Biodiversity and ecosystem functioning in stream detritivore systems: patterns and mechanisms.

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Summary

Global changes in biodiversity have prompted ecologists to examine the relationship between biodiversity and the functioning of ecosystems. The occurrence and form of such a relationship, and the mechanisms driving it, are critical for predicting the effects of biodiversity loss.

The aim of this study was to address whether species diversity is important for ecosystem function in streams, focusing on the relationship between the diversity of leaf-shredding macroinvertebrates and detritus processing. An initial field study revealed that there was no simple positive relationship between shredder diversity and leaf processing at a regional scale (i.e. between streams), but when combined with other biotic and abiotic factors did contribute significantly to explaining leaf-processing rate. The presence of particular species also appeared to be important for leaf processing. A second field study tested whether an increased variety of leaf types might lead to increased detritus processing in high, compared to low, diversity shredder communities. Again, particular species, or species combinations, appeared to be important in processing a mixed leaf resource, but shredder diversity was unimportant.

Artificial streams were then used to examine experimentally the effects of shredder identity and species number on detritus processing. Once more shredder diversity had little effect on processing rates, while shredder identity was important, on single and mixed leaf resources. A final experiment quantified the extent of resource-use complementarity among a set of shredder species, and then tested whether differences in complementarity among species pairs influenced leaf-processing rates. Although shredders did show differences in their leaf diets, experimental increases in complementarity did not translate into positive effects on leaf processing rates.

Both field and experimental studies provided little clear evidence for a positive diversity-function relationship, or the mechanisms proposed to underpin it. Results imply that the consequences of biodiversity loss for stream ecosystem function are dependent on which species are lost.

Thesis contents

1. General introduction.

1.1. Introduction.

1.1.1. The biodiversity-ecosystem function issue.

Alteration of the environment through human activities has brought about dramatic changes in the abundance and distribution of species at a global scale (Chapin III *et al.* 2000). It is estimated that anthropogenic activities have already caused the extinction of 5 – 20% of species in the major taxonomic groups including fish, plants, birds and mammals (Pimm *et al.* 1995). Current rates of extinction are estimated to be up to 1000 times greater than pre-human rates (Pimm *et al.* 1995, Lawton & May 1995). Such estimates raise the pressing question: "Can the current decline in biodiversity alter the functioning and stability of ecosystems….." (Loreau *et al.* 2002a). Here, the term 'biodiversity' refers to the variety of life across all levels of organisation, from genetic to taxonomic to ecological, across all spatial and temporal scales. The functioning of an ecosystem is, in the general sense, an aggregate property of the rate and stability of ecosystem-level processes (e.g. productivity, nutrient uptake) and properties (e.g. community invasibility), though from a practical point of view it is usually measured in terms of the rate and stability of individual processes.

The nature of the relationship between biodiversity and ecosystem functioning is important from several different perspectives. From an economic viewpoint, the loss of biodiversity could have serious implications for the provision and maintenance of ecosystem goods and services that are of importance to human societies, such as nutrient cycling, climate regulation, food and fresh water (Chapin III *et al.* 2000). Estimates of the monetary value of various ecosystem goods and services (e.g. Daily 1997, Costanza *et al.* 1997) have provided a strong economic incentive to understand the relationship between biodiversity and ecosystem functioning. For example, Costanza *et al.* (1997) estimated that ecosystems provide at least US$33 trillion worth of services per annum. From a management perspective, information about the relationship between biodiversity and ecosystem function could be usefully integrated into conservation strategies (Hector *et al.* 2001) and used to influence policy and management decisions, in agriculture and forestry for example. From an academic perspective, ecologists wish to understand the biological consequences of changes in biodiversity, and explore whether biodiversity is among the biotic and abiotic influences on ecosystems along with, for example, disturbance, nutrient supply, and climate (Tilman 1999).

1.1.2. The development of hypotheses.

Theoretical and empirical studies to explore the relationship between biodiversity and ecosystem function have been sporadic through time. The issue was initially considered by Darwin (1859), when he suggested that there might be a connection between greater biodiversity and higher productivity. The 'diversity-stability hypothesis' was developed in the following century. Elton (1958) argued that high species diversity and trophic complexity should increase stability at the population and ecosystem level, although he presented only indirect and anecdotal evidence to support his hypothesis (Pimm 1984). Other theoretical work of the 1950's also appeared to support the 'diversity-stability hypothesis' (MacArthur 1955, Hutchinson 1959) and it became a widely accepted theory in ecology. However, this hypothesis was later challenged by May (1972, 1973), who demonstrated theoretically that the stability of model systems decreased as species diversity increased. Thereafter, interest in the consequences of biodiversity on stability declined. However, interest has been rekindled over the past decade in a different light, stimulated by worries that human activity may cause a loss of biodiversity that will have an impact on ecosystem functioning (Tilman 1999). Recent interest in the functional impact of biodiversity loss has shifted focus, from the effects on populations and communities, to the effects on ecosystem-level properties and processes (Loreau *et al.* 2002b).

Investigation of the relationship between biodiversity and ecosystem functioning has become a major research goal for ecologists over the last decade, and has focused on three basic questions: (1) is there a relationship between biodiversity and ecosystem processes and properties? (2) Is the relationship positive or negative? And (3) what shape is the relationship? (Schläpfer & Schmid 1999). Predictions of the shape of the relationship between biodiversity and ecosystem function are represented by four central hypotheses. These hypotheses, described below, make predictions specifically about the shape of the trajectory between the point of zero biodiversity and the initial level of biodiversity in a system (Naeem *et al.* 2002; Figure 1.1).

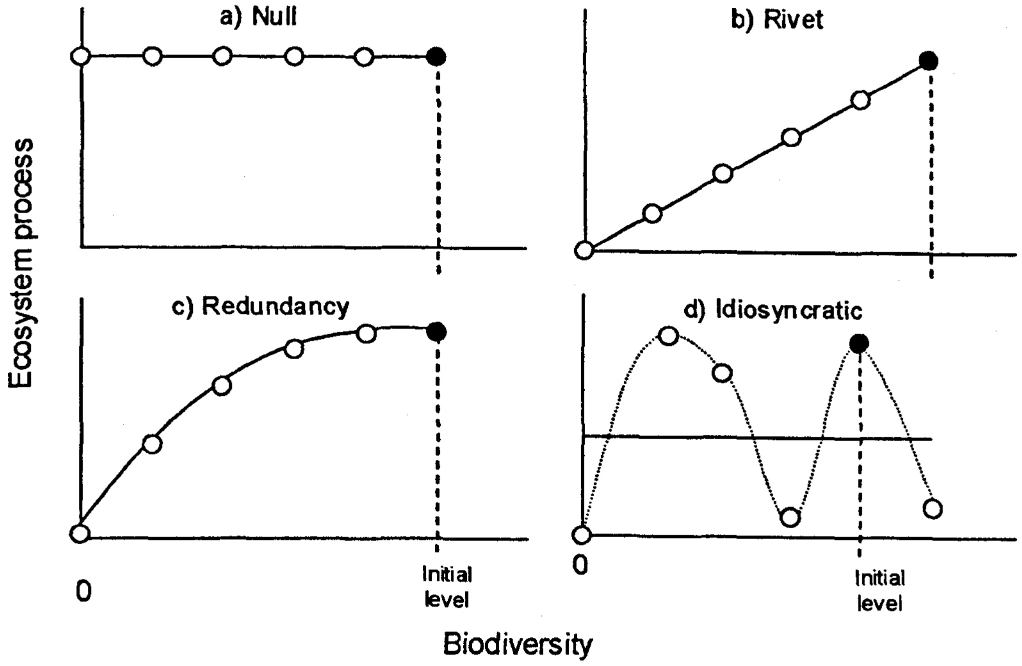

Figure 1.1. Graphical representation of the null hypothesis and the three classes of hypothesis that predict the shape of the relationship between biodiversity and an ecosystem process. Solid lines represent regression lines and the fine dashed line (---------) represents a trajectory plotted from point-to-point for (d).

The null hypothesis states that there is no effect of variation in biodiversity on ecosystem functioning and therefore a slope of zero for the trajectory between zero biodiversity and the initial level of biodiversity (Vitousek & Hooper 1993; Figure 1.1 a). The 'rivet hypothesis' (Ehrlich & Ehrlich 1981) is based on the assumption that every species is similarly and uniquely important for a given process. This hypothesis therefore predicts a positive linear relationship between biodiversity and ecosystem function (Figure 1.1 b) because the addition, or loss, of each individual species will increase, or degrade, ecosystem function to a similar extent. The 'redundant species hypothesis' assumes that species are at least partly substitutable in terms of their contribution to a given ecosystem process. The 'redundant species hypothesis' therefore predicts that as biodiversity increases, the contribution of each species to a given process is less likely to be unique, as niches begin to overlap and species become 'redundant'. This results in a positive, asymptotic relationship between biodiversity and ecosystem function (Lawton & Brown 1993; Figure 1.1 c).

Finally 'the idiosyncratic hypothesis' predicts no simple relationship between biodiversity and ecosystem function. This is because the effect of the addition, or loss, of a particular species on a given ecosystem process may be dependent on the functional traits of that particular species and/or dependent on local conditions, such as the composition of the remaining community, or local nutrient levels. In this case, certain species may have a strong influence on an ecosystem process while other species may not, which results in a hypothetical trajectory that exhibits changes in slope across the biodiversity gradient (Lawton 1994; Figure 1.1 d). Although the patterns predicted by both the null hypothesis and the 'idiosyncratic hypothesis' may result in a regression line with a slope of zero (Figure 1.1 a and d), there is an important distinction between the two. The null hypothesis predicts that there will be no variation in levels of ecosystem function as biodiversity changes, while the 'idiosyncratic hypothesis' predicts that changes in biodiversity do alter function, but in an inconsistent manner.

1.2. Biodiversity-ecosystem functioning experiments.

The body of empirical and observational work concerning biodiversity-ecosystem function relationships has grown rapidly over the last decade (Schwartz *et al.* 2000). Primarily, researchers have been concerned with discovering whether there is any relationship between the two, and whether this is positive or negative, rather than the precise shape of any relationship. Increasingly, experimental work has been aimed at examining what mechanisms might drive the observed relationships.

1.2.1. Measures of biodiversity, response variables and types of system used.

The general approach of biodiversity-ecosystem function experiments has been to quantify a range of response variables across an artificially constructed diversity gradient. The large majority of studies are experiments on terrestrial plant assemblages, where species richness (e.g. Naeem *et al.* 1994, 1995, Tilman & Downing 1994, Tilman *et al.* 1996), [1]functional group richness (i.e. the number of plant functional groups represented by the species present; Hooper & Vitousek 1997) or both (Tilman *et al.* 1997a, Hector *et al.* 1999), have been manipulated experimentally. Experiments using plant assemblages have commonly used above-ground, and sometimes below-ground, plant biomass, as an indicator of productivity, in order to quantify levels of ecosystem functioning.

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[1] A functional group is a group of species that play a similar functional role in a specific ecosystem process (Naeem *et al.* 2002). The concept of functional groups is discussed more fully in Section 1.4.2.3.

However, other response variables used include: nitrogen retention and uptake, CO_2 flux, water retention and decomposition rates. A few studies have also examined the relationship between species diversity and stability of plant communities (e.g. Tilman & Downing 1994, Tilman 1996, Sankaran & McNaughton 1999), while others have examined different aspects of plant systems, including the effect of plant diversity on below-ground leaf litter decomposition rates (Wardle *et al.* 1997a, Hector *et al.* 2000), and the effect of plant diversity on plant biomass across multiple sites (Hector *et al.* 1999).

Biodiversity-ecosystem function relationships have been investigated for few other types of system, and only recently has research been extended to marine (Emmerson & Raffaelli 2000, Emmerson *et al.* 2001), freshwater (e.g. Jonsson & Malmqvist 2000, Cardinale *et al.* 2002, Ruesink & Srivastava 2001) and wetland (Engelhardt & Ritchie 2001) systems. Microbial microcosms have also been used to examine the long-term effects (i.e. over many generations) of biodiversity on ecosystem processes for multi-trophic communities (e.g. McGrady-Steed *et al.* 1997, Naeem & Li 1997), and to examine the role of producer-decomposer interactions (Naeem *et al.* 2000).

1.2.2. The general patterns observed.

Across studies from a variety of ecosystems, positive relationships between biodiversity and various ecosystem processes and properties, are commonly reported (see reviews: Schläpfer & Schmid 1999, Schläpfer *et al.* 1999, Schwartz *et al.* 2000). For example, one review of observational and experimental studies reported that the null hypothesis was accepted on just four out of 38 occasions, while a positive relationship was observed for 34 of the tests (Schwartz *et al.* 2000). Another, more extensive, review of 91 field and laboratory trials, reported that 53 (58%) studies demonstrated a clear relationship between biodiversity and ecosystem functioning (Schläpfer & Schmid 1999). Of these 53 studies, a positive relationship was reported in 43 (81%) cases while negative relationships were reported for only ten (19%) studies.

One clear exception to the positive biodiversity-ecosystem function relationships observed is the effect of plant diversity on decomposition processes. Schläpfer & Schmid (1999) concluded that seven out of ten studies that examined plant diversity effects on soil microbial activity and decomposition rates, reported no effect, while two studies showed a positive effect, and one demonstrated a negative effect. Wardle *et al.* (2002) suggest that diversity effects in soil decomposer systems are inconsistent with those in plant diversity-productivity experiments, due to the different mechanisms that may be operating. However, decomposer systems are vastly under represented by biodiversity-ecosystem function studies, and such systems require more attention (see Section 1.5.3).

Empirical evidence has provided support for all four shapes of relationship between biodiversity and ecosystem function, for a range of ecosystem processes and properties, for different system types, and for the same system across different locations. For example, Hector *et al.* (1999) reported an overall log-linear decrease in above-ground plant biomass as plant species richness was reduced, across eight European experimental grasslands, corresponding with the 'redundant species hypothesis'. However, when the eight sites were analysed individually, a variety of relationships were observed including: log-linear (Switzerland and Portugal), linear (Germany and Sweden) and idiosyncratic (Ireland and UK (Silwood)). An experiment that examined the effect of diversity in aquatic microbial communities revealed a positive linear relationship between microbial species diversity and CO_2 production, but a positive asymptotic relationship between species diversity and decomposition of particulate organic matter (McGrady-Steed *et al.* 1997). Finally, patterns consistent with the idiosyncratic hypothesis have been observed across a range of system types including, terrestrial grasslands (e.g. Naeem *et al.* 1995, Symstad *et al.* 1998), marine coastal systems (Emmerson & Raffaelli 2000, Emmerson *et al.* 2001), and decomposition in soils (e.g. Wardle *et al.* 1997 a) and in streams (Jonsson *et al.* 2002, Jonsson & Malmqvist, in press).

Although many studies have provided evidence that reductions in biodiversity can alter the functioning and stability of ecosystems, the interpretation of this evidence has not been straightforward and indeed, has been the focus of much debate (e.g. Givinish 1994, Grime 1997, Tilman *et al.* 1997c, Wardle *et al.* 1997c, Huston 1997, Wardle 1999, Allison 1999, Naeem 1999, Kaiser 2000, Wardle 2001, Huston *et al.* 2000, Fukami *et al.* 2001). Discussion has centred on three core issues. First, the importance of species number versus the influence of particular individual species, or species composition, for ecosystem processes (e.g. Grime 1997, Hooper & Vitousek 1997, Tilman *et al.* 1997 a). Second, the relative contribution of two different classes of mechanism that might drive positive biodiversity-ecosystem function relationships, i.e. the selection effect and complementarity effects (e.g. Aarssen 1997, Huston 1997, Wardle 1999). Third, discussion has focused on the limitations of experiments including; the separation of the effects of different mechanisms (e.g. Loreau 1998a, Lepš *et al.* 2001, Loreau & Hector 2001, Špaèková & Lepš 2001), the relevance of experiments for natural systems (e.g. Grime 1997, Wardle *et al.* 1997c, Wardle 1999), and whether observed biodiversity-ecosystem function patterns can be generalised across different types of system (Loreau *et al.* 2002a). These three core issues are discussed the sections that follow.

1.3. Species identity and composition effects on ecosystem function.

1.3.1. Species identity effects.

Individual species may have large effects on an ecosystem process when there are large differences among species in their competitive abilities for a resource. According to resource competition theory, the species that can drive the resource to its lowest level will out-compete all others, become dominant, and the pattern of resource use will largely be a reflection of the activities of this particular species (Tilman 1990, Tilman *et al.* 1997b). In this case, the level of an ecosystem process will be influenced strongly by the presence of a particular species, i.e. the best competitor. At the point on the diversity gradient at which this species occurs, ecosystem function will show a marked, sudden change, leading, overall, to an idiosyncratic relationship between biodiversity and ecosystem function (Figure 1.1d).

The view that the functional traits of the dominant species are more important for ecosystem processes than the number of species present, is held strongly by some authors (e.g. Grime 1997, Aarssen 1997), and evidence from natural plant systems has provided support for this opinion (e.g. Lepš *et al.* 1982, Wardle *et al.* 1997b). For example, Lepš *et al.* (1982) reported that the response of two old-field successional plant communities to a drought, was determined by the reaction of the dominant species to stress, and was unrelated to their plant diversity.

The effects of particular species on ecosystem processes can be examined experimentally by deleting, or adding, different single species to intact assemblages. There have been few direct experimental tests of the relative importance of species identity versus species number for ecosystem functioning (e.g. Symstad *et al.* 1998, Ruesink & Srivastava 2001), however evidence from these studies also supports the contention that species identity can have large effects, above and beyond those of species number. For example, Symstad *et al.* (1998) reported that, although on average productivity decreased as plant diversity decreased, the magnitude and direction of the effect was dependent on the identity of the individual species that was removed. Other evidence for species identity effects comes from studies that have randomly allocated species to multiple replicates, within each diversity level, in order to construct a diversity gradient (e.g. Tilman *et al.* 1997a, 2001, Hector *et al.* 1999). For example, Hector *et al.* (1999) reported that each halving of the number of plant species, in experimental grassland assemblages, reduced productivity by 80 g m^{-2}, on average. However, one species in particular, the nitrogen-fixing plant *Trifolium pratense*, had marked effects on productivity. Productivity was reduced by 360 g m^{-2} on average, when this species was absent (Hector *et al.* 1999).

1.3.2. Species composition effects.

Community composition may be important when certain combinations of species have a marked effect on ecosystem process rates. This may occur through positive interactions among particular species (i.e. facilitation, Section 1.4.2.2), or the complementary use of resources among certain groups of species (i.e. the niche-differentiation effect, Section 1.4.2.1). As for the effects of single species, species composition effects should also lead to an idiosyncratic relationship between biodiversity and ecosystem function, since there will be a marked and sudden change in function at the point on the diversity gradient where a certain species combination occurs.

Experiments that have manipulated species composition, within levels of species diversity, have provided evidence that species composition can be a more important determinant of ecosystem functioning than species number for several different systems including: plant systems (e.g. Tilman *et al.* 1997a, Hooper & Vitousek 1997), soil decomposer systems (e.g. Wardle *et al.* 1997a, Mikola & Setälä 1998), and aquatic systems (e.g. Norberg 2000, Jonsson *et al.* 2002, Downing & Leibold 2002). For example, Jonsson *et al.* (2002) tested the effect of increasing diversity from one up to three species, on the breakdown of alder leaf litter in aquatic mesocosms, using three species of leaf-eating macroinvertebrate. They tested every species combination at each diversity level, with replication. The authors reported no effect of species diversity on leaf processing, but there were significant differences between individual species, and different two-species combinations. Downing & Liebold (2002) manipulated species richness and composition across multiple trophic levels in pond food webs. The authors reported that species composition could have larger effects on productivity, respiration and decomposition, than those of species richness.

Evidence that species identity and composition can have large effects on ecosystem processes appears to be at odds with the observation of positive biodiversity-function relationships, since strong identity and composition effects should result in idiosyncratic relationships (as described above). However, species identity and composition effects can lead to positive biodiversity-function relationships through a particular class of mechanism known as the 'selection effect' (Loreau 2000) (see below). The realisation that different mechanisms may drive positive biodiversity-function relationships has led to much discussion on the relative importance of these mechanisms (Section 1.4), and the development of techniques to separate their effects (Sections 1.4.2.4 and 1.5.1).

1.4. Mechanisms that drive positive biodiversity-ecosystem function relationships.

1.4.1. The selection effect.

The interpretation of early experiments that demonstrated positive biodiversity-function relationships (e.g. Naeem *et al.* 1994, 1995, Tilman *et al.* 1996, Tilman *et al.* 1997a) was questioned, based on a criticism of experimental design (Huston 1997, Aarssen 1997, Wardle 1999). Specifically, when species are assigned randomly to diversity treatments from a finite species pool, there is an increased probability that high diversity treatments will contain either, (1) a single species with particular functional traits that have a large influence on an ecosystem process or, (2) specific groups of two or more species that interact positively (i.e. facilitation, Section 1.4.2.2) or have complementary niches (i.e. the niche-differentiation effect, Section 1.4.2.1), and therefore act to increase the rates of an ecosystem process.

This effect is considered as a purely statistical phenomenon by some authors, who regard it as an artefact of the experimental design of random sampling from a species pool. For example, Huston (1997) interpreted this effect as a 'hidden treatment' that invalidated the conclusions of some experiments, and termed it 'the selection probability effect'. However, other authors consider this effect as a valid mechanism through which increases in species diversity can lead to an increase in ecosystem functioning, and have termed it the 'sampling effect' (Tilman 1997, Tilman *et al.* 1997b) or the 'selection effect' (Loreau 1998b, 2000). For simplicity, the 'selection effect' term will be used throughout this thesis.

Tilman *et al.* (1997b) used models of interspecific plant competition for nutrients, to predict the effect of plant diversity on productivity through alternative mechanisms. They demonstrate that, on average, "total plant biomass increases with diversity because better competitors produce more biomass and because the chance of having better competitors present increases with diversity". Loreau (1998b, 2000) further developed the selection effect theoretically, building a mechanistic model based on plant competition for a limiting nutrient, in a spatially heterogeneous environment. He demonstrated that productivity should increase with species diversity when species with a greater resource-use intensity (i.e. species that are able to depress a resource to the lowest levels) are favoured through natural selection processes. Similarly, he showed that productivity may decrease with species diversity, if species with a lower resource-use intensity are favoured (a 'negative selection effect'). Building on the model of Tilman *et al.* (1997b), Loreau (2000) emphasised two stages of the selection effect mechanism. First, greater species diversity represents a greater available range of trait variation among species and second, natural selection processes favour species with a higher resource-use intensity (or a lower resource-use intensity in the case of a negative selection effect).

While the selection effect has been recognised as a mechanism that may drive positive biodiversity-ecosystem function relationships in some experiments (e.g. Tilman 1997, 2001, Hector *et al.* 1999), the validity of this effect as a legitimate mechanism remains a contentious issue. Authors who have taken opposing views on this issue from its origin (i.e. Huston 1997, Tilman 1997) have recently contributed to the same book, but continue to disagree ("We will not argue the semantics of causation, but consider such sampling effects to be fundamental and ecologically important effects of diversity", Tilman *et al.* (2002)). Continued disagreement is mainly due to debate over whether such a mechanism is relevant for natural systems (see Section 1.5.2.1). However, so far there have been relatively few explorations of biodiversity-function relationships for natural communities (but see Tilman *et al.* 1996, Emmerson *et al.* 2001, Jonsson *et al.* 2001, Huryn *et al.* 2002).

1.4.2. 'Complementarity effects'.

Other mechanisms that may drive positive biodiversity-function relationships are those arising from complementarity between species. 'Complementarity effects' or 'complementarity' have been widely used in the literature as general terms under which to subsume all mechanisms that arise from complementarity among species (e.g. Hector 1998, Hooper 1998, Loreau & Hector 2001, Tilman *et al.* 1997b, Loreau *et al.* 2001). However, Petchey (2003) clarifies that complementarity is a property of a set of species, and not in itself a mechanism. Williams (2001) defines complementarity as "a property of sets of objects that exists when at least some of the objects in one set differ from the objects in another set". Complementarity among a group of species may give rise to mechanisms whereby ecosystem function increases with species number, including: 'the niche–differentiation effect' (Tilman *et al.* 1997b, Tilman 1999) and 'facilitation' (Fridley 2001, Loreau & Hector 2001). With this definition in mind, the term 'complementarity effects' will be used throughout this thesis in reference to all mechanisms that arise from complementarity between species.

1.4.2.1. The niche-differentiation effect.

The niche-differentiation effect can result when species differ to some extent in their requirements for a resource. Niche theory predicts that there must be at least some partitioning of resources among species in order for them to coexist (Giller 1984). Resources that may be partitioned between species include time, space and food (defined by quality (type) and size) (Schoener 1974). For example, different rooting depths of plant species (Hooper & Vitousek 1997), distinct sizes of algae consumed by different cladoceran species (Norberg 2000), interspecific variation in net-spinning sites used by caddisfly larvae in streams (Hildrew & Edington 1979), and different periods of feeding activity throughout the day in cyprinid fish (Baker & Ross 1981). If species differ in their resource use in at least one niche dimension, they may be considered to be complementary. If so, then each species can utilise a certain portion of the resource, but no single species can utilise the entire range of resources. In this case, the greater the number of species present in a community, the greater the resource range utilised, and hence the more complete the resource use (Tilman *et al.* 1997b, Loreau 1998b, Tilman 1999, Loreau 2000).

1.4.2.2. Facilitation.

Facilitation occurs when one species modifies a resource in a way favourable to another co-occurring species (Fridley 2001), such that overall resource use is increased when certain combinations of species occur together. For example, the presence of nitrogen fixing plants may increase the availability of this nutrient to other plant species in nitrogen-limited habitats (Hector *et al.* 1999, Tilman *et al.* 1997a). Jonsson *et al.* (2002) suggested that the cutting of leaf discs, by the feeding action of one species of stream detritivore, may increase the availability of the leaf edges on which another species preferred to feed. As for the niche-differentiation effect, ecosystem function is predicted to increase asymptotically with species number, as the strength or frequency of facilitative interactions increases, and then becomes saturated (Tilman *et al.* 1997, Loreau 1998b, Tilman 1999, Loreau 2000).

Methodologies have been developed to allow separation of the selection effect from mechanisms arising from complementarity between species, and use of these has produced evidence for the occurrence of both types of effect (see Section 1.5.1.). However, distinguishing the effects of niche-differentiation and facilitation may be very difficult in practise (Loreau & Hector 2001).

1.4.2.3. Functional groups and complementarity.

One approach taken by some researchers has been to ask whether functional group diversity affects ecosystem processes (e.g. Hooper & Vitousek 1997, Tilman *et al.* 1997a, Symstad & Tilman 2001). Functional groups can be defined as groups of species that have similar responses to the environment, or similar effects on ecosystem processes (Hooper *et al.* 2002). Species have commonly been assigned to functional groups using information about their physiological and morphological differences, which influence the way in which they respond to the environment, or effect ecosystem processes (e.g. Tilman 1997a, Hooper & Vitousek 1997).

The degree of variation in functional traits among species determines the degree of complementarity. Species belonging to different functional groups are more likely to be complementary, since they have, by definition, variation in their functional traits. While studies have manipulated species diversity across several different functional groups (e.g. Tilman & Downing 1994, Tilman *et al.* 1996, Emmerson *et al.* 2001), or functional group diversity itself (Hooper &

Vitousek 1997, Tilman *et al.* 1997a, Hector *et al.* 1999, Symstad & Tilman 2001), few studies have addressed whether species diversity within the functional group level is important for ecosystem processes (but see e.g. Cardinale *et al.* 2002, Jonsson & Malmqvist 2000, Jonsson *et al.* 2002, Duffy *et al.* 2001, Norberg 2000).

Studies that have manipulated functional group diversity are based on an underlying rationale that is somewhat circular. If species are designated to functional groups, defined by their similar roles in an ecosystem process (for example, species that are grouped according to the role they play in nitrogen cycling, Hooper & Vitousek 1997), the removal or addition of a functional group will inevitably affect that process (Hooper *et al.* 2002). For example, Tilman *et al.* (1997a) reported that the presence of a single plant functional group, nitrogen-fixing legumes, determined the level of plant total nitrogen in plant assemblages that varied in their functional group composition and diversity.

A *functional group approach*, as described above, is based on the assumption that all species within a functional group fulfil a similar functional role, and therefore are substitutable. However, functional classifications are not discrete, since many traits may vary continuously (Hooper *et al.* 2002), and species within a functional group may vary in their functional traits and therefore be complementary, to at least some extent. A functional group approach ignores natural trait variation among species, and therefore may underestimate the importance of species diversity for ecosystem processes. In contrast, a species diversity approach avoids predefining the degree of trait variation (or complementarity) among groups of species, and therefore avoids assuming redundancy within groups of species. If there is redundancy between species, a relationship between diversity and ecosystem function, consistent with the 'redundant species hypothesis' (Figure 1.1c), would reveal this.

A small number of studies have examined the effects of diversity within a functional group on ecosystem processes, but no consistent pattern has yet emerged. Cardinale *et al.* (2002) examined the effect of increasing species number within the filter-feeding functional group (see Section 1.6.1) of aquatic detritivores. Filter-feeders are one of five main functional feeding groups of stream macroinvertebrates, which are classified based on their feeding strategies (Cummins 1973, 1974, Cummins & Klug 1979). Species belonging to the filter-feeding functional group use a suspension feeding strategy to filter fine particulate organic matter from the water column. Cardinale *et al.* (2002) reported that total resource capture was increased, when the number of filter-feeding caddisfly larvae was increased from one to three. Another study examined the effect of species diversity on resource use within the shredder functional feeding group of aquatic detritivores (Jonsson & Malmqvist 2000). The shedder group primarily includes those species that use a chewing action to feed on large pieces of detritus, principally leaf material (but see Section 1.6.1). The study revealed that leaf decomposition rates were increased when the number of species of shredding stonefly larvae was increased from one to three.

In contrast, Duffy *et al.* (2001) reported that the three species of crustacean grazer that they examined had similar affects on epiphyte accumulation in aquatic mesocosms, suggesting a high level of redundancy within the group of three species. However, another process, secondary production, was affected by the removal of one species in particular, indicating its unique, non-redundant role among species belonging to the same functional group. Norberg (2000) tested whether an increase in diversity, within a closely related group of four cladoceran grazer species, affected various ecosystem processes in aquatic microcosms. There was no positive relationship between species diversity and any of the ecosystem processes. Rather, particular combinations of species, within diversity treatments, showed positive effects on ecosystem-level variables, primarily thought to be a result of resource-niche complementarity (Norberg 2000).

1.4.2.4. Distinguishing between different mechanisms.

The identification and separation of different mechanisms that drive positive biodiversity-function relationships (Section 1.4.) has recently become a central focus for researchers (e.g. Loreau 1998a, Hector 1998, Hooper 1998, Lepš *et al.* 2001, Loreau & Hector 2001, Špaèková & Lepš 2001, Hector *et al.* 2002b). Testing whether complementarity between species is responsible for positive effects on ecosystem processes is difficult in practical terms, since ideally it requires testing all species combinations, at all diversity levels, with replication (Loreau *et al.* 2001). If more than a small number of species are to be tested (i.e. three to four), this design becomes logistically impractical for most types of experimental system. Therefore, assessing the relative importance of the selection effect and complementarity effects has so far been achieved indirectly, using simple experimental designs that compare the performance of single-species treatments with species mixtures (Loreau 1998a, Hector *et al.* 1999, Huston *et al.* 2000, Loreau *et al.* 2001, Loreau & Hector 2001, Hector *et al.* 2002b).

Hector (1998) suggested the use of the Relative Yield (RY) and Relative Yield Total (RYT) measures, to compare the performance of plant species grown alone, and in a mixture, for replacement series designs, where each species is represented by an equal proportion of the total plant density. The RY of a species is its biomass in mixture as a proportion of its biomass in monoculture. The RYT of a mixture is simply the sum of the RY's of the component species. This measure therefore takes into account any shifts in numerical dominance among species in the mixture. If there are no positive effects of growing species in a mixture, compared to monocultures, then the value of RYT will be equal to one. However, a value of RYT greater than one indicates that at least one species has performed better in the mixture than in monoculture. A selection effect, brought about by the increased performance of a single species in the mixture, can be separated from complementarity effects, by examining the RY's of individual species. Loreau (1998a) observed that a limitation of the RYT metric was that an RYT value of greater than one could result through a number of possible interactions between species. Loreau (1998a) therefore developed metrics related to RY and RYT values, but based on the proportional deviation from expected values, a combination of which, he suggests, can be used to control for the selection effect.

Recently, a new method has been developed that unifies the two approaches mentioned above, and is based on the 'additive partitioning' of the 'selection effect' and the 'complementarity effect' (Loreau & Hector 2001). In this method, the selection effect is estimated based on the Price equation used in evolutionary genetics (Frank 1997). The sum of the selection effect and complementarity effect is the net biodiversity effect, all three of which have an expected value of zero under the null hypothesis of no effect of diversity on ecosystem function. All three effects may be positive or negative, in which case the possibility arises that the selection and complementarity effects may cancel each other out to give a net biodiversity effect of zero. An advantage of this approach is that the relative contribution of selection and complementarity effects can be compared quantitatively (Loreau & Hector 2001).

The methods described above have been used to examine the contribution of different mechanisms in some recent biodiversity experiments (e.g. Hooper

1998, Emmerson & Raffaelli 2000, Loreau & Hector 2001, Cardinale *et al.* 2002). For example, Hooper (1998) examined the effect of plant diversity on primary productivity and plant nitrogen yield in serpentine grassland assemblages. Values of RYT indicated positive effects of diversity on above-ground biomass in some two-species mixtures and one four-species mixture. The additive partitioning method was recently used to reanalyse data from the BIODEPTH study on grassland systems in eight European countries (Hector *et al.* 1999). The reanalysis revealed positive complementarity effects at four out of the eight localities, positive selection effects at two localities, and negative selection effects at one locality (Loreau & Hector 2001). Cardinale *et al.* (2002) examined the resource capture of three species of filter-feeding caddisfly larvae in stream mesocosms. The authors compared the resource capture of three different single-species treatments to that of a mixed-species assemblage containing all three species. Application of the additive partitioning method revealed that the positive net biodiversity effect could be partitioned into 17% selection and 83% complementarity.

1.5. Limitations of the current evidence.

1.5.1. The mechanisms.

All of the methods described above (Section 1.4.2.4) for distinguishing between different mechanisms that drive positive biodiversity-function relationships have limitations. Firstly, mechanisms that arise from complementarity between species may be interpreted as a selection effect, when Loreau & Hector's (2001) additive partition method is used (Petchey 2003). For example, if species that dominate in mixtures are also those with the most complementary resource-niches, then an effect resulting from resource-use complementarity will be included in the partitioned selection effect (Petchey 2003). For example, an analysis performed by Tilman *et al.* (2001) indicated that interactions among just four or five dominant plant species, out of a total of sixteen in the highest diversity mixtures, seemed to account for the positive effects of diversity on total plant biomass. Second, none of the methods described above are able to separate the different mechanisms that can arise from complementarity between species (the niche-differentiation effect and facilitation). A final limitation, for all of the methods mentioned, is that they are of little use for assessing complementarity effects when the contribution of individual species within a species mixture can not be quantified. This is the case for many important types of ecosystem processes, for example, nutrient and gas fluxes (e.g. Emmerson *et al.* 2000) and decomposition rates (Jonsson & Malmqvist 2000).

One measure that can be used to overcome the first and third of the limitations mentioned is that of overyielding (Loreau 1998a, Hector 1998, Hector *et al.* 1999, Hector *et al.* 2002a). Overyielding occurs when a species mixture has a greater response than any single-species treatment of its component species. A selection effect can only increase the response of a species mixture to a response equal to that of the highest 'yielding' single-species treatment. Therefore, overyielding is the most stringent and unambiguous test for complementarity effects, and has been used to interpret the results of some biodiversity-function experiments (e.g. Hooper 1998, Hector *et al.* 1999, Emmerson & Raffaelli 2000, Špaèková & Lepš 2001, Tilman *et al.* 2001, Emmerson *et al.* 2001).

Moreover, the overyielding test can be applied in systems where the response of individual species within a mixture can not be quantified. For example, Emmerson *et al.* (2001) examined the effect of the diversity of intertidal invertebrates on nutrient flux (ammonia nitrogen (NH_4-N)) to the water column. Invertebrate diversity was increased from one up to four species, using species pools from three different locations, in artificial mesocosms. Results revealed that, overall, less than 25% of the species mixtures showed evidence of overyielding, but that overyielding was much more common in higher diversity mixtures (75% of four-species mixtures), indicating niche-differentiation and/or facilitation between species.

Although simple experiments that compare the response of single-species treatments with species mixtures can provide insight as to whether complementarity effects may be important for certain ecosystem processes, direct experimental investigations (Stevens & Carson 2001), and direct observations (Cardinale *et al.* 2001), of such effects have been extremely rare. Stevens & Carson (2001) used naturally occurring grassland assemblages to test whether complementarity between species, in terms of their phenology (i.e. resource use and growth rates), led to an increase in total annual cover with an increase in plant diversity. Although a positive relationship between species diversity and total annual cover across plots was observed, there was no increase in phenological complementarity with an increase in plant diversity, and phenological complementarity explained little of the variation in plant cover.

However, to date, no study has directly tested the effects of species diversity on an ecosystem process over an experimentally manipulated gradient of resource-niche differentiation.

1.5.2. Relevance of experiments to natural systems.

1.5.2.1. Relevance of the selection effect in natural communities.

Some authors have argued that the selection effect is not likely to be a mechanism relevant for natural communities (Huston 1997, Aarssen 1997, Wardle 1999), since it is driven partly by the process of random allocation of species to diversity treatments (Section 1.4.1). Another part of the selection effect mechanism is the dominance of a highly competitive species, through a process of interspecific competition (Tilman *et al.* 1997b). While patterns of dominance are common in natural systems (e.g. Whittaker 1975, Ricklefs 1990), it is unclear whether stochastic processes are likely to be common for the assembly, or disassembly, of natural communities.

Loreau *et al.* (2001) argue that the loss of species could be random with respect to the ecosystem process that they influence, as climate change progresses, and species are lost gradually as their tolerance limits for abiotic conditions are exceeded. However, the assembly of most natural communities is not likely to be governed by random processes (e.g. Drake 1991, Wilson & Roxburgh 1994, Pardo 2000). Moreover, the loss of species through extinction events is not likely to be random (Kunin & Gaston 1997). The acceptance of the selection effect, as a mechanism through which biodiversity positively affects ecosystem function, requires the testing of hypotheses about the way in which natural communities are assembled and disassembled, and an exploration of biodiversity-ecosystem function relationships in natural communities.

A limited number of studies have explored whether biodiversity affects ecosystem function in natural communities (Tilman *et al.* 1996, Emmerson *et al.* 2001, Jonsson *et al.* 2001, Huryn *et al.* 2002). For example, Tilman *et al.* (1996) found a positive effect of plant species diversity on total plant cover and nitrogen uptake in an undisturbed grassland in Minnesota. However, the authors do not address whether the positive diversity effect was driven by the presence of dominant species in high diversity communities. Emmerson *et al.* (2001) reported a positive relationship between the number of sediment dwelling invertebrate species and the flux of ammonia nitrogen to the water column, for three different natural marine communities. Further analyses revealed that particular dominant species contributed disproportionately to ammonia nitrogen production at each of the three sites, however such species were present across the range of species richness examined. In general, evidence suggesting that the selection effect is a valid mechanism leading to positive biodiversity-ecosystem function relationships in natural communities is sparse. There is a crucial need to explore whether positive biodiversity-function relationships are prevalent in natural communities, and whether the selection effect is relevant.

1.5.2.2. Scale of experiments.

Biodiversity-ecosystem function experiments have often been conducted at small spatio-temporal scales (e.g. Tilman *et al.* 1996, 1997a, Jonsson & Malmqvist 2000), with only a few exceptions (e.g. Jonsson *et al.* 2001, Wardle *et al.* 1997b). For example, grassland experimental plots, which represent a large portion of experimental studies, are usually less than 100m^2 and have spanned only a small number of generations (<1 to 10) (Bengtsson *et al.* 2002). One source of controversy for interpreting the results of biodiversity-function experiments, has been whether patterns observed at such small experimental scales are relevant at larger spatial and temporal scales, for example, landscape or regional scales, or over many generations (Schwartz *et al.* 2000, Loreau 2000, Loreau *et al.* 2001, Tilman *et al.* 1997c, Wardle *et al.* 1997c).

Small spatial scale studies have addressed whether biodiversity is important for ecosystem function on a local scale, while environmental variables are held constant (Loreau *et al.* 2001). However, at larger scales, the biodiversity-ecosystem function relationship is likely to be affected by variation in environmental factors that might strongly influence ecosystem processes. Loreau (1997b, 2000) used the same mechanistic model of plant competition for a limiting nutrient, as described above (Section 1.4.1), to examine the relationship between variation in environmental factors, diversity, and productivity. Loreau's model demonstrates that any local effect of diversity on ecosystem function should be masked by the effect of environmental parameters when across-site comparisons are made, providing that there is variation in environmental parameters across sites. Loreau (2000) suggests that environmental variables will therefore be the primary influence on ecosystem function across large spatial scales, either by acting directly on ecosystem processes, or indirectly through influencing species number.

The limited number of large spatial scale studies that have addressed the biodiversity-ecosystem function relationship show mixed evidence for Loreau's (1998b, 2000) mechanistic model. Wardle *et al.* (1997b) found that the frequency of burning caused by wildfire, across fifty islands of varying size, was a major determinant of several ecosystem-level processes for plant communities. The strong environmental controls on the plant communities of different islands actually brought about a negative relationship between species diversity and ecosystem process rates. Emmerson *et al.* (2001) found that a positive species richness effect of marine invertebrates on ammonia nitrogen flux was primarily driven by differences between the three study sites used, Scotland, Sweden and Australia. A European wide study, that included eight different countries, reported that geographical location was an important determinant of plant community productivity (Hector *et al.* 1999). Finally, Jonsson *et al.* (2001) examined detritus processing rates in twenty-three streams across a region spanning from mid to northern Sweden, using study sites that were separated by up to 700km. Mass loss from experimental leaf packs was used as the dependent variable, in a partial least-squares regression analysis, along with eleven independent variables that included both biotic and abiotic factors. The authors reported that the main determinants of detritus processing rates across streams were 'year', (a factor that represented variation in all the factors that were not quantified between the two years of the study), followed by water temperature. However, species richness within the shredder functional feeding group (see Section 1.6.1) also showed positive relationship with detritus processing rates.

Temporal scales are also an important consideration for biodiversity-function experiments. Short-term experiments can reveal whether biodiversity affects ecosystem functioning at a particular point in time. However, longer-term experiments are required to examine the effects of biodiversity on the variability of ecosystem functioning. That is, whether biodiversity can act as a buffer against environmental change because communities that are more diverse have a greater range of tolerance to, or responses to, changing environmental conditions (Yachi & Loreau 1999, Ives *et al.* 2000). According to this hypothesis, known as the 'insurance hypothesis' (Yachi & Loreau 1999), species that may appear redundant for an ecosystem process in the short-term, may become important as conditions change over time (Loreau 2000). So far, hypotheses concerning long-term ecosystem dynamics have been addressed in aquatic microcosms (e.g. McGrady-Steed *et al.* 1997, Naeem & Li 1997), where biodiversity effects can be measured across many generations (Petchey *et al.* 2002). Such experiments have generally reported that the predictability of ecosystem processes increases with increasing species diversity, both in space (i.e. between replicates) and in time. For example, Naeem & Li (1997) reported that total autotroph biomass and density were more consistent, as the number of species per functional group was increased, in multi-trophic microbial microcosms.

The issue of scale is obviously a crucial one for biodiversity-ecosystem function relationships. The spatial and temporal scale at which experiments are conducted are likely to influence the relationships observed, and the interpretation of results. While studies using microbial microcosms can contribute to experimental evidence about the effects of biodiversity on long-term ecosystem dynamics, studies conducted in the same habitat type across space, may reveal the relative influence of biodiversity and environmental factors on ecosystem processes at larger spatial scales. However, both small and large-scale investigations are important since they complement one another by exploring causal relationships under different circumstances.

1.5.3. Generalising across ecosystem types.

The majority of experiments that have examined the biodiversity–ecosystem function relationship have been conducted for primary producers in grassland communities (e.g. Tilman & Downing 1994, Tilman *et al.* 1996, Hooper & Vitousek 1997, Tilman *et al.* 1997a, Hector *et al.* 1999, Sankaran & McNaughton 1999), while other ecosystem types and trophic levels remain largely unexplored. As a result, although positive relationships have commonly been reported between plant diversity and productivity (Schwartz *et al.* 2000, Hector *et al.* 2001), it is unknown to what extent such patterns can be generalised to other types of ecosystem.

The relationship between biodiversity and ecosystem function for different ecosystem types is likely to be dependent on variation in the major factors that drive species diversity, species abundance and process rates (Bengtsson *et al.* 2002). It is unlikely, therefore, that the patterns observed for production in grassland communities are generic across ecosystem types. For example, no consistent effect of plant species richness on soil decomposition processes has been revealed (e.g. Blair *et al.* 1990, Rustad 1994, Wardle *et al.* 1997a), possibly because this particular ecosystem process is influenced to a greater extent by microbial and invertebrate decomposers. However, decomposers (both microbial and invertebrate) are among the least well studied groups, in terms of their effects on ecosystems processes (Schläpfer & Schmid 1999), partly due the difficulty of their taxonomic identification (Behan-Pelletier & Newton 1999). There is little evidence to suggest that the biodiversity of soil fauna is important for decomposition. Six out of thirteen studies reviewed by Mikola *et al.* (2002) showed positive effects, but these were often weak, or inconsistent. The effect of biodiversity in soil decomposer systems is likely to be complicated, however, by the multiple trophic levels represented by the organisms present in such communities, and interactions between these trophic levels (Mikola & Setälä 1998).

Multi-trophic interactions are likely to affect both diversity and ecosystem processes, and therefore complicate any relationship between the two (Loreau *et al.* 2001, Raffaelli *et al.* 2002). Experiments that have tested the effects of manipulating species diversity within one trophic level upon another trophic level (e.g. Mikola & Setälä 1998, Laakso & Setälä 1999, Norberg 2000) have not provided any consistent evidence. Few studies have manipulated species diversity within more than one trophic level simultaneously (but see Naeem *et al.* 1994, McGrady-Steed *et al.* 1997, Petchey *et al.* 1999). Naeem *et al.* (2000) used simple aquatic microcosms to independently manipulate algal (producer) and bacterial (decomposer) diversity. Results were complex and indicated that ecosystem function (measured as the amount of biomass generated) was dependent on both producer and decomposer diversity, with no simple relationship between the two. In general, experiments performed in multi-trophic systems indicate that feedbacks between trophic levels may have complex effects on ecosystem processes. Raffaelli *et al.* (2002) propose that further experimental tests, and the development of theory and models, are required in order to increase our understanding of biodiversity effects in multi-trophic systems.

In general, the effect of biodiversity on ecosystem function is likely to be variable across ecosystem types due to fundamental differences in biotic and abiotic factors such as; the nature of the limiting resources, disturbance frequency, the strength of interspecific interactions, mobility of organisms, and the nature and complexity of the trophic web, all of which are likely to vary considerably across different ecosystem types. Aquatic ecosystems, in particular, are under represented in the current empirical evidence (Schläpfer & Schmid 1999), and are of particular interest since they are subject to quite different biotic and abiotic controls than terrestrial systems (Dobson and Frid 1998, Giller *et al.* in press).

1.6. Biodiversity and ecosystem function in streams.

Little attention has so far been paid to biodiversity-ecosystem function relationships in stream systems, despite evidence that they are particularly at risk of species loss through habitat destruction, fragmentation, invasion by exotic species and increased inputs of nutrients, sediment and various pollutants (Richter *et al.* 1997, Harding *et al.* 1998, Sala *et al.* 2000). Most freshwater that is accessible to humans (geographically and temporally) has already been affected by human activity in some way (Postel *et al.* 1996), and the scenario for biodiversity loss in freshwater systems may be far graver than for any terrestrial system (Ricciardi & Rasmussen 1999).

Levels of ecosystem functioning in streams have usually been evaluated indirectly, through bioassessment procedures that are based on measures of invertebrate species diversity and community structure (Lenat & Penrose 1996, Karr 1999). Links between the impacts of pollutants and associated changes in macroinvertebrate community structure have been well established (Wallace *et al.* 1996). However, the consequences of changes in invertebrate diversity and community structure for ecosystem function are poorly understood (Walker 1992, Bunn *et al.* 1999, Covich *et al.* 1999), and have frequently been inferred rather than tested directly in freshwater systems (Huryn *et al.* 2002). Empirical studies to understand how changes in community structure are related to ecosystem function are therefore urgently required for freshwater systems.

1.6.1. Detritus processing in streams.

The main energy input for forested low-order streams is organic matter that originates from bankside vegetation (Vannote *et al.* 1980, Graça *et al.* 2001), and is referred to as being 'allochthonous'. The decomposition of allochthonous organic matter plays a "central role in the functioning of many flowing water systems" (Maltby 1996), in the sense that detrital pathways are the routes for the major flows of energy and cycling of nutrients in streams (Webster & Benfield 1986, Giller & Malmqvist 1998). The fundamental role of decomposition processes in streams therefore provides an ideal model system for relating rates of an ecosystem process to ecosystem functioning.

Leaf litter represents the majority of allochthonous inputs in forested headwater streams, and any material greater than 1mm in diameter that enters a stream is referred to as coarse particulate organic matter (CPOM). The decomposition of CPOM proceeds through three main processes. First, the rapid loss of dissolved organic matter (DOM, < 0.5μm) and soluble inorganic leaf components, a process known as 'leaching', is thought to be responsible for a substantial initial mass loss (up to 30 %) (Petersen & Cummins 1974, Benfield 1996) and thereafter further gradual mass loss. Second, the chemical-structural modification of leaf material through the enzymatic activities of bacteria and fungi results in further mass loss. Aquatic hyphomycete fungi are especially important for this process (Maltby 1996), known as 'conditioning', which also acts to enhance leaf litter palatability for macroinvertebrate detritivores. Finally, the breakdown of CPOM, to smaller particle sizes, is mediated through both physical abrasion, and the feeding and digestive activities of macroinvertebrate detritivores. This process is referred to as 'fragmentation', and produces fine particulate organic matter (FPOM, < 1mm > 50μm) which can be utilised downstream by other macroinvertebrate functional feeding groups (Wallace *et al.* 1982).

Stream macroinvertebrates are classified into five functional feeding groups based on their feeding strategy; shredders, collectors, scrapers, macrophyte piercers and predators (Cummins 1973, 1974, Cummins & Klug 1979). The shredder group comprises primarily those species that use a chewing action to feed on CPOM and macrophytes, but also those species that use a gouging action to feed on woody detritus. Species belonging to the collector functional feeding group use either a suspension feeding strategy to filter FPOM from the water column (filterers), or a deposit feeding strategy to feed on sediment-related FPOM (gatherers). Scrapers include those species that feed on algae and biofilms that adhere to surfaces, using a grazing/scraping action. Macrophyte piercers feed on the cell and tissue fluids of living plants by piercing and sucking fluid, and predators engulf or pierce other animals. It is acknowledged that the functional feeding group classification is not without flaws (Giller & Malmqvist 1998). Many species may be omnivorous, and others may shift from one group to another at different stages in their life cycle, or depending on habitat or season. However, this classification scheme provides an important framework for linking particular groups of macroinvertebrates to specific ecosystem processes.

The shredder functional feeding group includes species from non-insect orders (e.g. Amphipoda, Isopoda), and the larvae of species from several insect orders (e.g. Plecoptera, Trichoptera, Diptera), and is clearly associated with the breakdown of leaf detritus. Many studies that have compared leaf decomposition rates in fine mesh bags, from which shredders are excluded, and coarse mesh bags, to which shredders have access, have reported faster breakdown rates in coarse mesh bags (see Webster & Benfield 1986). Moreover, evidence from several studies reveals that variation in leaf processing rates is positively related to both shredder abundance and biomass (e.g. Wallace *et al.* 1982, Webster & Benfield 1986, Wallace *et al.* 1986, Cuffney *et al.* 1990, Jonsson *et al.* 2001, Huryn *et al.* 2002). Further, several studies have shown that shredders increase the conversion of CPOM into FPOM and DOM in both laboratory (Cummins *et al.* 1973, Petersen & Cummins 1974, Mulholland *et al.* 1985), and field experiments (e.g. Wallace *et al.* 1982, Cuffney *et al.* 1990), increasing the availability of detritus for downstream transfer to other functional feeding groups. While there is a wealth of evidence to support the importance of the shredder functional feeding group for leaf processing in streams, there is currently very little evidence to suggest whether shredder diversity is positively related to leaf litter processing rates, and this is the focus of the work in this thesis.

1.6.2. Relationship between shredders and detritus processing.

The relationship between biodiversity and function is dependent on the major factors that influence species diversity, species abundances and process rates in communities (Bengtsson *et al.* 2002). Bengtsson *et al.* (2002) present a framework of possible relationships between species diversity and function with regard to these factors. Positive relationships between species diversity and ecosystem processes are expected in systems where there is; 1) exploitative competition between species for a limiting resource, and therefore the potential for the niche-differentiation mechanism, and/or 2) positive interactions between species, and therefore potential for the facilitation mechanism. No relationship between species diversity and an ecosystem process is expected in disturbance-driven systems, or systems where resources are not limited, or cannot be partitioned. In systems where interference competition between species dominates' a negative relationship, or no relationship at all, is predicted.

Finally, the predicted relationship between species diversity and ecosystem processes is unclear in systems where top-down effects dominate.

The frequency and strength of competition is not well known for stream communities. One view is that physical disturbance and chance act to structure communities in a stochastic way (e.g. Tokeshi 1994), and therefore macroinvertebrate assemblages are not interactive. An alternative view is that macroinvertebrate communities are deterministic assemblages structured mainly by species interactions (e.g. Minshall & Peterson 1985). However, the influence of physical factors and species interactions on community structure are not necessarily mutually exclusive (Giller & Malmqvist 1998), therefore it is difficult to predict whether a positive relationship between shredder diversity and leaf processing may be expected, given the framework presented above.

Most studies of interspecific competition among stream macroinvertebrates have been performed with 'sessile' organisms such as net-spinning caddisfly larvae and blackfly larvae (Hildrew & Giller 1994). Exploitative competition has been demonstrated for more mobile species, belonging to the grazer functional feeding group (e.g. Hill & Knight 1987, 1988, Kohler 1992, Hill 1992), but has not yet been demonstrated experimentally for shedders. However, several studies have provided evidence for resource limitation among shredding detritivores (e.g. Smock *et al.* 1989, Dobson & Hildrew 1992, Rowe & Richardson 2001), and leaf litter resources may potentially be partitioned between species in several ways. For example, shredder species may show spatial niche-differentiation by utilising different microhabitats within leaf packs, or temporal differentiation by utilising leaf resources at different times throughout the day, or at different times during the period of leaf-fall. Shredders may utilise different parts of the leaf tissue, for example, the isopod, *Asellus aquaticus* (L.), is known to feed preferentially on fungi present on the leaf surface (Graça *et al.* 1993), while the amphipod *Gammarus pulex* (L.) uses a chopping action to break off whole leaf pieces leaving only the major veins intact (Graça *et al.* 1993) and the trichopteran larvae *Sericostoma personatum* (Spence) consumes all parts of the leaf including the veins (Jonsson *et al.* 2002). There is also potential for resource-differentiation in terms of leaf type, between shredder species, since natural leaf packs often consist of several different leaf species (Leff & McArthur 1989, Boulton & Boon 1991).

The extent of positive interactions between species is not known for freshwater systems in general. Jonsson *et al.* (2002) proposed that the cutting of leaf discs, by the feeding action of the cased caddisfly larvae *Sericostoma personatum*, may have increased the availability of the leaf edges on which another species, the amphipod *Gammarus fossarum*, preferred to feed. However, it is difficult, in practical terms, to test the effect of such subtle behavioural interactions directly, and currently there does not appear to be any direct evidence to indicate how important they might be for shredders in streams.

A negative, or no, diversity-function relationship is predicted for communities that are dominated by interference competition (Bengtsson *et al.* 2002). Interference competition has been demonstrated experimentally in streams for filter-feeders (Hemphill 1988, Hart 1985) and grazers (Dudley *et al.* 1990). In general, interference competition is most apparent for sedentary, space-limited taxa in streams (Allan 1995), and there is no evidence to suggest that shredder communities are dominated by interference competition. Bengtsson *et al.* (2002) propose that the relationship between species diversity and ecosystem function may take a variety of forms when communities are structured by top-down effects. Hildrew & Giller (1994) suggested that some freshwater communities may be structured by predation, and studies of stream macroinvertebrate communities have provided evidence to support this (e.g. Peckarsky & Dodson 1980, Harvey & Hill 1991, Malmqvist 1993). However, it is unclear how important, or wide-spread, top-down control might be for shredder communities.

Overall, a variety of factors may influence species diversity, species abundances and process rates in shredder communities. Competition for a limiting resource, that can be partitioned, seems likely, and therefore the niche-differentiation effect may operate in shredder communities. However, the influence of other factors, such as positive interactions between species, and top-down control, are largely unknown for shredder communities, and therefore other relationships are possible.

To date, very few experiments have examined the effects of shredder diversity on leaf litter processing (Jonsson & Malmqvist 2000, 2003, Jonsson *et al.* 2002). Jonsson & Malmqvist (2000) tested the effect of increasing shredder species diversity from one to three, on the breakdown of alder leaf litter in aquatic mesocosms, using three different species of shredding stonefly larvae. They tested every species combination at each diversity level, with replication, and used a nested ANOVA design to test the effects of both species identity and species number. Leaf breakdown rates were significantly greater in three- than in two-species treatments, indicating possible complementarity effects, but there were no species identity effects, either between different single-species treatments, or between different two-species combinations. A similar study examined the effect of shredder diversity on alder processing for three species belonging to different taxonomic groups, including an amphipod, a trichopteran and a plecopteran (Jonsson *et al.* 2002). Using the same experimental design as described above (Jonsson & Malmqvist 2000), the authors found no effect of species number, but there were strong effects of species identity and species combination.

Interpretation of the wider significance of such sparse evidence is difficult. One possibility is that species identity effects may be more important when species are less closely related, since they are more likely to have morphological and physiological differences, and therefore play different functional roles in detritus processing. If one particular species has strong effects on leaf processing rates, this would manifest itself as an idiosyncratic response at low levels of species diversity (i.e. from one to three species), as observed in the study by Jonsson *et al.* (2002). However, over a greater range of species diversity, the strong influence of one shredder species may result in a positive effect of shredder species number on leaf processing, driven by the selection effect (Section 1.4.1).

The positive effect of increasing shredder species number for three closely related stonefly shredder species (Jonsson & Malmqvist 2000) is somewhat surprising, since they are less likely to be functionally different with regard to leaf processing. Indeed, there were no significant differences between the three individual stonefly species in their alder processing rates (Jonsson & Malmqvist 2000). However, subtle differences between the three stonefly species, may have been sufficient for niche-differentiation or facilitation to drive a positive diversity effect. Jonsson & Malmqvist (2000) proposed that facilitation between the three stonefly species may have driven the positive diversity effect, and presented evidence in a subsequent study in support of this mechanism (Jonsson & Malmqvist 2003). However, without direct behavioural observations, any effect of facilitation between species can not be separated from niche-differentiation.

1.7. Aims.

The overall aim of this thesis was to address whether species diversity is important for ecosystem function in streams, focusing specifically on the relationship between shredder diversity and leaf litter processing, since this represents a clear functional link between a group of species and an ecosystem process. This study had four main objectives.

Objective 1. To examine the influence of macroinvertebrate species richness, species identity and community composition on detritus processing at a regional scale (*i.e.* between streams).

The goal here was to test whether there was a detectable effect of macroinvertebrate species diversity on leaf litter processing at scales over which there was likely to be variation in other biotic and abiotic factors, that may have strong influences on leaf processing rates. Moreover, this objective addressed the issue of whether species identity or species composition effects are important for detritus processing in natural systems, and also whether there was any evidence for a selection effect in natural communities.

Objective 1 was addressed by asking the following questions:

(1) What is the importance of species diversity among the other biotic and abiotic factors important for leaf processing across natural streams?

> If species diversity is important, it is predicted that there will be a positive relationship between species diversity and leaf processing.

(2) What is the influence of species identity on leaf processing across natural streams?

> If a particular species has strong effects on leaf processing, it is predicted that leaf processing will vary according to the presence, or absence, of that species, and/or that variation in leaf processing across stream sites will be positively, or negatively, related to the abundance or biomass of that species.

(3) What is the influence of species composition on leaf processing?

> If particular species combinations influence leaf processing it is predicted that particular kinds of macroinvertebrate communities will be related to either increased or decreased levels of leaf processing.

These questions were addressed in a field study that examined leaf breakdown rates in eighteen streams, across a natural gradient of shredder diversity (Chapter 2).

Objective 2. To investigate the effect of leaf diversity on detritus processing in low and high diversity shredder communities.

Shredder diversity may positively affect leaf processing through complementarity effects. Objective 1 addresses whether there are complementarity effects of shredder diversity on a single leaf resource (i.e. facilitation, niche-differentiation in time or space). Whether or not a diversity effect is evident on a single leaf resource, shredders may also be complementary in terms of their leaf diets. A mixed leaf resource was used to test whether resource-niche differentiation is an important mechanism for the diversity-ecosystem function relationship in shredder communities. If shredder species are complementary in their leaf diets, it was hypothesised that resource niche-differentiation would lead to increased utilisation of a mixed leaf resource in high, but not in low, shredder diversity communities.

Objective 2 was addressed by asking the following questions:

(1) Is mixed leaf litter among the most fully decomposed litterbag type at high, but not at low, shredder diversity sites?

(2) Is mass loss from mixed leaf litter greater than the overall mass loss from single leaf-types at high, but not at low, shredder diversity sites?

(3) Is there a positive relationship between mass loss from mixed leaf litterbags and shredder species number?

(4) Is mass loss from mixed leaf litter greater than that predicted from single leaf types at high, but not at low, shredder diversity sites?

These questions were addressed by examining the breakdown rates of single and mixed leaf resources in a sub-set of the stream sites used in the first field study (Chapter 3).

Objective 3. To examine shredder identity and complementarity effects on leaf processing on a) a single leaf resource and b) a mixed leaf resource, under controlled conditions.

Objectives 1 and 2 address whether shredder diversity is important for leaf processing in natural streams, as other biotic and abiotic factors vary. Objective 3 tested for small-scale local effects of shredder diversity on leaf processing, while eliminating variation in biotic and abiotic factors that may mask effects at larger scales. A laboratory approach allowed the possible mechanisms driving any positive diversity effects to be identified.

Objective 3 was addressed by asking the following questions:

(1) Does shredder species identity affect leaf processing rates?

If there are shredder identity effects, it is predicted that there will be significant differences in leaf processing rates between single-species treatments.

(2) Does shredder diversity positively affect leaf processing rates?

If there is a positive affect of shredder diversity, it is predicted that leaf processing rates will be greater for mixed-species streams than for single-species streams on average, and that leaf processing rates observed in mixed-species streams will be greater than predicted from combining estimates of leaf processing rates from single species streams.

(3) Are there any complementarity effects?

If there is any facilitation or niche-differentiation between shredder species, it is predicted that there will be overyielding in mixed-species streams. That is, the mean leaf processing rate for mixed-species assemblages will be greater than that of the single-species assemblage with the highest leaf processing rate (see Section 1.5.1).

These questions were addressed using laboratory based stream mesocosms, to eliminate variation in biotic and abiotic factors that might mask effects in natural streams (Chapter 4).

Objective 4. To test whether complementarity between shredder species in their leaf diets positively affects leaf processing rates.

Previous objectives have not provided any direct test of the possible mechanisms arising from complementarity between shredder species. The goal here was to test directly the niche-differentiation mechanism. The niche-differentiation hypothesis predicts that the utilisation of available resources increases as a wider range of resource-niches are represented by the species present (Section 1.4.2.1).

Objective 4 was addressed by asking the following questions:

(1) Is there potential for complementarity between shredder species in terms of their leaf diets?

> If shredder species are complementary in their leaf diets, it is predicted that there will be significant variation in their relative consumption rates across a range of different leaf litter types.

(2) What is the relationship between complementarity and leaf processing rates?

> If there is variation between shredder species in their leaf diets, it is predicted that leaf processing rates will increase as complementarity in leaf diet between species increases.

These questions were addressed by quantifying the consumption rates of several shredder species on a range of leaf types, and then using these data to construct a gradient of complementarity between shredder species in their leaf diet, in artificial stream mesocosms (Chapter 5).

2. The importance of macroinvertebrate species richness, identity and community composition for detritus processing in natural streams.

2.1. Introduction.

The majority of studies on diversity-ecosystem function relationships have involved experimental manipulations of species richness at a local scale, for example small grassland plots (e.g. Tilman *et al.* 1996) and microcosm experiments (e.g. McGrady-Steed *et al.* 1997, Naeem & Li 1997; see Section 1.5.2.2). Only a few studies have been conducted on larger, landscape or regional scales (Hector *et al.* 1999) and fewer still have focused on natural systems (Wardle *et al.* 1997b, Jonsson *et al.* 2001, Huryn *et al.* 2002). Little is known about how the patterns and processes observed from local-scale experimental manipulations of species richness relate to larger scale, regional patterns (Wardle *et al.* 1997c, Bengtsson *et al.* 2002).

Small-scale experiments have produced mixed evidence as to the importance of macroinvertebrate species richness, species identity and composition for detritus processing in streams (Jonsson & Malmqvist 2000, in press, Ruesink & Srivastava 2001, Cardinale *et al.* 2002, Jonnson *et al.* 2002). Jonsson & Malmqvist (2000) manipulated the richness of stonefly shredders from one to three species, in small aquatic mesocosms. They reported positive effects of species number on detritus processing while species identity and species combination were unimportant. In contrast, Jonnson *et al.* (2002) found that species identity and composition were important for detritus processing, whereas species number was not, when they examined another three, less closely related shredder species. A further study revealed the same conclusions for stream macroinvertebrates belonging to other functional feeding groups: filter feeders, grazers and predators (Jonsson & Malmqvist, in press). Similarly, an experiment that manipulated the identity of the dominant shredder in artificial stream communities, reported that species identity was the main factor affecting detritus processing (Ruesink & Srivastava 2001). However, the effects of species number and species identity need not be mutually exclusive. For example, Cardinale *et al.* (2002) partitioned the observed positive effect of increasing the number of species of filter-feeding caddisfly larvae on resource consumption, from one to three, into 83% 'complementarity' (species richness effect) and 17% 'selection' (species identity effect).

Laboratory–based experiments in aquatic mesocosms and experimental stream systems are crucial for providing insight as to the importance of local-scale effects of species richness and identity for detritus processing (i.e. within a small stretch of stream). However, such experiments are of limited use in providing predictions about diversity effects at a larger regional scale (i.e. comparisons between different streams). Studies of the latter form are required in order to predict the effects of diversity on ecosystem function at larger, more realistic scales. However, at the regional scale, any effect of diversity on ecosystem function may be overshadowed by the effects of environmental factors, and other biotic factors, that may vary between ecosystems (Loreau 2000, Loreau *et al.* 2001; Section 1.5.2.2). It is therefore necessary to take into account variation in diversity, environmental factors and other biotic factors, in order to adequately characterise the relative influence of diversity on function at a regional scale.

Various environmental and biotic factors (including diversity) influence detritus processing in streams, some of which are likely to be intercorrelated. To investigate whether macroinvertebrate species richness is important for detritus processing at a regional scale requires that other factors are quantified and controlled for statistically. In addressing the specific role of macroinvertebrate species richness in detritus processing, therefore, it is critical to examine its importance relative to the various environmental and other biotic factors that influence detritus processing across a regional scale.

2.1.1. Factors that influence detritus processing in streams.

2.1.1.1. Environmental factors.

Various environmental factors influence detritus processing in streams either directly, or indirectly through their influence on the detritivore community (Webster & Benfield 1986). The two main abiotic influences on detritus processing are temperature and pH (Webster & Benfield 1986). Faster litter breakdown rates are commonly observed at warmer stream temperatures (e.g. Petersen & Cummins 1974, Reice 1974, Suberkropp *et al.* 1975). Temperature is thought to affect detritus processing rates primarily through its influence on microbial processes (Paul *et al.* 1983, Webster & Benfield 1986, Irons *et al.* 1994). Low pH appears to reduce rates of detritus processing in streams (e.g. Minshall & Minshall 1978, Burton *et al.* 1985, Rowe *et al.* 1996). This is thought to be an indirect effect, primarily acting on detritivore community structure, by altering macroinvertebrate composition and causing a reduction in shredder biomass (Townsend *et al.* 1983, Griffith & Perry 1993). Other environmental factors that may potentially influence detritus processing rates either directly, or indirectly, include: dissolved oxygen (Webster & Benfield 1986), flow rate (Reice 1974, Poff & Ward 1989), and conductivity (Giller & Malmqvist 1998).

The River Continuum Concept (RCC) (Vannote *et al.* 1980) predicts that the importance of detritus processing varies with increasing stream size, from headwaters to mouth (i.e. stream order). One major prediction of the RCC is that: as canopy cover decreases and light penetration therefore increases, autochthonous primary production becomes more important than the processing of allochthonous organic material, in relative terms. The RCC predicts that shredders will predominate in small, shaded, headwater streams, whereas collectors will be the dominant functional feeding group in larger, open streams, and this pattern has been observed in the field (e.g. Canton & Chadwick 1983, Minshall *et al.* 1983, Grubaugh *et al.* 1996, Graça *et al.* 2001). Therefore, it may be expected that leaf detritus will be processed at a faster rate in smaller, shaded streams, due to the prevalence of shredders, although field studies have provided contrasting evidence for this prediction (e.g. Minshall *et al.* 1983, Graça *et al.* 2001).

2.1.1.2. Biotic factors

Abundance and biomass.

Evidence from several studies reveals that variation in leaf processing rates is positively related to both macroinvertebrate abundance and biomass (e.g. Short *et al.* 1980, Wallace *et al.* 1982, Benfield & Webster 1985, Webster & Benfield 1986, Wallace *et al.* 1986, Cuffney *et al.* 1990, Jonsson *et al.* 2001, Huryn *et al.* 2002). For example, in two related studies, insecticide-induced disturbance of two different streams resulted in reductions in macroinvertebrate density (particularly of the shredder and collector-filterer functional feeding groups), that were associated with significantly reduced leaf processing rates in comparison to control streams (Wallace *et al.* 1982, Cuffney *et al.* 1990). A follow-up study on one of the experimentally disturbed streams revealed that recovery in leaf processing rates, to pre-disturbance levels, was associated with the restoration of shredder biomass (Wallace *et al.* 1986).

Species richness.

To date, only two studies have specifically addressed whether macroinvertebrate species richness positively affects leaf processing in streams at regional scales (i.e. across different streams) (Jonsson *et al.* 2001, Huryn *et al.* 2002). Jonsson *et al.* (2001) quantified the decomposition of alder leaf material (*Alnus incana*) across twenty-three boreal streams in Sweden, and related this to various environmental and biotic factors including the abundance, biomass and diversity of the shredder component of the macroinvertebrate community. A different study aimed to assess the effect of catchment land-use on processing rates of red maple litter (*Acer rubrum*) across seventeen stream sites in Maine, U.S.A (Huryn *et al.* 2002). In contrast to the mixed evidence provided by small-scale experimental manipulations of species richness (Section 2.1), both of these field studies found a positive relationship between shredder richness and detritus processing.

Moreover, both studies concluded that shredder species richness was the strongest biotic determinant of detritus processing, over and above either shredder abundance (Jonsson *et al.* 2001) or shredder biomass (Huryn *et al.* 2002). The influence of shredder richness on detritus processing, in the former study, was secondary to that of water temperature and 'year', a factor which represented variation in all the factors that were not quantified between the two years of the study. Huryn *et al.* (2002), however, did not examine the effect of shredder richness relative to variation in environmental factors across stream sites.

An effect of species richness on detritus processing, stronger than that of either abundance or biomass, is suggestive of low redundancy among species. That is, low species richness cannot be compensated for by increases in abundance or biomass. A weak influence of species richness on detritus processing, compared to that of abundance or biomass, would suggest that although species richness is important, there is a greater degree of redundancy among species, whereby increases in abundance or biomass can compensate for low species richness.

2.1.2. Influence of individual species on detritus processing.

There has been little work on the role of individual macroinvertebrate species in leaf processing, and not much is known about whether there are strong species identity effects on leaf processing in natural communities (Covich *et al.* 1999). A study conducted in artificial stream channels tested whether a shredder community could maintain leaf processing rates after the removal of either one of two dominant shredder species, both cased caddisfly larvae (Ruesink & Srivastava 2001). The authors reported that while an increase in shredding rates by the remaining species was able to compensate for the loss of one of the dominant species (*Pteronarcys californica*), it was unable to compensate for the loss of the other species (*Lepidostoma unicolor*), and leaf processing was significantly reduced, indicating strong species identity effects of *L. unicolor*.

Strong species identity effects may occur in stream communities when leaf processing is strongly influenced by a particular dominant macroinvertebrate species. If species identity effects on leaf litter processing do occur, then the selection effect (Section 1.4.1) may drive a positive relationship between species number and detritus processing, i.e. the species with a strong identity effect on leaf litter processing is more likely to be present in species rich communities, rather than species poor communities. However, if a species with a strong species identity effect occurs at unpredictable points along the species richness gradient, then an idiosyncratic relationship between species richness and leaf processing may result (Section 1.1.2; Figure 1.1d).

2.1.3. Influence of community composition on detritus processing.

Community composition may have an effect on detritus processing independently of any diversity effect, and depends on the identity of the species present within a community and their relative abundances (Section 1.3.2). Any effect of macroinvertebrate community composition on detritus processing may be driven by certain combinations of species that interact in either a positive (facilitation, niche-differentiation) or negative (interference) way, to either increase or decrease leaf processing rates. The extent to which species composition influences leaf processing in streams may depend on the relative influence of physical factors and species interactions on macroinvertebrate community structure. Macroinvertebrate communities may be deterministic assemblages structured mainly by species interactions, or alternatively, physical disturbance and chance may act to structure communities in a stochastic way (see Section 1.6.2). For deterministic assemblages, where there are interactions among species, community composition could influence leaf processing rates through positive or negative interactions among groups of species. Alternatively, if macroinvertebrate assemblages are non-interactive, then the effects of particular individual species (i.e. species identity effects; see Section 2.1.2) may be more important for leaf processing than interactions among groups of species. However, the influence of physical factors and species interactions on community structure are not necessarily mutually exclusive (Giller & Malmqvist 1998), therefore it is difficult to predict how community composition may affect leaf processing in natural stream communities.

To date there have been no studies that have explored specifically whether macroinvertebrate community composition affects leaf processing rates in streams. However, one field study, that followed the recovery of a stream from an insecticide-induced disturbance, does provide some limited evidence (Wallace *et al.* 1986). Taxonomic differences between two streams increased after an insecticide-induced disturbance in one of the streams. After a recovery period of two years, there was no significant difference in total shredder biomass between the disturbed stream and the control stream. However, shredder community composition differed considerably between the two streams in terms of both the shredder taxa present, and their relative biomass. Four different leaf types were used to quantify detritus processing rates in the two streams. While the process rate of the fastest decomposing leaf type used was significantly higher in the control stream, process rates of the remaining three leaf types used were similar in both streams. Shredder community composition therefore appeared to influence the process rate of one leaf type, but was unimportant for the other three.

2.1.4. Aims.

The overall aim of this chapter is to examine the influence of macroinvertebrate species richness, species identity and community composition on detritus processing at a regional scale (i.e. between streams). The specific questions addressed here are: (1) does species richness influence leaf litter processing? (2) Is there any evidence for individual species identity effects on leaf processing through either (a) species presence/absence, and/or (b) their abundance/biomass? And if so: (3) do species identity effects influence the relationship between species richness and leaf processing (i.e. is there a selection effect)? And (4) are there distinct community types associated with varying degrees of leaf processing?

While it was expected that any effect of biotic factors on leaf litter processing would be most closely associated with the shredder component of the macroinvertebrate community, the influence of the whole macroinvertebrate community was also considered for two reasons. Firstly, to take into account the influence of other functional feeding groups that might play an indirect but important role in leaf breakdown through their feeding activities. Secondly, to account for the various interactions between species belonging to different functional feeding groups, and unknown food-web dynamics, that might affect detritus processing rates (Malmqvist 1993). The influence of macroinvertebrate biomass on leaf processing was considered only for the shredder component of the community since they are the functional feeding group that feed directly on, and assimilate energy from, large fragments of leaf litter.

2.2. Methods.

2.2.1. Study sites.

The stream sites included in the present study were selected from an existing database of forty-three sites, originally compiled for a separate study during 1997/1998 (Whittle 2000). Species diversity information for these forty-three sites was used to select a sub-set of eighteen sites, which represented the greatest natural range in macroinvertebrate species richness over a regional scale. The selected eighteen stream sites are distributed over an area of approximately 1695 km^2 in South Yorkshire and Derbyshire, England (Figure 2.1). Detailed site information is given in Table 2.1. The majority of stream sites are situated within the Peak District National Park, positioned to the south west of Sheffield. Of the remaining sites, five are situated to the north of Sheffield (Lowmill, Berrymoor, Cranemoor, Oughtibridge and Charltonbrook), two sites lie east of Sheffield (Stone and Lindrick Dale) and one site is located within Sheffield (Greystones).

All sites selected for the present study are small headwater streams, ranging from stream order 1 to 3 (assigned using the Strahler Method, Dobson & Frid 1998), for which allochthonous detrital inputs are likely to be the main source of energy (Vannote *et al.* 1980). Typical dominant riparian tree species include alder (*Alnus glutinosa* L. (Gaertner), sycamore (*Acer pseudoplatanus* L.), ash (*Fraxinus exelsior* L.) and hawthorn (*Crategus monogyna* Jacquin). The site at Strines (Figure 2.2) is notable for the dominance of beech (*Fagus sylvatica* L.)

Figure 2.1. Map of study area with eighteen stream sites indicated by symbols (◆). Both maps reproduced from Ordnance Survey map data by permission of Ordnance Survey, ©Crown copyright.

Table 2.1. Summary of site information for the eighteen streams used in the field study. Stream names in brackets indicate that the site used was a tributary of the river name given. Geological information was taken from the 'Geological map of GB – sheet 2 (England and Wales)', 2nd edition, 1957, prepared by the Geological Survey. Land use type was ascertained from OS Landranger Maps (1:50 000) and personal observation. Land use type codes are: A = agricultural, WA = woodland surrounded by agriculture, WU = urban woodland, FP = forestry plantation. Stream order was ascertained from OS Landranger Maps (1:50 000) according to the Strahler Method (Dobson & Frid 1998).

Site name	Stream	NGR	Altitude (m above sea level)	Geology (Sedimentary formation)	Land use type	Stream order	Stream substrate composition (% cover)			
							Boulders	Pebbles	Sand	Silt
Stone	Maltby Dike	SK556897	50	Marl	A	2	80	15	5	0
Greystones	Porter Brook	SK318855	140	Coal measures	WU	2	40	50	10	0
Lindrick Dale	Anston Brook	SK540825	70	Magnesian limestone	A	3	5	80	15	0
Barlow Trout Farm	Barlow Brook	SK339757	110	Coal measures	A	3	5	90	5	0
Smeekly Wood	Barlow Brook	SK301772	220	Coal measures	WA	2	5	85	10	0
Hillhouses	(River Rother)	SK367671	140	Millstone grit	A	2	80	0	0	20
Highlightly Farm	Barlow Brook	SK326762	200	Coal measures	A	3	10	70	20	0
Charlton Brook	Hall Brook Dike	SK337967	120	Coal measures	WA	1	50	10	0	40
Crowdecote	River Dove	SK100652	250	Carboniferous limestone	A	3	0	30	10	60
Cranemoor	(River Dove)	SK304015	130	Coal measures	A	1	5	50	40	5

Table 2.1 continued.

Site name	Stream	NGR	Altitude (m above sea level)	Geology (Sedimentary formation)	Land use type	Stream order	Stream substrate composition (% cover)			
							Boulders	Pebbles	Sand	Silt
Strines	Strines Dike	SK220908	280	Millstone grit	FP	3	80	15	5	0
Oughtibridge	(River Don)	SK305933	100	Coal measures	A	1	10	70	30	10
Netherloads	(River Hipper)	SK329695	180	Millstone grit	A	1	70	0	0	30
Lowmill	(River Dearne)	SK296071	140	Coal measures	A	3	5	50	35	10
Holehouse	(River Etherow)	SK004921	180	Millstone grit	WA	1	20	60	20	0
Berrymoor	(River Dove)	SK292030	150	Coal measures	A	2	10	60	0	30
Brockhurst	River Amber	SK331646	220	Millstone grit	A	2	40	60	0	0
Barlow Brook	Barlow Brook	SK345755	125	Coal measures	A	3	50	40	10	0

Figure 2.2. Photograph of steam site at Strines.

Figure 2.3. Photographs of stream sites at a) Stone and b) Lindrick Dale.

and oak (*Quercus robur* L.) trees while birch (*Betula pendula* Roth) dominates the woodland surrounding the site at Holehouse. The stream sites at Stone and Lindrick Dale (Figure 2.3 a and b) run through private residential gardens. Consequently, the surrounding riparian vegetation is diverse and relatively unusual, including many exotic species.

The use of land surrounding stream sites is mainly agricultural, and largely pasture rather than crops. Strines is the only site situated within coniferous forest plantation, while Smeekly Wood, Charlton Brook and Holehouse are situated within non-coniferous woodland and surrounded by agricultural land. Greystones is the only urban site, but is also situated within non-coniferous woodland.

The underlying geology of the stream sites is of three main types. Coal measures is characteristic at sites to the north of Sheffield and at the north west edge of the Peak District. Millstone grit is typical of sites situated in the north east of the Peak District, while one site (Crowdecote) lies on the carboniferous limestone found further to the south west of the study area. There is unusual geology at the two sites situated east of Sheffield, with underlying marl at Stone and magnesian limestone at Lindrick Dale. Stone and Lindrick Dale are also situated at the lowest altitude (50 and 70 m respectively) while Strines is situated at the highest altitude at 280 m.

Streambed substrate composition (see Section 2.2.3) varied considerably across stream sites. Stone, Hillhouses, Strines and Netherloads are all notable for their high percentage cover of large boulders. Netherloads and Hillhouses have particularly homogenous substrates compared to the remaining sites, while Crowdecote is distinct due to the lack of large substrate components and high percentage cover of silt.

2.2.2. Quantifying leaf decomposition.

A single leaf type was used to quantify leaf decomposition for this study, alder (*Alnus glutinosa*). Alder is a common riparian tree species across the study area and is known to have a relatively rapid processing rate compared to other leaf types (Webster & Benfield 1986). Leaves were collected from alder trees just prior to abscission in early November 1999 from two locations near Sheffield:

the Rivelin Valley (NGR – SK313878) and Harper Lees (NGR - SK234806). Leaf material was air dried for one week before storage.

Rectangular litter bags (6 cm x 8 cm in size; Figure 2.4). were constructed from a plastic mesh material (standard garden shelter netting), with a mesh size of 0.5 cm x 0.4 cm. Each litter bag was filled with 5.0 g of air-dried alder material along with a small pebble to weigh down the litter bags, and was sealed using an electric heat sealer. Litter bags were strung together in groups of four with fishing line (60 lb. breaking strain), leaving a gap of 0.5 m between each bag. Eight litter bags (two strings of four) were deployed at each of the eighteen stream sites, over a period of five days, at the end of November 1999, in order to coincide with the period of peak leaf input into streams. Each string of litter bags was secured to tree roots or large boulders, on or near the stream bank. At each site, the two strings of litter bags were positioned approximately 5 m apart and on opposite banks.

Figure 2.4. Photograph of litter bags used for quantifying leaf litter decomposition.

Litter bags were collected after seven weeks in-stream exposure, over a period of five days. Upon collection each individual litter bag was detached from the fishing line and sealed into a labelled plastic bag. Litter bags were returned to the laboratory and stored by freezing at –10°C, until the material could be processed. Upon defrosting, macroinvertebrates were separated from the leaf material. Leaf material was then sieved through 0.5 cm x 0.4 cm mesh (i.e. the mesh used to construct the litter bags) in order to remove any small fragments of leaf material that may have been washed into the litter bag or retained after fragmentation by shredding detritivores. Leaf material retained by the sieve was washed carefully to remove any silt and air-dried until a constant mass was achieved. Leaf mass loss was subsequently recorded.

2.2.3. Physico-chemical measurements.

Measurements of dissolved oxygen (D.O.) (% saturation), temperature (°C), pH, conductivity (µS/cm) and flow rate (m/s) were made using hand-held meters (D.O. with a HANNA HI9142 meter, conductivity with a Jenway 4071 meter, pH and temperature with a Jenway 3310 meter and flow rate with a MeBfliigel current meter (Moulinet, type C2)). Readings were taken on two occasions, upon deployment of litter bags, and seven weeks later upon their collection. Two flow rate measurements were taken on each visit: one above the first litter bag of the first string of four, and the second further downstream, above the first litter bag of the second string of four. A visual judgement of percentage canopy cover was made on only one occasion (upon litter bag deployment) along with an estimation of stream substrate cover. Stream substrate cover was estimated using RIVPACS guidelines (Murray-Bligh *et al.* 1997) by assigning substrate to one of four different size categories: boulders (> 64 mm), pebbles (2 – 64 mm), sand (0.06 – 2 mm) and silt (< 0.06 mm), then judging the percentage cover of each.

2.2.4. Quantifying biotic variables.

The stream benthic macroinvertebrate communities were sampled upon litter bag collection, using a standard kick net (Murray-Bligh *et al.* 1997). Ten two-minute kick samples were taken at each site within the stretch of stream where litter bags were deployed (approximately a 10 to 12 m stretch), moving diagonally across and upstream in order to sample as many habitat types as possible. All kick sampling was performed by the same person and sampling effort was standardised across stream sites as far as is possible with this technique. The contents of each kick-net sample were preserved with 70% industrial methylated spirits in sealed pots for storage. Due to the drying out of a few kick-net samples, data from eight samples only from each site were used in the final analyses.

In the laboratory all macroinvertebrates were picked from each kick sample, identified to species level wherever possible (Macan 1977, Hynes 1977, Elliott &

Mann 1979, Edington & Hildrew 1981, Elliott *et al.* 1988, Wallace *et al.* 1990, Gledhill *et al.* 1993, Nilsson *et al.* 1996, Elliott 1996, Friday 1988) and counted. Notable exceptions included some of the dipteran larvae, which were identified to family level in most cases. Worms and water-mites were separated into different groups but not formally identified at the species level. Some early instars of cased caddisfly larvae belonging to the Limnephilidae and Leptoceridae families were too small to be identified beyond family level. Species belonging to the shredder functional feeding group were distinguished from other macroinvertebrate species using information from the literature (Nilsson *et al.* 1996, Giller & Malmqvist 1998). The wet mass of all shredder species were recorded by blotting animals twice on tissue paper to remove excess moisture and noting the weight (to the nearest 0.1mg) after exactly thirty seconds on the balance (Mettler ME30 microbalance).

2.2.5. Statistical analyses.

Multiple regression analysis was used to assess the relative influence of abiotic and biotic variables on leaf mass loss across the eighteen stream sites using mean leaf mass loss as the response variable. Multiple regression models were constructed using stepwise forward selection ($p < 0.25$ to enter) and best subsets regressions using MINITAB 13.2 for Windows. Best subsets regression identifies the best fitting regression models that can be constructed with a set of predictor variables. All possible subsets of the predictor variables are evaluated, beginning with models containing one predictor through to models containing the maximum number of predictors. Four separate multiple regression analyses were performed. One each using biotic predictor variables for a) the whole community, b) the shredder community only, c) the non-shredder community only and d) the shredder and non-shredder components of the community separately (Table 2.2). In all four analyses, all environmental factors were included as potential predictor variables. These included: pH, temperature (°C), conductivity (µS/cm), flow rate (m/s), dissolved oxygen (% saturation), % canopy cover and stream order. The biotic variables that were included as potential predictor variables in each of the four analyses are summarised in Table 2.2.

Collinearity between predictor variables was assessed visually using scatter plots between pairs of variables and by examining the variance inflation factor (VIF) for each predictor variable. The VIF measures how much of the variance of an estimated regression coefficient increases if the predictor variables are correlated. The largest VIF among all predictor variables was used as an indicator of collinearity. Variance Inflation Factor values of five or more were considered unacceptable (Montgomery *et al.* 2001).

Table 2.2. Summary of biotic factors entered as predictor variables in four separate multiple regression analyses.

Community components used in multiple regression analysis	Biotic factors entered as potential predictor variables.
a) Whole community	Total abundance. Total species richness.
b) Shredder community only	Shredder abundance. Shredder species richness. Shredder biomass.
c) Non-shredder community only	Non-shredder abundance. Non-shredder species richness.
d) Shredder and non-shredder community	Shredder abundance. Shredder species richness. Shredder biomass. Non-shredder abundance. Non-shredder species richness.

Where collinearity occurred, all alternative forward selection regression models were examined, i.e. including all variables simultaneously and each variable individually. In each case, the regression model that resulted in the best fit is presented. The goodness of fit of potential multiple regression models was assessed by examination of regression statistics and residual diagnostics. Models that generated residual plots that were closest to a normal distribution were favoured (i.e. normal probability plots were linear, histograms were symmetrical and bell-shaped). Additionally, models that generated Individuals charts of residuals that showed the least number of failed points (i.e. points that indicate a non-random pattern in the data), were favoured.

All biotic predictor variables were log transformed (Ln (x +1)) to improve the fit to a normal distribution, except for species richness (shredder, non-shredder and total). Best subsets regression analysis was also used to identify potentially significant relationships between leaf mass loss and the abundance/biomass of individual shredder species. Regression analysis was used to test for significant relationships between leaf mass loss and individual biotic factors, including overall shredder abundance and biomass and the abundance and biomass of particular species.

Principal Component Analysis (PCA) was used to assess the similarity in macroinvertebrate community composition among stream sites. Raw data were transformed (Ln (x +1)) in order to overcome the sensitivity of PCA to abundance data that includes differences across orders of magnitude (Whittle 2000). PCA was performed on transformed data for a) the whole community and b) the shredder community only, using both correlation (abundances are standardised) and covariance matrices (abundances are not standardised).

2.3. Results.

2.3.1. Variation in environmental and biotic factors.

A summary of the environmental data collected across the eighteen study sites is given in Table 2.3. (see Appendix A for raw data). Dissolved oxygen (% saturation) and pH were the environmental factors that varied least across the eighteen stream sites (C.V. = 9 and 7 respectively) while flow rate (m/s) and conductivity (μS/cm) showed the greatest variation (C.V. = 54 and 49 respectively).

A summary of the biotic data collected across the eighteen stream sites is given in Table 2.4 (see Appendix B for raw data). The total number of species found across all eighteen sites was 138, ranging from 15 to 59 species found at any one site. The total number of shredder species found was 37, with a minimum of 2 species at Stone and a maximum of 20 species found at Holehouse. Abundance varied greatly across sites for both the shredder and non-shredder components of the macroinvertebrate community (C.V. = 123 and 90 respectively). The total number of individuals collected was 39 329 with a range of 293 to 7514 individuals found at any one site. Shredder abundance was maximal at Stone (3961 individuals) while the fewest number of shredders were found at Crowdecote with only 17 individuals. Shredder biomass (g, wet mass) showed the greatest variation out of all the biotic factors (C.V. = 202) and closely mirrored patterns in shredder abundance.

Table 2.3. Summary of environmental data collected across eighteen sites. The mean (n = 18), standard deviation, coefficient of variation (C.V.) and range of each variable are given.

Summary statistics	Temperature (°C)	Dissolved oxygen (% saturation)	Flow rate (m/s)	Conductivity (μS/cm)	pH	Stream order	Canopy cover (%)
Mean	6.6	87	0.33	432	7.2	2.1	76.4
Standard deviation	0.95	6.6	0.18	214	0.7	0.83	27.18
C.V.	14	7	54	49	9	39	36
Minimum value	5.1	75	0.14	158	4.7	1	15
Maximum value	8.2	98	0.78	926	7.9	3	100

Table 2.4. Summary of biotic data collected across eighteen sites. The mean (n = 18), standard deviation, coefficient of variation (C.V.) and range of each variable are given.

Summary statistics	Richness			Abundance			Biomass (g, wet)
	Total	Shredder	Non-shredder	Total	Shredder	Non-shredder	Shredder
Mean	40.5	11.7	28.8	2184.4	870.4	1314	4.8
Standard deviation	12.6	4.8	9.6	1934.8	1071.9	1231.7	9.7
C.V.	30	40	30	90	123	90	202
Minimum value	15	2	8	293	17	19	0.05
Maximum value	59	20	48	7514	3961	5565	37.9

2.3.2. Factors influencing leaf mass loss.

2.3.2.1. Whole macroinvertebrate community.

There was no significant relationship between total species richness and leaf mass loss ($F_{1,16} = 0.63$, $p > 0.05$; Figure 2.5 a). Using data for the whole macroinvertebrate community, the best fit multiple regression model included canopy cover, total macroinvertebrate abundance and temperature, and was successful in explaining 66.2% of the variation in leaf mass loss across sites (Table 2.5). Each factor was positively related to leaf mass loss. Canopy cover and total macroinvertebrate abundance had the largest influences on leaf mass loss, while the influence of temperature was smaller.

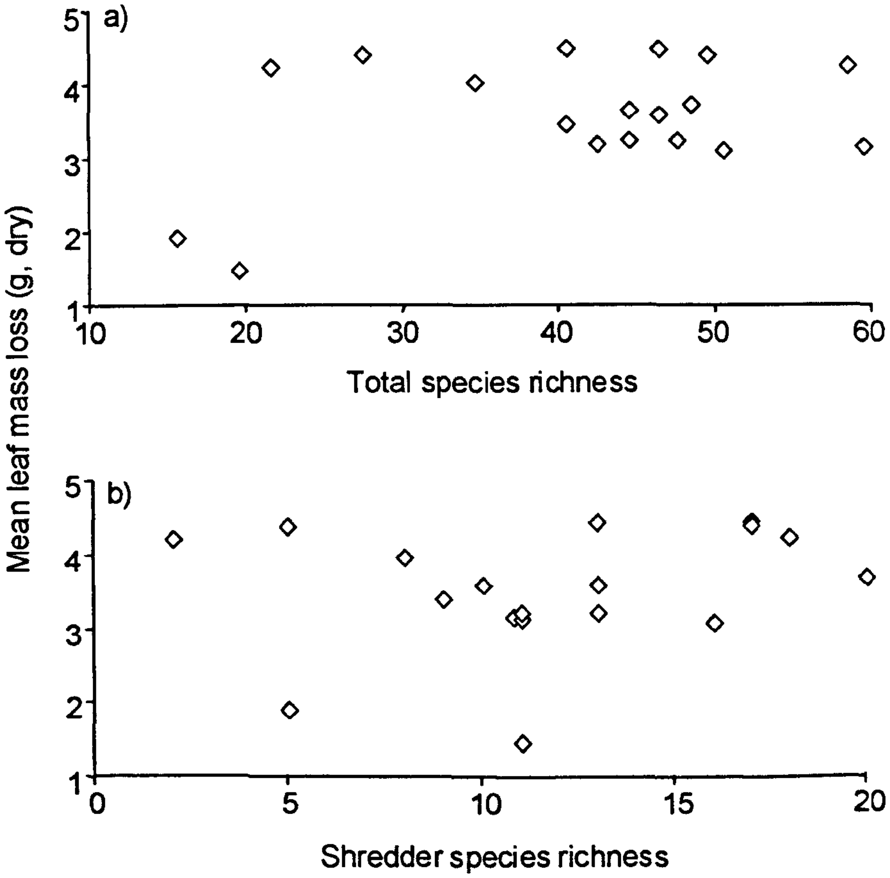


Figure 2.5. Relationship between mean leaf mass loss (g) and a) total species richness and b) shredder species richness.

Table 2.5. Summary of multiple regression results for each of four separate analyses on a) the whole community, b) the shredder community, c) the non-shredder community and d) an analysis entering shredder and non-shredder components of the community as separate predictor variables. For analyses where the exclusion of one site (Strines) made a difference to the best fit regression model, the alternative regression model is presented. Partial regression coefficients, their t-values and level of significance, are given for each factor included in each regression. * indicates $p < 0.05$, ** indicates $p \le 0.01$ and *** indicates $p \le 0.001$. R^2 values are adjusted for the number of predictors included in the model.

Component(s) of community data used for regression model	Sites used in analysis	R^2	F value	Intercept	d.f.	Factors included in best fit model	Partial regression coefficient	t value
Whole community	All sites	66.2	12.08***	-5.6**	3, 14	Canopy cover (%)	0.02**	3.59
						Whole community abundance	0.59**	3.46
						Temperature (°C)	0.49*	2.53
Shredder community	All sites	90.4	27.65***	-10.0***	6, 11	Canopy cover (%)	0.02***	7.11
						pH	0.54***	5.47
						Shredder species richness	0.08***	5.38
						Temperature (°C)	0.55***	4.98
						Shredder biomass (g)	0.43***	4.98
						D.O. (% saturation)	0.03*	2.92
Shredder community	Excluding Strines	84.3	18.18***	-5.7**	5, 11	Canopy cover (%)	0.02***	6.87
						Shredder biomass (g)	0.46***	5.13
						Shredder species richness	0.07***	4.72
						Temperature (°C)	0.44**	3.70
						D.O. (% saturation)	0.04**	3.14
Non-shredder community	All sites	64.5	11.3**	-4.6**	3,14	Canopy cover (%)	0.021**	3.56
						Non-shredder abundance	0.39**	3.28
						Temperatue (°C)	0.57**	3.00

Table 2.5 continued.

Component(s) of community data used for regression model	Sites used in analysis	R^2	F value	Intercept	d.f.	Factors included in best fit model	Partial regression coefficient	t value
Non-shredder community	Excluding Strines	38.7	4.37*	2.82***	3, 13	Conductivity (µS)	0.002**	3.03
						Stream order	-0.58*	-2.91
						Canopy cover (%)	0.06*	2.66
Non-shredder and shredder community	All sites	90.4	27.65***	-10.0***	6, 11	Canopy cover (%)	0.02***	7.11
						pH	0.54***	5.47
						Shredder species richness	0.08***	5.38
						Temperature (°C)	0.55***	4.98
						Shredder biomass (g)	0.43***	4.97
						D.O. (% saturation)	0.03*	2.92
Non-shredder and shredder community	Excluding Strines	84.3	18.18***	-5.7**	5, 11	Canopy cover (%)	0.02***	6.87
						Shredder biomass	0.46***	5.13
						Shredder species richness	0.07***	4.72
						Temperature (°C)	0.44**	3.70
						D.O. (% saturation)	0.04**	3.40

2.3.2.2. Shredder community.

There was no significant linear relationship between shredder species richness and leaf mass loss ($F_{1,16} = 0.63$, $p > 0.05$; Figure 2.5 b). Using data for the shredder component of the macroinvertebrate community only, a multiple regression model accounted for 90.4% of the variation in leaf mass loss and included six predictor variables (Table 2.5): canopy cover, pH, shredder species richness, temperature, shredder biomass and D.O. Canopy cover, pH and shredder species richness were the largest influences on leaf mass loss, while temperature, shredder biomass and D.O. had smaller influences. The influence of pH on litter mass loss was strongly driven by one site with a particularly low pH (Strines; Figure 2.6), while the remaining sites did not vary greatly in their pH (from 6.8 to 7.9). When Strines was removed from the analysis, pH was no longer included in the best fit multiple regression model and shredder biomass became a more important influence on leaf mass loss than shredder species richness (Table 2.5). Since shredder abundance and biomass were strongly linearly related ($r = 0.89$, $p < 0.001$, $n = 18$) only one of these factors (shredder biomass) was used in the final multiple regression models, however shredder abundance can be directly substituted for shredder biomass without any large changes to the final models.

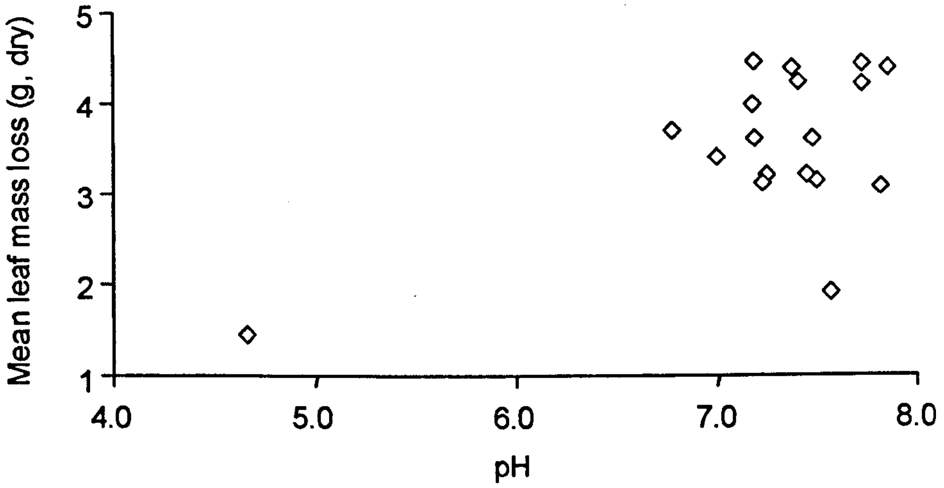


Figure 2.6 Relationship between mean leaf mass loss (g, dry) and pH.

2.3.2.3. Non-shredder community.

When data for the non-shredder component of the community was used in multiple regression analysis the best fit model included non-shredder abundance, canopy cover and temperature and explained 64.5% of the variation in leaf mass loss (Table 2.5). Canopy cover and non-shredder abundance were the largest influences, while the influence of temperature was smaller. The influence of non-shredder abundance was strongly driven by one particular site (Strines; Figure 2.7). When Strines was removed from the analysis, conductivity and stream order are included in the multiple regression model in place of temperature and pH. The resulting regression model explains only 38.7% of the variation in leaf mass loss.

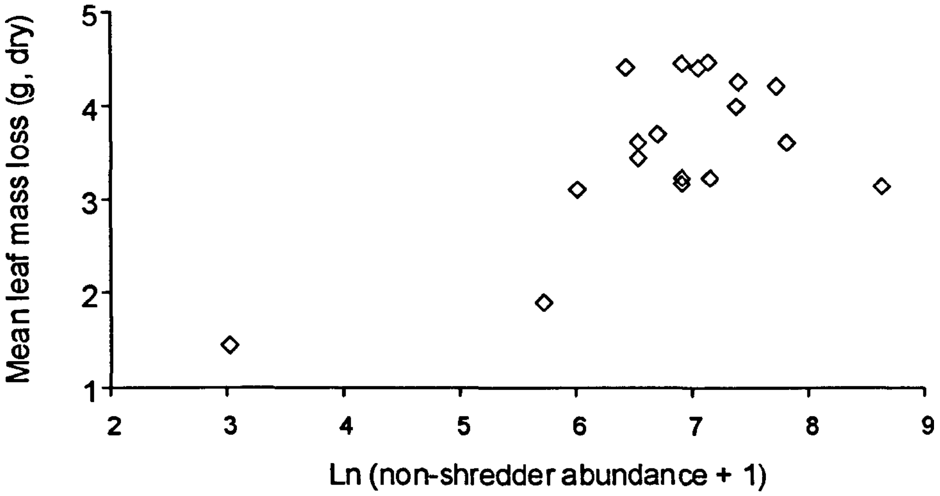


Figure 2.7 Relationship between mean leaf mass loss (g, dry) and non-shredder abundance.

2.3.2.4. All components of the macroinvertebrate community.

A multiple regression analysis, that included all shredder and non-shredder biotic factors as separate potential predictor variables, resulted in exactly the same model as for the shredder only analysis (see Section 2.3.2.2; Table 2.5). Adding non-shredder biotic variables to the potential predictor variables did not change the best fit model. As before, when Strines was removed from the overall analysis, pH was not included as an important predictor variable in the new regression model, which was identical to the model constructed from shredder only data (excluding Strines) (R^2 = 84.3%; Table 2.5). Again, shredder biomass can be substituted in both analyses for shredder abundance without any large changes to the final models.

2.3.2.5. General patterns.

The regression model that explained the greatest amount of variation in leaf mass loss, included all sites ($R^2 = 90.4\%$). The main effects were canopy cover, pH and shredder richness, with additional effects of shredder biomass (or abundance), temperature and D.O. Canopy cover was the environmental variable with the largest influence on leaf mass loss in all multiple regression models. pH was the next most important environmental predictor of leaf mass loss in models where Strines was included, but when this particular site was omitted, pH was unimportant and instead temperature became important. The best fit multiple regression model did not include any non-shredder biotic variables. Therefore, only the shredder component of the community was used to investigate the influence of particular species on leaf mass loss (Section 2.3.3).

2.3.3. Influence of individual shredder species on leaf mass loss.

2.3.3.1. Species presence/absence.

In order to test whether leaf mass loss was influenced purely by the occurrence of particular individual shredder species, the mean mass loss for sites where a species occurred was tested against the mean mass loss for sites where that species was absent, for each shredder species. There were no detectable effects of any of the thirty-seven shredder species ($H = 37.5$, d.f. = 51, $p > 0.05$).

2.3.3.2. Biomass.

Shredder biomass was linearly related to leaf mass loss ($F_{1,16} = 5.4$, $p < 0.05$; Figure 2.8 a). The biomass of each of the thirty-seven shredder species was assessed individually for a linear relationship with leaf mass loss. The biomass of only one species, *Gammarus pulex*, showed a linear relationship with leaf mass loss ($F_{1,16} = 6.77$, $p < 0.05$; Figure 2.8 b). A significant linear relationship continued between shredder biomass and leaf mass loss after *G. pulex* biomass was subtracted (i.e. between non-*G. pulex* shredder biomass and leaf mass loss) ($F_{1,16} = 7.1$, $p < 0.05$; Figure 2.8 c). This indicates that *G. pulex* was not wholly responsible for driving the overall shredder biomass-mass loss relationship.

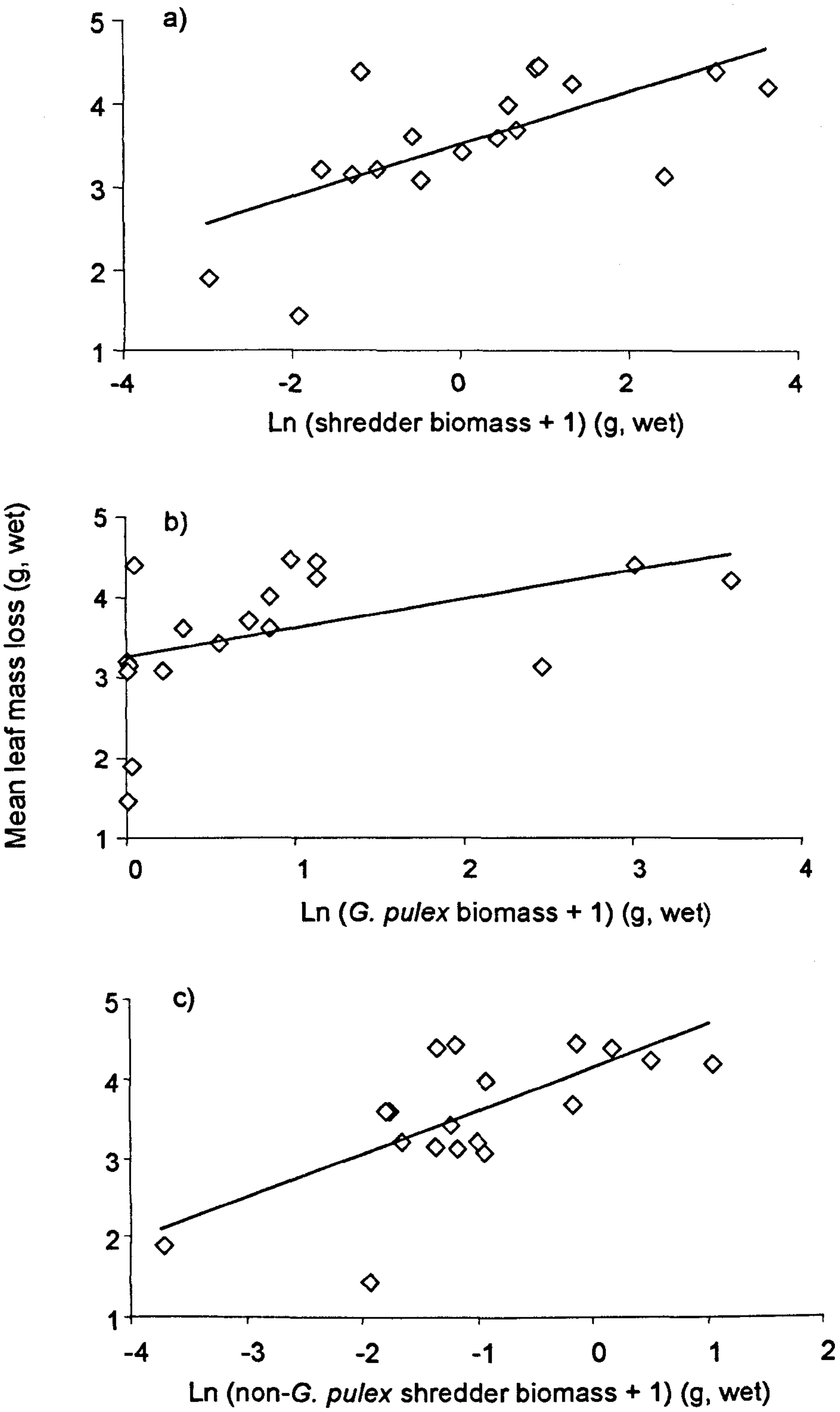


Figure 2.8. Relationship between mean leaf mass loss (g, dry) and;

a) Ln (shredder biomass + 1) (g, wet), $y = 3.13 + 0.41x$ and $R^2 = 25.2$,
b) Ln (*Gammarus pulex* biomass + 1) (g, wet), $y = 3.09 + 0.94x$ and $R^2 = 29.7$ and
c) Ln (non-*G.pulex* shredder biomass + 1) (g, wet), $y = 3.02 + 1.39x$ and $R^2 = 30.8$.

2.3.3.3. Abundance.

Total shredder abundance was linearly related to leaf mass loss ($F_{1,16} = 7.41$, $p < 0.05$; Figure 2.9). Individually, however, only two species' abundances showed significant relationships. These were, *Gammarus pulex* ($F_{1,16} = 9.69$, $p < 0.01$; Figure 2.10 a) and the cased caddisfly larva, *Potamophylax latipennis* (Curtis) ($F_{1,16} = 4.60$, $p = 0.048$; Figure 2.11 a).

The abundance of three other shredder species appeared to show significant negative relationships with leaf mass loss: larvae of the stonefly *Nemurella picteti* Klapálek, the cased caddisfly larva, *Adicella reducta* (McLachlan) and the dipteran larva, *Tipula* (*Savtshenkia* - subgenus). However, these relationships were driven primarily by the sole occurrence of these three species at Strines (a site with low leaf mass loss), and therefore these species were not considered further in this analysis.

A significant linear relationship continued between shredder abundance and leaf mass loss after *P. latipennis* abundance was subtracted (i.e. non-*P. latipennis* shredder abundance) ($F_{1,16} = 7.14$, $p < 0.05$; Figure 2.11 b), indicating that *P. latipennis* was not driving the shredder abundance-mass loss relationship. However, a significant relationship did not continue to occur between shredder abundance and leaf mass loss after *G. pulex* abundance was subtracted (i.e. non-*G. pulex* shredder abundance) ($F_{1,16} = 4.23$, $p = 0.06$; Figure 2.10 b) indicating that *G. pulex* has a strong influence on the shredder abundance-mass loss relationship. There was no relationship between the abundance of *G. pulex* and shredder species richness or total species richness (Figure 2.12 a and b), indicating that *G. pulex* did not drive a selection effect.

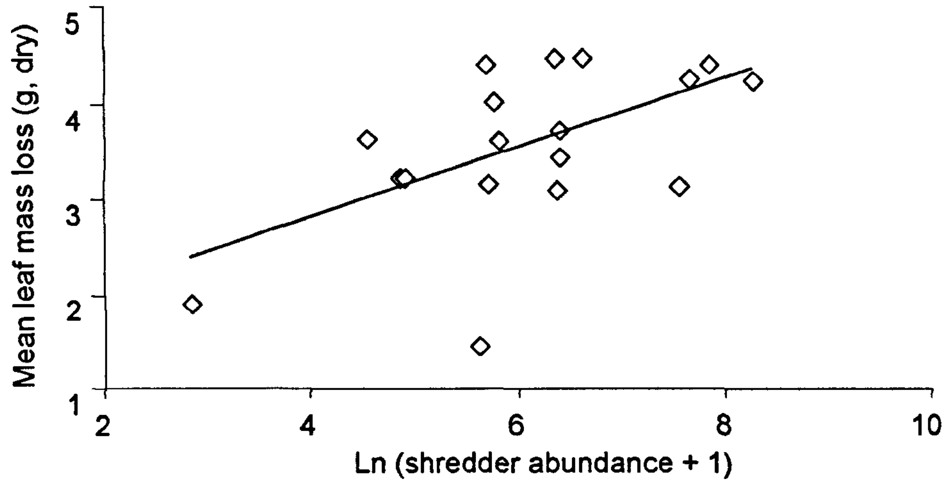


Figure 2.9. Relationship between mean leaf mass loss (g, dry) and Ln (shredder abundance + 1), y = 1.37 + 0.36x, and R^2 = 37.1.

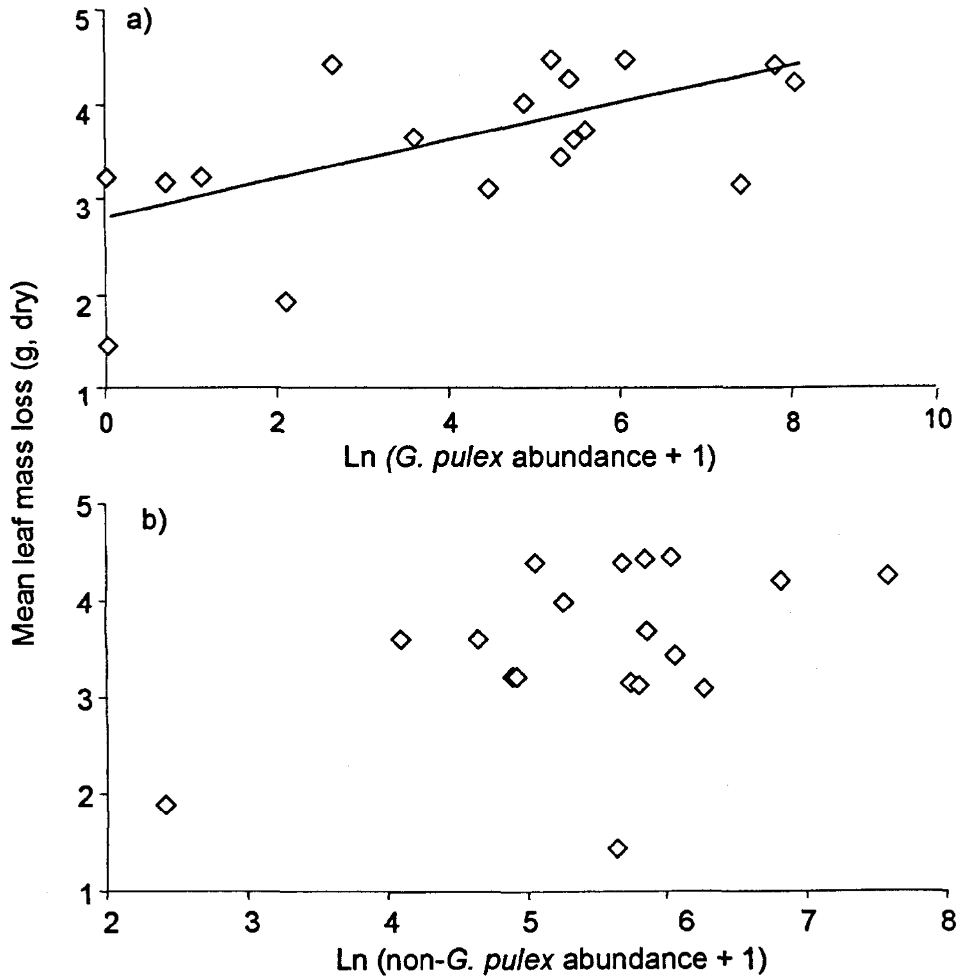


Figure 2.10. Relationship between mean leaf mass loss (g, dry) and
a) Ln (*Gammarus pulex* abundance + 1), y = 2.72 + 0.2x, and R^2 = 37.7, and
b) Ln (non-*G. pulex* shredder abundance +1), R^2 = 20.9 (not significant).

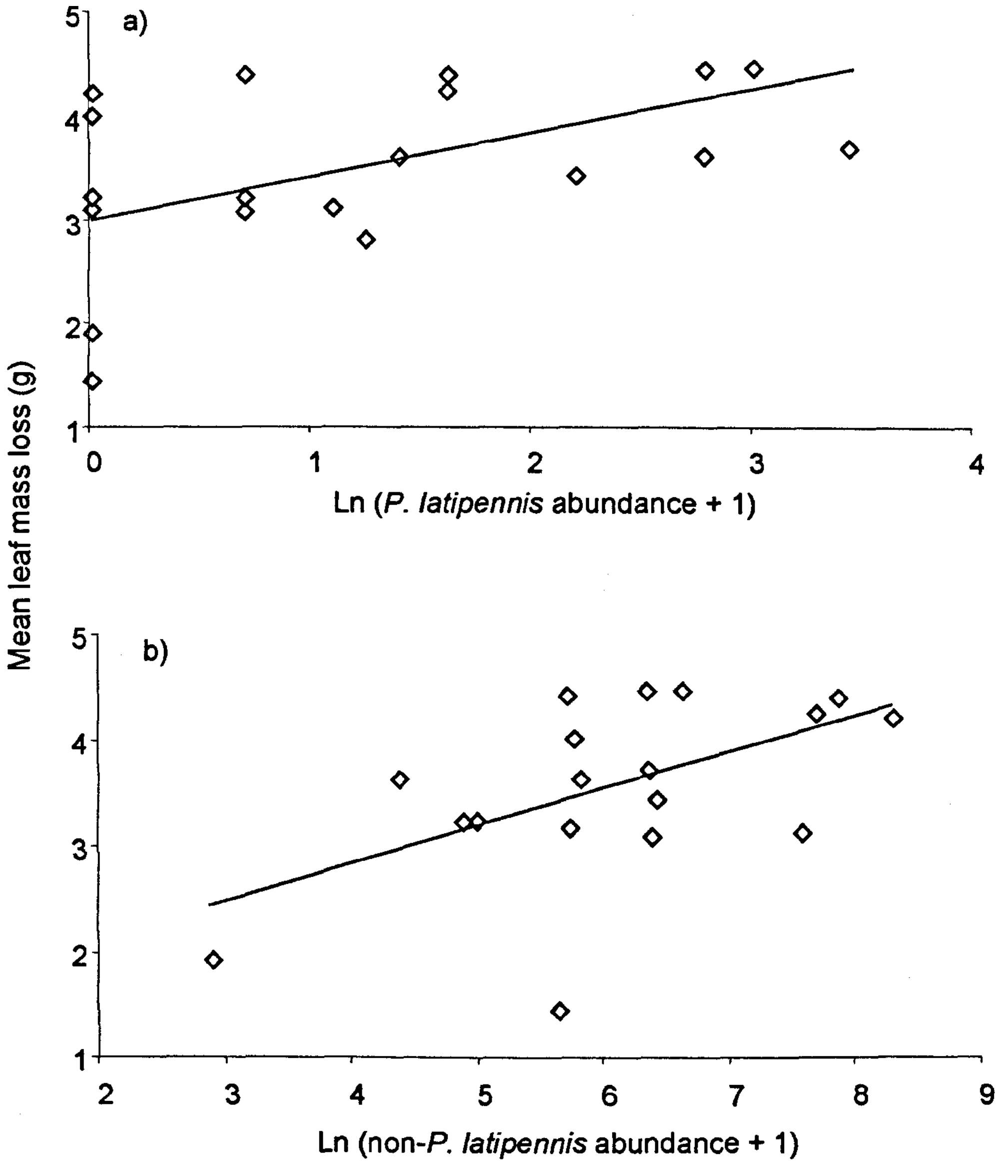


Figure 2.11. Relationship between mean leaf mass loss (g, dry) and
a) Ln (*Potamophylax latipennis* abundance + 1), y = 3.15 + 0.34x, and R^2 = 22.3, and
b) Ln (non-*P. latipennis* shredder abundance +1), y = 1.42 + 0.36x and R^2 = 30.8.

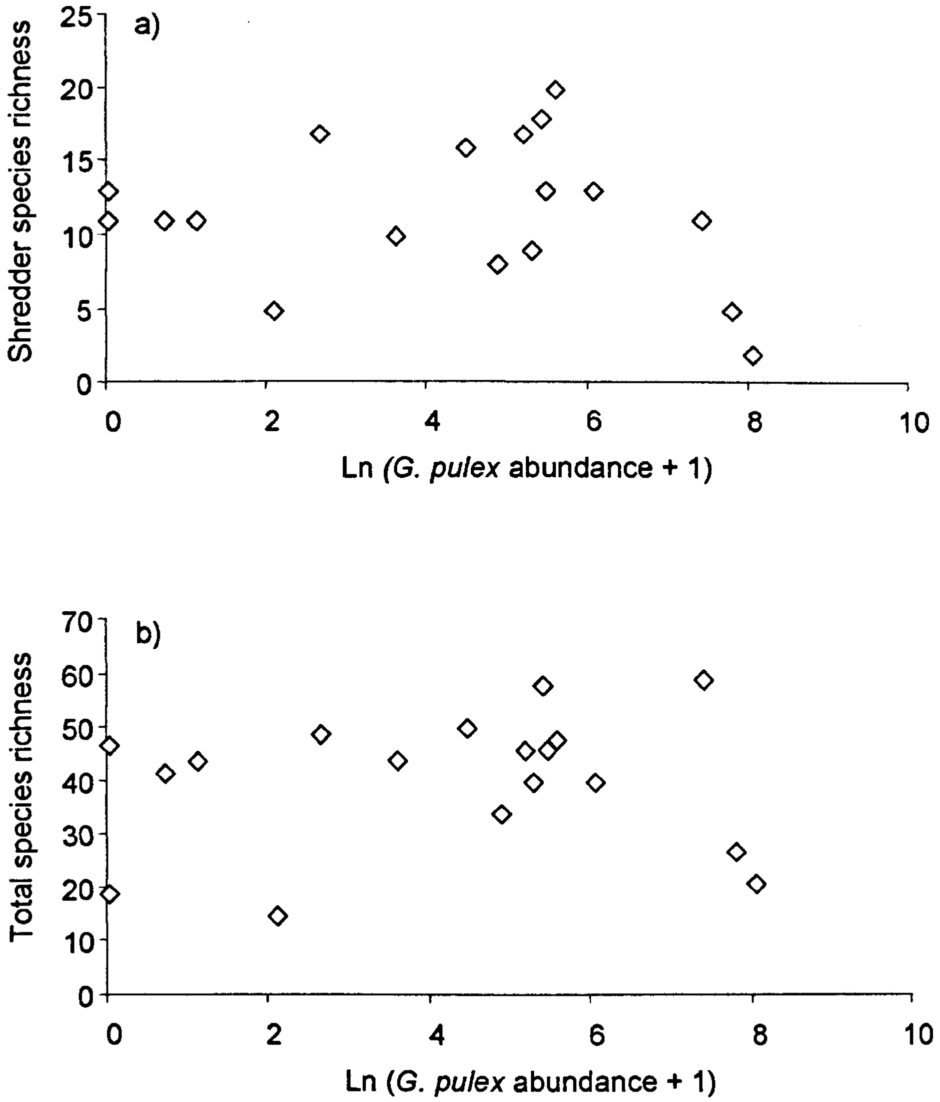


Figure 2.12. Relationship between Ln (*Gammarus pulex* abundance + 1) and a) shredder species richness, r = -0.18 (not significant) and b) total species richness, r = 0.11 (not significant).

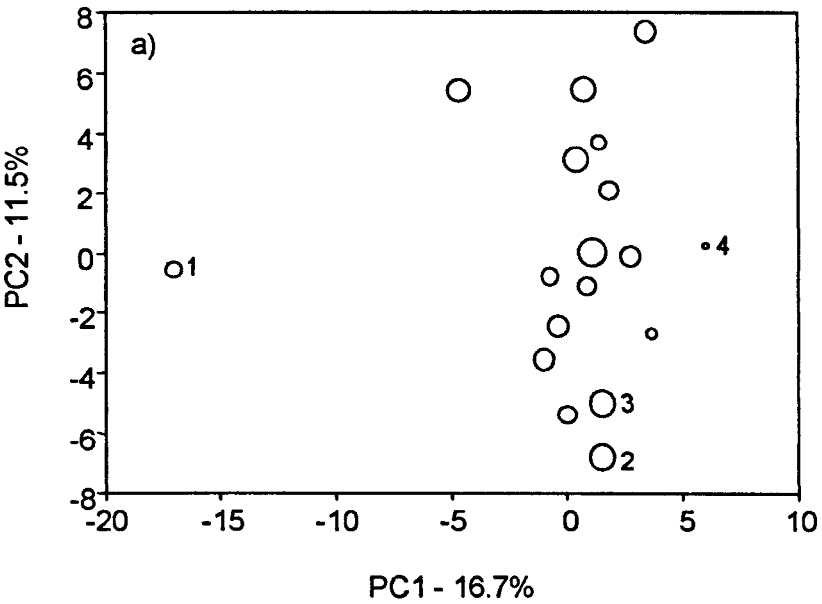
2.3.4. Influence of community composition on leaf mass loss.

2.3.4.1. Whole community.

A complete list of species, and their abundances at each site, is given in Appendix C. A Principal Component Analysis (PCA), based on a correlation matrix (abundances are standardised), for the whole macroinvertebrate community, encompassed 28.2% of the variation in species composition among sites, on the first two principal components (PC1 and PC2). A plot of PC1 against PC2 showed that only one site is obviously distinct from all others (on PC1) while the remaining sites tended to be distributed evenly across PC2 (Figure 2.13 a). Cranemoor had medium leaf mass loss (3.15 g) and was distinguished on PC1 primarily by the presence of fly larvae (e.g. *Tipula (Yamatapula* - subgenus) and *Spligona sp.*), a cased caddisfly larva species (*Drusus annulatus* Stephens) and several species of water-mite, all of which occurred solely at that site. Of the remaining sites, those positioned toward the positive end of PC2 were characterised by several stonefly species including *Isoperla grammatica* (Poda), *Leuctra nigra* (Olivier), *Leuctra hippopus* (Kempny), *Protonemura praecox* (Morton) and *Nemoura cambrica* (Stephens), the mayfly species *Rhithrogena semicolorata* (Curtis), and the cased caddis fly *Potamophylax rotundipennis* (Brauer).

Those sites positioned towards the negative end of PC2, principally Stone and Lindrick Dale, were characterised by the presence of the shredding isopod *Asellus aquaticus* (L.), several species of leech and worm, and the mollusc *Valvata cristata* Müll. In general, there was no distinct clustering of sites and no strong visual trends concerning leaf mass loss categories. Although Strines was at the extreme positive end of PC1 with a unique stonefly assemblage, including *Nemurella picteti*, *Protonemura praecox*, *Protonemura meyeri* (Pictet) and *Amphinemura sulcicollis* (Stephens), and was the site with the lowest leaf mass loss.

A second PCA was performed for the whole macroinvertebrate community using a covariance matrix (abundances are not standardised), and encompassed 43.1% of the variation among sites on the first two principal components (Figure 2.13 b). Although sites were less confined to one area of the plot, as in the correlation matrix analysis (Figure 2.13 a) there remained no distinct clustering of sites related to leaf mass loss. Cranemoor was distinguished at the negative



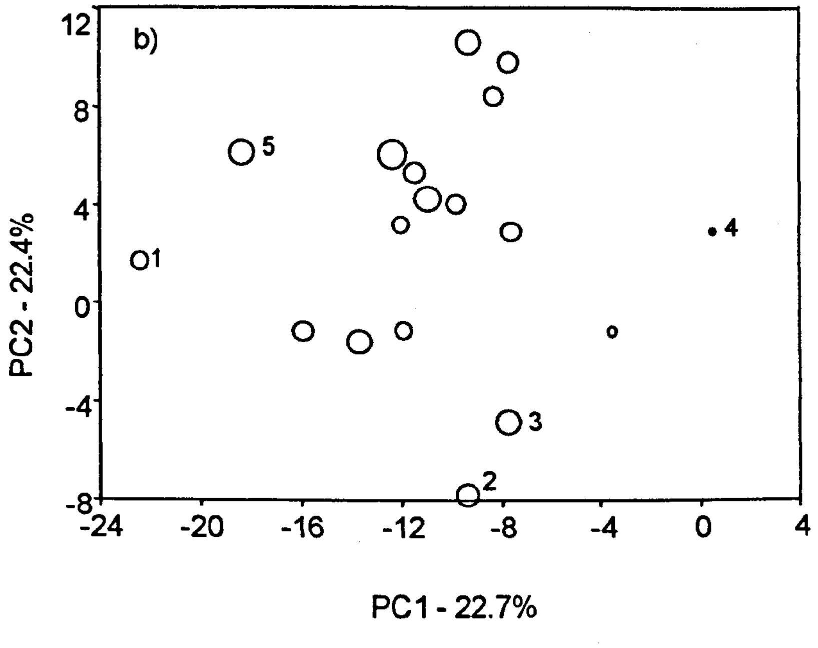


Figure 2.13. Plot of first two principal components from PCA on total macroinvertebrate community data using a) a correlation matrix and b) a covariance matrix. PC1 and PC2 capture for a) 28.2% of the variation and for b) 43.1% of the variation, in total macroinvertebrate composition across the eighteen stream sites. Mean leaf mass loss (untransformed data) is indicated by the relative size of each symbol. Sites referred to in the text are distinguished by numbers; 1 = Cranemoor, 2 = Stone, 3 = Lindrick Dale, 4 = Strines and 5 = Berrymoor.

end of PC1 as before, this time along with one other site, Berrymoor. The main influences included high numbers of the mollusc, *Potamopyrgus jenkinsi* (Smith), several species of fly and beetle larvae and *G. pulex*. Strines lay at the opposite end of PC1, as before, distinguished by its' unique stonefly assemblage (see above). Stone and Lindrick Dale were once again distinguished primarily by high numbers of *Asellus aquaticus* at the negative end of PC2. Stone and Lindrick Dale were among the highest mass loss sites, but were not clustered together with other high mass loss sites, which were positioned towards the middle and opposite end of PC2. In general, there was no distinct clustering of sites corresponding to leaf mass loss in the whole community PCA plots.

2.3.4.2. Shredder community.

A PCA based on a correlation matrix for the shredder community only, represented 36.2% of the variation among stream sites in species composition, on the first two principal components (Figure 2.14 a). Sites again showed an even spread across the PCA plot, rather than distinct clustering. Sites were distributed principally along PC1. Species that characterised sites towards the negative end of PC1 (including Stone and Lindrick Dale) were *Asellus aquaticus*, the stonefly *Nemoura avicularis* Morton, and two species of cased caddisfly larvae, *Halesus digitatus* (Schrank) and *Athripsodes sp.*. Toward the opposite end of PC1 the stonefly species *Protonemura praecox*, *Leuctra nigra* and *Protonemura meyeri* became more common, along with the cased caddisfly species *Potamophylax rotundipennis* and *P. latipennis*. However, there was no gradient in leaf mass loss to mirror the gradual changes in shredder composition along PC1. Strines and Berrymoor were positioned at the extreme opposite ends of PC2 and were characterised by different stonefly assemblages. *Capnia bifrons* (Newman), *Leuctra hippopus* and *Nemoura cambrica* were common at Berrymoor, which was the third highest leaf mass loss site, while Strines was the lowest leaf mass loss site and was characterised by the group of shredding stonefly species described above (Section 2.3.4.1).

A second PCA was performed using a covariance matrix, and captured 52.5% of the variation in shredder community composition among sites on the first two principal components (Figure 2.14 b). The strongest influences were *Asellus aquaticus* on PC1, and *G. pulex* on PC2, both of which resulted in the high leaf mass loss sites, Stone and Lindrick Dale, being grouped in the top right-hand corner of the plot. Sites positioned at the negative end of PC1 represented medium to high leaf mass loss and were characterised by several stonefly species including *Nemoura cambrica*, *Leuctra hippopus* and *L. nigra*.

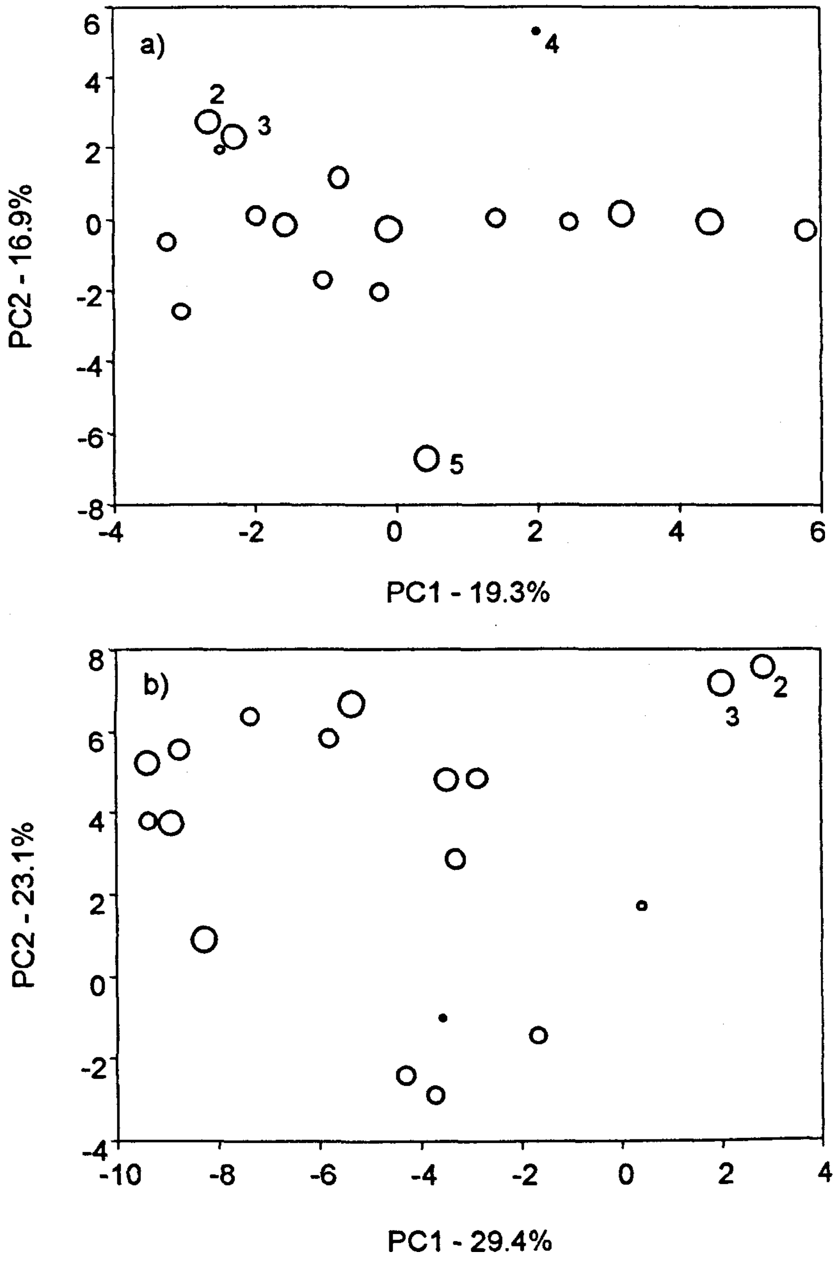


Figure 2.14. Plot of first two principal components from PCA on shredder community data using a) a correlation matrix and b) a covariance matrix. PC1 and PC2 capture for a) 36.2% of the variation and for b) 52.5% of the variation, in shredder composition across the eighteen stream sites. Mean leaf mass loss (untransformed data) is indicated by the relative size of each symbol. Sites referred to in the text are distinguished by numbers; 2 = Stone, 3 = Lindrick Dale, 4 = Strines and 5 = Berrymoor.

2.4. Discussion.

The overall aim of this chapter was to examine the influence of macroinvertebrate species richness, species identity and community composition on leaf processing in streams at a regional scale (i.e. between streams). The specific objectives of this chapter were (1) to examine whether species richness was among the factors that influence leaf processing across stream sites, (2) to explore whether there were any individual species identity effects on leaf processing either through (a) species presence/absence, and/or (b) their abundance/biomass and if so (3) to assess whether species identity effects influenced the relationship between species richness and leaf decomposition (i.e. was there a selection effect?) and (4) to explore whether there were any distinct community types associated with varying degrees of leaf decomposition.

2.4.1. Influence of species richness on leaf processing.

Although shredder richness did emerge as a correlate of leaf mass loss in multiple regression models (see below), there was no significant influence of shredder richness when used as a sole predictor variable for leaf mass loss across the eighteen stream sites in this study (Figure 2.8). This result is in contrast to two similar field studies that indicate significant positive relationships between shredder species richness and detritus processing across natural stream systems (Jonsson *et al.* 2001, Huryn *et al.* 2002). An important distinction that must be recognised for any study that uses field communities is that the species richness gradient is not a nested one of progressive species deletion, as assumed by the proposed theoretical relationships between diversity and function (Figure 1.1). Consequently, any species richness effect will always be confounded by changes in species composition in field studies of this nature. In addition, there are limitations to the present field study (as discussed below), but it is also true that neither of the two previous studies provide entirely satisfactory evidence for a positive effect of shredder richness on leaf processing.

The positive relationship between shredder richness and leaf mass loss observed across twenty-three Swedish stream sites (Jonsson *et al.* 2001), was driven by just one site that had only one shredder species ($F_{1,21} = 5.9$, $p < 0.05$; Figure 2.15). When the data from Jonsson *et al.* (2001) are reanalysed omitting this site, there is no significant relationship between shredder richness and leaf mass loss ($F_{1,20} = 0.2$, $p > 0.05$, $R^2 = 1.0$). In the study by Huryn *et al.* (2002), it is possible that the relationship between shredder richness and leaf processing rates was confounded by large differences in shredder composition across different catchment land-use types (Huryn *et al.* 2002). For example, all the sites with low taxonomic diversity were from urban catchment streams, which were characteristically dominated by fly larvae from the genus *Tipula*. In contrast, forest catchment streams showed a high level of taxonomic diversity and were characterised mainly by several species of shredding stonefly.

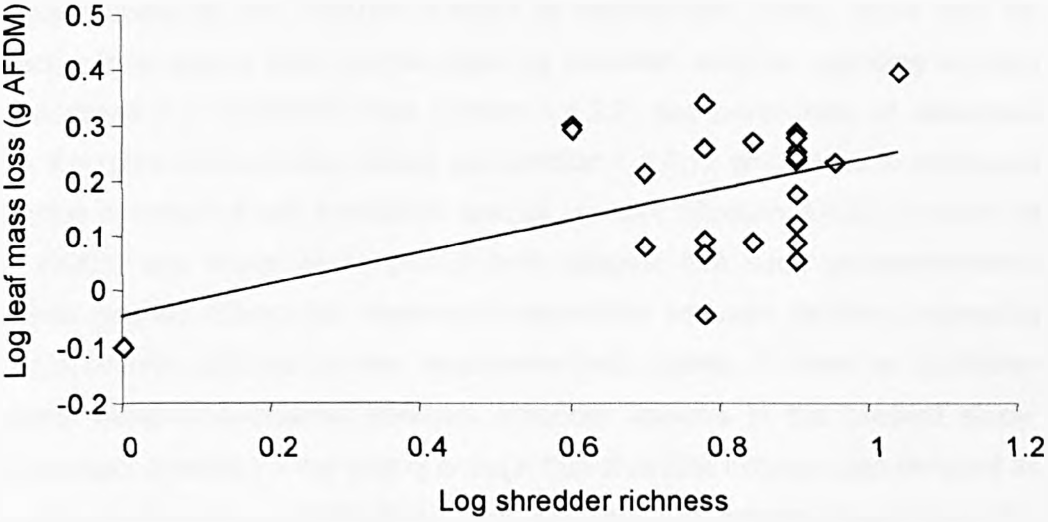


Figure 2.15. Relationship between shredder species richness and leaf mass loss across twenty-three Swedish stream sites, plotted using raw data from Jonsson *et al.* 2001. The fitted line is $y = -0.04 + 0.29x$ and $R^2 = 21.9$. AFDM = ash free dry mass. Data are transformed ($\log_{10}(x)$).

However, a similar criticism may be applied to the present field study. That is, the lack of a direct and simple relationship between shredder richness and leaf mass loss may have been confounded by the occurrence of particular species at sites with particular sets of environmental conditions. For example, conductivity was far higher at Stone and Lindrick Dale than at other sites at the lower end of the shredder richness gradient (see Appendices A and B), and these two sites were dominated by large numbers of *G. pulex* and *A. aquaticus*. It is likely that the two sites mentioned may also have been exposed to quite different nutrient levels than other low shredder diversity sites since they were characterised by a macroinvertebrate assemblage normally associated with polluted streams (i.e. large numbers of leeches and worms).

Additionally, the relationship between shredder richness and leaf mass loss in the present study may have been influenced by a particular aspect of the experimental design: the length of exposure time of the experimental leaf bags. It is possible that leaf mass loss approached the maximum possible after seven weeks in-stream exposure, at high mass-loss sites. If there was an artificial ceiling imposed on leaf mass loss at high mass-loss sites, any positive relationship between shredder richness and leaf processing may have been artificially depressed.

A strong positive effect of species richness on detritus processing could be brought about by two different classes of mechanism. Firstly, there may be mechanisms arising from complementarity between species, including positive interactions (i.e. facilitation; see Section 1.4.2.2) and partitioning of resources (i.e. the niche-differentiation effect; see Section 1.4.2.1), which lead to increased detritus processing with increased species number (Section 1.4.2). Jonsson *et al.* (2001) and Huryn *et al.* (2002) both suggest that such complementarity effects may be driving the observed relationships between detritus processing and shredder richness in their respective field studies. If there is facilitation and/or niche-differentiation between shredder species in the present study, these mechanisms are not strong enough that shredder richness can be used as the sole explanatory variable that drives leaf mass loss across stream sites. The second mechanism that could bring about a positive relationship is the selection effect (see Section 1.4.1) and this is discussed further below (Section 2.4.2).

The mechanistic model of Loreau (Loreau 1998b, 2000) suggests that environmental variables will be the primary influence on ecosystem function across large spatial scales, either by acting directly on ecosystem processes, or indirectly through influencing species number (see Section 1.5.2.2). Results from this study revealed that particular abiotic factors did have a strong influence on detritus processing across the stream sites. These factors included canopy cover, temperature, pH and dissolved oxygen. Canopy cover emerged as the environmental variable with the largest influence on leaf processing and reflects the importance of other environmental factors that were not measured directly (i.e. light levels, allochthonous inputs). The positive effect of temperature on leaf breakdown across the study sites probably acted through influencing rates of microbial processing (Paul *et al.* 1983, Webster & Benfield 1986). The influence of pH was principally driven by just one low pH site, Strines (Figure 2.6) and may have acted by altering community structure (Towsend *et al.* 1983), as is discussed further below (Section 2.4.3). Dissolved oxygen also entered regression models as a significant, but small, positive influence on leaf processing. There is no consistent evidence about the effects of variation in dissolved oxygen on leaf processing rates (Webster & Benfield 1986). The influence of dissolved oxygen in the present study may have been mediated by other abiotic factors, such as nutrient levels, temperature and flow rate. Nutrient levels were not quantified in the present study, but there was no direct correlation between dissolved oxygen and any of the other individual abiotic factors that were quantified. However, dissolved oxygen levels are known to be controlled by interplay between these, and other, physical and chemical factors (Walling & Webb 1992).

Loreau's model (see Section 1.5.2.2) demonstrates that any local effect of diversity on ecosystem function should be masked by the effect of environmental parameters when across-site comparisons are made, providing that there is variation in environmental parameters across sites. Despite variation in abiotic factors between stream sites, and their strong influences on leaf processing across the species richness gradient, biotic variables (including species richess) emerged as important correlates of leaf mass loss in this study. Although there was no simple positive relationship between shredder richness and leaf mass loss (Figure 2.5 b), shredder species richness emerged as a significant influence on leaf mass loss in every multiple regression model where it was entered as a potential predictor variable (Table 2.5). While Loreau's mechanistic model (Loreau 1998b, 2000) predicts that the influence of species richness across large scales should be an indirect effect of variation in environmental factors, there was no collinearity between shredder richness and any abioitc factors in the multiple regression models (see Section 2.2.5). Although it is possible that interplay between several factors, or unmeasured environmental factors, may have indirectly influenced the richness gradient.

Results from the present study suggest that shredder richness is a more important correlate of leaf mass loss than shredder biomass (or abundance) across the streams examined. Although this was dependent on the inclusion of a particular single site (Strines) in the analyses, and the influence of shredder richness and biomass (or abundance) were almost equally important when this site was removed. Jonsson *et al.* (2001) found shredder richness and then abundance to be important, while shredder biomass was relatively unimportant. The field study by Huryn *et al.* (2002) indicated that the influence of shredder richness on detritus processing rates was greater than that of shredder biomass, however they did not consider shredder abundance. Results from the present study suggest that there may be redundancy among shredders. That is, increases in shredder abundance, or biomass, may be able to compensate for low shredder richness (Walker 1992). Ruesink & Srivastava (2001) demonstrated that, in artificial stream mesocosms, leaf processing rates could be maintained in reduced-diversity shredder communities by increases in abundance. Although, results from the present study must be interpreted with some caution due to the method used to sample the shredder community. Kick sampling was used to gain the best estimate of shredder species richness within each stretch of stream, and although the sampling regime was standardised as much as possible across sites (see Section 2.2.4), it is a qualitative, rather than a quantitative technique. Therefore estimates of biomass and abundance across sites are not strictly comparable in relative terms.

While the shredder component of the macroinvertebrate community showed a substantial influence on leaf mass loss, the non-shredder component did not. In multiple regression models that were constructed using only the non-shredder component of the macroinvertebrate community, abundance did appear to be an important predictor variable (Table 2.5). However this was driven by just one site, Strines. Once Strines was excluded from the analysis, no biotic variables were included in the regression model. Therefore, there is no evidence that the non-shredder component of the macroinvertebrate community was important for patterns of detritus processing across stream sites.

The non-shredder component of the macroinvertebrate community was examined to account for the influence of other functional feeding groups that might play a role in leaf breakdown. For example, some mayfly species belonging to the collector functional feeding group, scrape fine particles from the leaf surface (Anderson & Sedell 1979), and therefore may directly influence leaf breakdown. Also, predator species may play an indirect role in detritus processing through their interaction with shredder species (e.g. Obemdorfer *et al.* 1984, Malmqvist 1993). The non-shredder component of the community is generally ignored in studies that examine leaf breakdown, and therefore there is little evidence with which to compare results from the present study. However, many studies have provided both indirect (e.g. Kaushik & Hynes 1971, Benfield & Webster 1985, McArthur & Bames 1988, Robinson *et al.* 1998) and direct (e.g. Cummins *et al.* 1973, Wallace *et al.* 1982, 1986, Cuffney *et al.* 1990; see

Section 2.1.1.2) evidence for the importance of the shredder functional feeding group in particular, for leaf processing.

2.4.2. Influence of individual species on leaf processing.

Evidence from the present study suggests that one species in particular has a strong influence on leaf processing in the study streams, the shredding amphipod *Gammarus pulex*. Detecting any presence/absence effect of *G. pulex* was not possible since it occurred at sixteen out of the eighteen stream sites and varied considerably in abundance across the sites where it was present. Natural variation in the abundance of particular species across streams makes it difficult to test for presence/absence effects in the field however, such species identity effects have been observed for other shredder species, in controlled mesocosm experiments (Ruesink & Srivastava 2001, Jonnson *et al.* 2002). In the current study, the effect of *G. pulex* was one of abundance, whereby the shredder abundance-mass loss relationship was driven by *G. pulex* (Figure 2.10), indicating that increases in abundance of this single species can compensate for low shredder richness. For example, Stone and Lindrick Dale represent the lowest shredder diversity sites, but were among the highest leaf mass loss sites, and have by far the greatest abundance of *G. pulex*.

While leaf processing was influenced by a particular dominant species in this study (i.e. *G. pulex*), there was no selection effect, as observed for some randomly assembled experimental plant communities (e.g. Naeem *et al.* 1994, Tilman *et al.* 1996, Symstad *et al.* 1998). That is, *G. pulex* was not more likely to occur at high abundances in high shredder diversity communities (Figure 2.12). There has been a great deal of controversy surrounding the issue of whether the selection effect can be a legitimate mechanism for species diversity effects on function in nature (see Section 1.5.2.1), since natural communities are not assembled, and do not lose species, at random (Wardle 1999). Neither this study, nor that of Jonsson *et al.* (2001), provides any evidence that the respective observed positive relationships, between shredder richness and leaf processing, are driven by the selection effect.

The species identity effects of *G. pulex* in this study probably contributed to the idiosyncratic nature of the relationship between species richness (total and shredder only) and leaf mass loss across sites (Figure 2.5). The lack of evidence for a selection effect suggests that the small, but significant, positive influence of shredder species richness on leaf processing observed in the multiple regression models (Table 2.5) may be the result of complementarity effects.

2.4.3. Influence of community composition on leaf processing.

There was no strong evidence to suggest that macroinvertebrate community composition affected leaf mass loss across the eighteen stream sites. The differences in community composition across stream sites tended to be gradual, and driven by a single axis, in the correlation matrix plots (Figure 2.13 a and 2.14 a), but the leaf mass loss gradient did not map on to the observed gradient in compositional change. Once absolute species abundances were taken into account (using a covariance matrix for the PCA), the compositional differences between sites became larger, and sites became more evenly distributed along both axis of the PCA plot (Figure 2.13 b and 2.14 b), but there was no distinct clustering of sites and no obvious effect of macroinvertebrate composition on leaf mass loss.

In general, there was an absence of any distinct groups of sites however there were a few exceptions. Stone and Lindrick Dale were consistently positioned close together in all PCA plots. These two sites were distinguished by the occurrence and abundance of the isopod *A. aquaticus* and abundance of *G. pulex*, and were among the sites showing the greatest leaf mass loss. However, there is no evidence that leaf processing at Stone and Lindrick Dale was increased above that of other sites where *G. pulex* occurred in high abundances and *A. aquaticus* was absent.

The macroinvertebrate community at Strines was distinct from other sites, and was characterised by a unique stonefly assemblage including *Protonemura praecox*, *P. meyeri, Nemurella picteti*, and *Amphinemura sulcicollis*. Strines was the most acidic site and had the lowest leaf mass loss. The influence of pH on detritus processing, indicated by earlier multiple regression models (Table 2.5), was principally driven by Strines. It is possible that the low pH at Strines affected leaf processing through its influence on community structure. Community structure in acid streams is typified by reduced abundance and diversity of non-shredder macroinvertebrate species (Townsend *et al.* 1983), dominance by acid-tolerant stonefly shredder species, and the absence of crustaceans (Griffith & Perry 1993, Jonsson *et al.* 2002), as was observed at Strines. It is possible therefore, that the low pH at Strines affected leaf processing indirectly, through altering community composition. Although low pH may also have other indirect influences on detritus processing through negative effects on the microbial community (Hall *et al.* 1980, Griffith & Perry 1993).

Overall, the sites distinguished by the PCA correspond with the general patterns indicated by other analyses in this chapter. Shredder abundance had a strong positive influence on detritus processing, especially that of *G. pulex*, which is extremely abundant at the high leaf mass loss sites. In multiple regression analyses, Strines was identified as an unusual site due to its low pH, and this was reflected by its unique stonefly assemblage. However, overall there was no evidence that leaf processing was influenced by community composition.

2.5. Conclusions.

The non-shredder component of the macroinvertebrate community was not important for leaf processing.

There was no simple positive linear relationship between shredder species richness and leaf processing across natural stream communities. However, shredder species richness was important among several abiotic (canopy cover, pH and temperature) and biotic (shredder biomass and abundance) factors that positively influenced leaf processing across sites. The influence of shredder richness was comparable to that of shredder abundance and biomass, suggesting that there may be some degree of redundancy among shredder species.

Variation in the abundance of one species in particular, the amphipod, *Gammarus pulex*, was responsible for driving the overall relationship between shredder abundance and leaf mass loss.

There was no evidence that the positive influence of species richness on leaf processing was driven by the selection effect, i.e. *G. pulex* was not more likely to occur at high abundances in high shredder diversity communities.

There was no discrete grouping of sites according to community composition either for the entire macroinvertebrate community or for the shredder community only. Instead, there tended to be a gradual change in community composition across stream sites, but this was not associated with variation in leaf litter processing.

3. The influence of resource diversity on detritus processing in low and high shredder diversity streams.

3.1. Introduction.

3.1.1. Introduction.

Evidence from the previous chapter (Chapter 2), and from other ecosystem-scale investigations (Jonsson *et al.* 2001, Huryn *et al.* 2002), suggests that the number of shredder species in a community may have a positive influence on detritus processing in streams. Two separate classes of mechanism have been suggested to explain the positive influence of species diversity on ecosystem function, the selection effect (Section 1.4.1) and complementarity effects (Section 1.4.2). There was no evidence that the positive effect of shredder diversity on detritus processing observed in Chapter 2 was the result of the selection effect, i.e. that a species with a marked influence on an ecosystem process is more likely to occur in high diversity communities. The selection effect mechanism was also refuted by other authors who observed a positive effect of shredder diversity on detritus processing across natural streams (Jonsson *et al.* 2001, Huryn *et al.* 2002). Instead, these authors suggest that mechanisms arising from complementarity between shredder species are the most likely mechanisms driving positive effects of shredder diversity on detritus processing, although neither study examined these mechanisms directly.

Complementarity effects can be divided into facilitation and the niche-differentiation effect (Section 1.4.2). Both mechanisms predict that ecosystem function will increase with greater species diversity because of interactions among combinations of species that have complementary traits. In the case of facilitation, a species may modify a resource in a way favourable to another co-occurring species (Fridley 2001), such that overall resource use is increased when certain combinations of species occur together. Jonsson *et al.* (2001) and Huryn *et al.* (2002) suggested that facilitation among shredder species led to an increase in detritus processing rates in their respective field studies. In the case of shredders, facilitation may occur due to differences in feeding modes between species. Jonsson *et al.* (2002) proposed that the cutting of leaf discs, by the feeding action of the cased caddisfly larvae *Sericostoma personatum*, may have increased the availability of the leaf edges, on which another species, the amphipod *Gammarus fossarum*, preferred to feed. If certain shredder species do differ in the way in which they utilise a leaf resource, facilitation between shredder species may lead to an increase in leaf litter processing rates with increased shredder diversity, due to interactions among certain combinations of species. Evidence from laboratory-based experiments supports the facilitation hypothesis (Jonsson & Malmqvist 2000, Cardinale *et al.* 2002). For example, increasing the number of species of filter-feeding caddisfly larvae from one to three, in artificial stream channels, resulted in an increase in total resource consumption of a homogenous resource of suspended particulate matter (Cardinale *et al.* 2002). The observed positive diversity effect was attributed mainly to a 'complementarity effect', brought about by differences between species in the morphology of their filter-feeding nets such that they facilitated each others resource capture through biophysical interactions.

Complementarity between species in their resource niches may also act to bring about a positive diversity effect. The niche-differentiation hypothesis predicts that the use of a heterogeneous resource base should increase as species number increases (Tilman *et al.* 1997b, Tilman 1999, Loreau 2000; Section 1.4.2.1). This prediction is based on the assumption that species differ in their resource-niches. If so, a wider range of resource niches will be represented as species number increases, and therefore total resource use will be enhanced. So far, the potential role of the niche-differentiation effect for positive effects of shredder diversity on detritus processing in streams has remained unexplored. Previous studies, both laboratory and field based, have used only a single leaf resource (Jonsson & Malmqvist 2000, Jonsson *et al.* 2001, Huryn *et al.* 2002). These studies have the potential to detect the niche-differentiation effect if species are complementary in their resource niches in time or space, although this has not been suggested as a possible mechanism in these studies. However the niche-differentiation effect has not been explored for a heterogeneous resource, on which species may be complementary in their use of different resource types.

Natural accumulations of leaf material in streams are usually composed of several different leaf types (Leff & McArthur 1989, Boulton & Boon 1991), the precise composition depending on the type of riparian vegetation and how much leaf material is retained within the stream (e.g. Benfield *et al.* 1977, Dobson & Hildrew 1992, Pozo *et al.* 1997). The extent of competition between shredder species for leaf resources is unknown, since most studies that have addressed the nature of interspecific competition among stream macroinvertebrates have been performed with 'sessile' organisms such as net-spinning caddisfly larvae and blackfly larvae (Allan 1995). However, resource limitation is an important prerequisite for interspecific competition and several studies have provided evidence for resource limitation among shredding detritivores (e.g. Gee 1988, Smock *et al.* 1989, Dobson & Hildrew 1992, Rowe & Richardson 2001). Given the range of leaf resources available, and the possibility of competition between shredder species utilising leaf litter packs, it is not unreasonable to hypothesise that there may be resource-niche differentiation among species of shredding detritivores, in terms of their leaf diets.

Different types of leaf are known to vary in their breakdown rates (Petersen & Cummins 1974, Webster & Benfield 1986), and their food quality for stream detritivores (Kaushik & Hynes 1971), depending on nutrient concentrations, fibre content and the presence of chemical inhibitors (Webster & Benfield 1986). Leaf litter is broken down by both microbial and shredder activity (Section 1.6.1), and studies have revealed that conditioned leaves (i.e. leaves that have been colonised by microorganisms) are preferred over unconditioned leaves (Giller & Malmqvist 1998). The palatability of leaf litter to shredders is thought to be a function of leaf type, fungal species and incubation time (Graça *et al.* 1993). Although shredder species tend to prefer the same leaf types, evidence from various studies suggests that species vary in their preferences and degree of selectivity for different types of fungi and also in their enzymatic digestive capabilities (Maltby 1992). Therefore, although the same leaf types are generally preferred by shredders, there is scope for resource-niche differentiation between species.

The processing rates of different leaf types in streams have normally been quantified using monospecific leaf packs (Leff & McArthur 1989, Murphy & Giller 2000). If shredder species do differ in their leaf preferences, leaf packs containing a greater number of leaf species may attract and support a greater number of shredder species because of their increased structural and nutritional diversity, compared to monospecific leaf litter packs (Boulton & Boon 1991). The overall processing rates of diverse leaf packs may therefore be increased above that of single leaf-type packs. However, if there is no resource-niche differentiation between shredder species, then only the particular leaf types, preferred by all shredder species, would be utilised, and leaf litter diversity may be unimportant for detritus processing rates.

Moreover, there may be positive, non-additive, effects of resource diversity on leaf processing rates when different leaf types occur in mixtures. That is, processing rates of individual leaf types may be enhanced in mixtures, beyond that expected from monospecific leaf packs, if there is resource-niche differentiation between shredder species. This may occur especially for the less palatable leaf types. For example, the most palatable resource within a diverse leaf litter pack may initially attract a large number of shredder species. If shredder species remain within the leaf pack once the most palatable leaf type has been consumed, rather than using energy to search for new resources, the less palatable leaf types within the pack will be consumed more rapidly than if they were in a homogenous pack (Wardle *et al.* 1997b). The processing rates of 'fast' decomposing leaf types may also be enhanced in diverse leaf packs. Dobson (1994) reported that litter bags containing material of low palatability (old beech and paper 'leaves') became slowly colonised so that the number of detritivore species approached that of the surrounding benthos. In contrast, highly palatable leaf types (alder and young beech) were quickly consumed and therefore provided little opportunity for shredder colonisation over time. Processing rates in highly palatable leaf-type bags decreased as detritivores left the litter bags, having little remaining leaf litter to provide a stable substrate. 'Slow' decomposing leaf types within diverse leaf litter packs may therefore act to provide a stable substrate for highly palatable leaf types to be processed at a faster rate than if they were in monospecific leaf packs (Leff & McArthur 1989).

There have been few investigations of the effect of leaf diversity on detritus processing rates and the majority of these are represented by terrestrial rather than aquatic studies. Only two stream studies have compared the processing rates of single and mixed leaf litter bags (Meyer 1980, Leff & McArthur 1989). Leff & McArthur (1989) reported that the processing rate of red maple (*Acer rubrum*) was similar whether exposed in single litter-type bags, or in mixed litter bags along with cypress leaves (*Taxodium distichum*). Similarly, Meyer (1980) reported that mass loss from mixed litter bags containing sugar maple (*Acer saccharum*), yellow birch (*Betula alleghaniensis*) and beech (*Fagus grandifola*), was not different from that predicted from single litter-type bags.

In contrast, there have been many more studies that have examined the effects of leaf diversity on decomposition in terrestrial systems, (e.g. Wardle *et al.* 1997b, Finzi & Canham 1998, Bardgett & Shine 1999, Kaneko & Salemanca 1999, Knops *et. al.* 2001), although results from these studies have not provided any consistent evidence. Positive, non-additive, effects of leaf diversity on mass loss were reported by Kaneko & Salamanca (1999) and Hector *et al.* (2000). Negative, non-additive, effects were reported in another study that quantified nitrogen mineralisation in mixed and single leaf-type bags (Finzi & Canham 1998). Wardle *et al.* (1997b) increased leaf diversity from one to eight species and examined the effects on various aspects of leaf litter decomposition. Both positive and negative, non-additive, effects of leaf litter mixing were observed, but these were independent of leaf diversity.

The mechanisms that have been suggested to explain positive and negative effects of leaf diversity on decomposition rates in terrestrial studies have focused on the chemical properties of leaf litter, such as the translocation of nutrients or inhibitory compounds between leaf types (e.g. Seastadt 1984, Fyles & Fyles 1993), or the physical litter microenvironment (Hector *et al.* 2000). However, the role of the soil detritivore community in mediating leaf diversity effects on decomposition has been largely ignored in terrestrial systems (but see e.g. Wardle *et al.* 1997b, Hansen & Coleman 1998, Bardgett & Shine 1999, Kaneko & Salamanca 1999).

Only two studies in terrestrial systems have specifically addressed whether there is an association between leaf diversity, processing rates and macroinvertebrate detritivore diversity (Hansen & Coleman 1998, Kaneko & Salamanca 1999). Kaneko & Salamanca (1999) examined the decomposition of single and mixed litter bags, and their associated microarthropod detritivore communities, in Japanese forest soils. Results revealed that both the abundance and diversity of oribatid mites, which represent the dominant detritivores, was higher in mixed leaf litter bags than in single leaf-type litter bags. The increased diversity of detritivore species attracted to mixed litter bags may have resulted in the observed enhanced processing rates, in this study. Hansen & Coleman (1998) also reported increased oribatid mite diversity and increased processing rates in mixed compared to single leaf litter bags, for a different set of leaf types, in forest soils in North Carolina, U.S.A.

There is little evidence from stream studies to support patterns of positive effects of leaf diversity on decomposition associated with increased detritivore diversity. Leff & McArthur (1989) reported a tendency for greater macroinvertebrate biomass in mixed litter bags compared to single litter-type bags, but few differences between leaf pack types in terms of macroinvertebrate diversity. No positive effects of leaf diversity were reported for this study, as mentioned above, however shredding invertebrates were not a significant component of the coastal plain streams in which decomposition processes were investigated.

3.1.2. Aims.

As discussed above, the effect of resource diversity on leaf litter processing will depend on whether shredder species differ in their leaf preferences. If so, then mixed leaf resources will be more completely utilised than individual leaf types, through the niche-differentiation effect. We would expect to see this effect in high, but not in low, shredder diversity communities. Moreover, we may expect the processing of mixed leaf litter bags to increase with greater shredder diversity. If there is a large amount of overlap between shredder species in their leaf preferences, only one or a few, particular leaf types will be utilised, and leaf litter type will be more important for detritus processing than leaf litter diversity, in both high and low shredder diversity communities. However, processing rates of single leaf types may still increase with greater shredder diversity if there is facilitation among certain species, or if there is niche-differentiation between shredders in time or space.

The overall aim of this chapter is to examine the effect of leaf diversity on detritus processing in low and high diversity shredder communities. This was achieved by quantifying the decomposition of six different individual leaf types, and a mixed resource comprising all six leaf types, across stream sites. The leaf types used in this study represent a range of well-established breakdown rates (Webster & Benfield 1986). Therefore, it was anticipated that there would be variation in processing across different individual leaf types and that the same pattern of variation across leaf types would be observed despite differences in shredder diversity across sites. Variation in several physico-chemical variables was also quantified across the stream sites, along with a survey of the macroinvertebrate shredder community.

It was hypothesised that leaf resource diversity affects detritus processing in high, but not in low, shredder diversity streams. Four predictions were made in order to test this hypothesis. First, mass loss from mixed leaf litterbags would be comparable to that from the most fully decomposed single litter-bag type at high, but not at low, shredder diversity sites. Second, mass loss from mixed leaf litterbags would be greater than the overall mean mass loss from all single leaf types at high, but not at low, shredder diversity sites. If the first prediction is true, then the second prediction must also be true. However, if the first prediction is not true, then the second prediction can be either true or untrue. That is, there can be a positive effect of leaf diversity on decomposition rates (prediction 2), even if mixed leaf litter is not among the most fully decomposed single litter-bag types (prediction 1). Third, that there would be a positive relationship between mass loss from mixed leaf litter bags and shredder species number. Fourth, that the mass loss from mixed leaf litter would be greater than that predicted from single leaf types (i.e. positive, non-additive, effects of leaf diversity) at high, but not at low, shredder diversity sites. If there was facilitation, or niche-differentiation among shredder species in time or space, it was predicted that mass loss from the single leaf types would increase with shredder species number.

3.2. Methods.

3.2.1. Study sites.

Eight stream sites were selected from the previous field study (Field Study 1; Chapter 2) to represent a gradient of shredder diversity from low to high (Table 3.1).

Table 3.1. Summary of shredder species number (quantified in Field Study 1), for the eight sites selected for the present study. Number of species is the total found in eight kick samples. Stream names in brackets indicate that the site used was a tributary of the river name given.

Site name	River name	Total number of shredder species
Stone	Maltby Dike	2
Lindrick Dale	Anston Brook	5
Crowdecote	River Dove	5
Strines	Strines Dike	11
Oughtibridge	Coumes Brook	17
Brockhurst	River Amber	17
Berrymoor	(River Dove)	18
Holehouse	(River Etherow)	20

The sub-set of sites chosen for the present study spanned the full range of site-types encountered in Field Study 1 (Table 2.1). Stone and Strines represented the lowest and highest altitude sites (50 m and 280 m above sea level, respectively). Each of the different types of underlying geology and stream order encountered in Field Study 1 was represented by at least one site in the present study, and all land-use types, except urban woodland, were represented. Stream substrate composition was re-assessed (using the same method as described in Section 2.2.3) to encompass the larger stretch of each stream used in the present study (see Section 3.2.2). The only site for which this re-assessment significantly changed stream substrate composition was at Crowdecote, where a particularly silty section of the stream had been used in the previous study. However, percentage cover of silt remained high at Crowdecote, and also at Berrymoor, compared to the remaining sites.

3.2.2. Quantifying leaf decomposition.

Seven different leaf litter-type bags were deployed at each of the eight sites. These included six single leaf litter-type bags, and one mixed leaf litter bag containing equal proportions of each of the six different leaf types. Each different litter-bag type was replicated five times at each site. The six leaf types used in this study were: alder (*Alnus glutinosa*), ash (*Fraxinus exelsior*), sycamore (*Acer pseudoplatanus*), hawthorn (*Crategus monogyna*), oak (*Quercus robur*) and beech (*Fagus sylvatica*). These six leaf types were chosen based on a pre-study survey of the riparian zones of the eight study sites (Table 3.2). Each leaf type used commonly occurred in riparian zones at most of the study sites, and the range used represented the dominant riparian canopy species across the study sites. The order of breakdown rates predicted from the literature was ash > alder > sycamore > oak = beech (Webster & Benfield 1986). Breakdown rates of leaves from tree species belonging to the Rosaceae family (i.e. for hawthorn in the present study) were not included in the summary of published data.

Leaves were collected from trees just prior to abscission during October and November 2000 from two locations near Sheffield: the Rivelin Valley (NGR SK313878) and Harper Lees (NGR SK234806). Leaf material was air dried for one week before storage. Litter bags were constructed as described in Section 2.2.2, and each single litter-type bag was filled with 5.0 g of air-dried leaf material.

Mixed litter bags were filled with 0.83 g of each of the six leaf types to give a total weight of 5.0 g. Litter bags were strung together with 60 lb breaking strain fishing line in groups of five, leaving a 0.5 m gap in between litter bags. Thirty-five litter bags (seven strings of five) were deployed at each of the eight stream sites, over a period of three days, during mid-November 2000, in order to coincide with the period of peak leaf input into streams. At each site, litter bags were deployed over an approximately 30 m stretch of stream, each string of five being secured on alternate sides of the stream bank. Litter bags were collected after eight weeks in-stream exposure, over a period of three days. Upon collection, leaf material was treated as described in Section 2.2.2, to ascertain air-dried mass loss.

Table 3.2. Summary of tree species survey across eight study sites. All tree species within 10 m of the river bank were recorded for a distance of 50 m upstream of the study site. Canopy cover was estimated visually. Latin names for species not mentioned in the text: goat willow (*Salix caprea* L.), wych elm (*Ulmus glabra* Hudson) and rowan (*Sorbus aucuparia* L.).

Site name	Total canopy cover (%)	Dominant riparian tree species (> 50 % of total canopy cover)	Other tree species present
Stone	30	Sycamore	Goat willow, hawthorn, wych elm, alder, ash
Lindrick Dale	90	Alder, sycamore, goat willow	Ash, hawthorn, birch, wych elm
Strines	90	Beech, oak	Alder, hawthorn, birch, rowan
Crowdecote	40	Alder, sycamore	Ash, hawthorn, beech, wych elm
Oughtibridge	60	Sycamore, ash	Hawthorn, alder, goat willow
Berrymoor	60	Sycamore	Alder, hawthorn, ash, wych elm
Brockhurst	98	Alder, ash	Beech, hawthorn, oak, sycamore, wych elm
Holehouse	60	Birch, oak, alder	Hawthorn

3.2.3. Physico-chemical measurements.

Measurements of dissolved oxygen (D.O.) (% saturation), temperature (°C), pH, conductivity (μS/cm) and flow rate (m/s) were made as described in Section 2.2.3. Readings were taken on five occasions, upon deployment (week one) and collection (week eight) of litter bags, and at weeks three, four and six. Two flow rate measurements were taken upon each visit: one above the first litter bag of the first string of five, and the second further downstream, above the first litter bag of the last string of five.

3.2.4. Quantifying biotic variables.

The stream macroinvertebrate communities were sampled, sorted, and identified as described in Section 2.2.4. Species belonging to the shredder functional feeding group were distinguished from other macroinvertebrate species (Section 2.2.4) and counted, but were not weighed.

3.2.5. Statistical analyses.

The effect of resource diversity on mass loss from individual leaf components in mixed litter bags was tested by comparing the observed mass loss from mixed litter bags with an expected value (*L*) that was calculated using mean mass loss from single litter-type bags using equation 3.1.

$$L = \sum p_i m_i \qquad \text{Equation 3.1}$$

Where p_i is the proportion of leaf type i in mixed litter bags and m_i is the observed mean mass loss from leaf type i in single litter-type bags.

A visual assessment of the difference between observed and expected mass loss values was made for each site. Variation around the expected value was estimated by using the expected maximum and expected minimum values as error bars. These were calculated using Equation 3.2.

$$L_{\max(or\ \min)} = \sum p_i m_{i\ \max(or\ \min)} \qquad \text{Equation 3.2}$$

Where $L_{\max\ (\text{or min})}$ is the maximum (or minimum) expected mass loss from mixed litter bags, and $mi_{\max\ (or\ min)}$ is the maximum (or minimum) observed mass loss from leaf type *i* in single litter-type bags.

3.3. Results

3.3.1. Shredder diversity categories.

Study sites were selected using data from Field Study 1 (Section 3.2.1). The shredder community was re-sampled at each site and there was a positive significant relationship for the total number of shredder species at each site between study years ($r = 0.93$, $p < 0.01$, $n = 8$; Figure 3.1). The gradient of shredder diversity, from low to high, was therefore confirmed, and was used to categorise sites in some of the analyses that follow (Table 3.3). Detailed information on shredder species composition and abundance is given in Appendix D.

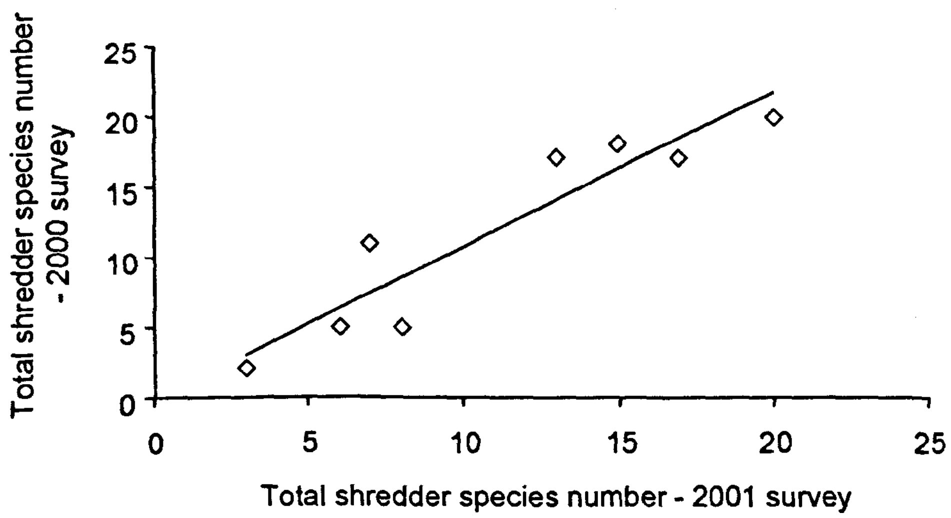


Figure 3.1. Relationship between total number of shredder species at each site between Field study 1 (2000) and Field Study 2 (2001).

Table 3.3. Total number of shredder species found at each stream site in the present study and assigned diversity category.

Site name	Total number of shredder species	Diversity category
Stone	3	Low
Lindrick Dale	6	Low
Strines	7	Low
Crowdecote	8	Low
Oughtibridge	13	High
Berrymoor	15	High
Brockhurst	17	High
Holehouse	20	High

3.3.2. Litter bag retrieval.

Thirty-five litter bags were deployed in total at each of the eight field sites, consisting of five replicates of each of the seven litter-bag types. However, not all litter bags were retrieved, and retrieval success varied across sites and across the seven litter-bag treatments (Table 3.4). Some litter bags were missing from the fishing lines altogether, presumably having been detached during periods of fast flow. Other litter bags were retrieved, but found to have large holes, possibly caused by debris catching onto, and tearing, them.

Table 3.4. Percentage of replicates retrieved for each litter-bag type, across stream sites. Litter-bag type codes are: Ald = alder, Syc = Sycamore, Hwn = hawthorn, Bch = beech, Mx = mixed.

Site	Litter-bag type							Total % retrieval per site
	Ald	Syc	Ash	Hwn	Oak	Bch	Mx	
Stone	60	60	100	80	60	80	60	71
Lindrick Dale	80	80	40	20	80	60	100	66
Strines	100	80	100	60	80	100	80	86
Crowdecote	60	20	80	80	80	40	100	66
Oughtibridge	80	100	60	40	100	20	100	71
Berrymoor	100	80	60	100	80	80	60	80
Brockhurst	20	40	20	40	0	20	80	31
Holehouse	100	80	100	100	100	100	100	97

3.3.3. Effect of leaf type versus leaf diversity on detritus processing.

The full two-factor analysis of sites x leaf litter types was unbalanced because no oak litter bags were retrieved from one site (Brockhurst). Therefore, two separate ANOVAs were performed. The first analysis included all leaf types, but excluded Brockhurst (analysis 1). The second analysis included all sites, but excluded oak litter-bag data (analysis 2). Both analyses indicated that mass loss was significantly different across different leaf types ($F_{\geq 5,126} \geq 68.3$, $p < 0.001$) and across different stream sites ($F_{\geq 6,126} \geq 31.1$, $p < 0.01$).

Both analyses showed that, overall, mass loss from mixed litter bags was significantly lower than from ash, hawthorn or alder litter bags, but significantly greater than that from beech litter bags (Figure 3.2). Analysis 1, which included oak litter-bag data, indicated that mass loss from beech and oak litter bags was not significantly different, but both were significantly lower than mixed litter bag mass loss (Figure 3.2 a).

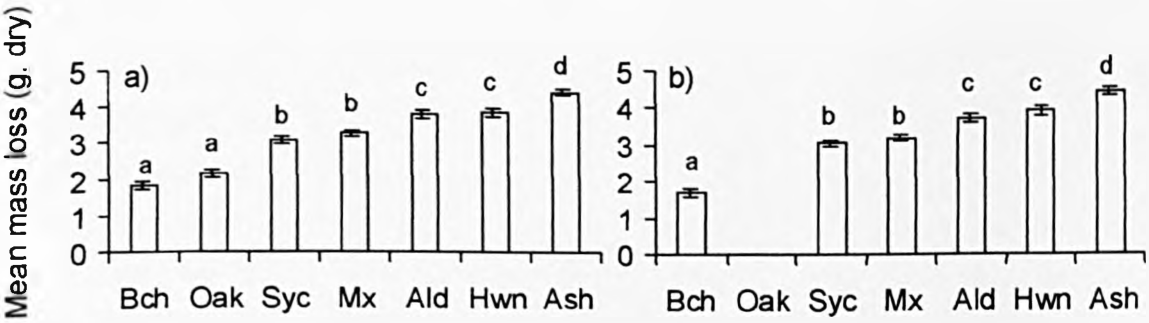


Figure 3.2. Mean mass loss (g, dry) from different litter-bag types from two alternative analyses, a) analysis 1: including all leaf types but excluding Brockhurst and b) analysis 2: including all stream sites but excluding oak litter bags. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). Error bars are 1 S.E. Litter-bag type codes are as for Table 3.4.

Overall, the mean mass losses from litter bags at Stone and Lindrick Dale were significantly greater than at Berrymoor (high shredder diversity), Strines and Crowdecote (both low shredder diversity), but not from the other two high shredder diversity sites in analysis 1 (Figure 3.3 a). Mean mass loss at Strines and Crowdecote was significantly less than at any other site. The second analysis, which included the eighth site (Brockhurst), showed a similar pattern to analysis 1 (Figure 3.3 b). Mean mass loss from litter bags was significantly greater at all high shredder diversity sites than at two of the low shredder diversity sites (Strines and Crowdecote), but significantly lower than that at the remaining two low shredder diversity sites (except for one site, Oughtibridge).

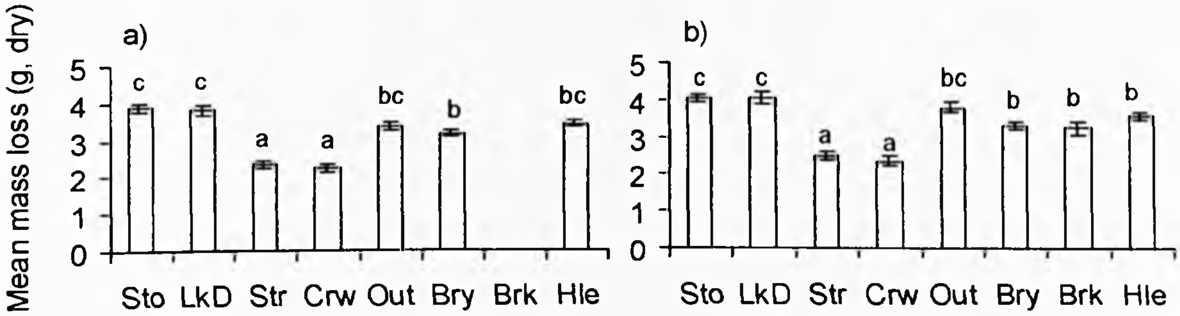


Figure 3.3. Mean mass loss (g, dry) across different stream sites from two alternative analyses, a) analysis 1: including all leaf types but excluding Brockhurst and b) analysis 2: including all stream sites but excluding oak litter bags. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). Error bars are 1 S.E. Site name codes are: Str = Strines, Crw = Crowdecote, Sto = Stone, LkD = Lindrick Dale, Bry = Berrymoor, Hle = Holehouse, Brk = Brockhurst and Out = Oughtibridge.

There was a significant interaction effect in both analyses ($F_{\geq 35,126} \geq 3.6$, $p < 0.01$) indicating that the pattern of mass loss across different litter-bag types varied across sites (Figure 3.4). At most sites, mean mass loss from beech and oak litter bags was significantly lower than that from alder, hawthorn and ash, but not from each other. At two sites (Strines and Brockhurst), mean mass loss from beech litter bags was not significantly different than that from alder (Figures 3.4 c and g), and at Oughtibridge mean mass loss from beech litter bags was not significantly different from any other leaf type (Figure 3.4 e). The patterns revealed at Brockhurst and Oughtibridge were likely influenced by the small sample sizes of beech litter bags at these sites. Ash, alder and hawthorn showed the greatest mean mass loss at all sites, and were never significantly different from one another, except at Crowdecote where mean mass loss from ash litter bags was significantly greater than for all remaining leaf types (Figure 3.4 d).

Mass loss from mixed litter bags was not significantly different from that of the litter-bag type with the greatest mean mass loss at six out of the eight sites (Table 3.5). The two sites where mean mass loss from mixed litter bags was significantly lower than the leaf type with the greatest mass loss included both a low (Crowdecote) and a high (Berrymoor) shredder diversity site.

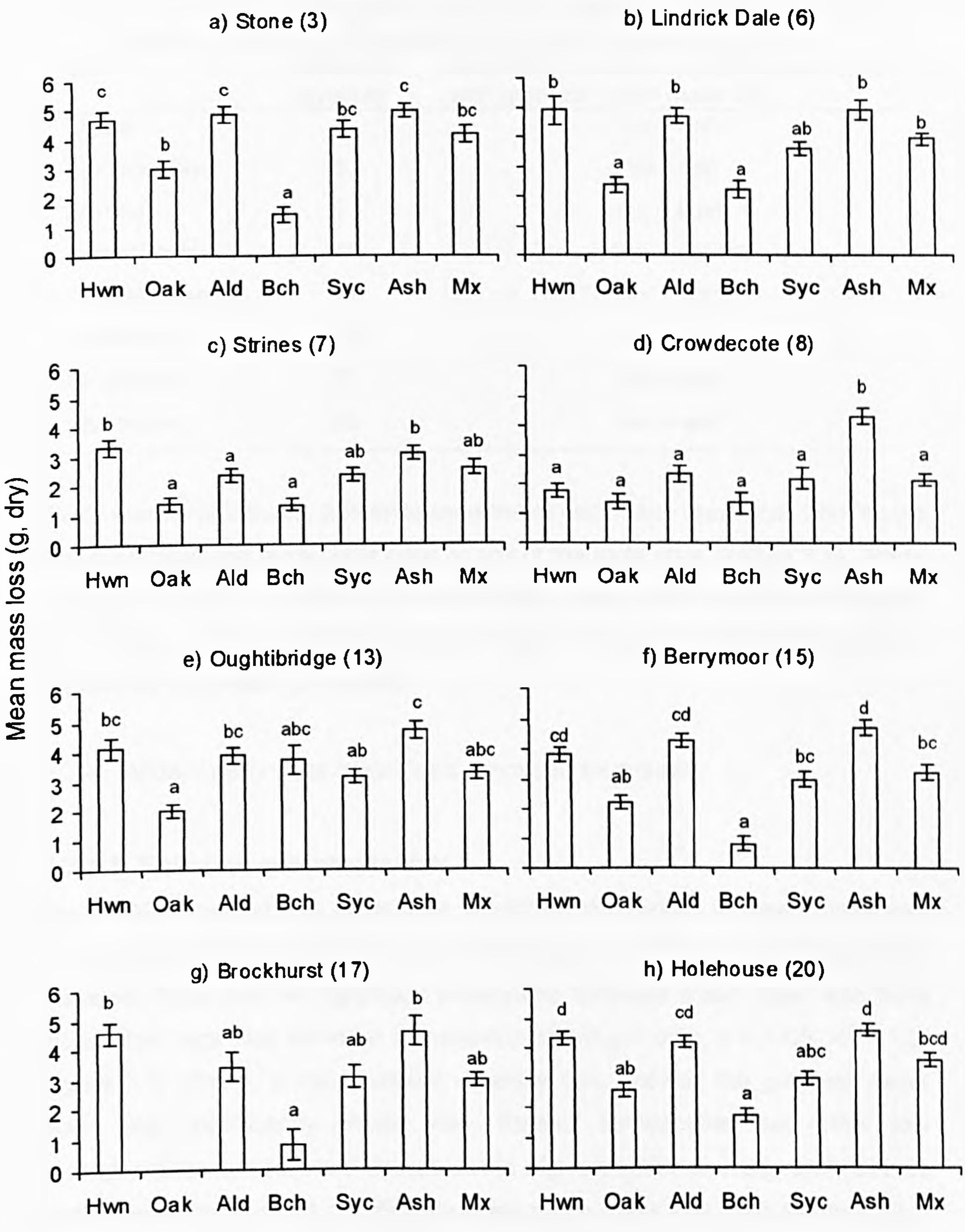


Figure 3.4. Mean mass loss (g, dry) from different litter-bag types at eight different stream sites. Numbers in parentheses indicate shredder species diversity at each site. a – f, and h are plotted using means and S.E. from analysis 1 (including oak litter-bag data) and g is plotted using means and S.E. from analysis 2 (excluding oak litter-bag data). Within each plot, bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison tests, $p > 0.05$). Standard errors are values calculated by the General Linear Model used to perform the 2-way ANOVA and are 1 S.E. Litter-bag letter codes are as for Table 3.4.

Table 3.5. Mixed litter bag mass loss (g, dry) relative to the leaf type with the greatest mass loss. = indicates no significant difference. * indicates $p < 0.05$, *** indicates $p < 0.001$. Litter-bag type letter codes are as for Table 3.4.

Site	Shredder diversity	Mean Mx mass loss relative to leaf type with greatest mean mass loss.
Stone	3	mx = ash
Lindrick Dale	6	mx = ald
Strines	7	mx = hwn
Crowdecote	8	mx < ash***
Oughtibridge	13	mx = ash
Berrymoor	15	mx < ash*
Brockhurst	17	mx = ash
Holehouse	20	mx = ash

There was no significant difference between overall mean mass loss from single litter-type bags and mixed litter bags at any of the eight sites (Figure 3.5). There was an indication that mean mass loss from mixed litter bags at Strines was greater than that from single litter-type bags, although this difference was not statistically significant ($p = 0.068$).

3.3.4. Influences on leaf mass loss across stream sites.

3.3.4.1. Shredder species number.

An ANOVA revealed that there were significant differences in mean mass loss from mixed litter bags among the eight sites ($F_{7,27} = 11.16$, $p < 0.01$; Figure 3.6). However, there was no significant relationship between mean mass loss from mixed litter bags and shredder species number ($F_{1,6} = 0.08$, $p > 0.05$, $R^2 = 1.3$; Figure 3.7). Stone, a low shredder diversity site, showed the greatest mean mass loss, significantly greater than Strines, Crowdecote (two other low shredder diversity sites) and Brockhurst (a high shredder diversity site). Strines and Crowdecote showed significantly lower mean mass loss than all other sites except for Brockhurst. Moreover, there were no significant relationships between mean mass loss and shredder species number for any of the six single leaf types ($F_{1,6} \leq 0.35$, $p > 0.05$).

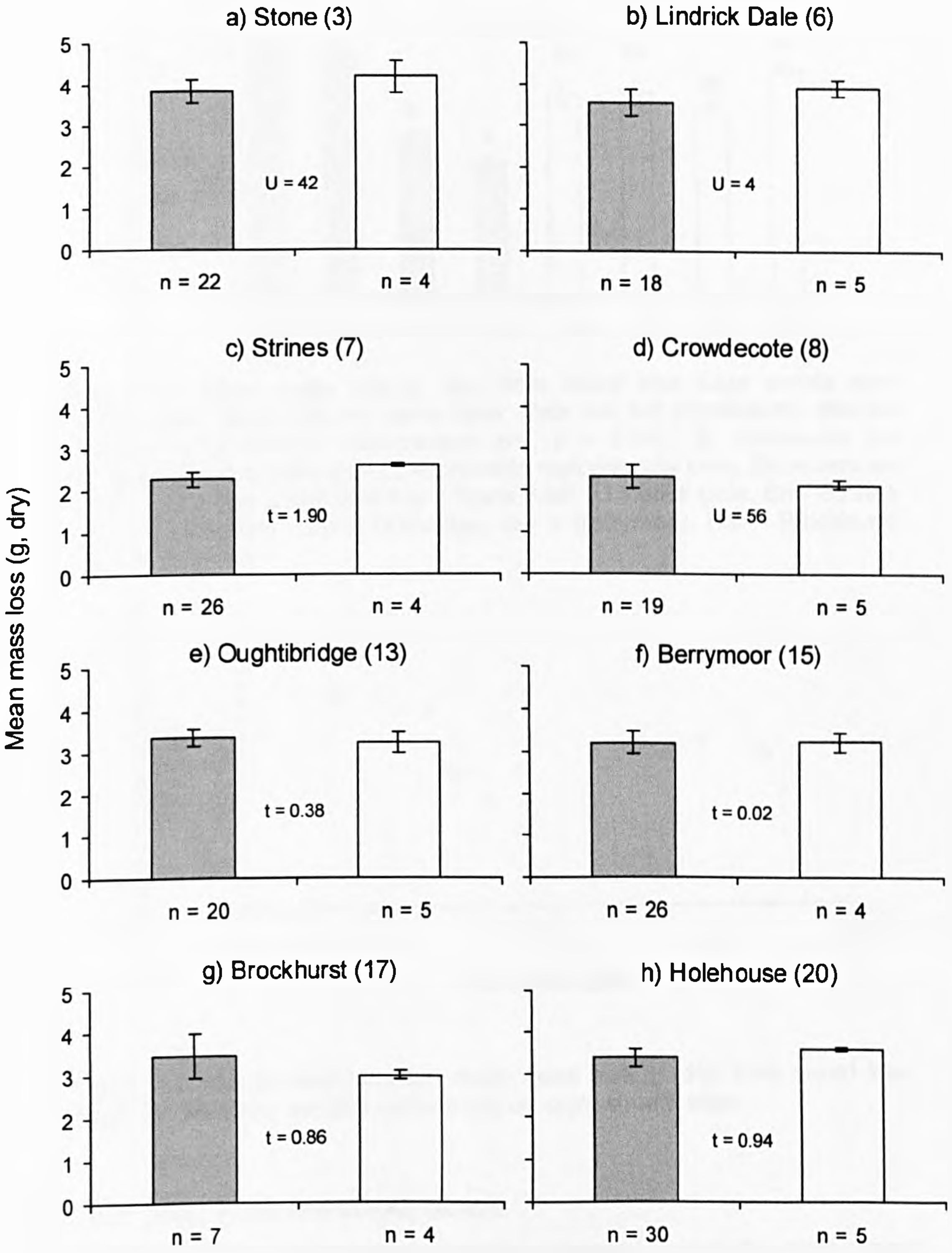


Figure 3.5. Mean mass loss (g, dry) from single litter-type bags (▨) compared to mixed litter bags (☐), for each of eight stream sites. Error bars are 1 S.E. Numbers in parentheses indicate shredder species number. Test statistics for comparisons between bars are given.

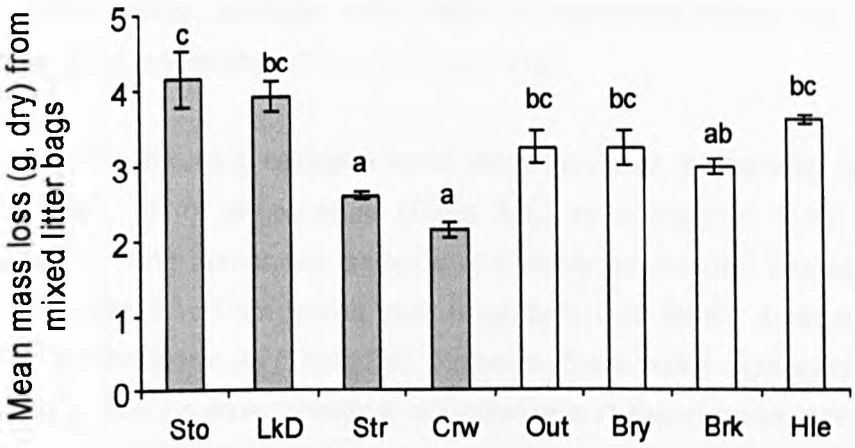


Figure 3.6. Mean mass loss (g, dry) from mixed litter bags across eight stream sites. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). ■ represents low shredder diversity sites and □ represents high diversity sites. Error bars are 1 S.E. Site name codes are: Sto = Stone, LkD = Lindrick Dale, Str - Strines, Crw = Crowdecote, Out = Outibridge, Bry = Berrymoor, Brk = Brockhurst, Hle = Holehouse.

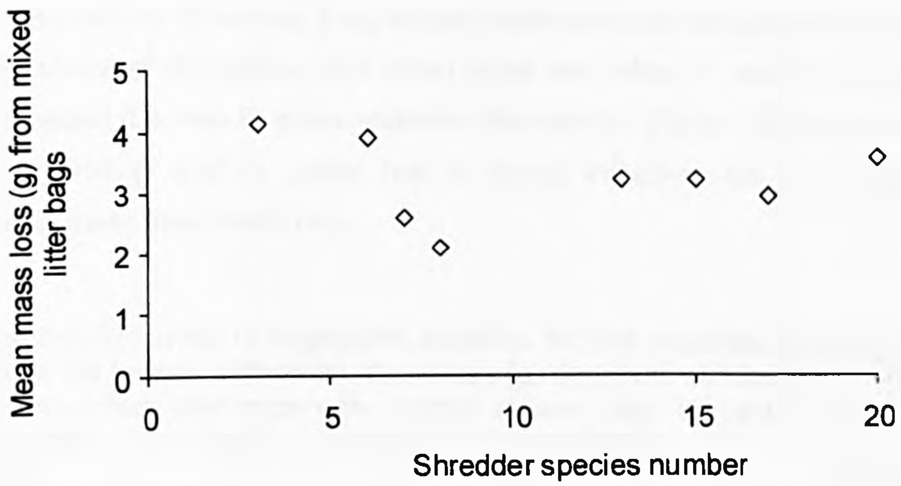


Figure 3.7. Relationship between mean mass loss (g, dry) from mixed litter bags and shredder species number across eight stream sites.

3.3.4.2. Other biotic and abiotic factors.

A summary of the physico-chemical factors recorded across the eight stream sites is given in Appendix E. Field Study 1 (see Chapter 2) indicated that shredder abundance, canopy cover, temperature and pH were factors that had a large influence on variation in mean mass loss from alder litter bags across natural streams. Canopy cover at the subset of sites used for the present study ranged from 30% up to 98%. There was significant variation between sites in both pH ($F_{7,32} = 20.3$, $p < 0.01$) and shredder abundance ($F_{7,64} = 19.2$, $p < 0.01$)

in the present study, although there were no significant differences between sites in terms of temperature ($F_{7,32} = 1.8$, $p > 0.05$).

There was no relationship between mean mass loss from all litter-bag types and canopy coverr, pH or temperature (Table 3.6), indicating that none of these factors were driving across-site patterns of detritus processing. The same was true when mass loss from mixed litter bags only was tested against canopy cover, pH and temperature (Table 3.6). However, there was a significant positive linear relationship between shredder abundance and mean mass loss from all litter-bag types, and from mixed litter bags only (Table 3.6; Figure 3.8 a and d). Results from Field Study 1 revealed that the relationship between shredder abundance and mass loss from alder litter was driven by one species in particular, *Gammarus pulex*. Similarly, there was a significant positive linear relationship between *G. pulex* abundance and mean mass loss, from all litter-bag types, and from mixed litter bags only, in the present study (Table 3.6; Figure 3.8 b and e). Moreover, a significant relationship did not continue to occur between shredder abundance and mean mass loss after *G. pulex* abundance was subtracted (i.e. non-*G. pulex* shredder abundance) (Table 3.6; Figure 3.8 c and f), indicating that *G. pulex* has a strong influence on the shredder abundance-mass loss relationship.

Table 3.6. Summary of regression statistics for five separate analyses of each of the factors with mean mass loss (g, dry) from all litter-bag types, and from mixed litter bags only, across stream sites. d.f. are 1, 6 for all regressions. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Factor	F	R^2
Regressions with mass loss from all litter-bag types		
Canopy cover	0.08	1.4
pH	3.61	27.2
Temperature (°C)	4.78	35.0
Ln (shredder abundance +1)	12.61*	62.4
Ln (*G. pulex* abundance +1)	20.57**	73.7
Ln (non-*G. pulex* shredder abundance + 1)	0.33	0.0
Regressions with mass loss from mixed litter bags only		
Canopy cover	0.09	1.4
pH	1.14	15.9
Temperature (°C)	3.49	36.7
Ln (shredder abundance +1)	46.8***	88.6
Ln (*G. pulex* abundance +1)	33.9***	85.0
Ln (non-*G. pulex* shredder abundance + 1)	0.73	10.9

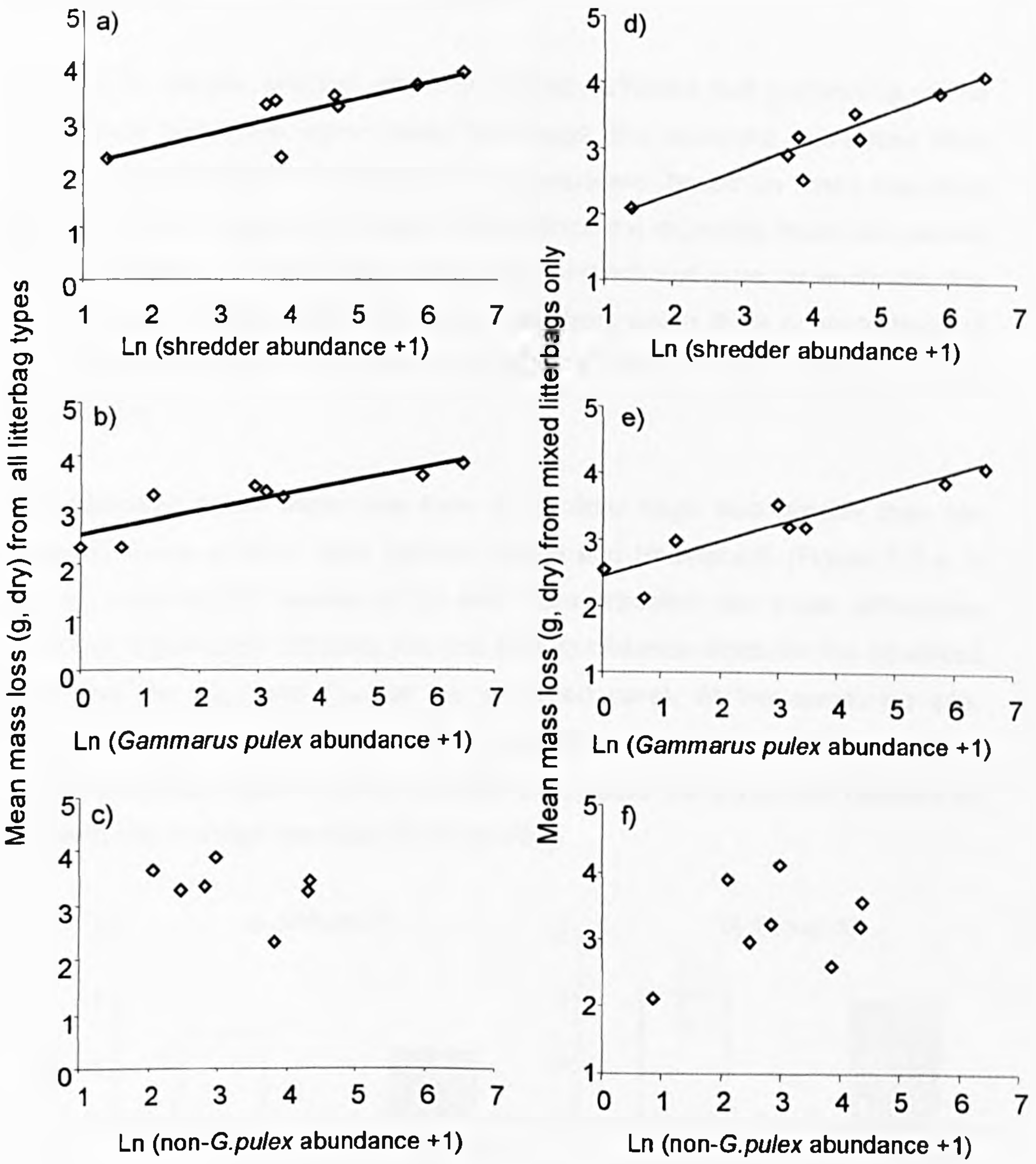


Figure 3.8. Relationship between mean mass loss from all litter-bag types and a) Ln (shredder abundance +1), fitted line is y = 1.86 + 0.31 x; b) Ln (*G. pulex* abundance +1), fitted line is y = 2.52 + 0.22 x and; c) Ln (non-G. pulex abundance + 1) (not significant) and;

Relationship between mean mass loss from mixed litter bags only and d) Ln (shredder abundance +1), fitted line is y = 1.51 + 0.403 x; e) Ln (*G. pulex* abundance +1), fitted line is y = 2.45 + 0.266 x and; f) Ln (non-G. pulex abundance + 1) (not significant).

3.3.5. Effect of resource diversity on processing of component leaf types at high and low shredder diversity sites.

In order to explore whether resource diversity affected leaf processing of the component leaf types within mixed litter bags, the observed mass loss from mixed litter bags was compared with that expected, based on mass loss from single leaf type bags (see Section 3.2.5.). Since the expected mass loss values were calculated from the mean mass loss for each leaf type, at each site, the analysis was performed only for those sites from which three or more bags of each single leaf type were retrieved (Table 3.4; Stone, Strines, Berrymoor and Holehouse).

The observed mean mass loss from mixed litter bags was greater than the expected value at three sites (Strines, Stone and Holehouse) (Figure 3.9 a, b and c), however the overlap of the error bars indicated that these differences were not significantly different (i.e. the 95% confidence limits for the observed bars and the L_{max} and L_{min} for the expected bars). At the remaining site, Berrymoor, observed and expected mass loss from mixed litter bags were almost identical (Figure 3.9 d). Overall, there were no consistent differences between low and high shredder diversity sites.

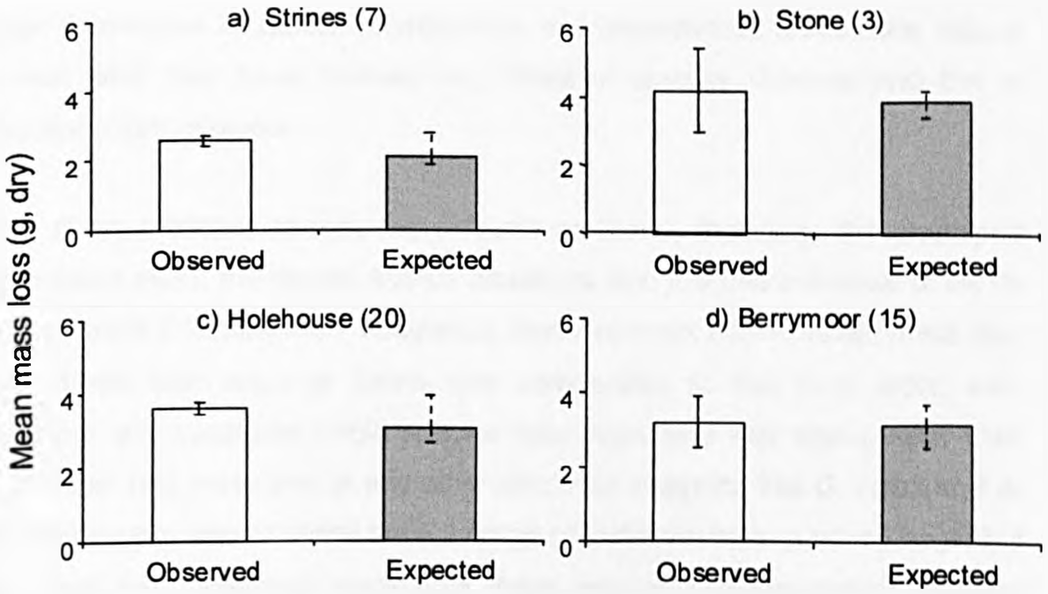


Figure 3.9. Comparisons of the observed mean mass loss from mixed litter bags with expected values (calculated from single leaf type bags, Equation 3.1), for four sites. Numbers in parentheses indicate the number of shredder species found at each site. Error bars are 95% confidence limits for the observed bars and L_{max} and L_{min} (calculated using Equation 3.2) for the expected bars.

3. 4. Discussion.

The overall aim of this chapter was to examine the effect of leaf diversity on detritus processing across low and high diversity shredder communities. It was hypothesised that resource diversity should have greater effects on leaf litter processing in high shredder diversity communities. This hypothesis is based on the assumption that there would be resource-niche differentiation between shredder species resulting in an increased potential for leaf litter processing with greater leaf diversity.

There was no evidence to support the niche-differentiation mechanism for positive effects of shredder diversity on detritus processing in natural streams. Although mixed litter bags were among the most fully decomposed litter-bag types at six out of the eight sites, there was no consistent pattern with shredder diversity. Moreover, mass loss from mixed litter bags did not increase with increasing shredder diversity. These results may be observed if shredder species do not differ in their leaf preferences, and so an increase in shredder diversity does not increase the range of resource-niches that are represented. The high mass loss from mixed litter bags at low shredder diversity sites suggests that just two shredder species, *Gammarus pulex* and *Asellus aquaticus* were adequate to utilise the range of leaf resources offered. However, large differences in species composition and abundances across the natural stream sites may have masked any effect of species richness and this is discussed further below.

Only three shredder species were found at Stone, including; the amphipod *Gammarus pulex*, the isopod *Asellus aquaticus*, and just one individual of the fly larvae *Tipula* (*Yamatapula* – subgenus) (see Appendix D). However, mass loss from mixed litter bags at Stone was comparable to that from alder, ash, hawthorn and sycamore single species litter bags, and was also greater than mixed litter bag mass loss at any other site. This suggests that *G. pulex* and *A. aquaticus* were able to utilise the full range of leaf resources in mixed bags, but this does not necessarily mean that there was niche-differentiation between these two species. The same results would have been observed if one, or both, of these species has a broad resource-niche range that covers all of the leaf types used in the study. Various studies have suggested that many shredder species are able to utilise a wide range of leaf types, and other resources, as a food source (Kaushik & Hynes 1971, Iversen 1974, Irons *et al.* 1988, Malicky 1990, Friberg & Jacobsen 1994).

For example, one study revealed that although *G. pulex* showed a preference for conditioned alder leaves when given a choice between six food sources including: conditioned beech (*F. sylvatica*), conditioned sitka spruce needles (*Picea sitchensis*), fresh beech leaves, a fresh macrophyte, and a fresh filamentous green alga, it did feed actively on all six of these food sources (Friberg & Jacobsen 1994). This evidence suggests that out of the two dominant shredders present at Stone, *G. pulex*, at least, is potentially able to feed on a range of resources. If the resource-niche ranges of shredders are generally broad and overlapping, then the niche-differentiation effect may not be an important mechanism for positive effects of shredder diversity on leaf processing in streams.

If shredder species do not partition resources in terms of their diet, then we may expect resources to be partitioned in another niche dimension in order that species can co-exist, for example, either time or space (Giller 1984). There are examples of niche partitioning in time (e.g. Grant & MacKay 1969, Elliott 1987, 1988) and space (e.g. Hildrew & Edington 1979, Edington *et al.* 1984) for stream macroinvertebrates. However, mass loss from any of the single leaf type litter bags did not increase with shredder species number in this study, providing no evidence for the niche-differentiation effect in niche-dimensions other than diet. A longer term study (over one year) is probably required to detect any effects of temporal separation of life-cycles over different seasons, which is frequent among univoltine insects in temperate streams (Allan 1995). Moreover, the patterns of mass loss from single leaf type litter bags provided no evidence for facilitation among shredder species. Examples of facilitation have been suggested for shredder species and observed for other stream macroinvertebrates (Section 3.1). Although there was not an increase in the processing of single leaf types with shredder diversity, this does not negate the possibility that facilitation may have occurred between certain combinations of species.

Results from this study indicate that species identity and abundance may be more important than shredder species number for detritus processing on mixed leaf resources. Mixed leaf processing was significantly lower at Crowdecote and Strines than at Stone and Lindrick Dale, all of which were low shredder diversity sites. The most obvious compositional difference between these two pairs of low diversity sites was the high abundance of *G. pulex* and *A. aquaticus* at Stone and Lindrick Dale while *A. aquaticus* was absent at Strines and Crowdecote and *G. pulex* was absent at Strines and occurred in very low abundances at Crowdecote. Field Study 1 (Chapter 2) indicated that processing of alder material was influenced by *G. pulex* abundance, while mass loss from mixed litter bags in the present study was also positively related to *G. pulex* abundance. Any influence of shredder species richness therefore would be difficult to detect in the field, given the large variation in *G. pulex* abundance across the field sites and it's strong influence on leaf processing. The role of species identity in affecting mass loss from mixed litter bags may be important if certain shredder species, for example *G. pulex*, have a wide resource-niche range, while other species do not.

Alternatively, particular combinations of shredder species may have been important for processing a mixed leaf resource. For example, if there is a high degree of resource-niche complementarity between certain species, while most other shredders share the same resource-niche range. Differences in leaf preferences between *G. pulex* and *A. aquaticus* in this study may have led to the greater mass loss from mixed litter bags at the sites where these two species co-occurred. One study revealed that there was little niche-differentiation between *G. pulex* and *A. aquaticus* in terms of their fungal preferences (Graça *et al.* 1994b), however there is no evidence to indicate whether these species differ in their leaf preferences.

As well as no overall effect of leaf diversity on detritus processing, there was no evidence to suggest that the processing of individual leaf types within mixed litter bags was enhanced above that of single litter-type bags, at either high or low shredder diversity sites, i.e. the effects of increasing resource diversity were purely additive. These results agree with two other studies performed in stream systems that examined the processing rates of single and mixed leaf litter bags for two (Leff & McArthur 1989) and three (Meyer 1980) different leaf types, but are in contrast to the positive and negative non-additive effects observed in some terrestrial leaf decomposition studies (e.g. Wardle *et al.* 1997b, Kaneko & Salamanca 1999).

The observed additive effects of leaf diversity in the present study may be a result of shredders utilising each individual leaf type within mixed bags discretely and in order of palatability. Evidence from the present study suggests that the range of leaf litter types tended to be processed in the same order at most sites, indicating a general sequence of shredder preference (i.e. ash > hawthorn > alder > sycamore > oak > beech, Figure 3.4). It was predicted that the processing of some 'slow' decomposing leaf types would be enhanced in leaf mixtures if shredder species remained within the leaf pack once the most palatable leaf type had been consumed, rather than using energy to search for new resources.

However, if shredders emigrated from, and recolonised, litter bags as the availability of different leaf resources changed within the mixed litter bags, and in the surrounding stream, through time, processing rates of individual leaf types would not be enhanced above that of homogenous litter bags. Some studies have suggested that shredders may have the ability to track leaf litter abundance and distribution in space and through time (e.g. Richardson 1991, Dobson & Hildrew 1992), and that the response of shredder populations to resource depletion may be rapid. For example, Rowe & Richardson (2001) manipulated resource abundance in artificial streams by reducing the number of resource patches (red alder (*Alnus rubra*) leaf packs) by half. Emigration, and aggregation of shredder species on remaining leaf resources, significantly increased above that of control streams within just seven days.

There are some factors that may have affected the ability of this study to detect effects of resource diversity and shredder diversity on detritus processing. For example, litter bags were deployed to coincide with the main period of autumn leaf fall into streams and therefore with the peak of feeding activity of shredding detritivores (Boulton & Boon 1991). However, the natural leaf input was likely to be variable in type and quantity across the eight stream sites, as indicated by the survey of riparian vegetation (Table 3.2). If shredder species are able to track leaf resources, as discussed above, the amount and type of natural leaf litter surrounding experimental litter bags may have influenced their mass loss. That is, if highly palatable leaf litter was abundant in the surrounding stream, we might expect mass loss from mixed litter bags to be low, and vice versa.

For example, Strines was the only site where the riparian canopy was dominated by the two slowest decomposing leaf types used in this study, beech and oak (Table 3.2). Strines was also the only site where it was indicated that mass loss from mixed bags was greater than the overall mass loss from single leaf-type litter bags, although this difference was not significant (p = 0.068, Figure 3.5 c). At the remaining stream sites the riparian canopy was dominated by leaf types that were among the most quickly decomposed in this study, and this may have negatively affected detritus processing in mixed litter bags. The precise nature of the affect of natural detritus on experimental litter bag mass loss can not be predicted, since the composition of riparian vegetation is not an accurate reflection of the composition of in-stream leaf litter packs. This is because of differences in throughfall processes, leaf transport distances and variation in the time of abscission (Boulton & Boon 1991). One way to overcome such affects may be to deploy experimental litter bags after most natural leaf inputs have been consumed, or to conduct studies in artificial streams where leaf inputs can be controlled.

A further factor that may have affected detritus processing is the influence of microbial processes. The decomposition of leaf litter in streams is mediated by the physico-chemical characteristics of different leaf types, environmental conditions and the detritivore community (Webster & Benfield 1986), which comprises both microbes and macroinvertebrates (Section 1.6.1). The colonisation of leaf litter by microbes acts to 'condition' the leaf material, increasing its palatability for consumption by macroinvertebrates, but also results in mass loss (Gessner & Dobson 1999). If mass loss caused by microbial activity outweighed that caused by shredders (i.e. shredders were not important for leaf processing), any effect of shredder diversity on leaf processing would be undetectable.

Evidence from both laboratory and field studies has demonstrated that macroinvertebrates play a significant role in leaf breakdown, especially in low-order streams where macroinvertebrates are abundant (e.g. Benfield & Webster 1985), and during winter months when stream temperatures are low (e.g. Short *et al.* 1980, Rowe *et al.* 1996), as in the present study. Macroinvertebrate activity has been found to be unimportant for leaf processing in larger streams where leaf inputs are low and shredders are numerically unimportant (Anderson & Sedell 1979, Webster & Benfield 1986). There may have been microbially mediated mass loss from experimental litter bags in the present study, since microbial activity has been demonstrated at stream temperatures of 0°C (Bãrlocher & Kendrick 1974). However, it is unlikely that this outweighed shredder mediated mass loss in the low-order streams used for this study, in which shredders were abundant. At only one site used in this study, may processing of leaf litter by shredders have been unimportant. Mass loss from different leaf types was very low, and far less variable, at Crowdecote than for any of the remaining sites. Moreover, there were no significant differences in mass loss between leaf types, except for ash, which showed greater mass loss than the five other leaf types. At this particular site, total shredder abundance was only twenty-six individuals, an order of magnitude less than at any other site.

Evidence from this study suggests that resource diversity is unimportant for detritus processing in natural streams where species composition and abundance vary greatly. There was no evidence from the field for resource-niche differentiation between shredder species in terms of their leaf preferences. It is possible that the effects of niche differentiation between shredders were not detectable under field conditions, especailly given variation in species' abundances across sites. Moreover, very few replicates of some leaf type treatments were recovered at some sites (see Table 3.4), and therefore estimates of processing rates may not be very robust in some cases. However, it is also possible that the niche-differentiation effect is not an important mechanism for effects of shredder diversity on detritus processing across these streams. One feasible reason for this may be the nature of resource availability through time, in streams. Petersen & Cummins (1974) proposed the idea that different leaf types become palatable to shredders, through microbial conditioning, after different periods of time within a stream, and therefore represent a 'dietary continuum' whereby different leaf types are utilised by shredders at different stages in time. Shredder species may have adapted to utilise this 'dietary continuum' by having a wide resource-niche range, in order to be able to utilise the different leaf types as they become palatable. The niche-differentiation effect may therefore be unimportant in a system where only a single resource is available for consumption by shredders at any one point in time. In this case, facilitation, or niche-differentiation in time or space, between shredder species utilising a single leaf resource may more important mechanisms for positive effects of shredder diversity on detritus processing in streams.

3.5. Conclusions.

There was variation in processing across different individual leaf types. A similar pattern of variation across leaf types was observed despite differences in shredder diversity across sites.

Decomposition in mixed litter bags was equivalent to that of the most fully decomposed single-litter type at six out of eight sites, but this was independent of shredder diversity.

Mass loss from mixed litter bags was not greater than the overall mean mass loss from single leaf types at high shredder diversity sites, nor at low shredder diversity sites. Leaf diversity was not important for detritus processing.

There was no evidence from the stream sites examined for:
-a positive relationship between mass loss from mixed litter bags and shredder species richness,
-a positive relationship between mass loss from single leaf types and shredder species richness or,
-positive non-additive effects of leaf diversity.

However, there was large variation in species composition and abundance across sites. In particular, *G. pulex* abundance appeared to have a strong influence on leaf mass loss across stream sites and may have masked any relationship between mass loss and species richness.

Given this caveat, it is unclear from this field study whether niche-differentiation in leaf diet and/or facilitation or niche-differentiation in niche dimensions other than leaf diet, are important mechanisms for positive shredder diversity effects on detritus processing across the study streams.

4. The affect of shredder species number and identity on detritus processing: a test using stream mesocosms.

4.1. Introduction.

4.1.1. Introduction.

Field studies have provided insights as to the role of shredder diversity, along with other biotic and abiotic factors, in influencing leaf decomposition at a regional scale (Jonsson *et al.* 2001, Huryn *et al.* 2002; Chapters 2 and 3), but have not provided any detailed insights as to the possible mechanisms that may be driving any positive diversity effects. A recent focus of attention has been to distinguish which of two different classes of mechanism is primarily responsible for driving positive biodiversity-ecosystem function relationships; the selection effect, whereby ecosystem function is affected by the presence of particular species (Section 1.4.1), or complementarity effects, whereby resource-niche differentiation and positive interactions between species lead to increased ecosystem function (see Section 1.4.2).

There has been a very limited exploration of the selection effect versus complementarity effects in freshwater decomposer systems. This is partly due to the logistical constraints of the experimental design that is required to test for complementarity among more than a few species (Loreau *et al.* 2001, see Section 1.4.2.4). In addition, recent methodologies for identifying and separating the effects of selection and complementarity have been developed exclusively for terrestrial plant systems, applying techniques adapted from agricultural and plant competition experiments (Loreau 1998a, Hector 1998, Hector *et al.* 1999).

Measures such as the relative yield, and relative yield total (Hector 1998), and D_i and $\check{D}$ (Loreau 1998a), have been developed to detect positive effects of increasing species number on ecosystem function, after accounting for shifts in numerical dominance among species (see Section 1.4.2.4). These metrics can be applied to simple experimental designs whereby the response of a multi-species mixture is compared with that of the single-species treatments of each of the component species. However, these methods can only be fully applied in experimental systems where the response of individual species can be quantified within a mixed-species assemblage, and therefore their application to ecosystem processes such as nutrient fluxes and decomposition rates, is limited.

Moreover, neither measures of the metrics mentioned above can provide unambiguous evidence for complementarity effects (see Loreau 1998a), for which the most stringent test is the detection of 'overyielding' (e.g. Loreau 1998a, Hector *et al.* 1999, Hector *et al.* 2002a; see Section 1.5.1). That is, if the observed response for a multi-species assemblage is greater than that for the single-species assemblage with the greatest response; an effect that can only be brought about by resource-niche complementarity or positive species interactions (e.g. Hector *et al.* 2002a). The detection of overyielding can be applied to a broader range of experimental systems since it does not require that the response of individual species within a mixed-species assemblage be quantified. Therefore overyielding can be used to indicate whether complementarity effects are occurring in stream decomposer systems, where it is difficult, in practical terms, to separate the effects of different species on leaf processing rates.

The few studies that have examined the influence of macroinvertebrate species richness on detritus processing in streams, under controlled laboratory conditions (Jonsson & Malmqvist 2000, Cardinale *et al.* 2002, Jonsson *et al.* 2002, Jonsson & Malmqvist (in press)), do not provide consistent evidence. While two studies have provided evidence for complementarity effects (Jonsson & Malmqvist 2000, Cardinale *et al.* 2002), two others have indicated that species identity was the main factor affecting detritus processing rates (Jonsson *et al.* 2002, Jonsson & Malmqvist (in press)).

Cardinale *et al.* (2002) examined the resource capture of three species of suspension-feeding caddisfly larvae in stream mesocosms. The authors compared the resource capture of three different single-species treatments to that of a mixed-species assemblage, containing all three species. The additive partitioning method of Loreau & Hector (2001) (see Section 1.4.2.4) was used to partition the observed net diversity effect into 17% selection and 83% complementarity. These results suggested a strong complementarity effect, although the additive partitioning method is subject to limitations (see Section 1.5.1), and the authors did not test for overyielding (i.e. whether resource capture in mixed-species assemblages was significantly greater than that in the single-species treatment with the greatest resource capture). Despite this, observations of larval feeding performance and near-bed hydrodynamics did provide direct evidence for complementarity effects on resource capture. Differences in the morphology of the nets used for filter feeding allowed different species to facilitate each others resource capture through biophysical interactions.

Cardinale *et al.* (2002) propose that the kind of facilitation that they observed, i.e. alteration of the physical environment increasing the availability of resources, is likely to be widespread in both aquatic and terrestrial systems. In stream systems, such facilitation is likely between other groups of filter-feeders (e.g. blackfly, and some other, fly larvae, some mayfly larvae (Allan 1995)), but could also be important among shredders. For example, the fragmentation of large particles of detritus by the feeding action of larger shredder species, with chewing (e.g. *Gammarus pulex*; Graça *et al.* 1993) or cutting (e.g. *Sericostoma personatum*; Friberg & Jacobsen 1994) feeding strategies, into smaller particle sizes that may be more readily consumed by smaller shredder species (e.g. stonefly larvae).

The overall positive diversity effect could be partitioned for the experiment described above, because the resource capture of individual caddisfly larvae species could be quantified in the mixed-species streams. However, the other studies that have examined the effect of macroinvertebrate diversity on leaf breakdown in streams, discussed below, have not been amenable to this method. Jonsson & Malmqvist (2000) tested the effect of increasing shredder species diversity from one to three, on the breakdown of alder leaf litter in aquatic mesocosms, using three different species of shredding stonefly larvae. They tested every species combination at each diversity level, with replication, and used a nested ANOVA design to test the effects of both species identity and species number. Results indicated no species identity effects on leaf breakdown, either between different single-species treatments, or between different two-species combinations. Leaf breakdown rates were significantly greater in three- than in two-species treatments, indicating possible complementarity effects. The authors suggested that the increased leaf processing rates in more diverse mixtures may have been a result of facilitation between species and also propose that intraspecific interference may be reduced in mixed-species assemblages, allowing increased processing rates. A subsequent study has provided evidence to support both the facilitation and intraspecific interference hypotheses (Jonsson & Malmqvist 2003).

Jonsson *et al.* (2002) used three shredder species belonging to different taxonomic groups (Amphipoda, Plecoptera and Trichoptera) to test the effect of species identity and number on the processing rates of two different leaf types (alder and beech), using the same design as described above. In contrast to the former experiment, there was no significant effect of species number on processing rates for either of the leaf types used, indicating no complementarity effects. Instead, variation in leaf processing rates was driven by species identity and species combination. One more study used the same experimental design to examine three other functional feeding groups of stream macroinvertebrates; filter feeders, grazers and predators (Jonsson & Malmqvist (in press)). Results indicated no evidence for an increase in resource consumption rates with increased species number. Again, resource consumption was dependent on species identity and species combination.

Current evidence for shredder identity and complementarity effects on leaf breakdown in streams comes mainly from studies that have tested a range of one to three species only. However, this represents only the very lowest end of the range of shredder diversity found in natural streams in field studies that have provided evidence for positive effects of shredder richness on leaf processing. For example, of the stream sites surveyed by Jonsson *et al.* (2001) and in Chapter 2 of this thesis, 83 % of sites had six or more shredder species, while only one site in each study had three or fewer shredder species. Clearly it is necessary to investigate the effects of shedder diversity, and the possible mechanisms driving any effects, for a larger number of species.

Only one study has examined the effect of shredder diversity on leaf processing for more than three species. Jonsson & Malmqvist (2003) examined the effect of shredder species richness on alder processing rates along a gradient from one to six species. Six species of shredding stonefly larvae were used to create four levels of species richness (one, three, four and six species). Results indicated that processing rates in single-species treatments were significantly lower than the three- and six-species treatments, but not from the four species treatments, and that there was no difference between the three- four and six-species treatments. However, the experimental design did not allow for the separation of species identity effects from complementarity effects, and without the ability to ascertain which mechanisms may be driving the observed patterns, these results are difficult to interpret. For example, no data are presented to indicate whether there were differences in processing rates between single species treatments, and therefore whether a particular species may have had a strong effect on leaf processing. Moreover, the authors did not indicate whether the processing rate for the six species treatment was greater than that expected from the single-species treatments, or whether there was any overyielding.

The possible mechanisms that may drive positive species diversity-function relationships in shredder-leaf decomposition systems have been discussed above. However, all evidence so far, comes from studies that have used only a single leaf resource (Jonsson & Malmqvist 2001, Jonsson *et al.* 2002, Jonsson & Malmqvist (in press)). Such experiments have been able to detect complementarity effects that are brought about by facilitation between species, or niche-differentiation in time or space (see Section 1.6.2). However, resource-use complementarity between shredder species in terms of their leaf diets may also lead to a niche-differentiation effect, when a mixed leaf resource is available. Results from a field study (Chapter 3) provided no clear evidence to support the hypothesis that niche-differentiation may be driven by the partitioning of different leaf types between shredder species (Section 3.4). However, to date, there have been no controlled laboratory experiments that have examined species identity and complementarity effects on decomposition processes with more than one resource.

4.1.2. Aims.

The overall aim of this chapter is to examine shredder identity and complementarity effects on detritus processing on a) a single leaf resource and b) a mixed leaf resource, under controlled conditions. This was achieved by performing two separate experiments in artificial stream mesocosms, where many biotic and abiotic factors could be better controlled than in the field. A simple experimental design was employed in which the detritus processing rates for several different single-species shredder treatments were tested against that of a mixed-species assemblage composed of all the different single shredder species.

Three specific questions are addressed for both (a) a single leaf resource and (b) a mixed leaf resource: (1) does shredder species number affect leaf processing rates? (2) Are detritus processing rates greater for mixed-species shredder assemblages than for single-species shredder treatments? And if so: (3) is there any evidence for complementarity effects?

These questions were addressed by testing for the following effects. Firstly, if species identity does affect detritus processing, there should be significant differences in leaf processing rates between single-species treatments. Secondly, if an increase in species number has any positive effect (through species identity, complementarity, or both) on detritus processing rates should be greater for mixed-species streams than for single-species streams, and leaf processing rates observed in mixed-species streams should be greater than predicted from combining estimates of leaf processing rates from single species streams. Finally, if there were any positive effects of shedder species number on detritus processing through complementarity effects (i.e. facilitation and/or niche-differentiation in time or space, on a single leaf resource, and additionally niche-differentiation in leaf diet on a mixed leaf resource), there should be overyielding in the mixed-species streams.

4.2. Methods.

4.2.1. Experimental design.

Two separate experiments were performed. In Experiment 1, shredder assemblages were provided with a single leaf resource and for Experiment 2, a mixed leaf resource was used. Experiments were carried out over separate eighteen-day periods: Experiment 1 during February/March 2001 and Experiment 2 during March 2002. For both experiments, several different single-species treatments were tested against a multi-species assemblage composed of all the species used in the single-species treatments. For Experiment 1, there were six different single–species treatments, each replicated four times, and one multi-species assemblage that was replicated six times, resulting in a total of thirty mesocosms. For Experiment 2, there were only five different single-species treatments. This was because one of the stonefly species, *Protonemura praecox*, could not be used due to the high rates of emergence observed during laboratory acclimatisation (see Section 4.2.2). The remaining five single-species treatments were each replicated four times, and the multi-species treatment replicated six times, resulting in a total of twenty-six mesocosms.

4.2.2. Choice, collection and acclimation of test species.

Shredder species were selected using three criteria: representation of a range of taxonomic groups, representation of species that could be found together in the field (based on field data from Chapter 2) and, availability. The shredder species used, their taxonomic groups and collection locations are summarised in Table 4.1.

Table 4.1. Shredder species used in mesocosm experiments, taxonomic order, and collection locations. Stream names in parentheses are unnamed tributaries of the stream name given.

Species name	Order	Collection location	
		Stream name	NGR
Gammarus pulex	Amphipoda	Crags stream	SK 497745
Asellus aquaticus	Isopoda	Rivelin pond	SK 324889
Sericostoma personatum	Trichoptera	2001 – River Amber	SK 331646
		2002 – River Lathkill	SK 219647
Leuctra hippopus	Plecoptera	(River Dove)	SK 292030
Nemoura cambrica	Plecoptera	(River Dove)	SK 292030
Protonemura praecox	Plecoptera	Strines Dike	SK220908

Shredder species were collected by taking kick samples from the streambed with a standard kick net (Murray-Bligh *et al.* 1997). The kick net contents were tipped into sorting trays where the appropriate species were identified and collected using a pipette. This process was repeated until the target number of individuals had been collected (see Section 4.2.4). Collection techniques were modified slightly for *Gammarus pulex* and *Asellus aquaticus*. For the former species, a hand sieve was used for collection, while *Asellus aquaticus* was collected by dredging leaf litter from the pool bottom with a kick net, then separating animals from leaf material.

All animals were acclimatised to laboratory conditions for three days before transfer to the mesocosms. Animals were held in species-specific tanks and provided with alder leaf material as a food source. For the first twenty-four hours after collection animals were kept in aerated stream water. After twenty-four hours, stream water was replaced with Artificial Pond Water (APW) (H.S.E. 1982). After three days, animals were transferred to the mesocosms (see Section 4.2.3). Animals were collected over a period of four days. Therefore, although all animals were acclimatised to laboratory conditions in tanks for a standard period of time, not all animals were acclimatised to mesocosm conditions for the same period of time. The minimum period of acclimatisation to mesocosm conditions was twenty-four hours. Once transferred to mesocosms, shredders were provided with alder leaf material as a food source, which was removed twenty-four hours prior to the beginning of each experiment.

4.2.3. Experimental system.

Artificial stream mesocosms were constructed from white plastic electrical ducting material and small pumps (Aquaclear powerhead 201, HAGEN®) were used to recirculate water through plastic tubing (Figure 4.1). Each stream was compartmentalised with fine (400 μm mesh size) and coarse (0.4 cm x 0.5 cm mesh size) mesh in order to create compartments that were assigned to particular functions (Figure 4.1). Fine mesh barriers enclosed shredders within particular compartments, while coarse mesh was placed immediately upstream of each fine mesh barrier in order to prevent fine mesh becoming clogged with coarse particulate organic matter, and thereby restricting flow. Each stream channel was 150 cm long, 9.5 cm wide and 9 cm deep and was filled to a depth of 3 cm with pea gravel in certain compartments (see Figure 4.1). Streams were filled to a depth of 6 cm with APW and the water level was marked and maintained throughout the experiments with the addition of distilled water.

Each mesocosm consisted of seven compartments in total (Figure 4.1). The 'community compartments' contained the experimental shredder assemblages while a smaller compartment was assigned as a 'monitoring compartment' in each single-species treatment mesocosm (see Figure 4.1). In these monitoring compartments, five individuals (of the same species as in the corresponding community compartment) were kept with a small amount of alder litter and a few pieces of pea gravel in order that species-specific emergence and mortality could be monitored daily. Animals could be clearly observed in these compartments, but could not be in the experimental 'community compartments'. The equivalent compartments in mesocosms with multi-species experimental assemblages were set up in the same way but with no animals.

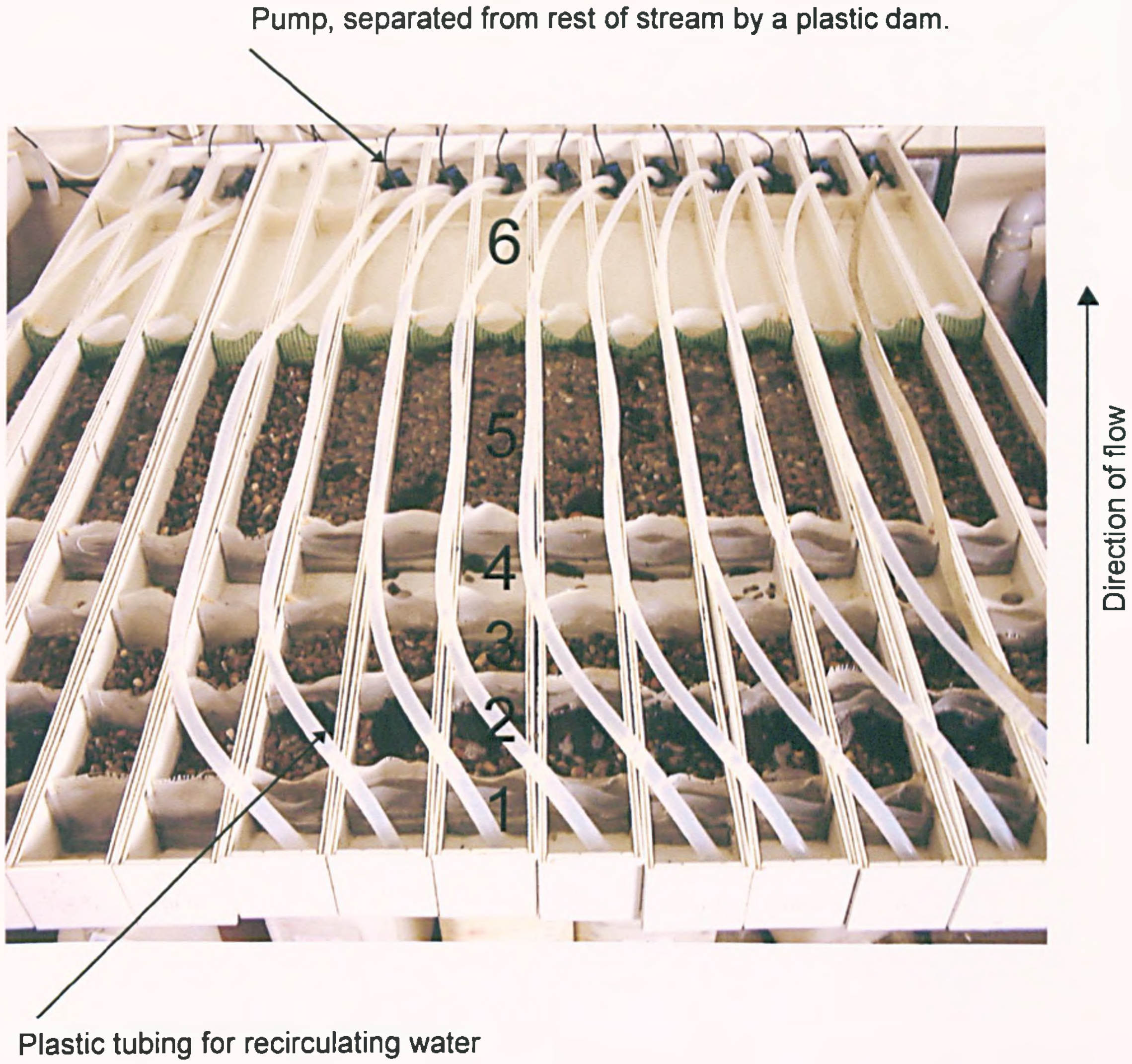


Figure 4.1. The artificial stream mesocosms. Individual compartments are numbered as follows: 1 = water inflow, 2 = gravel and control leaf material, 3 = gravel only, 4 = single species monitoring compartment with three to four pieces of gravel, 5 = community compartment with shredder assemblage, experimental leaf material and gravel, 6 = empty.

Each stream was assigned to one of seven treatments in Experiment 1, or to six treatments in Experiment 2, and labelled accordingly. The mesocosms were placed side by side on laboratory benches, and treatments were assigned at random. After stocking with shredders and leaf material (see Sections 4.2.4 and 4.2.5) the mesocosms were left to run for eighteen days in an unheated room with no natural light. Lights were operated on a 12-h light: 12-h dark photoperiod. Stream temperature (°C), pH, conductivity (µS/cm) and dissolved oxygen (mg/L) were recorded every second day for each stream for Experiment 1, and daily for Experiment 2, with hand held meters (see Section 2.2.3). Flow rates were recorded on every second day in both experiments by draining water from the plastic tubing in which water was re-circulated, into a measuring cylinder for ten seconds. This was repeated three times and the mean value (l/10 secs) was recorded for each stream.

Emergence and mortality in single-species monitoring compartments, and emergence from community compartments, were recorded daily for both experiments. Emergence was recorded in community compartments by removing and counting the number of final instar empty cases found in, and on the sides of, each stream. Any observed emergence from community compartments was compensated for by the addition of fresh animals, throughout both experiments. After eighteen days all gravel and animals were removed from each stream and preserved in 70% Industrial Methylated Spirits. Animals were later counted and their wet weights recorded.

4.2.4. Mesocosm stocking.

Mesocosms were stocked with an approximately equal shredder biomass. A range of shredder species of different size categories was used, and therefore equalising biomass across treatments minimised weight-specific feeding rate differences (Table 4.3). This design assumes that each of the eight shredder species used would be able to achieve similar biomasses in nature. The wet weight (mg) of twenty individuals of each species was recorded, prior to the beginning of each experiment. The mean wet weight for each species was used to calculate the number of individuals required to stock each stream with a target shredder biomass of 300 mg. The target biomass was based on the maximum number of individuals that could reasonably be collected of the species with the lowest mean wet mass, which was *Leuctra hippopus* in both experiments (see Table 4.3).

Only half of the available community compartment area within stream mesocosms was used ($0.378m^2$) (see Figures 4.1), in order to increase the overall density of shredder species, and therefore the effect of shredder feeding on leaf processing. However, equalising shredder biomass across treatments meant that stocking densities were variable across species (Table 4.3) and compared with estimates of natural densities. Estimates of natural densities for each species were made using data collected in Field Study 1 (Chapter 2). For each species, the number of individuals found at the site where it occurred at its highest densities, was compared with mesocosm densities. Stocking densities of shredder species in mesocosms varied relative to natural density estimates from less than one fifth (i.e. for *Gammarus pulex*), to greater than 78 times (i.e.

Protonemura praecox) natural densities. However, there was considerable variation in natural densities across the streams examined for Field Study 1 (e.g. densities of *Gammarus pulex* varied from 0.04 individuals per m^2 to 125.5 individuals per m^2). Moreover, the densities of certain species were found to be much higher when specific types of microhabitats were searched for collection of study animals (e.g. *Protonemura praecox* and *Sericostoma personatum*).

Table 4.3. Stocking levels for each shredder species in artificial stream mesocosms in single-species treatments (SS), and the mixed-species treatment (Mx), for Experiment 1 and Experiment 2.

Species	Mean biomass per individual (mg, wet weight)	SS treatments		Mx treatments	
		No. individuals	Biomass (mg, wet weight)	No. individuals	Biomass (mg, wet weight)
Experiment 1					
Gammarus pulex	29.7	10	297.0	3	89.1
Asellus aquaticus	13.5	22	297.0	4	54.0
Nemoura cambrica	6.8	44	299.2	7	47.6
Leuctra hippopus	2.9	104	301.6	17	49.3
Protonemura praecox	4.1	73	299.3	12	49.2
Sericostoma personatum	37.4	8	299.2	3	111.2
				Total per Mx stream	
				46	401.4
Experiment 2					
Gammarus pulex	37.4	8	299.2	3	112.2
Asellus aquaticus	47.3	6	284.0	3	141.9
Nemoura cambrica	3.9	77	300.0	15	58.5
Leuctra hippopus	2.4	125	300.0	25	60.0
Sericostoma personatum	32.3	9	290.7	3	96.9
				Total per Mx stream	
				49	469.5

In mixed-species streams, the target biomass was divided equally between the component species. However, for some species, less than one individual was required to make up one sixth (in Experiment 1), or one fifth (in Experiment 2), of the total target biomass, i.e. *Gammarus pulex* and *Sericostoma personatum* in Experiment 1 and additionally, *Asellus aquaticus* in Experiment 2. When this occurred, three individuals of each of these species were added to mixed-species assemblages.

4.2.5. Quantifying detritus processing.

For Experiment 1 shredder assemblages were provided with a single leaf resource only: alder (*Alder glutinosa*). For Experiment 2, shredder assemblages were provided with a mixed resource comprised of five different leaf types: alder (*Alder glutinosa*), sycamore (*Acer pseudoplatanus*), hawthorn (*Crategus *monogyna*), oak (*Quercus robur*) and beech (*Fagus sylvatica*). Leaves were collected from trees just prior to abscission during October/ November 2000 for Experiment 1, and at the same time the following year for Experiment 2, at locations given previously (Section 2.2.2). Leaf material was air dried for one week before storage.

Litter bags were constructed as described in Section 2.2.2. For Experiment 1, coarse mesh (0.5cm x 0.4cm) litter bags were constructed containing approximately 0.5 g (air-dried) of alder leaf material. For Experiment 2, coarse mesh litter bags were constructed, containing approximately 0.1 g (air-dried) of each of the five different leaf types, giving a total of 0.5 g (approx.) per litter bag. The exact air-dry weight (g) of each batch of leaf material was recorded, and each litter bag was identified using a code recorded on a plastic plant label, which was sealed in the litter bag. Two weeks prior to each experiment, leaf material was conditioned by deployment in a natural stream, in order that it could be colonised by a variety of microorganisms, to avoid shredder preferences for any one particular type of fungi or bacteria (see Section 3.1). Coarse mesh bags were sealed in larger fine mesh bags (30cm x 15cm; <400 μm mesh size), in groups of five, in order to exclude macroinvertebrates. Fine mesh bags were then strung together in groups of three, using 60lb breaking strain fishing line, and deployed in the Porter Brook, Sheffield (SK 319855). After ten days, litter bags were retrieved and stored at -10°C prior to use.

Leaf material was defrosted overnight in a refrigerator at 6°C in APW before placing in the mesocosms on day 1 of each experiment, after stocking with shredders. Leaf material was removed from the coarse mesh litter bags then placed in the stream mesocosms. Two batches of leaf material were placed in each mesocosm: one in the 'community compartment', along with the experimental shredder assemblage, and a second in a compartment that was isolated from the shredder assemblage, to provide a measure of detritus processing in the absence of shredders (see Figure 4.1). After eighteen days all leaf material was removed from each mesocosm, washed, and placed in a labelled dish for air-drying. For Experiment 2 each leaf type, from each mesocosm, was isolated and air-dried separately. Leaf material was air-dried until a constant mass was achieved. Leaf mass loss was subsequently recorded.

4.2.6. Statistical analyses.

Detritus processing rates were expressed as a mass-specific consumption rate (C) (i.e. mg of leaf material/mg of shredder/day) using Equation 4.1:

$$C = \frac{((W_i \times F) - (W_t))}{S \times t} \qquad \text{Equation 4.1.}$$

Where W_i is the start weight of leaf material (mg, air-dried), W_t is the end weight of leaf material (mg, air-dried), S is shredder biomass (mg, wet weight), and t is the number of days. F is a correction factor representing the mean proportional change in leaf mass for control leaf material. For Experiment 2, F was calculated for each different leaf type. Mass-specific consumption rates will be expressed as mg/mg/day, throughout the remainder of this chapter.

To test whether shredder species number had any positive non-additive effect on overall consumption rates, the observed mean consumption rate in mixed-species streams was compared with an expected value (Cx) that was calculated from the mean consumption rates in single-species streams using Equation 4.2.

$$Cx = \sum s_i o_i \qquad \text{Equation 4.2.}$$

Where s_i is the proportion of species i in mixed treatments and o_i is the observed consumption rate of species i in single species treatments. A visual assessment of the difference between observed and expected consumption rates was made for each of the experiments. Variation around the expected value was estimated by using the expected maximum and expected minimum values as error bars. These were calculated using Equation 4.3.

$$Cx_{\max(or \min)} = \sum s_i o_{i \max(or \min)} \qquad \text{Equation 4.3.}$$

Where $Cx_{max(\ or\ min)}$ is the maximum (or minimum) expected consumption rate in mixed-species streams, and $o_{i\ max(\ or\ min)}$ is the maximum (or minimum) observed consumption rate of species i in single-species streams.

4.3. Results.

4.3.1. Mesocosm physico-chemical conditions.

The mean physico-chemical conditions in mesocosms for Experiments 1 and 2 are summarised in Table 4.4.

Table 4.4 Mean (S.D) physico-chemical conditions in stream mesocosms for Experiments 1 and 2.

Physico-chemical factor	Mean	S.D
Experiment 1		
Temperature (°C)	15.1	1.36
Dissolved oxygen (mg/L)	9.1	0.68
Conductivity (µS/cm)	618	86.81
pH	7.9	0.11
Flow (L/min)	5.1	0.27
Experiment 2		
Temperature (°C)	16.8	0.91
Dissolved oxygen (mg/L)	7.7	0.46
Conductivity (µS/cm)	550	63.88
pH	8.1	0.11
Flow (L/min)	5.3	0.22

There were no significant differences in any of the physico-chemical factors between treatments, during either of the two experiments, except for conductivity in Experiment 2 ($F_{5, 488} = 14.3$, $p < 0.001$). In Experiment 2, conductivity was significantly lower in the *Asellus aquaticus* and *Sericostoma personatum* single-species treatments than for any other treatment, across the experimental period (Figure 4.2).

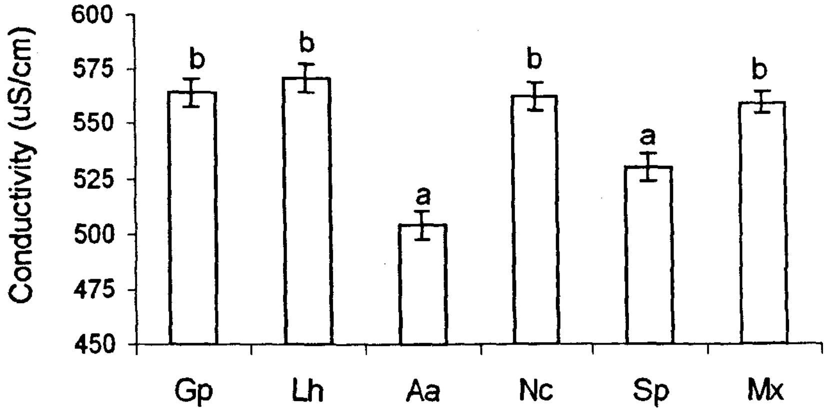


Figure 4.2. Mean conductivity (µS/cm) across different treatments for Experiment 2. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). Error bars are 1 S.E. Species codes are Gp = *Gammarus pulex*, Lh = *Leuctra hippopus*, Aa = *Asellus aquaticus*, Nc = *Nemoura cambrica*, Sp = *Sericostoma personatum*, Mx = mixed-species.

4.3.2. Changes in shredder assemblages.

Although any animals emerging from stream mesocosms were replaced throughout the experiments, the number of individuals counted in each stream at the end of each experiment indicated that there were further, unobserved, changes in shredder abundance. Changes in abundance varied across different shredder species (Figure 4.3). Considering only the single-species treatments, the greatest mean reduction in shredder abundance was found for the *Leuctra hippopus* and *Protonemura praecox* treatments in Experiment 1 and for the *Leuctra hippopus, Gammarus pulex* and *Nemoura cambrica* treatments in Experiment 2.

The pattern of reduction in abundance for individual species within mixed-species streams, reflected that of the single-species treatments (Figure 4.3). The reduction in abundance in mixed-species treatments in Experiment 1 was driven mainly by *Leuctra hippopus* and *Protonemura praecox*. In Experiment 2 reductions in abundance in mixed treatments were driven mainly by the two stonefly species, *Leuctra hippopus* and *Nemoura cambrica* and *Gammarus pulex*.

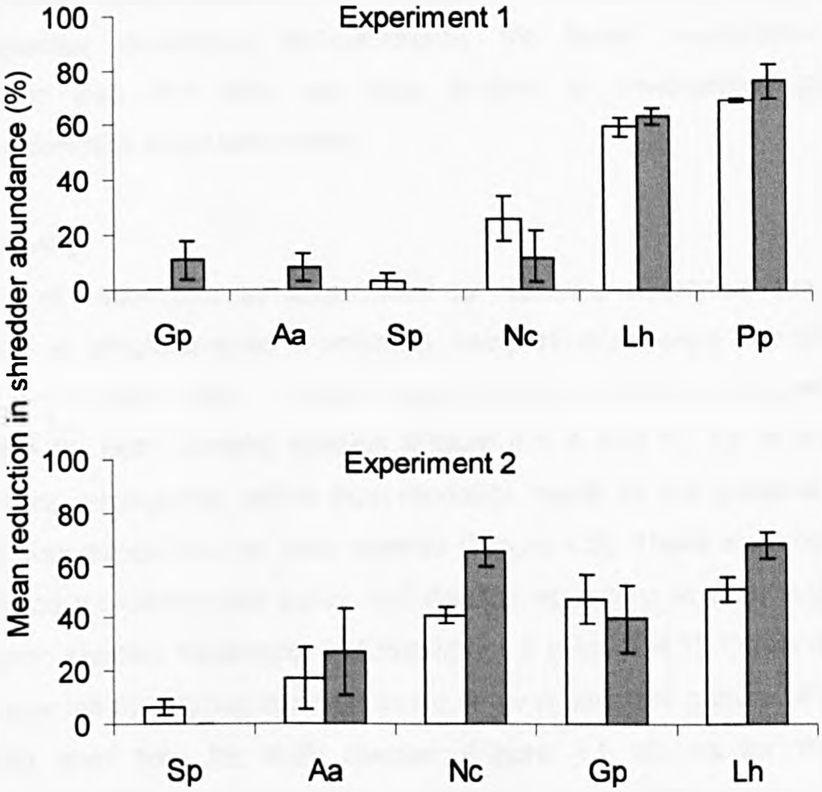


Figure 4.3. Mean reduction in shredder abundance (%) in single-species (□), and mixed-species streams (▨) for a) Experiment 1 and b) Experiment 2. Error bars are 1 S. E. Species codes are as for Figure 4.2 and Pp = *Protonemura praecox*.

Observational data from single-species monitoring chambers was used to ascertain the patterns and causes (i.e. mortality and emergence) of reductions in abundance through time, for different species during both experiments.

Experiment 1.

Reductions in abundance of the three stonefly species, *Leuctra hippopus*, *Protonemura praecox* and *Nemoura cambrica* were fairly constant over the experimental period and emergence, rather than mortality, was the primary cause of reductions in abundance (Figure 4.4). For *Asellus aquaticus* and *Gammarus pulex* there was no reduction in abundance in single–species treatments, but there was a small reduction in abundance in mixed-species treatments, represented by the loss of one *Gammarus pulex* individual and two *Asellus aquaticus* individuals. Three *Gammarus pulex* individuals were lost in total, in single-species monitoring chambers, and this mortality occurred on days 3, 9 and 14. Only one individual of *Asellus aquaticus* was lost from single-species monitoring chambers, on day 13. A linear relationship between mortality and time was therefore assumed for *Gammarus pulex* and *Asellus aquaticus*. Only one individual of *Sericostoma personatum* was lost during Experiment 1. In the absence of any mortality or emergence of *Sericostoma personatum* in the single-species monitoring compartments, the linear relationship between abundance loss and time was also applied to *Sericostoma personatum* consumption rate data (see below).

Experiment 2.

Patterns of reductions in abundance for *Leuctra hippopus* and *Nemoura cambrica* in single-species monitoring compartments were similar to those observed for Experiment 1. There was a constant pattern of abundance loss over time for both stonefly species (Figure 4.5 a and b). As in the previous experiment, emergence, rather than mortality, made up the greatest proportion of total abundance loss for both species (Figure 4.5). There were reductions in abundance for *Gammarus pulex* and *Asellus aquaticus* in both single-species and mixed-species treatments in Experiment 2 (Figure 4.3). Observations from single-species monitoring compartments show a constant pattern of abundance loss (%) over time for both species (Figure 4.5 c). As for the previous experiment, there was very little reduction in abundance for *Sericostoma personatum* (Figure 4.3). In the single-species monitoring compartments only one individual was lost, due to mortality. Therefore, the linear relationship

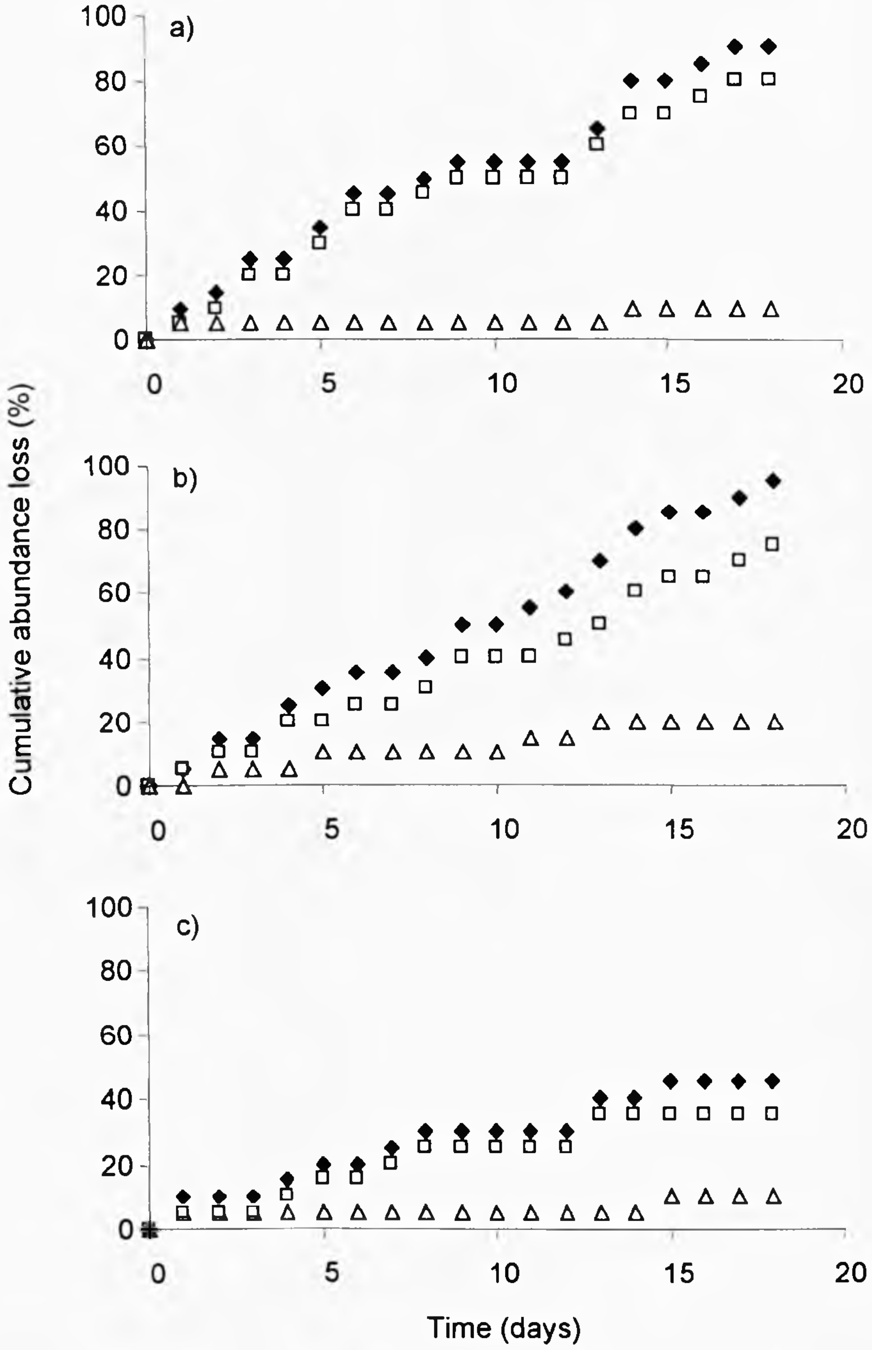


Figure 4.4. Cumulative abundance loss (%) over the 18 day experimental period in Experiment 1 for three stonefly species a) *Leuctra hippopus*, b) *Protonemura praecox* and c) *Nemoura cambrica*, based on observational data from single-species monitoring compartments. Data from four stream mesocosms were pooled. ◆ represents total abundance loss (%), □ represents abundance loss (%) due to emergence and △ represents abundance loss (%) due to mortality.

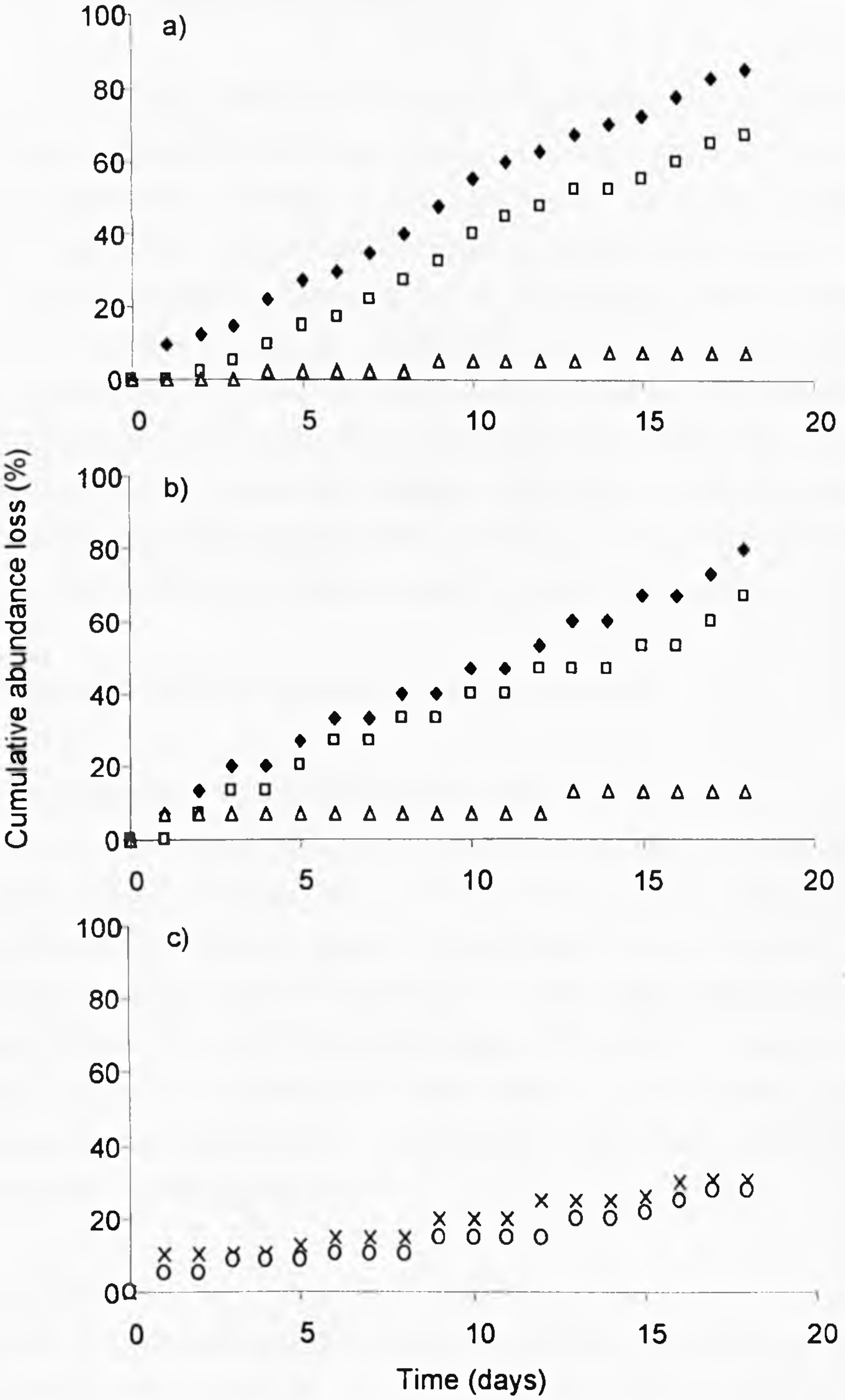


Figure 4.5. Cumulative abundance loss (%) over the 18 day experimental period in Experiment 2 for a) *Leuctra hippopus*, b) *Nemoura cambrica* and c) *Gammarus pulex* (×) and *Asellus aquaticus* (○) based on observational data from single-species monitoring compartments. Data were pooled across four stream mesocosms for each species. ◆ represents total abundance loss (%), □ represents abundance loss (%) due to emergence and △ represents abundance loss (%) due to mortality.

between abundance loss and time was also applied to *Sericostoma personatum* consumption rate data, as for Experiment 1.

The observed linear patterns of cumulative abundance loss in single-species monitoring compartments were assumed to represent patterns of abundance loss in experimental streams. In order to account for a linear decrease in shredder abundance (and therefore a linear decrease in shredder biomass) in experimental treatments, consumption rates (mg/mg/day) were calculated from Equation 4.1, using the mid-point shredder biomass (see Section 4.2.6). The mean biomass per individual, for each shredder species, was calculated from the shredder biomass in each stream at the end of the experiment, rather than pre-experiment mean values (see Section 4.2.4), and was used to convert mid-point shredder abundance into shredder biomass (S). All the analyses that follow were performed using consumption rates calculated in this way.

4.3.3. Species identity effects on detritus processing.

4.3.3.1. Experiment 1 – single leaf resource.

There was a significant difference in mean consumption rate of alder leaf material between treatments ($F_{6,23} = 6.88$, $p < 0.001$), though this was driven by just one treatment: *Asellus aquaticus* showing significantly lower consumption rates than the other species (Figure 4.6). The mean consumption rate in mixed-species streams was also significantly greater than that for *Asellus aquaticus* streams, but was not greater than *Protonemura praecox*, which showed the greatest mean consumption rate, indicating no overyielding and therefore, no complementarity effects (Figure 4.6).

4.3.3.2. Experiment 2 – mixed leaf resource.

There was a significant difference in the mean consumption rate of a mixed leaf resource between treatments ($F_{5,19} = 10.34$, $p < 0.001$; Figure 4.7). *Asellus aquaticus* again showed a significantly lower mean consumption rate than the remaining treatments, but there were also further species identity effects the stonefly *Nemoura cambrica* showing a significantly greater mean consumption rate than either *Gammarus pulex* or the mixed-species treatment (Figure 4.7). As for Experiment 1, the mean consumption rate of mixed-species streams was not significantly greater than the single-species treatment with the greatest consumption rate (in this case, *Nemoura cambrica*), indicating no overyielding and therefore, no complementarity effects, on a mixed leaf resource. A previous analysis indicated that there were significant differences between treatments in terms of conductivity (Section 4.3.1, Figure 4.3). Regression analysis was used to test whether consumption rates were associated with mean stream conductivity. There was no linear relationship between mean conductivity and consumption rate, across replicates ($F_{1,24} = 2.78$, $p > 0.05$, $R^2 = 10.4$).

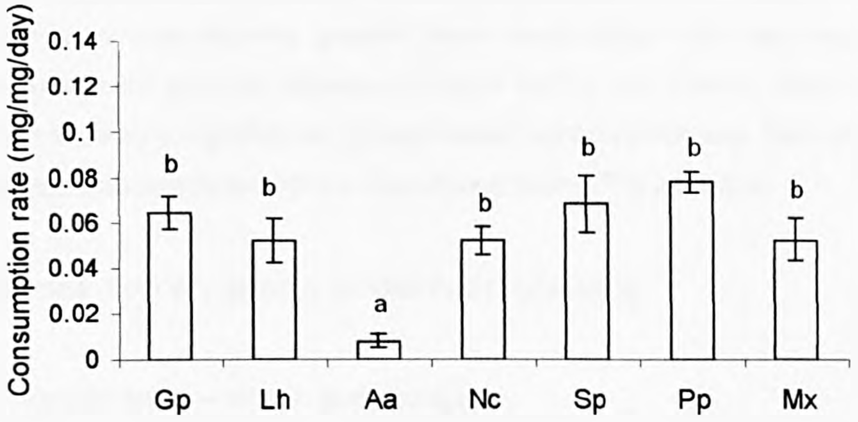


Figure 4.6 Mean consumption rates (mg/mg/day) on a single leaf resource across single- and mixed-species treatments. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). Error bars are 1 S.E. Treatment codes are as for Figure 4.2. and Pp = *Protonemura praecox*.

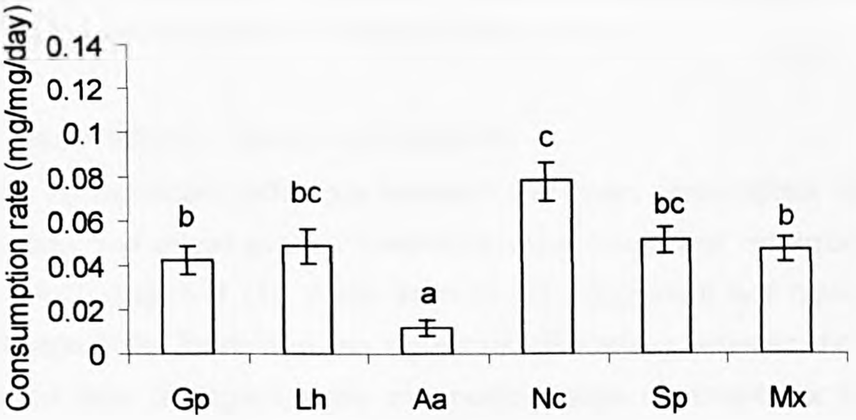


Figure 4.7. Mean consumption rates (mg/mg/day) on a mixed leaf resource for single- and mixed-species treatments. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). Error bars are 1 S.E. Species codes are as for Figure 4.2.

Each leaf component of the mixed leaf resource was also tested for significant differences in mean consumption rates between treatments using a separate analysis for each leaf type. There were significant differences in mean consumption rates between treatments for four out of the five leaf types: alder, hawthorn, oak and beech ($F_{5,19} \geq 3.6$, $p < 0.05$). The mixed-species treatment did not show the greatest mean consumption rate for any of these four leaf types, indicating no overyielding and therefore, no complementarity effects on any of the individual leaf types (Figure 4.8).

Species identity effects varied on different leaf types. *Nemoura cambrica* had a significantly greater mean consumption rate on alder than *Sericostoma personatum* or *Asellus aquaticus* (Figure 4.8 a). However on oak, *Nemoura cambrica* showed a significantly greater mean consumption rate than any other treatment except for *Leuctra hippopus* (Figure 4.8 b). On beech, *Sericostoma personatum* showed a significantly greater mean consumption rate than all other single-species treatments except for *Gammarus pulex* (Figure 4.8 e).

4.3.4. Species diversity effects on detritus processing.

4.3.4.1. Experiment 1 – single leaf resource.

There was no significant difference between the mean consumption rates of single-species and mixed-species treatments on a single leaf resource (t_9 = 0.11, $p > 0.05$; Figure 4.9). Moreover there was no difference between the mean consumption rate observed in the mixed-species treatment and that expected from single-species treatments (Figure 4.10), indicating purely additive effects of increasing shredder diversity on alder consumption rates.

4.3.4.2. Experiment 2 – mixed leaf resource.

There was no significant difference between the mean consumption rates of single-species and mixed-species treatments on a mixed leaf resource (t_{13} = 0.08, $p > 0.05$; Figure 4.11). When each of the component leaf types were analysed separately, there were no significant differences between the mean consumption rates of single-species and mixed-species treatments for four out of the five leaf types tested ($t_{22} \leq 0.60$, $U_{20,5} \leq 35$, $p > 0.05$). However, the mean consumption rate of alder was significantly greater for single-species assemblages compared to mixed-species assemblages (t_{22} = 2.3, $p < 0.05$; Figure 4.12 a). There was also some suggestion that the mean consumption rate of beech was greater in mixed-species than in single-species assemblages, however this was not statistically significant ($U_{20,5}$ = 25, p = 0.096; Figure 4.12 b).

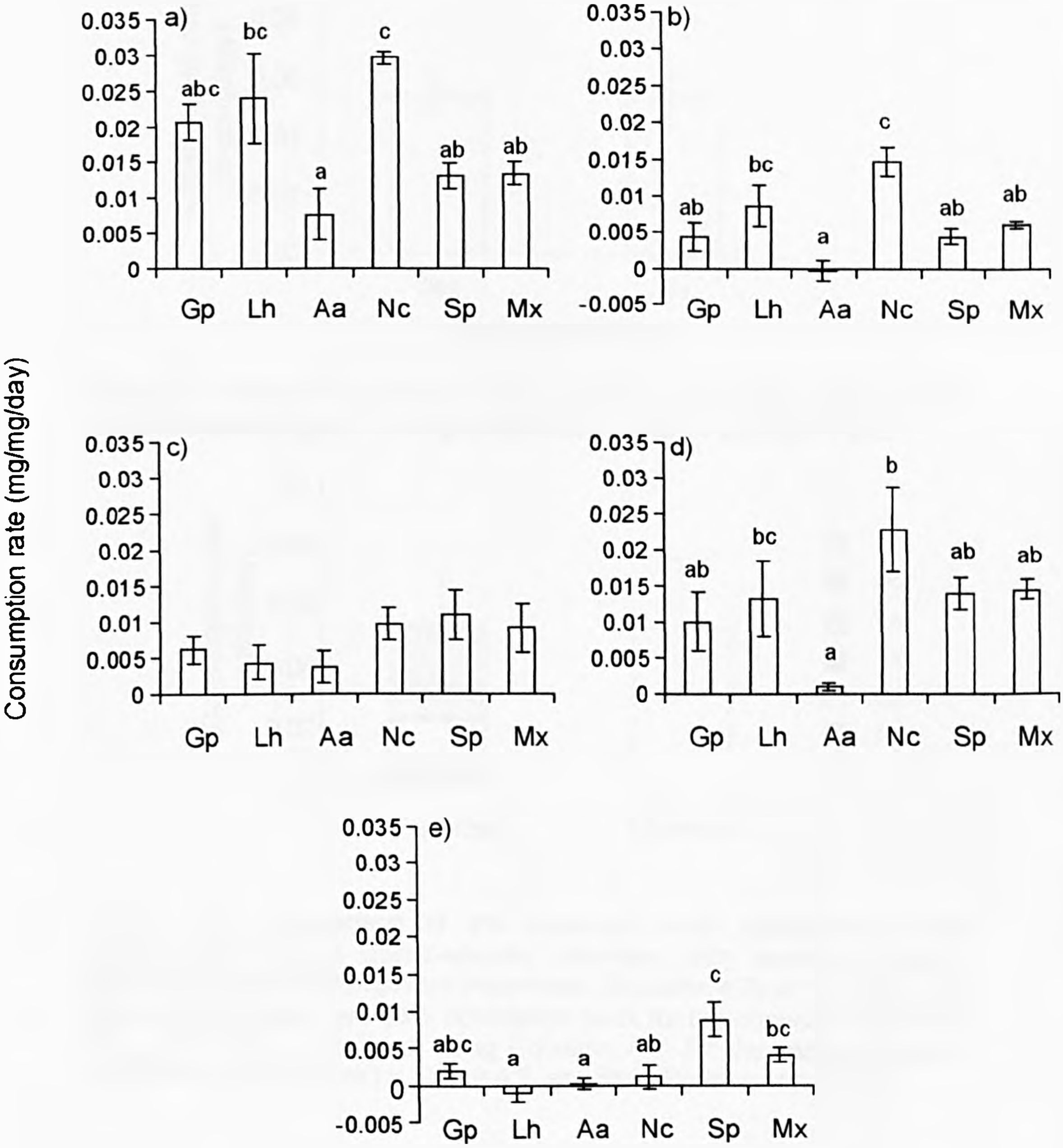


Figure 4.8. Mean consumption rates (mg/mg/day) on a) alder, b) oak, c) sycamore, d) hawthorn and e) beech, when presented as part of a mixed leaf resource. Within each plot, bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, p > 0.05). Error bars are 1 S.E. Treatment codes are; Gp = *Gammarus pulex*, Lh = *Leuctra hippopus*, Aa = *Asellus aquaticus*, Nc = *Nemoura cambrica*, Sp = *Sericostoma personatum*, Mx = Mixed.

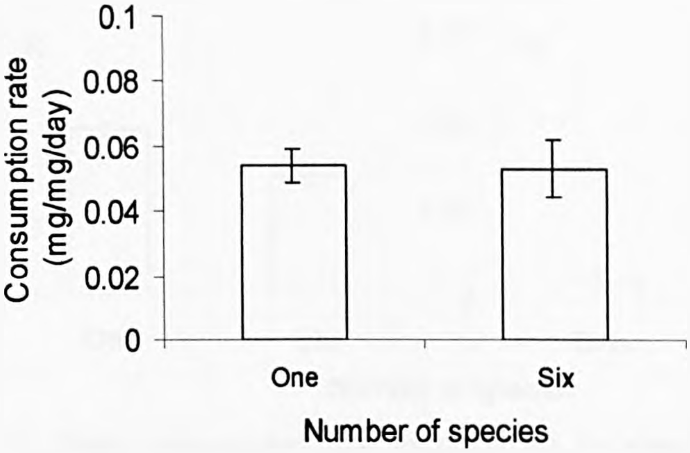


Figure 4.9. Mean consumption rate (mg/mg/day) for single- and mixed-species assemblages on a single leaf resource. Error bars are 1 S.E.

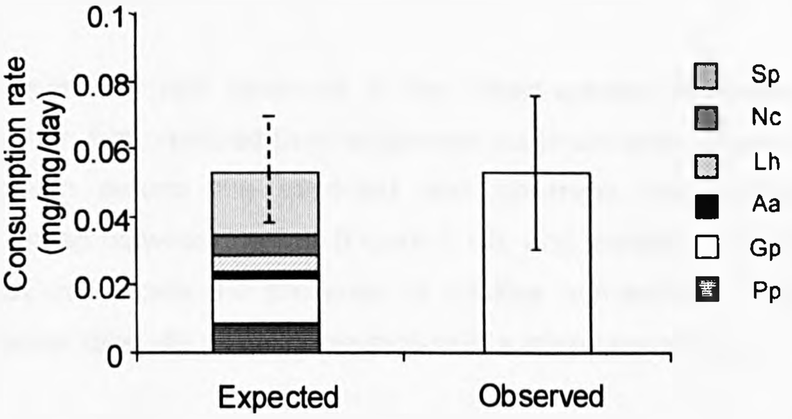


Figure 4.10. Comparison of the observed mean consumption rate (mg/mg/day) for the mixed-species treatment with expected values (calculated from single-species treatments, Equation 4.2) on a single leaf resource. Error bars are 95% confidence limits for the observed bars and Cx_{max} and Cx_{min} (calculated using Equation 4.3) for the expected bars. Treatment codes are as for Figure 4.8. and Pp = *Protonemura praecox*.

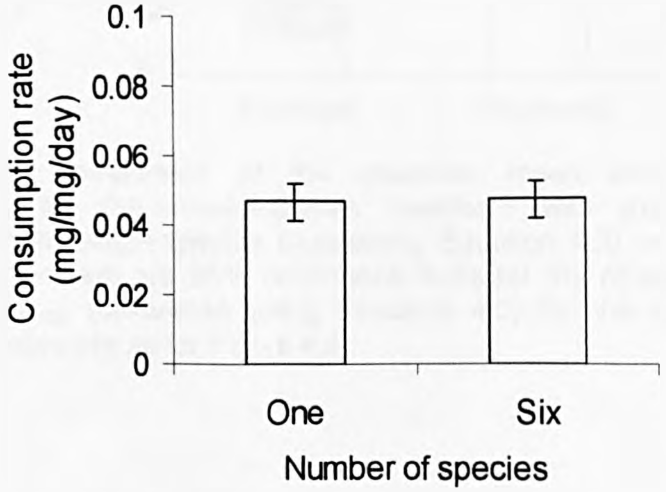


Figure 4.11. Mean consumption rate (mg/mg/day) for single- and mixed-species assemblages on a mixed litter resource. Error bars are 1 S.E.

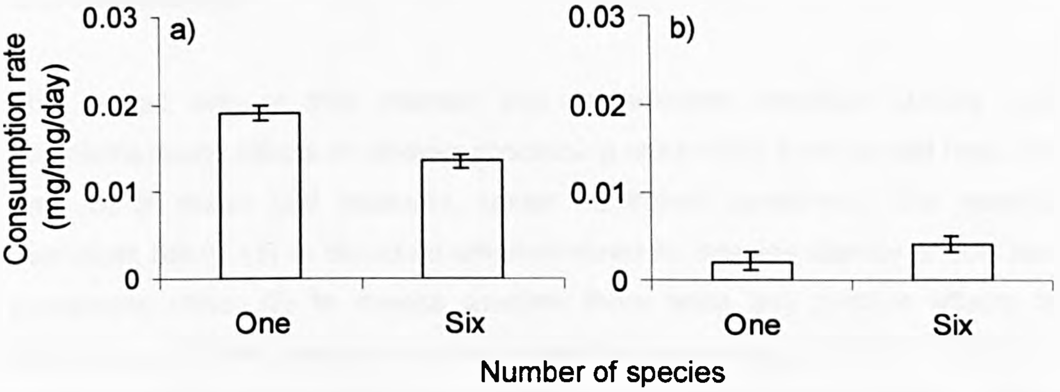


Figure 4.12. Mean consumption rate (mg/mg/day) for single- and mixed-species assemblages on a) alder and b) beech, as components of a mixed leaf resource. Error bars are 1 S.E.

The mean consumption rate observed in the mixed-species treatment was slightly greater than that predicted from single-species treatments (Figure 4.13). However, variation around the expected and observed values indicates considerable overlap between the two (Figure 4.13), and therefore, there is no strong evidence to indicate the presence of positive non-additive effects of increasing shredder diversity on the consumption of a mixed resource.

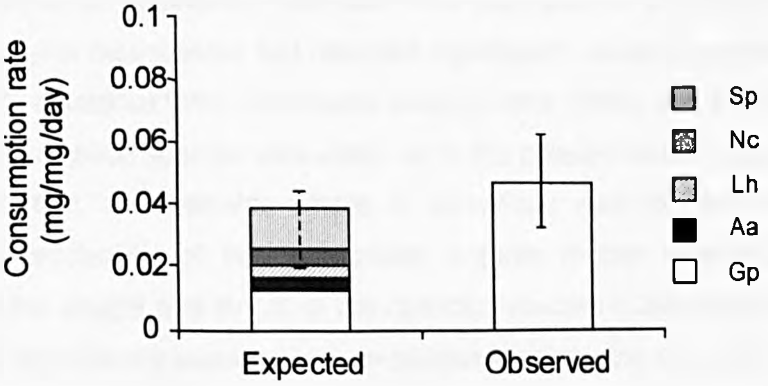


Figure 4.13. Comparison of the observed mean consumption rate (mg/mg/day) for the mixed-species treatment with expected values (calculated from single-species treatments, Equation 4.2) on a mixed leaf resource. Error bars are 95% confidence limits for the observed bars and Cx_{max} and Cx_{min} (calculated using Equation 4.3) for the expected bars. Treatment codes are as for Figure 4.8.

4.4. Discussion

The overall aim of this chapter was to examine shredder identity and complementarity effects on detritus processing rates of (a) a single leaf resource and (b) a mixed leaf resource, under controlled conditions. The specific objectives being: (1) to elucidate whether shredder species identity affects leaf processing rates, (2) to assess whether there were any positive effects of increasing shredder species number on detritus processing rates and if so (3) to examine whether there was any evidence for complementarity effects. These objectives were addressed for both (a) and (b) above.

4.4.1. Species identity effects.

When shredders were offered a single highly palatable resource (alder), the processing rate of most shredder species was similar. Only the isopod, *Asellus aquaticus*, showed a significantly lower processing rate than the remaining five shredder species. These results imply that there may be functional redundancy among the shredder species tested, whereby any species can compensate for the loss of any other species in terms of processing alder litter, with the exception of *A. aquaticus*. The low alder processing rate by *A. aquaticus* indicates that it would be unable to fulfil the role of the other shredder species, if it was present at an equivalent biomass. This supposition is supported by a study performed in mesocosms that reported significantly lower processing rates on alder by *A. aquaticus* than *Gammarus pulex* (Grant 1996), even although an equal biomass of each species was used, as in the present study. Grant (1996) also reported that in treatments where *A. aquaticus* was the sole shredder species, the production of fine particulate organic matter was significantly reduced and the weight and length of the collector species (*Chironomus riparius* Meigen) was significantly lower than in mesocosms containing *G. pulex*.

The relatively low processing rate of alder by *A. aquaticus* is probably a consequence of its feeding strategy. Experimental evidence indicates that *A. aquaticus* uses a scraping strategy to feed preferentially on fungi present on the leaf surface (Graça *et al.* 1993). This strategy appears to be unique among the shredder species used in the present study. For example, *G. pulex* uses a chewing action to break off whole leaf pieces leaving only the major veins intact (Graça *et al.* 1993). *S. personatum* has large mandibles (Friberg & Jacobsen 1994) which it uses to cut whole pieces from the leaf and consumes all parts of the leaf including the veins (Jonsson *et al.* 2002, C. Inglis pers. obs.). Further, many stonefly species tend to avoid veins but eat all other parts of the leaf (Wallace *et al.* 1970, Allan 1995). While several studies have reported significantly higher consumption of alder by *G. pulex* than by *A. aquaticus* (e.g. Graça 1990, Ash 1995, Grant 1996), there are currently no other studies that have compared the alder processing rates of *A. aquaticus* with the other shredder species used in the present study.

The similarity of the remaining five shredder species in their rates of alder consumption is perhaps not surprising, since alder is known to be a highly palatable food source to a range of shredder species of different taxonomic orders (e.g. Wallace *et al.* 1970, Kaushik & Hynes 1971, Otto 1974, Iversen 1974, Irons *et al.* 1988, Friberg & Jacobsen 1994, Canhoto & Graça 1995) due to its high nitrogen content and low levels of indigestible compounds (Graça 2001). However, other studies have reported differences in feeding rates on alder between the species and genera used in the present study. For example, Friberg & Jacobsen (1994) reported that consumption of alder by *G. pulex* was markedly higher than that of *S. personatum*. In contrast, results from the study by Jonsson *et al.* (2002) suggest that *Gammarus fossarum* processes alder at a slower rate than *S. personatum*. Evidence from the latter study also indicates that the stonefly larva *Nemurella picteti* processes alder at a faster rate than either *S. personatum* or *G. fossarum*.

These apparently contrasting results could be a consequence of differences in experimental design, or perhaps variation in feeding rates within genera or taxonomic order. For example, the density of *G. pulex* in the stream mesocosms in the present study was greater than that of *S. personatum* (one individual per 3.8 cm^2 and 4.7 cm^2 respectively). In contrast, Friberg & Jacobsen (1994) used an equal density of both shredder species (one individual per 19.6 cm^2), which was far lower than the densities used in the present study. Processing rates in the *G. pulex* treatment may therefore have been reduced relative to the *S. personatum* treatment in the present study, due to more intense intraspecific competition that may have hindered processing rates. In contrast to the present study, Jonsson *et al.* (2002) reported processing rate differences between the Plecoptera, Trichoptera and Amphipoda. This may simply be a result of the different species used across the two studies however, there is little evidence to indicate the extent of variation in feeding rates among different species within the *Gammarus* genera or within the order of Plecoptera. Although several studies have reported interspecific differences within the *Gammarus* genera (*G. fossarum* and *G. roeseli*) in terms of thermal requirements, hatching success, maturation times and growth rates (Pockl 1995), there has been no comparison of feeding rates. For plecopterans, one study reported that there were no significant differences in feeding rates on alder between six stonefly species, belonging to five different genera (Jonsson & Malmqvist 2003). Although *Nemurella picteti* was among the six species tested, none of stonefly species used in the present study was included. It is therefore difficult to ascertain whether the difference in results reported by the present study and that of Jonsson *et al.* (2002), were a consequence of the different species used.

Experiment 2 was designed to examine species identity effects on leaf processing for a scenario more similar to that of natural streams, where leaf packs are comprised of several different leaf types (Leff & McArthur 1989, Boulton & Boon 1991). Results revealed that, once more, *A. aquaticus* had a significantly lower processing rate than all other species. Additionally, the stonefly *Nemoura cambrica* showed a significantly greater consumption rate than *G. pulex*, suggesting that *N. cambrica* may be able to utilise a wider range of leaf resources than *G. pulex*.

An examination of the processing rates of individual components of the mixed leaf resource reveals that the processing rates of *N. cambrica* and *G. pulex* were similar on all leaf types, except for oak, on which *N. cambrica* showed a significantly greater processing rate than either *G. pulex* or *S. personatum*. This suggests that the greater processing rates observed for *N. cambrica* streams were driven by increased consumption of oak. Variation between shredder species in their ability to utilise different leaf types is thought to be influenced by a combination of several factors including, differences in chewing abilities, nutrient requirements and their ability to process indigestible compounds (Graça 2001). However, the variation in feeding rates between the three species may partly be explained by differences in feeding strategies. The strategy of cutting through leaf material to remove whole pieces (see above) practised by *G. pulex* and *S. personatum* may be disadvantageous on tougher leaf types with thicker cuticles and higher fibre contents, such as oak and beech (Webster & Benfield 1986). In contrast *N. cambrica* (and the other stonefly species used in this experiment) tended to feed on the leaf material in layers, removing the epidermal then the mesophyll cells until only the veins remained (C. Inglis. pers. obs.), which may have allowed it to utilise oak more efficiently.

However, there must have been further factors influencing the difference in leaf processing rates between species, since *S. personatum* showed a significantly higher processing rate on beech than all other species except for *G. pulex*. Although beech also has a thick cuticle and high fibre content, it appeared that *S. personatum* could utilise this leaf type with its 'cutting' strategy. Jonsson *et al.* (2002) also reported that *S. personatum* showed the fastest processing rate on beech litter followed by *Nemurella picteti* and then *G. fossarum*. *Sericostoma personatum* was the least mobile of the species used in the present study and this may partly explain its ability to utilise beech leaf material at a faster rate than most of the other species. Bärlocher (1983) suggested that shredder species that are less mobile are unable to search widely for leaf material, and therefore have digestive systems adapted to process whatever leaf types they encounter. In contrast, more mobile species can search more widely for the highest quality resource patches, and therefore have digestive systems adapted to utilise particular leaf types.

The difference in species identity effects on a single highly palatable leaf resource, on a mixed resource, and on the individual components of a mixed resource, illustrate that the importance of particular species and the degree of redundancy among species may change depending on the range and type of leaf litter available. In the present study, certain species varied in their ability to process the more refractory leaf types, beech and oak, however there were fewer differences between species on alder and hawthorn, and no difference between species on sycamore. The latter three leaf types are fast-decomposers while beech and oak are processed much more slowly (Webster & Benfield 1986). Species identity may therefore be more important for detritus processing rates towards the end of the leaf-fall season, when leaf types of low quality, such as beech and oak, remain in streams. For example, the processing rate of beech was slightly greater in mixed-species streams than in single-species streams, although the difference was not statistically significant ($p = 0.096$), and was probably a result of the presence of *S. personatum* in mixed-species streams.

4.4.2. Complementarity effects.

Two experiments using stream macroinvertebrates have provided evidence for increased resource-use driven by facilitation between species on a single resource (Jonsson & Malmqvist 2000, Cardinale *et al.* 2002). Field studies have also reported a positive relationship between shredder species number and detritus processing rates of a single leaf resource (Chapter 2, Jonsson *et al.* 2001, Huryn *et al.* 2002). However, the present study provides no evidence for a positive effect of shredder species number on leaf processing rates driven by complementarity effects, on either a single or mixed leaf resource. Results from this study therefore suggest that mechanisms such as facilitation, or the niche-differentiation effect, are not necessarily important for detritus processing in streams.

However, it is likely that the occurrence of these mechanisms and the strength of the effect are dependent on the particular combination of species that is examined. That is, whether the species examined differ in their feeding physiology or resource-niches. For example Jonsson *et al.* (2002) suggested that differences between *G. fossarum* and *S. personatum* in the way in which they utilised leaf material led to facilitation between these two species, and therefore increased alder processing rates (see Section 3.1.1). Norberg (2000) reported that increased grazing efficiency was most pronounced for combinations of cladoceran species that included the two species with the greatest difference in their prey-size range.

If there were such differences, in feeding physiology or resource-niches, between the particular shredder species used here, they did not translate into effects on leaf processing rates in this study, since leaf processing was not increased in multi-species communities. This is somewhat surprising, since a wide range of feeding strategies were represented by the six shredder species used, providing the potential for facilitation, or niche-differentiation, between species (see Section 4.4.1). For example, one possibility for facilitation between species may have been the removal of epidermal layers by stonefly shredders, reducing the difficulty of cutting through tough epidermal layers for species with cutting strategies, like *G. pulex* and *S. personatum*. Moreover, results suggest that there were differences between some species in their ability to utilise different leaf types (see Section 4.4.1), providing the potential for niche-differentiation, driven by differences in leaf diet. For example, the ability of *N. cambrica* to process oak material at a faster rate than most other species, and the high processing rates of beech by *S. personatum*.

A small increase in the observed leaf processing rate in mixed-species streams, above that expected from single-species streams, was detected when shredders were provided with a mixed leaf resource, indicating that there may have been complementarity effects. Complementarity effects may therefore have occurred, although they were not strong enough to bring about a significant difference between the observed and expected values. This may have occurred if positive complementarity effects between certain combinations of species were cancelled out by negative interactions, resulting from physical interference, between other species (Loreau & Hector 2001, Hector *et al.* 2002b).

Aggressive interactions have been observed for stream macroinvertebrates both within (e.g. Hildrew & Townsend 1980) and between species (e.g. Bovbjerg 1970, Hemphill 1988). Moreover, interference competition based on aggressive physical interactions has been experimentally demonstrated for a range of stream macroinvertebrates including filter-feeders (Hart 1985, Hemphill 1988) and grazers (Dudley *et al.* 1990), although not for shredders. Generally, the effect of interference between species reported by such studies is a reduction in the chance to feed, either due to disturbance by neighbours, or displacement from preferred locations. Larger size tends to confer an advantage in terms of aggressive interactions (Allan 1995), and therefore interference of the small stonefly species (*Leuctra hippopus* and *Nemoura cambrica*) by *S. personatum* or *G. pulex* seems the most likely direction of any negative interaction in this study.

The intensity of intra- versus interspecific competition may provide a further explanation as to why no positive complementarity effects were observed in the present study. Jonsson & Malmqvist (2000) proposed that if intraspecific interactions are more intense, then shredder feeding may be hampered in species poor situations compared to multi-species assemblages where interactions take place mainly between different species. Jonsson & Malmqvist (2002) suggested that this might be one reason why alder processing rates increased with stonefly species number in their mesocosm experiment. Although, a further study indicated that only one of the stonefly larvae species used in their former experiment (*Nemurella picteti*), showed a significant increase in alder processing rates with a decrease in density (Jonsson & Malmqvist 2003).

However, the converse may also be true, whereby interspecific competition is more intense than intraspecific interactions. If so, feeding rates may be hampered in more species rich situations where interactions are primarily between different species. If such an effect were strong, it would result in much reduced processing rates in mixed-species streams compared with that expected from single-species treatments. Although this overall pattern was not observed for the present study, it is possible that at least some species will have suffered reduced consumption rates in the mixed-species streams. Without the ability to quantify the processing rates for individual species within the mixed-species streams, it is not possible to ascertain which of the explanations outlined above is most likely.

Results from field studies have indicated that shredder diversity is among the factors that positively affect leaf processing in natural streams (Jonsson *et al.* 2001, Huryn *et al.* 2002, Chapter 2). However, this study could not detect any evidence that complementarity effects are among the mechanisms responsible for the relationships observed in the field. Some points must be considered in interpreting these results, and assessing their implications for natural streams. Firstly, the high losses of individuals from mesocosm treatments and the way in which leaf processing rates were calculated. The median biomass of shredders was used to calculate the amount of leaf material eaten (mg) per biomass of shredder (mg) per day, based on the linear pattern of mortality and emergence observed in the monitoring chambers (see Section 4.3.2). However, there was a substantial loss of shredders in some mesocosm treatments, that was undetected (Figure 4.3). If this undetected biomass loss did not follow a linear pattern, consumption rates may have been artificially elevated or depressed in some treatments. However, alternative analyses using consumption rates calculated from shredder biomass both at the beginning and at the end of the experiments, revealed the same overall patterns as reported in Sections 4.3.3 and 4.3.4 of this chapter. Therefore the high losses of individuals from some treatments was not considered to be a factor that may have effected the interpretation of the observed results.

Secondly, only one six-species combination was examined in the mixed-species streams. Although this is a greater number of macroinvertebrate species than has usually been used in other similar studies (e.g. Jonsson & Malmqvist 2001, Jonsson *et al.* 2002, Cardinale *et al.* 2002), it nevertheless only represents one possible combination, at the lower end of the diversity range that has been observed across streams in field studies. For example, the number of shredder species found at any one site ranged from two to twenty in Chapter 2 of this thesis, and from one up to eleven in the field study by Jonsson & Malmqvist (2001). Therefore, although complementarity effects appeared to be unimportant for leaf processing using the particular six-species combination in this study, this does not provide information about the possible positive interactions between other combinations of species, at other diversity levels in natural systems.

Third, is the effect of an artificial stream environment on shredder species interactions. Interactions between species are the basis of any complementarity effects, however there are several reasons why interactions between shredders may be altered in the artificial stream systems, compared with those in natural streams. For example, competitive interactions may become more intense in the relatively stable abiotic conditions in mesocosms, where there is no disturbance from physical factors, such as flow rates. The homogenous pea gravel substrate of the stream mesocosms would have provided little opportunity for certain species to take refuge. For example the larger species, *A. aquaticus* and *G. pulex*, are usually found under flat stones and pebbles in nature (Graça *et al.* 1994a). These species may have found it difficult to find refugia in the mesocosms, and therefore may have been less able to avoid any aggressive interactions. Conversely, shredders never experienced resource limitation within the mesocosms, since there was always leaf material left over, therefore competitive interactions may have been weaker in mesocosms compared with nature. Moreover, shredder species were stocked in mesocosms at densities estimated to be different from those at which they were found in nature (see Section 4.2.4). These factors may have combined to alter the intensity of interactions among individuals in stream mesocosms compared with natural streams, and also may have affected particular interactions to different extents.

4.5. Conclusions.

There were shredder species identity effects on detritus processing. There were more differences between shredder species on a mixed leaf resource than on a single leaf resource.

There was no evidence for any overall positive effect of increasing shredder species number on detritus processing (either through selection effects or complementarity effects), on either a single or a mixed leaf resource.

There was no evidence that facilitation, or the niche-differentiation effect, increased detritus processing rates in mixed-species streams.

5. Complementarity between shredder species and its effect on detritus processing.

5.1. Introduction.

5.1.1. Introduction.

Much attention has been paid to identifying and separating the selection effect from complementarity effects, as mechanisms for driving positive biodiversity-ecosystem function relationships (e.g. Loreau 1998a, Lepš *et al.* 2001, Loreau & Hector 2001, Hector *et al.* 2002a; see Section 1.4.2.4). Evidence from previous chapters in this thesis has suggested that shredder species identity effects are important for detritus processing in streams, while species number is potentially less important (Chapters 2, 3 and 4). There is no evidence from previous chapters that strong identity effects result in positive species diversity-leaf processing relationships, driven by the selection effect. However, results from an artificial stream study (Chapter 4) did suggest that some shredder species differed in their resource-use of different leaf types and therefore, that there may be the potential for complementarity between species. In Chapter 4, any potential for complementarity between shredder species in terms of their leaf diet, did not translate into positive effects on leaf processing rates, and the possible reasons for this have been discussed (Section 4.4.2). The present chapter focuses on testing one particular mechanism that can arise through complementarity between species: the niche-differentiation effect, by examining the extent of potential complementarity between shredder species in terms of their leaf diets and, by directly testing whether an increase in complementarity among shredder species has a positive effect on detritus processing in streams.

The 'niche-differentiation effect' can result when species differ in their requirements for a heterogeneous resource (i.e. are complementary to some extent). If so, then each species can utilise a certain portion of the available resources, but no single species can utilise the entire range of resources. In this case, the greater the number of species present in a community, the greater the resource range utilised, and hence the more complete the resource use (Tilman *et al.* 1997b, Loreau 1998b, Tilman 1999, Loreau 2000). Theoretical models developed by Tilman (1999) and Loreau (1998b), based on competition in plant communities (see Section 1.4), predict that when species are complementary in their resource requirements, ecosystem function will always increase asymptotically with species number. This is because a point will eventually be reached where the entire range of resources can be utilised by all the species present and additional species do not add to the overall resource-niche range. In this scenario, any differences between species in their competitive abilities (i.e. ability to depress resource levels) for the range of resources, will affect the steepness of the relationship, but not the shape (Loreau 1998b, 2000). However, if species are identical in their requirements for a heterogeneous resource (i.e. species are redundant), Loreau's mechanistic model (1998b, 2000) predicts that ecosystem function will not change with species number. Although, if such a group of species did differ in their competitive abilities for a set of resources, a positive or negative relationship between species number and ecosystem function could result, determined by the identity of the species added or removed from the assemblage.

Early biodiversity-ecosystem function experiments were not designed to examine or separate specific mechanisms (e.g. Naeem *et al.* 1994, Tilman *et al.* 1996). More recently, experimenters have sought to examine mechanisms by comparing the performance of single-species treatments with multi-species assemblages (e.g. Jonsson & Malmqvist 2000, Cardinale *et al.* 2002, Hector *et al.* 2002; see Section 1.4.2.4). Several methods have been developed to detect positive effects of increasing species number on ecosystem function, after accounting for species-specific effects (see Section 1.4.2.4). However, the most stringent test for complementarity effects is the detection of 'overyielding' (Loreau 1998a; see Section 1.4.2.4).

While not all studies that have tested for complementarity effects find evidence for it (e.g. Špaèková & Lepš 2001), several do support the occurrence of complementarity effects (e.g. Tilman *et al.* 2001, Hector *et al.* 1999, Hooper 1998). In a seven-year grassland experiment, species number had highly significant effects on above-ground and total (above- and below-ground) plant biomass in years six and seven, after effects of functional group composition were controlled for (Tilman *et al.* 2001). The experiment revealed that many species mixtures outperformed the highest yielding monocultures, providing evidence for overyielding, and therefore mechanisms such as niche-differentiation and facilitation. Recent reanalysis of data from the pan-European BIODEPTH study on grassland systems (Hector *et al.* 1999), using the additive partitioning method mentioned above, revealed positive complementarity effects at four out of the eight localities, and for the overall analysis across all sites (Loreau & Hector 2001).

Hooper (1998) examined the effect of plant diversity on primary productivity and plant nitrogen yield in serpentine grassland assemblages. Relative yield totals (see Section 1.4.2.4) indicated positive effects of complementarity on above-ground biomass in some two-species mixtures and one four-species mixture. However, it was revealed that complementarity effects were influenced by relative increases in productivity of species from particular functional groups, rather than productivity increases across all species. Moreover, no overyielding was detected for plant nitrogen yield in mixtures compared to monocultures.

Špaèková & Lepš (2001) tested for overyielding in plant mixtures of meadow species in a greenhouse pot experiment. They compared the yields of species mixtures and monocultures using an overyielding index (equivalent to other overyielding measures such as D_{max} of Loreau (1998a)), and also used the additive partitioning method of Loreau & Hector (2001). Although there was a highly significant increase of plant biomass (above- and below-ground) as species number increased from one to six, no overyielding was detected. In fact, there was a significant tendency for overyielding to decrease in more species rich mixtures. In contrast, the additive partitioning method revealed that there were complementarity effects in species mixtures, although such effects did not increase with species number. The different conclusions arise because the additive partitioning method is a much less stringent test than the detection of overyielding, and can reveal complementarity effects even when there is no overyielding (see discussion in Špaèková & Lepš 2001, Petchey 2003).

A limited number of experiments have attempted to explore whether complementarity effects are important for ecosystem function in animal systems (Jonsson & Malmqvist 2000, Norberg 2000, Emmerson *et al.* 2001, Cardinale *et al.* 2001, Jonsson *et al.* 2002, Jonsson & Malmqvist in press; see Section 4.1) and overall, results are inconsistent. For example, experiments that have examined the effects of benthic invertebrate diversity on nutrient flux (ammonia nitrogen (NH_4-N)) to the water column have produced mixed evidence for complementarity effects in such systems (Emmerson & Raffaelli 2000, Emmerson *et al.* 2001). These experiments have involved the manipulation of invertebrate diversity in artificial microcosms, across a gradient of biomass, using several different species pools. One study that manipulated invertebrate diversity from one up to four species at three different locations revealed that, overall, less than 25% of the species mixtures showed evidence of overyielding, although overyielding was much more common in higher diversity mixtures (75%

of four-species mixtures) (Emmerson *et al.* 2001). Another study that compared single-species treatments with three-species mixtures, for two different species pools, found no evidence for overyielding in any of the three-species mixtures (Emmerson & Raffaelli 2000).

In contrast, experiments in stream systems have suggested that complementarity effects may be important for detritus processing (Cardinale *et al.* 2002, Jonsson & Malmqvist 2000, see Section 4.1). In both experiments, authors attributed the effect of increasing species diversity to the facilitation mechanism. While Cardinale *et al.* (2002) provided direct evidence to support the occurrence of facilitation among filter-feeding invertebrates, Jonsson & Malmqvist (2000) suggested this mechanism was based on possible, subtle, physiological differences between stonefly shredder species. However, so far, no study has directly investigated the importance of niche-differentiation for driving complementarity effects in animal systems, and only one study has addressed this for a plant system (see below).

For most of the experiments described above, evidence for complementarity effects has been derived indirectly using measures such as the Relative Yield Total, $\check{D}$ and the additive partitioning method (Section 1.4.2.4). However, such methods have limitations (see Section 1.5.1), and therefore a more direct approach is required to elucidate the mechanisms that arise from complementarity between species. One way in which this may be achieved is by directly manipulating species along a known gradient of resource-use complementarity, to test the niche-differentiation effect. For example, Norberg (2000) examined the effect of cladoceran zooplankton diversity on several ecosystem processes for four species with well known niche widths (prey-size range) and grazing efficiencies on phytoplankton. In this way, Norberg (2000) was able to ascertain whether niche-differentiation was a likely mechanism for any observed diversity effects. The study revealed strong species identity effects, and effects of particular species combinations on ecosystem function including biomass, productivity and nutrient concentrations. In particular, observed responses were significantly increased above predicted responses for species combinations that included the two cladoceran species with the most complementary prey-size range (*Daphnia magna* and *Chydorus sphaericus*), suggesting the niche-differentiation effect as the primary mechanism for increased levels of ecosystem processes.

To date only one study, has directly examined the relationships between species diversity, complementarity and ecosystem function. Stevens & Carson (2001) used naturally occurring early successional grassland species to test the relationship between plant diversity (measured as species number and evenness) and total annual cover in one hundred and sixty permanent plots. They further examined whether phenological complementarity (PC – asynchrony in species' growth rates) was the mechanism responsible for any positive relationship between the two. Although there was a positive relationship between diversity and total annual cover across plots, there was no increase in PC with increases in plant diversity and PC explained little of the variation in plant cover. The authors suggest that PC may have been unimportant because levels of diversity in the natural plots were at moderately high levels compared to the experimental plots used in other studies, and therefore PC was already at an almost maximum level even in the lowest diversity plots. The solution to this problem is to directly manipulate species assemblages to represent the desired gradient of resource-use complementarity, and this is the novel approach adopted for the present study.

The overall aim of the study reported in this chapter is to test whether complementarity between shredder species has the potential to positively affect leaf processing rates through the niche-differentiation mechanism. The two assumptions of the niche-differentiation mechanism are that 1) species differ to some extent in their resource-niches and therefore are potentially complementary and 2) utilisation of available resources increases as a wider range of resource-niches are represented by the species present.

The first stage of this study was to quantify resource-use differentiation within a group of shredder species on a range of leaf types. Evidence from the literature suggests that many shredder species, from various taxonomic groups, show clear preferences when offered a range of leaf types and generally prefer those leaf types with the highest nutritional quality (i.e. high nitrogen levels, low lignin content and low levels of indigestible compounds) (Kaushik & Hynes 1971, Anderson & Sedell 1979, Nolen & Pearson 1993, Canhoto & Graça 1995). Moreover, field data shows that shredders tend to be found in greater numbers on the leaf types for which they show preferences in laboratory experiments, and are less abundant on low quality leaves (Webster & Benfield 1986, Graça 2001). This evidence suggests that shredder species may show limited differentiation in their leaf diets when offered several leaf types simultaneously, since leaves of the highest nutritional quality will be chosen above the other leaf types.

Friberg & Jacobsen (1994) examined the preferences of *Gammarus pulex* and the cased caddisfly larvae, *Sericostoma personatum*, on six different food types: including conditioned alder, beech and sitka spruce and fresh beech leaves, macrophyte and a filamentous green alga. They concluded that feeding preferences were not simply correlated with nitrogen content, C:N ratios or leaf toughness, and suggest that shredder species may use chemoreception to select food items, based on other parameters that were not measured in the study. This evidence suggests that shredder preferences for different leaf types may be driven by more complex factors, and therefore, there may indeed be potential for differentiation between shredder species. Further differences between shredder species in digestive and feeding behaviour adaptations, such as chewing abilities, nutrient requirements, ability to detoxify inhibitory chemicals and gut enzyme capabilities, may also result in different shredder preferences for different leaf types.

In addition to differentiation in leaf preferences, shredders may also differ in their ability to utilise individual leaf types as a sole food source, that is, when no choice is available. Resource-use differentiation on isolated leaf types could be important for the degree of complementarity between shredder species, after resource preferences have been exercised. For example, towards the end of the leaf-fall season when only the more recaltricant leaf types, such as beech and oak, remain in a stream. If the shredder species present do not show any preference for either of these leaf types, but do differ in their ability to utilise them when given no other choice, then there would still be the potential for complementarity between these species. However, if shredder species did not show any preference for the leaf types, or differ in their ability to utilise them, there would be no potential for complementarity. Therefore, differentiation in shredder preferences, and in the potential ability to utilise different leaf types as a sole food source, may both be important for the extent of complementarity in leaf diet, between shredder species.

Overall, there is little information to predict the degree of differentiation in leaf diet between shredder species. However, one factor that may influence it is the strength of interspecific competition. The frequency and strength of competition is not well known for stream communities, and most studies have been performed on sessile filter feeders (see Allan 1995, Giller & Malmqvist 1998). Accumulating evidence does suggest that competitive interactions may be important among more mobile organisms, such as grazers (e.g. Kohler 1992). However, thus far, there have been no studies on shredders.

Strong competitive interactions between species result in resources being partitioned in order for species to coexist (see review by Vandermeer 1972, Giller 1984). Resources that may be partitioned between species include time, space and food (defined by quality (type) and size) (Schoener 1974). While there is evidence for food partitioning in other functional feeding groups in streams, such as grazers (Hill & Knight 1988), predators (Townsend & Hildrew 1979, Sheldon 1972) and filter-feeders (Malas & Wallis 1977), food partitioning has not been demonstrated for shredder species. Since many shredder species have life cycles that are synchronised with the annual input of autumn-shed leaves (Giller & Malmqvist 1998), and share the habitat created by discrete patches of leaf litter while feeding, partitioning of the food source appears the most likely strategy for coexistence. Therefore, at least some degree of resource-use differentiation may be expected between those shredder species that co-occur in nature.

5.1.2. Aims.

The overall aim of this study is to test whether complementarity between shredder species positively affects leaf processing rates through the niche-differentiation mechanism. This was addressed by asking the following questions; 1) was there the potential for complementarity between shredder species in terms of their leaf diets? 2) What was the relationship between complementarity and detritus processing rates, and 3) was there any evidence that species identity affected the relationship between complementarity and detritus processing rates?

Questions 1 and 2 were addressed through two separate experiments. Question 1 was addressed by quantifying the consumption rates of eight shredder species on a range of leaf types in single-species feeding tests (Experiment 1). Individuals were offered five different leaf types either a) simultaneously, to assess the preferences of each shredder species or b) in isolation, to assess the potential ability of each species to consume individual leaf types as a sole food source. Data from these feeding trials were used to calculate the complementarity between every pair-wise combination of shredder species, using three alternative indices (see Section 5.2.5)

To address Question 2, a gradient of complementarity was established by stocking twenty-five stream mesocosms with different pair-wise combinations of shredder species (Experiment 2). The processing rates of a mixed leaf resource were quantified across this gradient. If there was potential for complementarity between shredder species in terms of their leaf resource-use, it was predicted that there would be a positive relationship between complementarity and detritus processing rates, as predicted by the niche-differentiation mechanism. Stream mesocosms were stocked in order to minimise differences in consumption rates between different species (see Section 5.2.4.2.), in order to reduce any species identity effects on detritus processing. Whether or not particular species did have an affect on leaf processing rates was addressed in the analysis (Question 3).

5.2. Methods.

5.2.1. Collection and acclimation of test species.

The same six shredder species used for the studies described in Chapter 4 (Section 4.2.2) were also used in the present study, along with two additional species (*Nemoura avicularis* Morton and *Potamophylax latipennis* (Curtis)). The taxonomic groups and collection locations of the shredder species are summarised in Table 5.1. Shredder species were collected by the same methods as described in Section 4.2.2.

For Experiment 1, all animals were acclimatised to laboratory conditions for a minimum of three days, as described in Section 4.2.2. All food was removed from acclimatisation tanks twenty-four hours prior to the start of feeding trials, to provide a period of starvation, after which animals were transferred to individual feeding chambers containing experimental leaf discs (Section 5.2.3.2). For Experiment 2 all animals were acclimatised to laboratory and mesocosm conditions as detailed in Section 4.2.2. Once more, animals were starved for twenty-four hours before the beginning of the experiment.

Table 5.1. Taxonomic order and collection location details for the eight shredder species used in the present study. Stream names in parenthesis are unnamed tributaries of the stream name given

Species name	Order	Collection location	
		Stream name	NGR
Gammarus pulex	Amphipoda	Crags stream	SK 497745
Asellus aquaticus	Isopoda	Rivelin pond	SK 324889
Protonemura praecox	Plecoptera	Strines Dike	SK220908
Nemoura avicularis	Plecoptera	Barlow Brook	SK 339757
Nemoura cambrica	Plecoptera	(River Dove)	SK 292030
Leuctra hippopus	Plecoptera	(River Dove)	SK 292030
Sericostoma personatum	Trichoptera	River Lathkill	SK 219647
Potamophylax latipennis	Trichoptera	(River Dove)	SK 292030

5.2.2. Quantifying leaf decomposition.

Leaves were collected from alder (*Alnus glutinosa*), sycamore (*Acer pseudoplatanus*), hawthorn (*Crategus monogyna*), oak (*Quercus robur*) and beech (*Fagus sylvatica*) trees, just before abscission. Leaves were collected during October/November 2000 for Experiment 1, and at the same time the following year for Experiment 2, at locations given previously (Section 2.2.2). Leaf material was air-dried for one week before storage.

For both experiments, leaf material was conditioned by deployment in a natural stream (see Section 4.2.5) for a period of ten days. For Experiment 1, material of a single leaf type was loosely packed into several large (20 cm x 15 cm) coarse mesh bags (see Section 2.2.2), and these were subsequently sealed into larger (30 cm x 20 cm) fine mesh (<400 μm mesh size) bags before deployment in the stream. This was repeated for each of the five leaf types. For Experiment 2, mixed litter bags were constructed and deployed exactly as described for Experiment 2 in Section 4.2.5. Upon retrieval all leaf material was stored by freezing at –10 °C before use.

For Experiment 1, leaf material was defrosted overnight in APW before being cut into standard leaf discs (10 mm diameter). Leaf discs were oven-dried at 60 °C for four days before being weighed. Five leaf discs in total were required for each feeding trial replicate. For feeding trials on a sole food source, the mass of five leaf discs of the same leaf type was recorded. For feeding trials that examined shredder preference, the mass of a single leaf disc of each of the five leaf types was recorded separately. Leaf discs were rehydrated in the experimental vessels, in aerated APW, for four days prior to the beginning of the experiment. For the preference feeding trials, the discs of different leaf types were identified with different colours of map pin. After six- to eight- days exposure to a shredder, leaf discs were removed and oven-dried at 60 °C for five days before reweighing. For Experiment 2, leaf material was handled exactly as described for Experiment 2 in Section 4.2.5, except that leaf material was removed from mesocosms after thirteen, rather than eighteen, days.

5.2.3. Quantifying complementarity (Experiment 1).

5.2.3.1. Experimental design.

The consumption rates of eight shredder species were quantified on five leaf types in a series of feeding trials. Consumption rates were quantified for individual animals exposed to five leaf discs in small glass jars (Section 5.2.3.2). Animal were exposed to either a) five leaf discs of different types, to quantify any differentiation in shredder preferences for different leaf types or, b) five leaf discs of the same type, to quantify the potential ability of shredder species to consume different leaf types when presented as a sole food source. There were six different leaf treatments per shredder species; five single leaf-type treatments and one mixed leaf treatment, each treatment replicated between twelve to fifteen times.

Four distinct sets of feeding trials were performed between the end of October 2001 and mid-January 2002, as dictated by the availability of each of the shredder species throughout the leaf-fall season. Each trial lasted between six and eight days. To provide a temporal control, consumption rates were quantified for one shredder species (*Gammarus pulex*) on the same leaf type (alder), during all four sets of trials. Moreover, six control treatments were included in each trial to quantify leaf mass loss in the absence of shredders; five different single leaf-type control treatments and one mixed leaf control treatment, each replicated fifteen times.

5.2.3.2. Experimental system.

Individuals of each shredder species were exposed to leaf discs in small (60 ml) glass jars (Figure 5.1). Each glass jar contained 40 mls of APW (which was aerated via a small needle), three small pieces of pea gravel, five leaf discs and a single animal. Treatments were assigned randomly to glass jars, which were contained in trays in sets of thirty-five (Figure 5.1), in a constant temperature room (15 °C ± 1 °C) with lights operated on a 12-h light: 12-h dark photoperiod. Water levels were maintained by refilling with distilled water. Animals were monitored daily for mortality and moulting. The progress of feeding was monitored, and feeding trials were terminated when leaf resources in any of the replicates were almost completely consumed.

Figure 5.1. Photograph of experimental system used for quantifying leaf consumption by individuals of different shredder species.

5.2.4. Testing the affect of complementarity (Experiment 2).

5.2.4.1. Indices of complementarity.

Data from Experiment 1 were used to quantify the potential resource-use complementarity between each pair-wise combination of shredder species in terms of their leaf diets. Three different methods were used to calculate an index of complementarity: Schoener's Dietary Overlap Index, Sørenson's Similarity Coefficient and Euclidean distance. The first index is considered one of the most robust indices of dietary overlap (Wallace 1981), and has been used in previous studies with stream invertebrates (Graça *et al.* 1994b), leafhoppers (McClure & Price 1976) and wolf-spiders (Uetz 1977). Sørenson's Similarity Coefficient is a quantitative index that is widely used in plant ecology to assess similarity in species composition between habitats (Southwood & Henderson 2000). Here, it was used as an alternative index, to represent the similarity between shredder species in their leaf diets. Finally, Euclidean distance is the simplest index for calculating the geometric distance between objects in multi-dimensional space (Mardia *et al.* 1994), and was used here as a further alternative index, for calculating the dissimilarity between shredder species in their leaf diets.

5.2.4.1.1. Schoener's Dietary Overlap Index.

Dietary overlap between each pair of shredder species was calculated using the Dietary Overlap Index (Schoener 1968), $C\hat{c}$ (Equation 5.1).

$$C\hat{c} = 1 - \left[0.5\left(\sum_{i=1}^{n} \left|p_{xi} - p_{yi}\right|\right)\right] \qquad \text{Equation 5.1.}$$

Where p_{xi} is the mean relative consumption of leaf type i by species x, and p_{yi} is the mean relative consumption of leaf type i by species y, for n leaf types. The Dietary Overlap Index gives values from 0 (no overlap between species) to 1 (complete overlap between species). No dietary overlap between species indicates the maximum potential for resource-niche complementarity, therefore complementarity was calculated as $1 - C\hat{c}$.

5.2.4.1.2. Euclidean distance.

Euclidean distance is a measure of geometric distance in multi-dimensional space and was used directly as a coefficient of dissimilarity, since the Euclidean distance between two points increases as 'dissimilarity' or 'divergence' increases between those two points (Mardia *et al.* 1994). The Euclidean distance between species x and y ($d(x, y)$) is given by Equation 5.2.

$$d(x,y) = \sqrt{\sum_{i=1}^{n} \left(C_{xi} - C_{yi}\right)^2} \qquad \text{Equation 5.2.}$$

Where C_{xi} is the mean consumption of leaf type i by species x, and C_{yi} is the mean consumption of leaf type i by species y, for n leaf types. Small values of Euclidean distance therefore represent low levels of complementarity between species pairs, while large values represent a greater degree of complementarity between species pairs.

5.2.4.1.3. Sørenson's Similarity Coefficient.

A modified Sørenson's Similarity Coefficient (Bray & Curtis 1957), C_n was used to calculate the similarity between each species pair (Equation 5.3). For shredder species a and b,

$$C_n = \frac{2j_N}{(a_N + b_N)} \qquad \text{Equation 5.3.}$$

Where a_N and b_N are the sums of the mean consumption rates on all leaf types for each species, and j_N is the sum of the lesser mean consumption rates across all leaf types for species a and b. Sørenson's Similarity Coefficient gives values from 0 (no similarity between species) to 1 (complete similarity between species). No similarity between species gives the maximum potential for resource-use complementarity, therefore complementarity was calculated as 1 – C_n.

5.2.4.2. Experimental design.

A regression design was employed to ascertain whether there was any relationship between complementarity and the processing rate of a mixed leaf resource. A gradient of potential complementarity (as determined from Experiment 1, see Section 5.2.4.1) was represented by distinct pair-wise combinations of shredder species, each one established in a separate mesocosm. The original eight shredder species used in Experiment 1 gave 28 possible different pair-wise combinations of shredder species, however only 25 of these were used. This was due to the inability to collect a large enough number of certain species from the field. Therefore, three pair-wise combinations of species were eliminated from the design; *Sericostoma personatum-Asellus aquaticus*, *Sericostoma personatum-Nemoura avicularis* and *Protonemura praecox-Nemoura avicularis*, without reducing the overall range of complementarity that was represented. Leaf consumption rates were quantified across the gradient of complementarity.

5.2.4.3. Experimental system.

Mesocosms were the same as those used for previous experiments (see Section 4.2.3; Figure 4.1). Mesocosms were set up and maintained as previously described (Section 4.2.3), with the exception that two compartments (compartments 3 and 4; Figure 4.1) were assigned as single-species 'monitoring' compartments in the present study. Five individuals, of each of the two species in the corresponding 'community' compartment, were kept separately in these two compartments, with a small amount of alder material and a few pieces of pea gravel. Emergence and mortality was recorded daily for 'monitoring' and 'community' compartments as described in Section 4.2.3. After stocking with shredders (see below) and leaf material (Section 5.2.2), the mesocosms were left to run for thirteen days. Stream temperature (^{0}C), pH, conductivity (μS/cm) and dissolved oxygen (D.O.) concentration (mg/l) were recorded daily with hand held meters (see Section 2.2.3). Flow rates were recorded on every second day as described in Section 4.2.3. A summary of initial physical and chemical conditions in mesocosms is given in Table 5.2.

Table 5.2. Values of the physical and chemical factors recorded in stream mesocosms on day 0.

Physico-chemical factor	Mean	S.D.
Temperature (^{0}C)	17.4	0.10
pH	7.9	0.06
D.O. (mg/l)	7.3	0.49
Conductivity (μS/cm)	570.6	77.92
Flow rate (l/min)	5.3	0.19

The experiment was carried out during February 2002. After thirteen days all gravel and animals were removed from each stream and preserved in 70 % Industrial Methylated Spirits. Animals were later counted and their wet mass recorded.

Mesocosms were stocked with shredders in order to achieve an approximately equal processing power of 15.6 mg/day across all streams, to minimise differences in species-specific consumption rates. The target processing power was based on the processing rate required for at least two of the leaf types to become completely consumed over a period of sixteen days (i.e. 250 mg/16 days). Sixteen days was the expected minimum time period for running the experiment. If leaf material was utilised in a particular order of preference, it was therefore anticipated that shredder assemblages would become limited on at least their most preferred food sources. The target processing power was divided equally between the two shredder species in each stream mesocosm. The number of individuals of each species required to achieve the target of 7.8 mg/day for each shredder species (*N*) was estimated from feeding trial data from Experiment 1, using Equation 5.4.

$$N = \frac{T}{Cm \times M} \qquad \text{Equation 5.4.}$$

Where T is the constant target processing power of 7.8 mg/day, Cm is the mean consumption rate (mg/mg/day) of the shredder species across all five leaf types and M is the mean mass of an individual of that species (mg, dry). Stocking levels for each species are given in Table 5.3. Rounding the number of animals required up to whole numbers generated some variation in processing power across species (mean = 7.9 ± 0.15 mg/day).

Table 5.3 Number of individuals of each shredder species required for equalising processing power to 7.8 mg/day across all shredder species, calculated using Equation 5.4, and actual stocking levels and estimated processing power for each shredder species after rounding up to whole numbers. Abbreviations are the same as for Equation 5.4.

Shredder species	Cm (mg/mg /day)	M (mg, dry)	N	Actual number of individuals used.	Estimated processing power (mg/day)
Gammarus pulex	0.076	8.77	11.7	12	8.0
Asellus aquaticus	0.011	7.47	94.9	95	7.8
Protonemura praecox	0.317	0.57	43.2	44	7.9
Leuctra hippopus	0.220	0.32	110.7	111	7.8
Nemoura cambrica	0.218	0.41	87.2	88	7.9
Nemoura avicularis	0.069	1.26	89.7	90	7.8
Sericostoma personatum	0.128	5.31	11.4	12	8.2
Potamophylax latipennis	0.380	3.54	5.8	6	8.1

5.2.6. Statistical analyses.

For both Experiments 1 and 2, mass-specific consumption rates (C) were expressed as mg of leaf material/mg of shredder/day, calculated using Equation 5.5.

$$C = \frac{((W_i \times F) - (W_t))}{S \times t} \qquad \text{Equation 5.5.}$$

Where W_i is the start weight of leaf material (mg), W_t is the end weight of leaf litter (mg), S is shredder biomass (mg), and t is the number of days. For quantifying complementarity (Experiment 1), leaf material and shredders were oven-dried. For testing the effect of complementarity (Experiment 2), leaf material was air-dried while the wet mass of shredders was recorded. A correction factor, representing the mean proportional leaf mass remaining for control leaf material, is represented by F, and was calculated for each different leaf type.

For Experiment 1 consumption rates were standardised by conversion into 'percentage of total consumption' ($\%C$) per leaf type, using Equation 5.6. For leaf type i:

$$\%C = \frac{100 \times Ci}{\sum_{i=1}^{n} C} \qquad \text{Equation 5.6.}$$

Where Ci is the mass-specific consumption rate of leaf type i, and there are n leaf types. To generate $\%C$ for the feeding trials where different leaf types were presented as the sole food source, replicates from each different leaf type were grouped together.

All statistical analyses were performed using MINITAB 13.2 for Windows. General Linear Models were used for all two-way and one-way unbalanced ANOVA tests and associated multiple comparison tests (using the Tukey-Kramer method for unequal sample sizes). Consumption rates on a sole leaf resource were transformed for input into two-way ANOVA analyses (Ln (x + 1) for the absolute consumption data and $\sin^{-1}\sqrt{x}$ for the percentage of total consumption data), to improve the normality of the data.

The data generated from shredder preference feeding trials could not be analysed using ANOVA since each of the different leaf types did not represent an independent replicate. That is, if an animal is eating one type of food, then less of another type is likely to be taken. The statistical problem of testing for significant preferences for a single species in choice experiments has been addressed (Roa 1992, Manly 1993, 1995, Lockwood 1998). However, no statistical test has yet been developed that allows a test of the variation in food choice between different species. For this reason, differences in leaf preferences between species were examined via Principal Component Analysis (PCA). Leaf consumption values (percentage of total consumption) from each replicate, for each shredder species, were used as input for the PCA (i.e. between 12 –15 sets of values for each shredder species), using a covariance matrix. Subsequently, ANOVAs were used to test for significant differences between species, using the co-ordinates generated by the PCA. Separate ANOVA tests were performed for each of the main PC axis (PC1 and PC2).

Repeated measures ANOVAs were used to test for between-stream differences in temperature (°C), dissolved oxygen (mg/L) and conductivity (µS/cm). Flow rate (L/min) and temperature (°C) data were not suitable for this type of analysis and therefore one-way ANOVAs were used to test for differences in mean values between streams, over the experimental period.

Regression analysis was used to ascertain whether there were significant linear relationships between complementarity and consumption rates (mg/mg/day) in mesocosms, for each of the different complementarity indices (see Section 5.2.4.1), calculated using both consumption rates on a sole food source ('no choice' data) and consumption rates when shredders were offered a choice ('preference' data). The complementarity index and consumption rate values were transformed (Ln (x)) for regression analysis to improve the normality of the data.

Assessing the *niche breadth in streams containing particular species* was one method used to examine species identity effects on leaf processing. Niche breadth (B) was calculated using the inverse of the Simpson Index (Arsuffi & Suberkropp 1989) (Equation 5.7).

$$B = \frac{1}{\sum_{i=1}^{n} r_i^2} \qquad \text{Equation 5.7.}$$

Where r_i is the relative consumption of each leaf type. Since five leaf types were used, values of B can range from 1 (narrow niche breadth) to 5 (wide niche breadth). Niche breadth (B) was calculated for each pair-wise combination of shredder species. Mean niche breadth (B) was calculated for a shredder species using the B values for all streams in which it occurred. Mean niche breadths for each shredder species were compared using an ANOVA.

5.3. Results.

5.3.1. Potential for complementarity between shredder species - Experiment 1.

5.3.1.1. Shredder preferences (choice data).

A PCA plot showing the relative positions of all eight shredder species based on their similarity in leaf preference, suggested that there were differences between shredder species (Figure 5.2). The PCA plot encompassed 69.1 % of the variation in leaf preferences across species on the first two principal components (PC1 and PC2). PC1 alone explained 38.9 % of the variation in shredder preferences and was driven by high a percentage consumption of oak and sycamore towards the positive end of the axis and a high percentage consumption of alder towards the negative end. *Asellus aquaticus* is represented by points mainly located to the positive end of PC1 (Figure 5.2), suggesting a higher percentage consumption of sycamore and oak for this species than for the others. There are three points towards the negative end of PC1 for *Asellus aquaticus*, representing three replicates in which consumption of alder material was much higher (between 68 and 93 %) than in the other replicates.

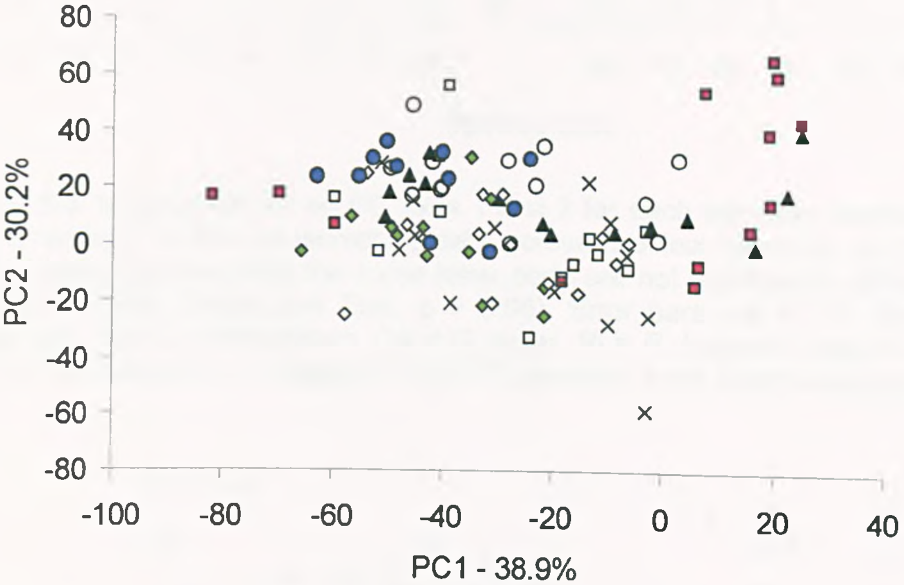


Figure 5.2. Plot of first two principal components from PCA using percentage of total consumption data for shredder preference feeding trials. The plot captures 69.1% of the variation in the feeding preferences of all eight shredder species, on five litter types. Symbols represent each of the shredder species as follows: *Gammarus pulex* (◆), *Asellus aquaticus* (■), *Protonemura praecox* (▲), *Nemoura cambrica* (×), *Nemoura avicularis* (○), *Potamophylax latipennis* (◇), *Leuctra hippopus* (□), *Sericostoma personatum* (●).

The coordinates generated from the PCA were used to test for significant differences between species on each of the two main PCA axes (i.e. PC1 and PC2). There were significant differences in mean coordinates between species on PC1 ($F_{7, 96} = 3.8$, $p < 0.001$; Figure 5.3 a). *Asellus aquaticus* showed a significantly higher mean value than *Sericostoma personatum* or *Gammarus pulex*. The PCA plot showing the positions of these three species only, visually clarifies the differences between them on PC1 (Figure 5.4 a). While *Asellus aquaticus* tended to prefer sycamore and oak, *Sericostoma personatum* and *Gammarus pulex* consumed only a small percentage of these two leaf types, and tended to prefer alder. The remaining five shredder species did not show significantly different mean coordinates from *Asellus aquaticus* on PC1 (Figure 5.3 a).

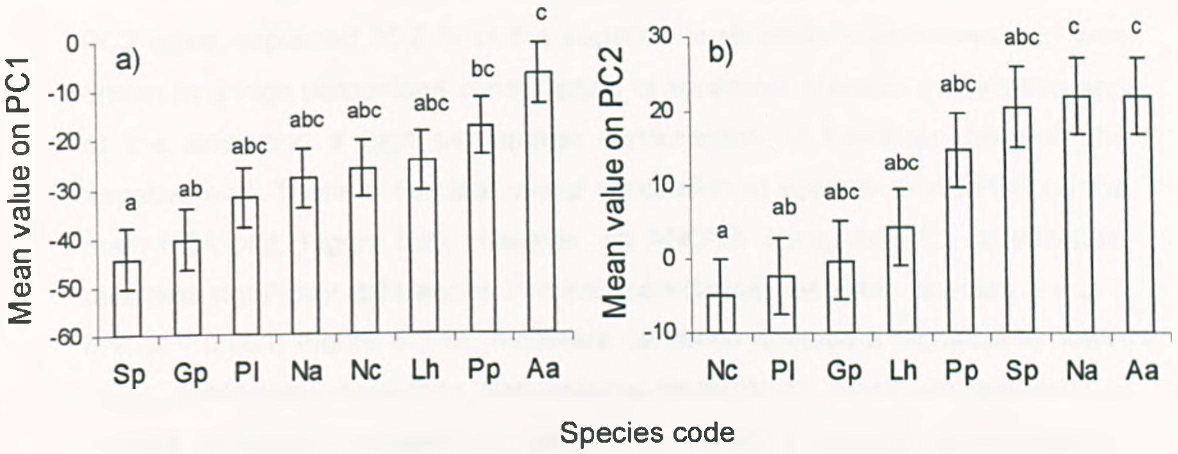


Figure 5.3. Mean positions on PC axes 1 and 2 for each shredder species from PCA on percentage of total consumption data across five leaf types for a) PC1 b) PC2. Within each plot, bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison Test, p > 0.05). Error bars are 1 S.E. Species name codes are: Sp = *S. personatum*, Gp = *G. pulex*, Pl = *P. latipennis*, Na = *N. avicularis*, Nc = *N. cambrica*, Lh = *L. hippopus*, Pp = *P. praecox*, Aa = *Asellus aquaticus*.

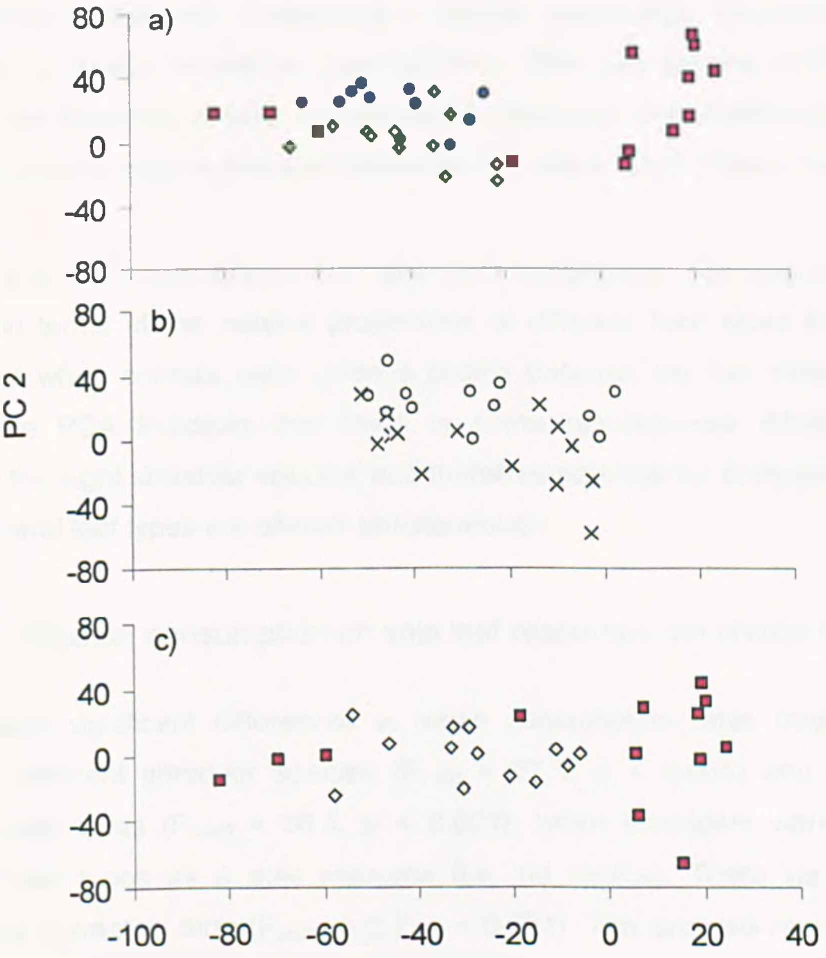


Figure 5.4. PCA plots for certain groups of species, extracted from main PCA plot (Figure 5.2); a) *Asellus aquaticus* (■), *Gammarus pulex* (◆) and *Sericostoma personatum* (●), b) *Nemoura cambrica* (✕) and *Nemoura avicularis* (○), c) *Asellus aquaticus* (■) and *Potamophylax latipennis* (◇).

PC2 alone explained 30.2 % of the variation in shredder preferences and was driven by a high percentage consumption of sycamore towards the positive end of the axis, and a high percentage consumption of hawthorn towards the negative end. There is no clear visual separation of species along PC2 on the main PCA plot (Figure 5.2). However, an ANOVA using the PC2 coordinates, revealed significant differences in mean coordinates between species ($F_{7, 96}$ = 4.9, $p < 0.001$; Figure 5.3 b). *Nemoura cambrica* showed a significantly lower mean coordinate value than *Sericostoma personatum*, *Nemoura avicularis* or *Asellus aquaticus*, suggesting that it consumed a greater percentage of hawthorn in its diet than any of these three species.

For example, a PCA plot showing the positions of only *Nemoura cambrica* and *Nemoura avicularis* allows a clearer visualisation of the dissimilarity between these two species on PC2 (Figure 5.4 b). Moreover, *Asellus aquaticus* showed a significantly higher mean coordinate value than either *Nemoura cambrica* or *Potamophylax latipennis*, suggesting a higher percentage consumption of sycamore by *Asellus aquaticus*, than by these other two species. A PCA plot showing the positions of only *Potamophylax latipennis* and *Asellus aquaticus* illustrates the dissimilarity between these two species on PC2 (Figure 5.4 c).

Overall, the PCA illustrated that there were differences between shredder species in terms of the relative proportions of different food types that were consumed when animals were given a choice between the five different leaf types. The PCA indicates that there is some resource-use differentiation between the eight shredder species, and therefore potential for complementarity when several leaf types are offered simultaneously.

5.3.1.2. Shredder consumption on sole leaf resources (no choice data).

There were significant differences in mean consumption rates (mg/mg/day) between different shredder species ($F_{7,522}$ = 67.1, $p < 0.001$) and between different leaf types ($F_{4,522}$ = 36.5, $p < 0.001$), when shredders were offered different leaf types as a sole resource (i.e. no choice). There was also a significant interaction term ($F_{28,522}$ = 2.7, $p < 0.001$). This analysis revealed that the eight shredder species varied in their absolute mean consumption rates on different leaf types (Figure 5.5 a).

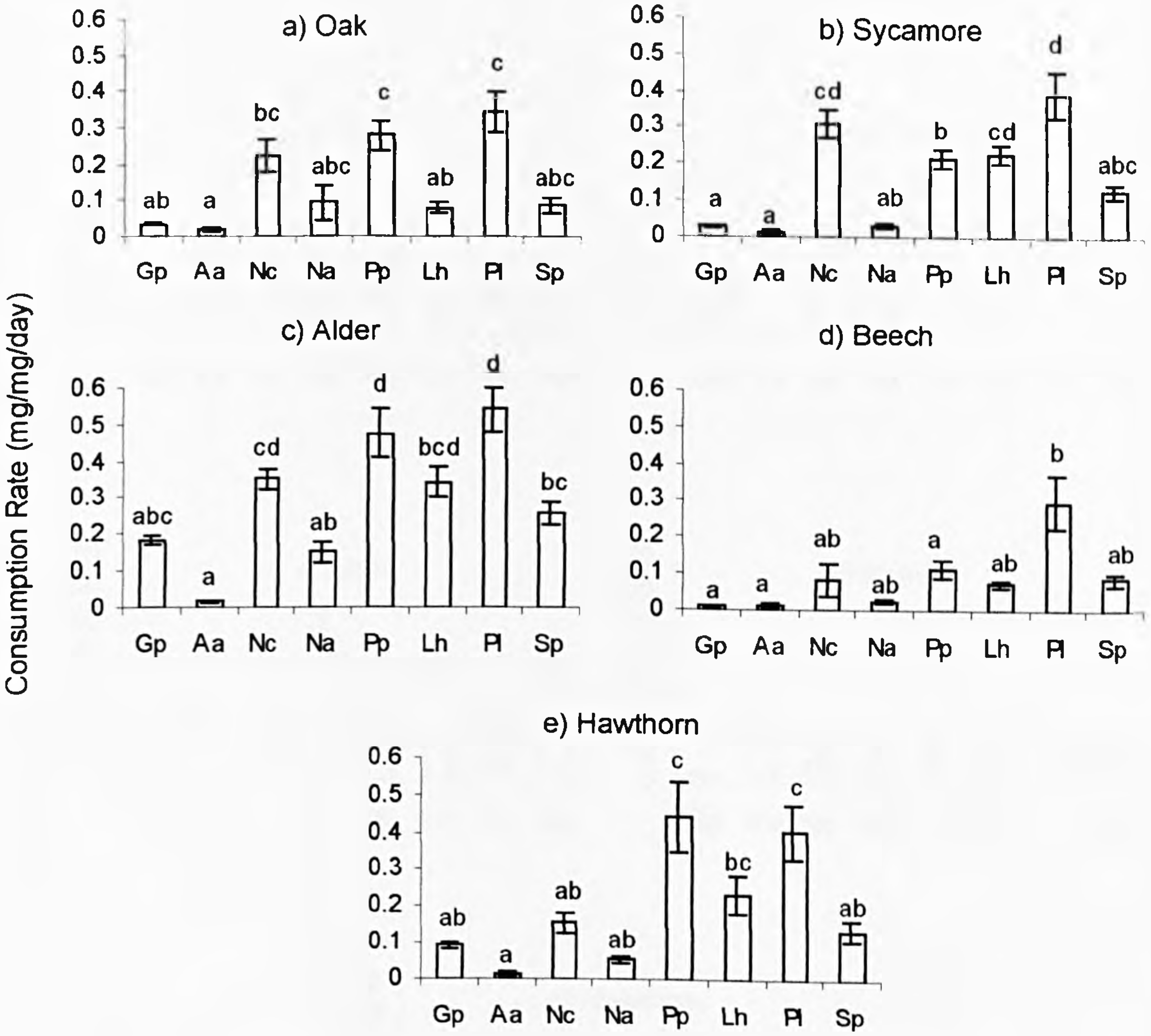


Figure 5.5. Mean consumption rates (mg/mg/day) across shredder species for each of five different leaf types, when shredders were exposed to each leaf type as a sole resource (i.e. no choice data). Error bars are S. E. Within each plot, bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison Test, $p > 0.05$). Shredder species codes are as for Figure 5.3.

In order to examine relative differences in leaf consumption between shredder species, consumption rates were standardised by calculating the mean percentage consumption of each leaf type, as a proportion of total consumption (see Section 5.2.6; Equation 5.6). A two-way ANOVA using the relative consumption data (performed on transformed data ($\sin^{-1}\sqrt{x}$)), revealed a significant overall effect of leaf type ($F_{4,435} = 50.3$, $p < 0.01$) and a significant interaction term ($F_{28,435} = 4.92$, $p < 0.01$; Figures 5.6 and 5.7). Shredder species was not a significant main factor due to the standardisation across species, i.e. the mean percentage consumption for each species was always 20%.

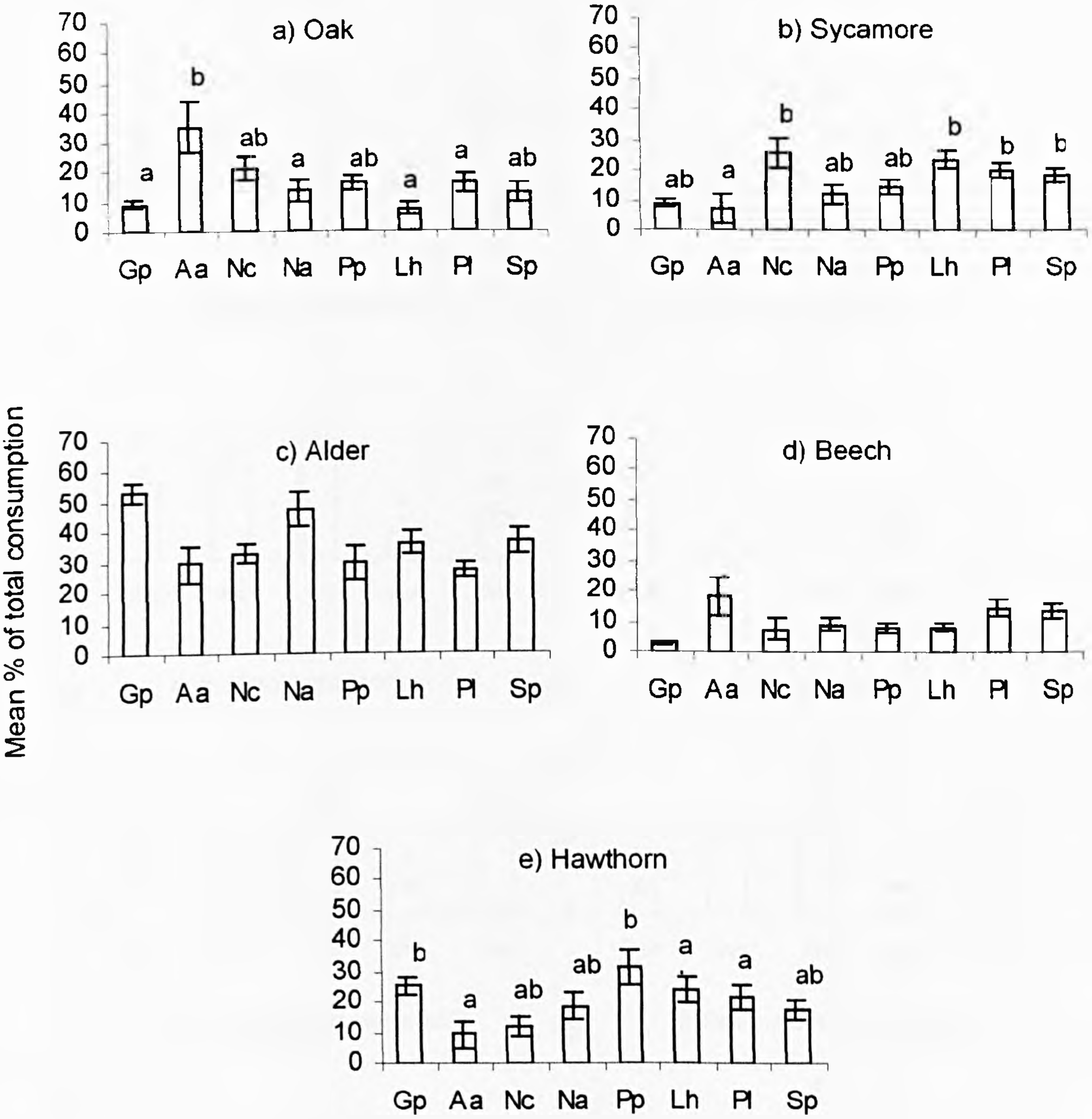


Figure 5.6. Mean relative consumption (% of total consumption) across shredder species for each of five different leaf types, when shredders were exposed to each leaf type as a sole resource (i.e. no choice data). Error bars are S. E. Within each plot, bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison Test, p > 0.05). Shredder species codes are as for Figure 5.3.

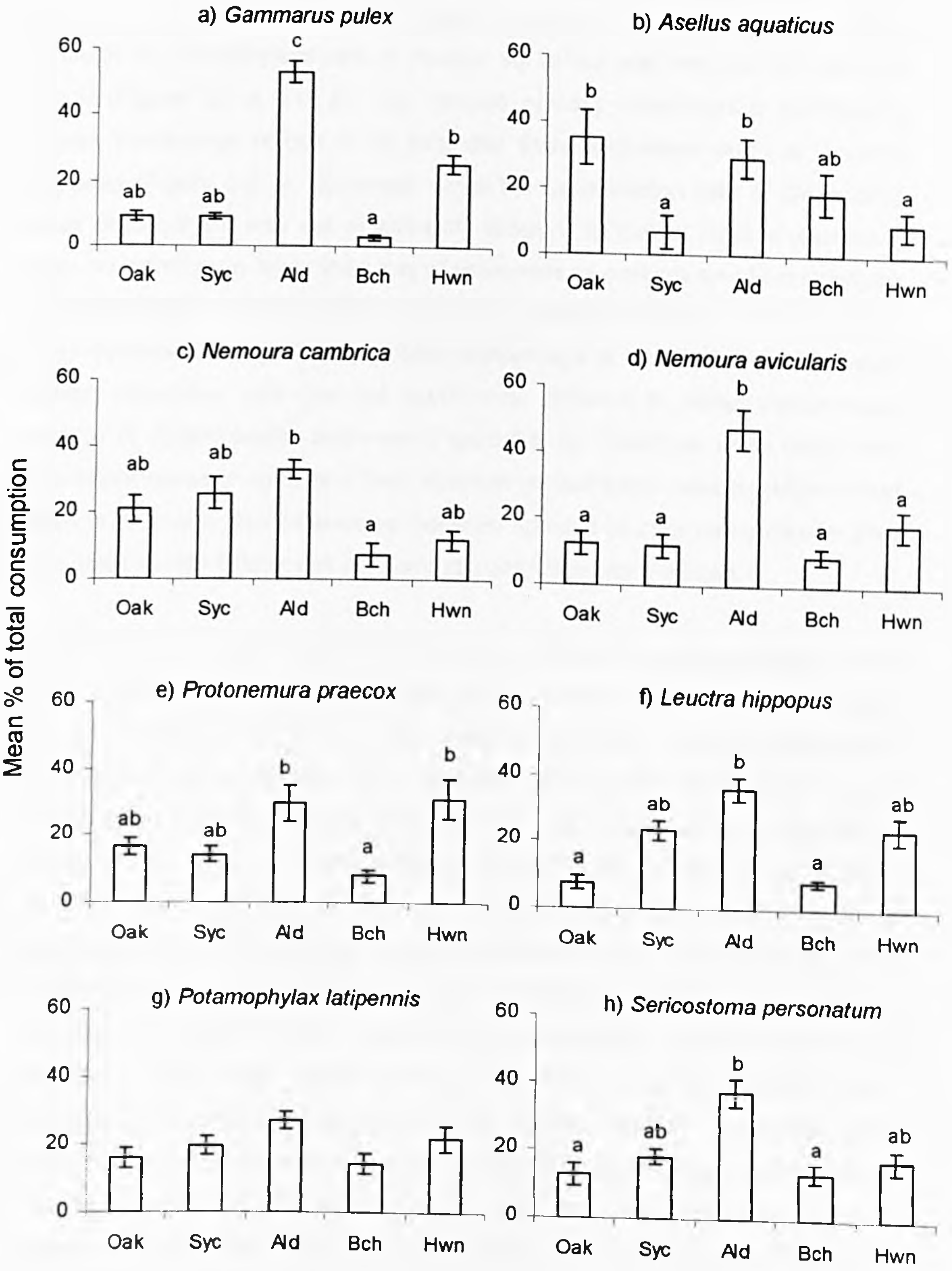


Figure 5.7. Mean relative consumption (% of total diet) of each leaf type for each of the eight shredder species, when shredders were exposed to each leaf type as a sole resource (i.e. no choice data). Within each plot, bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison Test, p > 0.05). Error bars are 1 S.E. Leaf type codes are: Syc = sycamore, Ald = alder, Bch = beech and Hwn = hawthorn.

Patterns of relative shredder consumption on each leaf type differed from patterns in absolute consumption rates (Figure 5.5 and 5.6). For example, although the consumption rate of *Asellus aquaticus* was very low on oak and beech (Figure 5.5 a and d), this species actually consumed a significantly greater percentage of oak in its total diet than *Gammarus pulex* or *Leuctra hippopus* (Figure 5.6 a). Moreover, while the consumption rate of *Gammarus pulex* on hawthorn was not significantly different to that of *Asellus aquaticus*, and was significantly lower than that of *Protonemura praecox* and *Potamophylax latipennis* (Figure 5.5 e), relative consumption patterns revealed that *Gammarus pulex* consumed a significantly greater percentage of hawthorn in its diet than *Asellus aquaticus*, and was not significantly different to either *Protonemura praecox* or *Potamophylax latipennis* (Figure 5.6 e). Therefore, while there were differences between species in their absolute consumption rates on different leaf types, there were also differences between species in their resource-use after consumption rate differences between species were standardised.

A second set of plots reveal the differences between shredder species in their patterns of relative consumption (percentage of total diet) across the different leaf types (Figures 5.7). For example, *Gammarus pulex* consumed significantly more alder as a percentage of its total diet than of any other leaf type and consumption of beech and oak was very low (2.9 % and 9.3 % respectively) (Figure 5.7 a). This is a very different pattern to that observed for *Asellus aquaticus*, for which the percentage consumption of alder, oak and beech is not significantly different, and consumption of beech and oak is relatively high (18.8 % and 35.3 % respectively; Figure 5.7 b). The different patterns of percentage consumption suggest a high degree of complementary between these two species in their leaf resource-use. In contrast, *Leuctra hippopus* and *Sericostoma personatum* show a very similar pattern of relative leaf consumption (Figure 5.7 f and h). For both species, percentage consumption of alder was significantly different from beech and oak, but not from hawthorn and sycamore, suggesting a low degree of complementarity between these two species in their resource-use.

5.3.2. Testing the effect of complementarity – Experiment 2.

5.3.2.1. Mesocosm physico-chemical conditions.

Over the thirteen-day experimental period there were no significant differences between stream mesocosms in terms of mean conductivity (µS/cm), mean dissolved oxygen (mg/l) or mean flow rate ($F_{\leq 24, 300} \leq 1.48$, $p > 0.05$). There were differences between streams in terms of temperature and pH ($F_{\geq 24,288} \geq 5.78$, $p < 0.001$). However, the maximum difference between streams in mean temperature was 0.4°C, compared to a maximum difference of 2.6°C between days of the experiment. Similarly, the maximum difference between streams in terms of pH was only 0.2, while the maximum difference between days was 0.1. Therefore, differences in temperature and pH between streams were considered to be unimportant, given the variation in these factors over the experimental period.

5.3.2.2. Changes in shredder assemblages.

Although any animals observed emerging (i.e. metamorphosing to adults) were immediately replaced during the experiment, the final number of individuals in each stream indicated that had been further, unobserved, changes in shredder abundance. These varied across different shredder species (Table 5.6). Two out of the six treatments that included the shredder *Protonemura praecox* (i.e. *P. praecox-G. pulex* and *P. praecox-N. cambrica*) had particularly high losses (> 80%) and were removed from this, and all remaining analyses.

Table 5.6 Mean (S.D.) overall reduction in shredder abundance (%) for each species.

Species name	Reduction in shredder abundance (%)	
	Mean	S.D.
Sericostoma personatum	1.7	3.7
Potamophylax latipennis	4.8	8.2
Gammarus pulex	16.7	9.1
Asellus aquaticus	21.8	5.8
Leuctra hippopus	30.2	10.4
Nemoura avicularis	30.9	4.5
Nemoura cambrica	35.2	17.3
Protonemura praecox	64.2	7.1

Observational data from single-species monitoring chambers were used to ascertain the patterns and causes of reductions in shredder abundance through time, for different species. Very few individuals of *Sericostoma personatum* or *Gammarus pulex* emerged (relevant only for the former species) or died within single-species monitoring compartments (zero and one respectively). Therefore it was not possible to predict the pattern of abundance loss through time in experimental compartments for these particular species. For the remaining six species, emergence and/or mortality appeared to occur at a constant rate over the experimental period, giving linear patterns of cumulative abundance loss (%) (Figure 5.8). Emergence, rather than mortality, appeared to be the central cause of reductions in abundance for the cased caddisfly *Potamophylax latipennis*, (Figure 5.8 a) and for the four stonefly species (Figure 5.8 b – e).

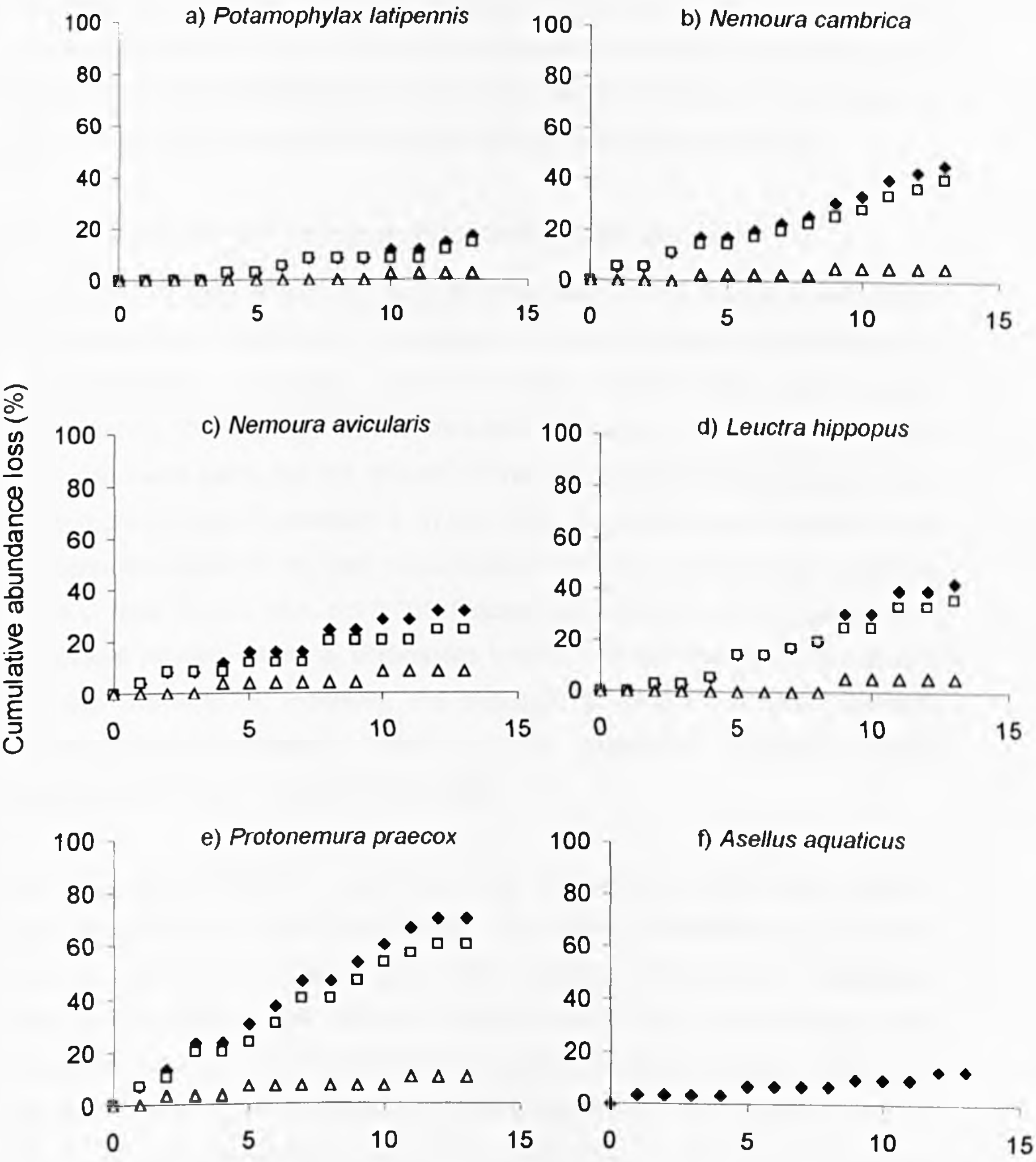


Figure 5.8. Cumulative loss (%) over the thirteen-day experimental period for six out of the eight shredder species, based on observational data from single-species monitoring compartments. Data from single-species monitoring compartments in different mesocosms was pooled for each species. ◆ represents total abundance loss (%), □ represents abundance loss (%) due to emergence and Δ represents abundance loss (%) due to mortality.

The observed linear patterns of cumulative abundance loss in single-species monitoring compartments were assumed to represent patterns of abundance loss in experimental streams. In order to account for a linear decrease in shredder abundance (and therefore a linear decrease in shredder biomass) in experimental treatments, consumption rates (mg/mg/day) were calculated using the mid-point shredder biomass (Section 5.2.6; Equation 5.5). The mean biomass per individual, for each shredder species, was calculated from the shredder biomass in each stream at the end of the experiment, and was used to convert mid-point shredder abundance into shredder biomass. All analyses that follow were performed using consumption rates calculated in this way.

5.3.2.3. Effect of complementarity on leaf processing rates.

The values of complementarity calculated for each of the 23 shredder species pairs are given in Appendix F. There was no positive relationship between log complementarity (calculated using the Niche Overlap Index) and log leaf consumption (mg/mg/day) across mesocosms, either when complementarity was calculated using the 'no choice' or the 'choice data' (percentage of total consumption), from Experiment 1. In fact, there were significant negative linear relationships between log leaf consumption and log complementarity for both types of data ($F_{1,21} \geq 18.4$, $p \leq 0.001$; Figures 5.9 a and 5.10 a). Earlier analysis suggested physico-chemical differences between mesocosms in terms of both pH and temperature. However, the inclusion of neither of these variables improves the explanatory power of the regression models between complementarity and leaf processing rates.

The general conclusion, that there was no positive relationship between complementarity and leaf consumption, was robust to changes in the method used to calculate complementarity. Both Euclidean distance and Sørenson's Similarity Coefficient were used as alternative indices of complementarity (see Section 5.2.4.1). For both methods, a significant negative linear relationship between log leaf consumption and log complementarity was observed when 'no choice' shredder consumption data were used ($F_{1,21} \geq 23.5$, $p < 0.001$; Figure 5.9 b and c). Negative trends were also observed when 'choice data' were used to calculate both alternative indices, however the relationships were not significant ($F_{1,21} \leq 1.7$, $p > 0.05$; Figures 5.10 b and c).

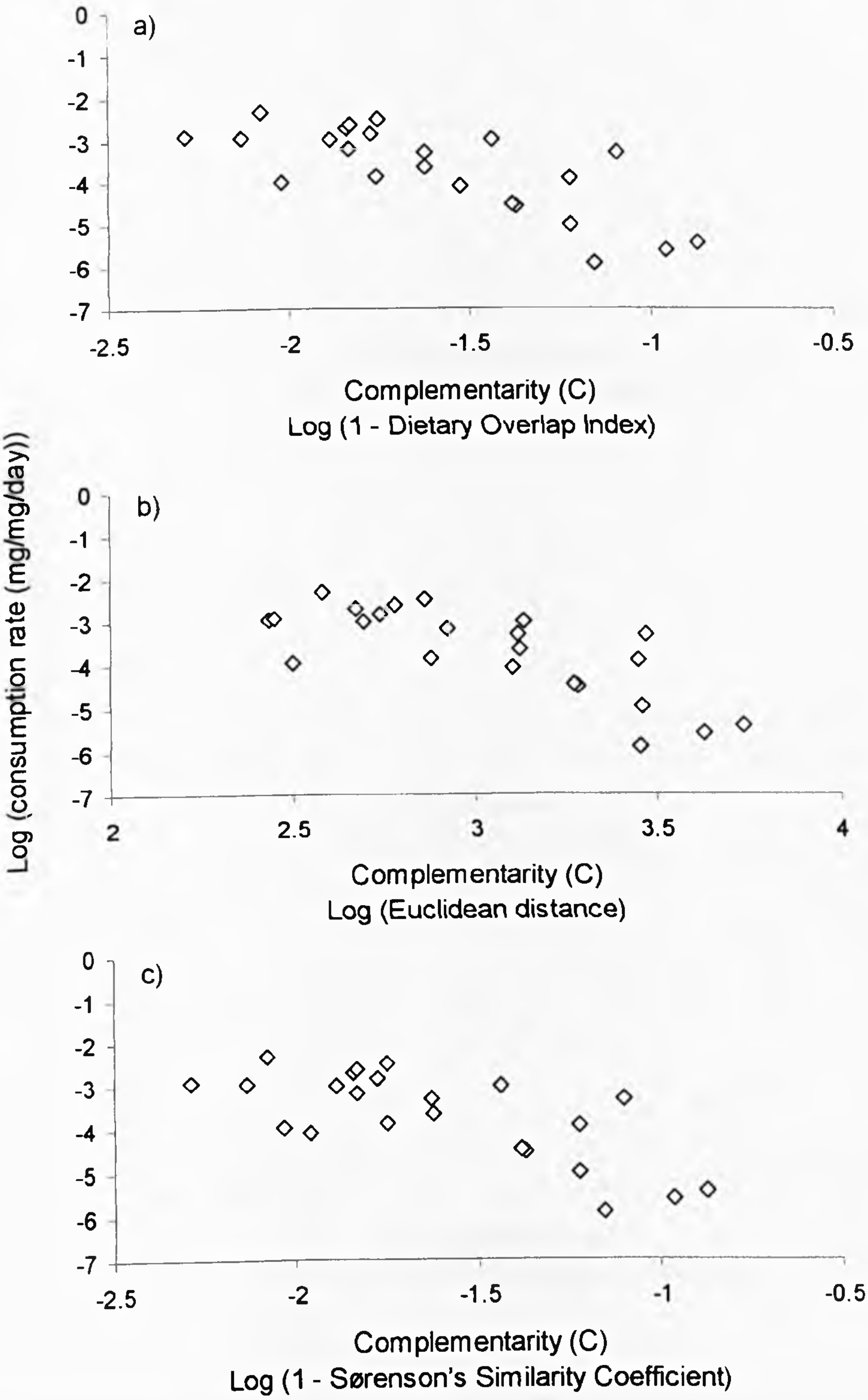


Figure 5.9. Relationship between log consumption rate (mg/mg/day) and three different indices of complementarity (C), each calculated using 'no choice' shredder consumption data (% of total consumption); a) log (1 - Dietary Overlap Index), y = - 6.9 - 2.1 x, R^2 = 57.6, b) log Euclidean distance, y = - 2.5 - 2.0 x, R^2 = 57.8 and c) log (1 - Sørenson's Similarity Coefficient), y = - 6.8 - 1.9 x, R^2 = 52.8.

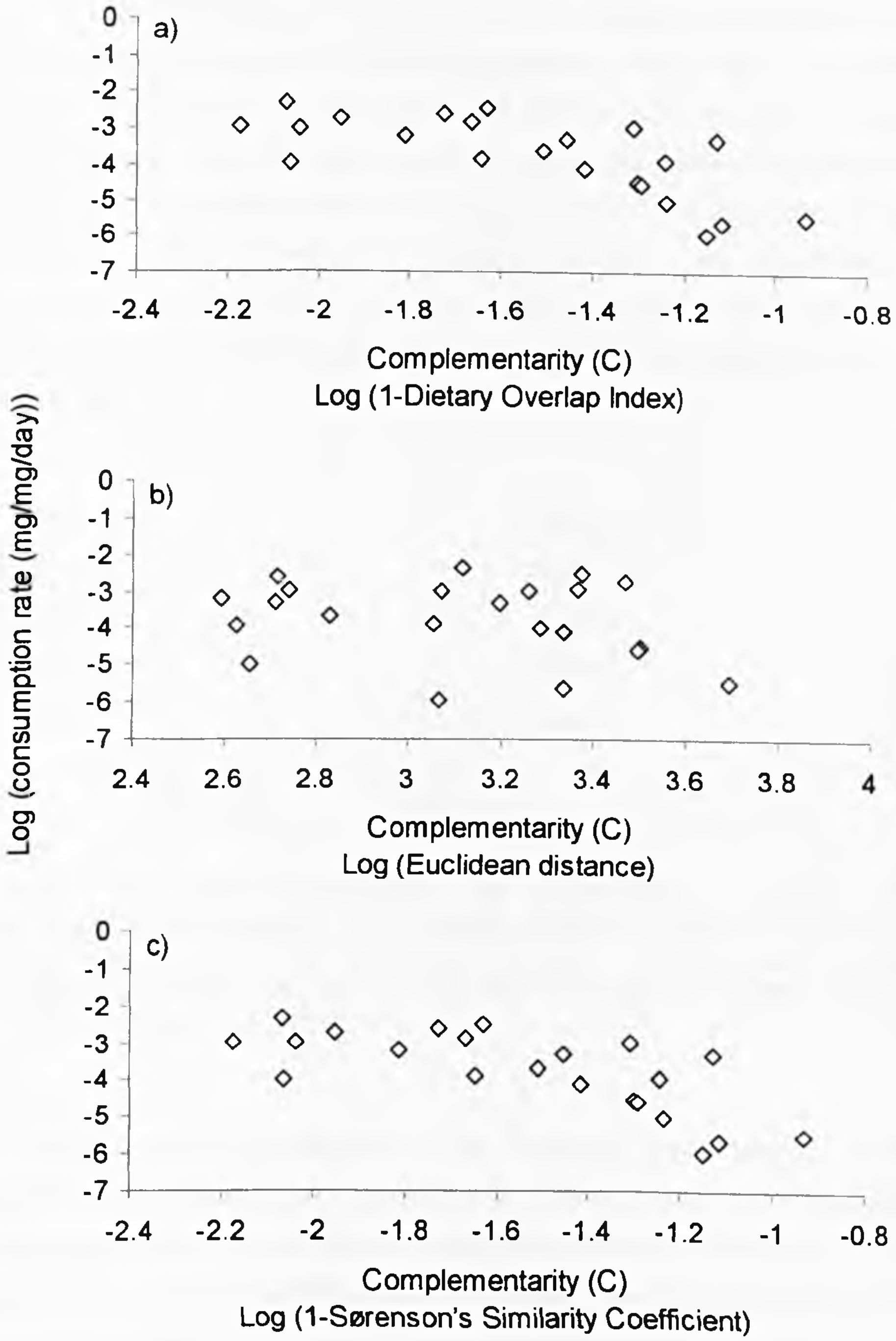


Figure 5.10. Relationship between log consumption rate (mg/mg/day) and three different indices of complementarity (C), each calculated using 'choice' shredder consumption data (% of total consumption); a) log (1 - Dietary Overlap Index), y = - 6.5- 1.8 x, R^2 = 46.7, b) log Euclidean distance, y = - 1.5 – 0.7 x, R^2 = 7.3, and c) log (1 - Sørenson's Similarity Coefficient), y = - 4.7 - 0.6 x, R^2 = 4.8.

5.3.3. Species identity effects on leaf processing rates.

A series of Mann-Whitney U tests were used to compare consumption rates for streams where a particular species was present with those for all remaining streams, for all eight shredder species. Analyses revealed that consumption rates in streams where *Sericostoma personatum* was present were significantly higher than for all remaining streams ($U_{5,18} = 12$, $p < 0.05$; Figure 5.11 a), while consumption rates in streams with *Asellus aquaticus* were significantly lower than for all other streams ($U_{6,17} = 0$, $p < 0.001$; Figure 5.11 b). No significant differences were detected for the remaining six shredder species ($U_{n1 \geq 4, n2 \geq 16} \geq 16$, $p > 0.05$).

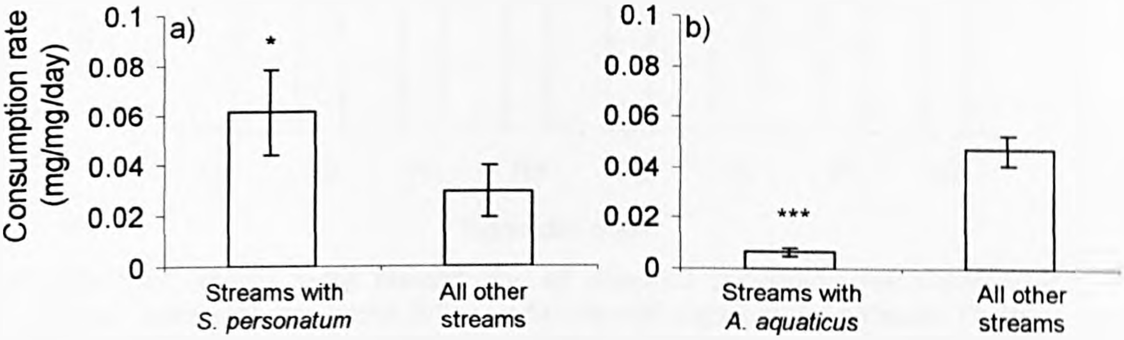


Figure 5.11. Mean consumption rate (mg/mg/day) in streams with a) *Sericostoma personatum* and b) *Asellus aquaticus*, compared with the mean consumption rate in all remaining streams. * represents a significant difference between bars at $p < 0.05$ and *** a significant difference at $p < 0.001$. Error bars are 1 S.E.

The greater mean consumption rate observed for streams containing *Sericostoma personatum* may have been a result of the ability of this species to utilise a greater number of different leaf types, i.e. it's niche breadth. The niche breadth (see Section 5.2.6) for streams containing *Sericostoma personatum* was significantly greater than for streams containing *Nemoura avicularis*, *Leuctra hippopus* or *Asellus aquaticus*, but not different from streams containing the remaining four shredder species ($F_{7,38} = 4.11$, $p < 0.01$; Figure 5.12).

It is possible that differences in consumption rates between streams containing particular species were the result of experimental artefact rather than species identity effects *per se*. Differential survival and emergence of different shredder species throughout the experiment (Table 5.6) may have influenced consumption rates. There were significant differences between shredder species in the mean percentage of individuals lost (through emergence and mortality)

($F_{7,\,38}$ = 20.9, $p < 0.001$). Both *Sericostoma personatum* and *Potamophylax latipennis* lost a significantly lower mean percentage of individuals than any other shredder species (Table 5.6). If increased rates of mortality or emergence affected consumption rates, a negative relationship between the percentage of individuals lost in streams and consumption rates might be expected. However no such relationship was observed (r_{23} = 0.26, $p > 0.05$; Figure 5.13).

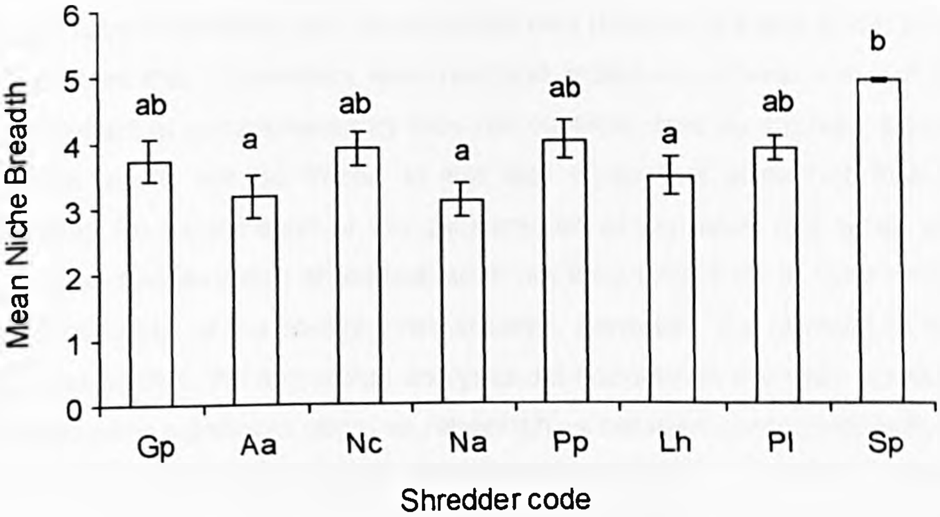


Figure 5.12. Mean niche breadth for all streams containing each shredder species. Bars with the same letter code are not significantly different (Tukey-Kramer Multiple Comparison test, $p > 0.05$). Error bars are 1 S.E. Shredder species name codes are; Gp = *G. pulex*, Aa = *A. aquaticus*, Nc = *N. cambrica*, Na = *N. avicularis*, Pp = *P. praecox*, Lh = *L. hippopus*, Pl = *P. latipennis*, Sp = *S. personatum*.

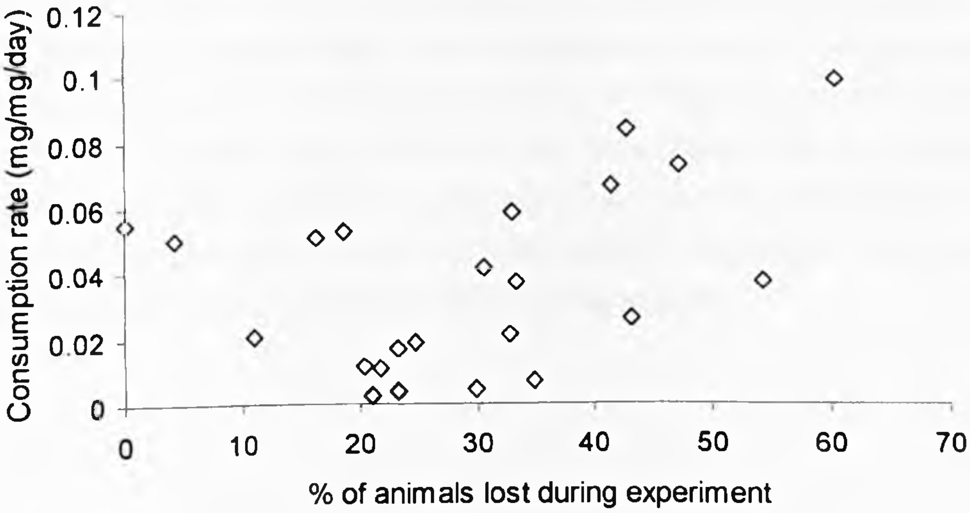


Figure 5.13. Relationship between percentage of individuals lost in each mesocosm and consumption rate (mg/mg/day). Correlation performed on transformed data ($\mathrm{Sin}^{-1}\sqrt{x}$).

Mesocosms were initially stocked in order to equalise the processing power (mg/day) between shredder species, and across streams. The target processing power was based on the estimated minimum processing rate required for shredder assemblages to become food limited on at least two leaf types over the experimental period. However, the differential loss of individuals of different shredder species (Table 5.6) led to a differential reduction in processing power across streams. This may have had two possible effects on the relationship between complementarity and consumption rate (Figures 5.9 and 5.10). First, it was expected that if shredders were not food limited on at least one leaf type, then the effect of complementarity may not manifest itself as strongly, because shredders would not be forced to eat leaf types that were not their first preference. An examination of the consumption of individual leaf types within mesocosms revealed that shredders were not food limited on at least one leaf type, in eight out of the twenty-three streams. However, the removal of these eight streams from the regression analyses did not change the main conclusion that there were significant negative relationships between complementarity and consumption rate, for both 'choice' and 'no choice' data ($F_{1,13} \geq 42.5$, $p < 0.001$, $R^2 \geq 76.8$).

Second, variation in reductions in processing power may have affected the extent of food limitation in mesocosms. The observed negative relationships between complementarity and consumption rate (Figures 5.9 and 5.10) may have resulted if streams with high predicted complementarity, were also those streams with large reductions in processing power and therefore very little or no food limitation. However there was no relationship between the percentage reduction in processing power (mg/day) and food limitation ($r_{23} = -0.35$, $p > 0.05$; Figure 5.14). Overall, these results provide no evidence that the observed negative relationships between complementarity and consumption rates, and the observed species identity effects of *Sericostoma personatum* and *Asellus aquaticus*, were the consequence of experimental artefact.

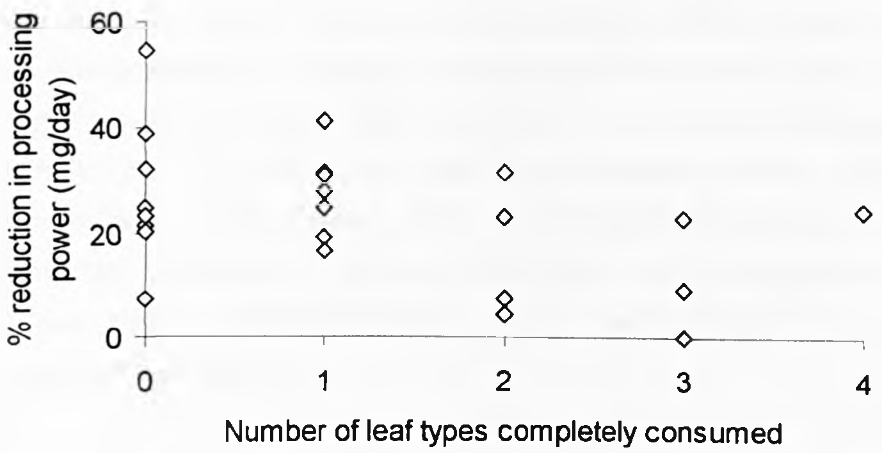


Figure 5.14. Relationship between the percentage reduction in processing power (mg/day) and extent of food limitation (represented as the number of leaf types completely consumed) across mesocosms.

5.4. Discussion.

The overall aim of this chapter was to test whether complementarity between shredder species in their leaf diets positively affected leaf processing rates through the niche-differentiation mechanism. The specific questions addressed were: 1) was there the potential for complementarity between shredder species in terms of their leaf diets? 2) What was the relationship between complementarity and detritus processing rates, and 3) was there any evidence that species identity affected the relationship between complementarity and detritus processing rates?

While this study did provide evidence for potential complementarity between shredder species in terms of their leaf diets, there was no evidence that this complementarity positively affected leaf processing rates. In fact, the observed relationship between complementarity and processing rates was negative, a pattern observed independent of the type of index (see Section 5.2.4.1) that was used to calculate complementarity. However, there was evidence that species identity affected leaf processing rates, despite an experimental design that minimised differences in species-specific processing rates.

5.4.1. Complementarity between shredder species.

Differentiation in leaf diet between shredder species was assessed both for shredder preferences (i.e. when shredders had a choice of leaf types), and for the ability of shredder species to utilise individual leaf types as a sole food source (i.e. when shredders had no choice). Two different methods of quantifying differences in leaf diets were used to represent different scenarios of leaf litter availability. Quantifying shredder preferences was used to represent a scenario in which many different leaf types are abundant simultaneously. For example, this may occur in the middle of the leaf-fall season, after most tree species have shed their leaves, but before any particular leaf type has become completely decomposed. Evidence from this study indicates that shredder species vary in their preferences when a range of leaf types of varying palatability's is available.

Shredder preference for alder leaves, over other leaf types, has been consistently reported in the literature, for a number of different shredder species (e.g. Wallace *et al.* 1970, Iversen 1974, Otto 1974, Canhoto & Graça 1995). However, in the present study, there was variation in shredder leaf preferences, and a large percentage (38.9 %) of this was driven by the difference between *A. aquaticus* and the other species. While *A. aquaticus* tended to consume more sycamore than any other leaf type when given a choice, all other species tended to consume less sycamore when allowed to choose (Figure 5.2). These results suggest that *A. aquaticus* should be relatively complementary with most of the other shredder species tested. When complementarity indices were calculated for each pair-wise combination of species, those species pairs with *A. aquaticus* tended to have the highest values (see Appendix F). The species pair with the highest complementarity index value was always *G. pulex* - *A. aquaticus*, irrespective of which index was used to calculate complementarity (Appendix F). Indeed, *A. aquaticus* had significantly more positive coordinates than *G. pulex* on PCA axis 1 (Figure 5.3), which explained 38.9% of the variation between shredders in their leaf preferences and represented increased consumption of sycamore towards the positive end, and increased consumption of alder towards the negative end.

This evidence may provide insight as to the results of a previous field study (Chapter 3), where litter bags containing a range of six different leaf types (all those used in this study along with ash) were almost completely consumed in a *low shredder* diversity stream, where the dominant shredder species were *G. pulex* and *A. aquaticus*. One explanation for the wide range of resource use observed at this site, may be the high degree of complementarity between *G. pulex* and *A. aquaticus*, in terms of their leaf preferences, as suggested by the present study.

However, variation in shredder leaf preferences was not driven solely by the difference between *A. aquaticus* and all other species in their consumption of alder and sycamore. Analyses indicated that there were also differences between other shredder species on other leaf types. For example, *Sericostoma personatum* and *Protonemura praecox* differed in their relative consumption of alder and sycamore (Figure 5.3 a). Further, *Nemoura cambrica* differed from *Sericostoma personatum, Nemoura avicularis* and *A. aquaticus*, showing a significantly greater percentage consumption of hawthorn (Figure 5.3 b), while the other three species consumed less hawthorn and more sycamore. Therefore results indicate that complementarity between shredders is not dependent on the presence of *A. aquaticus*, and that there is potential for complementarity between species even after the most commonly preferred leaf type, alder, is completely consumed.

Results from this study also revealed that there were significant differences between species in their ability to utilise different individual leaf types, when offered as a sole food source. This method of quantifying resource-use differences between shredder species was used to represent a scenario where leaf resources are limited and of a narrow range. For example, towards the end of the leaf-fall season, when the most palatable leaf types have been consumed, or at the very beginning of the leaf-fall season, when only one or two tree types have begun to senesce. Under this scenario, the ability to utilise whichever leaf resources may be available, rather than shredder preferences, may be important for complementarity.

Once more, *A. aquaticus* tended to show a different pattern of consumption from the other shredder species. In general, *A. aquaticus* tended to consume a higher percentage of oak in its diet, and a lower percentage of hawthorn. The results suggest that there should be a relatively high degree of complementarity between *A. aquaticus* and many of the other shredder species tested, but especially with *G. pulex*. Indeed, complementarity index values were always greatest for the *G. pulex* - *A. aquaticus* pairing (Appendix F), as for the choice data. However, there were further species pairs that showed a relatively high degree of potential complementarity in their leaf diets (e.g. *Nemoura cambrica* and *Nemoura avicularis* (Figure 5.7 c and d), and also pairs that were very similar in their pattern of leaf consumption (e.g. *Leuctra hippopus* and *Sericostoma personatum* (Figure 5.7 f and h), providing a range of potential complementarity over which to test the niche-differentiation mechanism.

Overall, shredder species varied in both their preferences and ability to utilise individual leaf types as a sole food source. This suggests that the niche-differentiation mechanism could be important for detritus processing rates in streams, throughout the leaf-fall season, whether a wide range of abundant resources are available or whether a narrow range of limited resources are available.

It is unclear what the basis for differentiation in leaf diet between the shredder species used might be, especially in terms of their preferences. Evidence from several studies indicates that a clear order of preference is exhibited by several different shredder species (Giller & Malmqvist 1998) associated with leaf nutrient content (e.g. Iversen 1974, Irons *et al.* 1988), leaf toughness (e.g. Nolen & Pearson 1993) and levels of plant secondary compounds (tannins, lignins) (e.g. Irons *et al.* 1988, Canhoto & Graça 1999). However, evidence from other studies suggests that shredder preference, and variation in their ability to utilise individual leaf types, may be more complex, and influenced by a combination of several factors (Friberg & Jacobsen 1994, Graça 2001). Variation between shredder species in their chewing abilities, nutrient requirements and ability to process indigestible compounds (and different combinations of these characteristics), may all influence shredder consumption of different leaf types.

It may be expected that more closely related taxa will vary less in the digestive and feeding characteristics mentioned above, and therefore will be more similar in their leaf preferences and abilities to utilise individual leaf types when given no choice. However, there was no evidence from this study to suggest that complementarity was associated with the taxonomic relatedness of the shredder species'. While the very highest values for complementarity tended not to be represented by species pairs that belonged to the same taxonomic order, and usually included the only isopod (*A. aquaticus*), many of the lower values for complementarity were represented by species pairs belonging to different taxonomic orders (Appendix F).

Variation in chewing abilities between the shredder species used may be one factor influencing leaf diet differentiation. For example, while species such as *S. personatum* (Jonsson *et al.* 2002) and *G. pulex* (Graça *et al.* 1993) tend to cut through leaf material, *A. aquaticus* tends to scrape the surface of the leaf (Graça *et al.* 1993). It is thought that the feeding strategy of *A. aquaticus* allows it to selectively feed on fungi from the leaf surface. Graça *et al.* (1993) reported that *A. aquaticus* preferred pure fungal mycelia over fungally colonised leaf material, and that food preference was positively associated with fungal biomass, supporting the contention that fungi are important as a food source for this species. *A. aquaticus* may therefore be expected to feed preferentially on those leaf types that become rapidly colonised by fungi, i.e. alder, while avoiding those leaf types that are slowly colonised by fungi, such as oak and beech. Fungal colonisation of leaf material is also important for *G. pulex*, but as a modifier of the physical and chemical structure of the leaf, rather than as a food source itself (Graça *et al.* 1993, Graça 2001). Species such as *G. pulex*, and especially *S. personatum*, which has mouthparts with large mandibles (Friberg & Jacobsen 1994), however, may have mouthpart morphology that is better equipped to feed on tougher leaf types, especially when there is no choice.

However, results from this experiment are contrary to this prediction. *S. personatum* and *G. pulex* tended to prefer alder when given a choice, as reported in other feeding studies on these species (e.g. Nilsson 1974, Iversen 1974). *A. aquaticus* however, tended to prefer sycamore, the reason for which is unclear. When shredders were given no leaf choice, *A. aquaticus* consumed similar proportions of alder, oak and beech in its diet, and a significantly greater percentage of oak than *G. pulex*. In contrast, *S. personatum* and *G. pulex* consumed a significantly smaller proportion of beech and oak, than of alder, suggesting that they were unable to feed substantially on the tougher leaf types. Perhaps in this case, the scraping strategy of *A. aquaticus* was an advantage for utilising oak and beech, since it may have been able to scrape fungi from the leaf surface without ingesting the toxic compounds found in these leaf types, such as high levels of tannins (Giller & Malmqvist 1998). In contrast, *S. personatum* and *G. pulex*, unable to derive nutrition from oak and beech in this way, were not able to feed substantially on these leaf types since the thick cuticles may have been difficult to chew through. Evidence from other studies in detritus-based systems, both aquatic and terrestrial, has suggested a relationship between consumption and leaf-toughness (Wakefield & Murray 1998, Graça 2001). For example, leaf toughness was a more important determinant of food preference for the salt-marsh crab, *Armases cinereum*, than other factors such as protein and secondary chemicals content (Pennings *et al.* 1998).

A further mechanism that may contribute to differentiation in leaf diet between shredder species is variation in digestive capability. Bärlocher (1983) suggested that variation in digestive abilities may be a functional adaptation, whereby species that are mobile, are able to search widely for the highest quality leaf material, and therefore have digestive systems adapted to particular leaf types. In contrast, species that are less mobile are unable to search to the same extent and have digestive systems that are adapted to a wider range of leaf types, since they must be able to utilise whatever leaf types are encountered.

The least mobile shredder used in the present study was the cased caddisfly larvae, *Potamophylax latipennis,* which tended to attach itself firmly to the undersides of large flat stones or to leaves within leaf packs (C. Inglis, pers. obs.). Since *P. latipennis* lacks the ability to swim, like *G. pulex* or the stonefly larvae species used in this study, movement is by crawling over the stream bed (Solem & Gullefors 1996). *Potamophylax latipennis* showed a similar pattern of preference across leaf types as the more mobile species such as *G. pulex* and *Nemoura cambrica*. However, while these more mobile species were unable to utilise any of the leaf types to the same extent as alder, when exposed as a sole food source, *P. latipennis* was able to utilise all five leaf types to the same extent. *P. latipennis* and *G. pulex* were one of the most complementarity species pairs, based on 'no choice' consumption data, since *P. latipennis* is able to consume those leaf types that *G. pulex* is not.

Factors other than the nutritional quality or toughness of leaves may play a role in their selection by shredder species. Leaf packs in streams provide shelter against periods of high flow and predation (Dobson & Hildrew 1992). Therefore, leaf packs are of value to shredders both as a food source and as a habitat. Leaf types that remain in streams for an extended time after leaf fall, such as beech and oak, may be of value to shredders since they provide a stable substrate and a lasting food source (Friberg & Jacobsen 1994). Such characteristics are likely to be particularly valuable for shredder species that are present in streams all year round, such as non-insects (e.g. *A. aquaticus*, *G. pulex*) and insects with biannual life cycles (e.g. *S. personatum*), rather than those species whose life cycles are synchronised with autumnal leaf inputs. There is evidence from choice experiments in marine systems, that the value of seaweed as a habitat may outweigh its value as a food source, for marine herbivore species (e.g. Duffy & Hay 1991, 1994, Nicotri 1980). Therefore, *A. aquaticus* may have adapted to use more refractory leaf types as a food source because of the stability of such leaf types as a habitat and food source in nature. This may be one reason for the apparent preference of *A. aquaticus* for oak and sycamore in the present study. Neither of the other two species used in this study, that remain in streams year-round (i.e. *G. pulex* and *S. personatum*) exhibited a similar pattern of preference to *A. aquaticus.* However, shredder preferences may be influenced by interactions between the various factors discussed above, and are therefore unlikely to be straightforward.

5.4.2. Relationship between complementarity and detritus processing rates.

Despite clear evidence for resource-differentiation between shredder species, both in their leaf preferences and in their ability to utilise individual leaf types, no positive relationship was observed between complementarity and leaf processing rates in mesocosms. In fact, this study revealed a negative relationship between complementarity and leaf processing rates. It is unlikely that this negative relationship was a causal one, but rather that other factors and mechanisms influenced detritus processing rates, and there are several possible reasons for the observed results.

Firstly, other mechanisms that can result from complementarity between shredder species may have been operating in the mesocosms, i.e. facilitation, or niche-differentiation on a single leaf type. Both of these mechanisms can operate within a single leaf type, therefore, species pairs with a low complementarity index with regard to their leaf diets (i.e. species that consume the same leaf types), could be potentially highly complementary with regard to facilitation, or niche-differentiation on a single leaf type. These mechanisms are therefore more likely between species pairs at the lower end of the complementarity gradient quantified on the basis leaf diet. If such mechanisms operate, and are important for increasing leaf processing rates in shredder communities, they could have driven the observed negative relationship between complementarity in leaf diet and detritus processing in mesocosms.

Facilitation has been demonstrated for a group of filter-feeding caddisfly larvae (Cardinale *et al.* 2002), and was shown to be mediated through alteration of the physical environment. Such facilitation may be also be important among shredders. For example, the fragmentation of large particles of detritus by the feeding action of larger shredder species, with chewing (e.g. *Gammarus pulex*;

Graça *et al.* 1993) or cutting (e.g. *Sericostoma personatum*; Friberg & Jacobsen 1994) strategies, into smaller particle sizes that may be more readily consumed by smaller shredder species (e.g. stonefly larvae). Jonsson & Malmqvist (2000) have also suggested that differences in the feeding morphologies of stonefly shredders, may have led to facilitation in their study.

There is no experimental evidence to indicate the extent of niche partitioning between shredder species on a single leaf resource, however, this could be an important mechanism. For example, given the range of feeding strategies exhibited within the shredder functional feeding group, shredders may partition different parts of the leaf tissue. For instance, some species of stonefly larvae are known to consume mainly the cuticle, epidermal and mesophyll cells, leaving the leaf venation intact (e.g. Wallace *et al.* 1970), whereas species of caddisfly larvae belonging to the Limnephilidae family (Allan 1995), and *S. personatum* (Jonsson *et al.* 2002), consume all parts of the leaf, including the veins. In this way, consumption of the leaf resource may be increased, since one species can utilise leaf tissues that another can not.

It is not possible to ascertain whether facilitation or niche-differentiation on a single leaf type, were important between the shredder species used in this study, since no direct behavioural observations were made. However, such interactions may have occurred between species pairs at the lower end of the calculated complementarity gradient (Appendix F). For example, partitioning of leaf tissues between larvae of the stonefly species *Leuctra hippopus* and *S. personatum*, as described above. Facilitation may have occurred between *G. pulex* and *Nemoura avicularis*, whereby *G. pulex* may have fragmented leaf material into smaller particles, that were more accessible for *Nemoura avicularis* larvae. However, facilitation between shredders may be subtler in many cases, and it is not clear how important this mechanism may have been in the present study, for increasing leaf processing rates.

A further factor that may have influenced the observed relationship between complementarity and leaf processing rates is the way in which complementarity was quantified. Replicate feeding trails were performed with a single individual of each shredder species, and therefore measured the fundamental resource-niche (Vandermeer 1972, Giller 1984). That is, the optimum leaf consumption by an individual in the absence of any predators, intra- or interspecific competition. Consequently, the calculated gradient of complementarity was a theoretical one, since it was determined using the fundamental niche of each species. Therefore, it may not have reflected the true resource complementarity between species pairs when they were established together in mesocosms, since aggressive interactions and interference between species (see Section 4.4.2) may have affected leaf consumption. This problem may be partially addressed by examining the effect of increasing the density of animals used for quantifying species-specific consumption rates. For example, Jonsson & Malmqvist (2003) quantified the consumption rates of three different stonefly shredder species (*Protonemura meyeri*, *Taeniopteryx nebulosa* and *Nemurella picteti*) on alder leaves, at three different densities (four, six and twelve individuals). They found that leaf mass loss decreased with increasing density, for two out of the three species, suggesting that increasing intraspecific competition may affect consumption rates.

5.4.3. Species identity effects.

Experiment 1 provided clear evidence that shredder species differed in their consumption rates on different leaf types. Experiment 2 of this study was therefore designed to eliminate species-specific effects by equalising processing power (mg/day) across shredder species (see Section 5.2.4.3). Despite this, results indicated that species identity effects were a strong influence on leaf processing rates in mesocosms. If there were effects of complementarity in leaf diet on detritus processing, these were weak compared with species identity effects, which appeared to drive the observed negative relationship between complementarity and leaf processing rates.

Two separate species identity effects were detected; *S. personatum* had a positive effect on leaf processing rates, while processing rates in streams with *A. aquaticus* were significantly lower than in all other streams. This appeared to drive the negative relationship between complementarity and leaf processing rates, because species pairs with high complementarity index values tended to include *A. aquaticus*, and species pairs with low complementarity index values tended to include *S. personatum*. The mechanisms driving these species identity effects however, are unclear.

Streams that included *S. personatum* showed a significantly greater range of leaf resource use (as indicated by niche breadth; see Section 5.2.6) than streams with *A. aquaticus*, *N. avicularis* and *L. hippopus*. Studies have shown that *S. personatum* is able to feed on a range of food sources including beech and ash leaves, needles of Sitka and Norway spruce, macrophytes and filamentous algae (Iversen 1974, Friberg & Jacobsen 1994, 1999), suggesting that this species may be a relatively non-selective feeder. The ability of *S. personatum* to consume a range of leaf types is thought to be related to; its mobility (see above), its large mandibles, and low respiration rates relative to, for example, *G. pulex* (Friberg & Jacobsen 1994). Despite these attributes, *S. personatum* was unable to consume oak and beech material to the same extent as alder, when given no choice (Figure 5.7 h). Therefore it seems unlikely that the positive identity effect of *S. personatum* was through an increased range of resource use.

A previous mesocosm experiment (Chapter 4), did not provide any evidence that single-species treatments of *S. personatum* had strong identity effects on either a single or a mixed leaf resource. However, the species identity effect of *S. personatum* in the present study may have been a result of its interaction with other shredder species in each of the pair-wise treatments. Strong intraspecific competitive interactions may have hindered feeding rates in *S. personatum* single-species treatments (Chapter 4). In the present study *S. personatum* may have been released from intraspecific competition by the presence of another species, resulting in increased feeding rates. Release from intraspecific competition has been observed for the fly larvae shredder *Tipula abdominalis*, which showed higher survivorship and better growth rates when reared together with the shredding caddisfly larvae *Pycnopsche lepida*, than when reared with conspecifics (Cummins *et al.* 1973). Furthermore, there is evidence for strong effects of intraspecific competition among individuals of the grazing caddisfly larva *Helicopsyche borealis* (Feminella & Resh 1990), while Hildrew & Townsend (1980) have observed interference within populations of the predatory net-spinning caddisfly larva *Plectrocnemia conspersa*. However, there is no evidence from the literature to indicate whether intraspecific competition may affect leaf consumption rates in *S. personatum* populations.

Although *S. personatum* suffered the lowest loss of individuals out of the eight shredder species used, leaf processing rates did not seem to be affected by differences in shredder survival (Figure 5.13). However, the high survival rate of *S. personatum* in mesocosms suggests that the experimental system may be more suitable for *S. personatum* than for the other shredder species. For example, in natural streams *S. personatum* is normally found buried under gravel in the stream bed (Solem & Gullefors 1996). *A. aquaticus* can be found in a variety of microhabitats, but is found least commonly in gravel substrates (Graça *et al.* 1994a). Therefore, the gravel substrate of the experimental mesocosms may have been more suitable for *S. personatum* than for *A. aquaticus*. It is possible that *S. personatum* was better able to take refuge, and perhaps avoid aggressive interactions from other species, than *A. aquaticus*.

Although species-specific consumption rates were equalised in the experimental design, it is not possible to eliminate all differences between shredder species such as, competitive behaviour, microhabitat preferences and feeding strategies, for example. Therefore, it is not possible to design an experiment where differences between species, other than in their leaf diets, do not affect leaf consumption. Although it is unclear precisely why *S. personatum* and *A. aquaticus* appeared to have such strong species identity effects on leaf processing rates, it is clear that they outweighed any affects of complementary use of different leaf types between shredder species, in the present study.

5.5. Conclusions.

There was potential for complementarity between shredder species in their leaf diets, both in terms of preferences and in their ability to utilise individual leaf types as a sole food source.

However, no positive effect of complementarity in leaf diet on detritus processing rates was observed. Instead, there was a negative relationship between complementarity and detritus processing rates in mesocosms.

The overall shape of the relationship between complementarity and leaf processing rates was the same irrespective of which index was used to calculate complementarity.

There were species identity effects on leaf processing rates, despite an experimental design that minimised differences in species-specific processing rates.

6. General discussion.

The overall aim of this thesis was to examine whether species diversity is important for ecosystem function in streams, focusing specifically on the relationship between shredder diversity and leaf litter processing. This aim was tackled by addressing four objectives. Objective 1 (Chapter 2) examined the influence of macroinvertebrate species richness, species identity and community composition on detritus processing at a regional scale (i.e. between streams). Objective 2 (Chapter 3) assessed whether resource diversity influenced leaf processing rates in a sub-set of the natural streams examined for Objective 1. The remaining two objectives were addressed through laboratory-based experiments. Objective 3 (Chapter 4) examined the effect of shredder diversity and identity on leaf processing in stream mesocosms, and Objective 4 (Chapter 5) examined more closely one of the possible mechanisms that may lead to positive effects of shedder diversity. In this chapter, the findings from each of these objectives are summarised (Section 6.1). Section 6.2 goes on to examine the contribution of these findings to, and their wider implications for, the biodiversity-ecosystem functioning relationship in stream detritivore systems. Finally, the patterns and mechanisms observed for stream decomposer systems are discussed in relation to those observed for other ecosystem types (Section 6.3).

6.1. Summary of objectives and main thesis findings.

6.1.1. Objective 1.

To examine the influence of macroinvertebrate species richness, species identity and community composition on detritus processing at a regional scale (i.e. between streams).

This objective tested whether macroinvertebrate species diversity was important for detritus processing, at scales over which there was likely to be variation in other biotic and abiotic factors (Section 2.1.1), that may have strong influences on leaf processing rates (Section 1.5.2.2). The effect of species identity (Sections 1.3.1, 2.1.2) and species composition (Sections 1.3.2, 2.1.3) on detritus processing in natural systems was also examined, along with evidence for the selection effect in natural communities (Sections 1.4.1, 1.5.2.1).

In Chapter 2 leaf decomposition was quantified across eighteen natural streams that varied in their biotic and abiotic conditions. Results indicated that there was no positive linear relationship between shredder species richness and leaf processing across streams. However, shredder species richness was important among several abiotic (canopy cover, pH and temperature) and biotic (shredder biomass and abundance) factors that positively influenced leaf processing across sites. Shredder richness had a marginally greater influence than shredder abundance and biomass, but this was strongly dependent on the inclusion of one particular site in the analysis, and overall results suggested at least some redundancy among shredder species.

One species in particular, *Gammarus pulex*, appeared to be responsible for driving the overall relationship between shredder abundance and leaf mass loss, suggesting a species identity effect. However, there was no evidence that the positive influence of species richness on leaf processing was driven by the selection effect, i.e. *Gammarus pulex* was not more likely to occur at high abundances in high shredder diversity communities. The occurrence of high numbers of *Gammarus pulex* was most likely driven by differences in physico-chemical factors across the stream sites. Finally, there was no discrete grouping of stream sites according to community composition. Instead, there tended to be a gradual change in community composition across stream sites, but this was not associated with variation in leaf litter processing.

6.1.2. Objective 2.

To investigate the effect of leaf diversity on detritus processing in low and high diversity shredder communities.

Whether or not a diversity effect was evident on a single leaf resource (Objective 1, Chapter 2), shredders may also be complementary in terms of their leaf diets (Sections 1.6.2, 3.1.1). To address Objective 2, a mixed leaf resource was used to test whether resource-niche differentiation, in terms of leaf type, was an important mechanism in natural shredder communities. If shredder species were complementary in their leaf diets, it was hypothesised that resource niche-differentiation would lead to increased utilisation of a mixed leaf resource in high, but not in low, shredder diversity communities, because the former would have the potential to utilise a wider resource range (Section 1.4.2.1).

In Chapter 3 the decomposition of a range of single leaf types, and of a mixed leaf resource, was quantified across low and high shredder diversity sites, which represented a sub-set of the natural streams used in Chapter 2. Single leaf types showed the same relative pattern of decomposition across the stream sites, suggesting a general pattern of shredder preference. There was no evidence to indicate that mass loss from a mixed leaf resource was increased in high shredder diversity communities, indicating that high shredder diversity does not necessarily increase the resource-niche range represented by a shredder community. In fact, mass loss from the mixed leaf resource was independent of shredder diversity, and was equivalent to the most fully decomposed single leaf type, at most low and high shredder diversity sites.

Overall, niche-differentiation in leaf diet did not appear to be an important mechanism for positive shredder diversity effects on detritus processing across the study streams. Moreover, mass loss from single leaf types did not increase with shredder species number, providing no evidence for facilitation, or niche-differentiation on a single leaf type, between shredder species. However, there was large variation in species composition and abundance across sites. In particular, *G. pulex* abundance appeared to have a strong influence on leaf mass loss across stream sites and may have masked any relationship between mass loss and species richness. These results suggested that particular species, or species combinations, might be more important than shredder diversity for the breakdown of a mixed leaf resource in the field.

6.1.3. Objective 3.

To examine shredder identity and complementarity effects on leaf processing on a) a single leaf resource and b) a mixed leaf resource, under controlled conditions.

Objectives 1 and 2 addressed whether shredder diversity was important for leaf processing in natural streams, as other biotic and abiotic factors vary. Objective 3 tested for small-scale local effects of shredder diversity on leaf processing, while eliminating variation in biotic and abiotic factors that may mask effects at larger scales (Section 4.1.1). A laboratory approach allowed the possible mechanisms driving any positive diversity effects to be identified. The detritus processing rates for several different single-species shredder treatments were tested against that of a mixed-species assemblage, composed of all the different single shredder species. Two separate experiments were carried out in stream mesocosms. For Experiment 1 shredders were provided with a single leaf resource to test for any effect of facilitation (Section 1.4.2.2) or resource partitioning within a single leaf type (Sections 1.6.2, 4.1.1). For Experiment 2 shredders were provided with a mixed leaf resource to test for any effect of resource-niche differentiation in leaf diet (Sections 1.6.2, 4.1.1).

Significant differences between single-species treatments revealed that there were shredder species identity effects on detritus processing. On a single highly palatable leaf resource, alder, most species showed equivalent consumption rates, except for *Asellus aquaticus*, which had a significantly lower consumption rate than all other species. These results suggested a high level of redundancy among the group of shredder species, in terms of their roles in alder leaf breakdown. When shredder species were exposed to a mixed leaf resource, *Asellus aquaticus* again showed a significantly lower consumption rate than all other species. Additionally, *Nemoura cambrica* showed a significantly greater consumption rate than *Gammarus pulex*, indicating that these species differed in their ability to utilise the range of leaf resources. Therefore, there appeared to be less redundancy among the group of species when exposed to a mixed leaf resource.

There was no evidence of overyielding on either a single, or a mixed, leaf resource (i.e. mixed species assemblages did not show significantly greater consumption rates than the single-species treatment with the highest consumption rate). Therefore, there was no evidence for complementarity effects (facilitation, or the niche-differentiation effect). Moreover there was no evidence for any overall positive effect of increasing shredder species number on detritus processing (either through selection effects or complementarity effects), on either a single or a mixed leaf resource.

6.1.4. Objective 4.

To test whether complementarity between shredder species in their leaf diets positively affects leaf processing rates.

Previous objectives did not provided any direct test of the possible mechanisms arising from complementarity between shredder species. Therefore, Objective 4 was concerned with testing directly one possible mechanism that may lead to positive shredder diversity effects on detritus processing: the niche-differentiation effect. Specifically, whether increasing complementarity in the leaf diets of shredder species, could lead to increased leaf processing rates. The niche-differentiation hypothesis predicts that the utilisation of available resources increases as a wider range of resource-niches are represented by the species present (Section 1.4.2.1).

Two separate experiments were performed to test the above hypothesis. Firstly, the consumption rates of a range of shredder species were quantified on a range of leaf types, to ascertain whether species varied in their leaf diets (Experiment 1). Both shredder preferences (shredders were offered a choice of leaf types), and shredder abilities to utilise individual leaf types (shredder were offered each leaf type individually), were quantified. Secondly, data from Experiment 1 were used to quantify the complementarity, in terms of leaf diet, between every pair-wise combination of shredder species. A gradient of complementarity was then established experimentally in stream mesocosms, using pair-wise combinations of shredder species, and the processing rates of a mixed leaf resource quantified.

Experiment 1 indicated that there was the potential for complementarity between shredder species in their leaf diets, both in terms of preferences and in their ability to utilise individual leaf types as a sole food source. However, no positive effect of complementarity in leaf diet on detritus processing rates was observed. Instead, there was a negative relationship between complementarity and detritus processing rates in mesocosms. Experiment 1 indicated that there were differences in species-specific consumption rates and therefore Experiment 2 was designed in order to minimise these as far as possible. Despite this, analyses suggested that there were species identity effects on leaf processing rates in stream mesocosms. While streams with *Sericostoma personatum* showed increased leaf consumption rates, streams with *Asellus aquaticus* tended to have lower consumption rates. These species identity effects may have masked any effects of complementarity in leaf diet, and may have driven the observed negative relationship between complementarity and detritus processing rates in mesocosms.

6.2. Relevance and implications of findings for the biodiversity-ecosystem function relationship in stream detritivore systems.

6.2.1. Relevance and contribution to current knowledge.

6.2.1.1. Patterns.

To date, very few experiments have examined the relationship between biodiversity and ecosystem functioning in stream detritivore systems, and the evidence presented by these is inconsistent (see Section 1.6.2). A study that increased the number of shredding stonefly species from one to three, in aquatic mesocosms, reported a positive effect of increasing species number on alder breakdown, but no differences between the three species used (Jonsson & Malmqvist 2000). A similar study, used three species belonging to different taxonomic groups, including an amphipod, a trichopteran and a plecopteran (Jonsson *et al.* 2002). The authors reported no effect of increasing species number, from one to three, on alder or beech processing rates. However, there were strong effects of species identity and species combination, which differed depending on leaf type.

Evidence from mesocosm experiments in this study (Chapter 4) support the conclusions of the latter study. That is, there were differences between different single-species treatments, but no effect of increasing shredder diversity on leaf processing rates. Similarly to Jonsson *et al.* (2002), shredders from a range of taxonomic groups were used. The apparently contrasting results reported by Jonsson & Malmqvist (2000) compared with Chapter 4 and Jonsson *et al.* (2002), may be a function of the taxonomic relatedness of the species used in the experiments. That is, species identity effects may be more important when species are less closely related (Section 1.6.2). Such species are more likely to have morphological and physiological differences, and therefore play different functional roles in detritus processing. Results reported in Chapter 4 of this thesis would seem, in part, to support this idea. There were effects of shredder species identity on alder processing rates, but these were confined to a significant difference between the only isopod used in the study, *Asellus aquaticus*, and all the species from other taxonomic orders, including Plecoptera, Trichoptera and Amphipoda. Species identity effects were, however, more apparent on a mixed leaf resource, where there were significant differences in consumption rates between species belonging to three different taxonomic orders (Plecoptera > Amphipoda > Isopoda).

One further study has provided evidence for species identity effects on leaf processing rates in streams. Ruesink & Srivastava (2001) tested the effect of removing either one of two dominant shedder species on alder processing rates, from stream detritivore communities that were experimentally assembled in field enclosures. The two dominant shredder species removed were the stonefly larva *Pteronarcys californica* and the caddisfly larva *Lepidostoma unicolor*. In general, shredder communities from which *Pteronarcys californica* was removed, were able to maintain leaf processing rates, but those from which *Lepidostoma unicolor* were removed could not. That is, the effect of reducing shredder diversity in the stream communities was dependent on the identity of the species that was lost.

Although current evidence is very limited, in general, and including the evidence from this study, it seems to support the idea that shredder species identity effects are important for detritus processing in streams. Moreover, there is also evidence that species identity effects are important for resource use within other functional feeding groups. Jonsson & Malmqvist (in press) manipulated species number from one to three, for three separate groups of stream macroinvertebrates, filter feeders, grazers and predators. For all three groups, the authors reported significant effects of species identity on rates of resource use, while there were no effects of increasing species number. Therefore, the importance of species identity effects may be relevant for stream macroinvertebrates in general.

Evidence for positive effects of increasing detritivore diversity on detritus processing rates is far sparser than for species identity effects. The only evidence in the present study was from a field study across eighteen stream sites (Chapter 2). Chapter 2 did not reveal a direct positive relationship between shredder diversity and leaf processing. Rather, species diversity was among various abiotic and biotic factors that positively influenced leaf processing (Section 6.1.1). This is in contrast to two other field studies (Jonsson *et al.* 2001, Huryn *et al.* 2002), that each revealed a direct positive relationship between shredder diversity and leaf processing rates; although, the results of these field studies have, for different reasons, been questioned (see Section 2.4.1).

Although the field study reported in this thesis (Chapter 2) suggested that species diversity may be important for leaf processing across natural streams, further laboratory-based experiments did not provide any evidence to support this (Chapter 4). However, other laboratory-based experiments have reported positive effects of shredder species number on leaf processing (Jonsson & Malmqvist 2000, 2003). Jonsson & Malmqvist (2000) reported a positive linear relationship between leaf processing rates and diversity when shredder species number was increased from one up to three. However, the linear relationship revealed by this study may be an artefact of the small number of species used. That is, the effects of adding species may not continue far beyond three species because each new species is less likely to play a unique functional role (the 'redundancy hypothesis', Section 1.1.2). Results reported by another study appear to support this idea (Jonsson & Malmqvist 2003). Jonsson & Malmqvist (2003) used a species pool of six shredding stonefly species to create one-, three-, four- and six-species treatments. Results revealed that the three- and six-species treatments had significantly greater alder processing rates that the one-species treatment, but were not different from each other, while the four-species treatment was not different to the one-species treatment. The overall pattern suggested a 'redundancy hypothesis' type curve (Section 1.1.2, Figure 1.1c), where an increase in shredder species number beyond three, had no further effects on leaf processing rates. The study presented in this thesis (Chapter 4), revealed that leaf processing rates in the six-species treatment were not significantly different from the one-species treatment, in contrast with the results of Jonsson & Malmqvist (2003). One reason for these contrasting results may be the different groups of shredder species used. That is, positive interactions and/or niche differentiation, may have been more prevalent among the group of stonefly species used by Jonsson & Malmqvist (2003), than among the group of species used in Chapter 4.

In general, experiments suggest that the relationship between shredder species number and leaf processing rates, across a wide diversity range, should follow that predicted by the 'redundancy hypothesis' (Section 1.1.2), or that shredder diversity should be unimportant. However, the use of laboratory-based experiments to predict the types of patterns that may be observed in natural systems is extremely limited. It is not possible, in practical terms, to replicate every possible combination of species, at every diversity level, across a broad diversity gradient. At best, experiments can test the effects of shredder diversity for a small number of species combinations, along a modest gradient of diversity. An experiment therefore, may or may not reveal positive diversity effects, depending on the species chosen, and the combinations used. For example, in Chapter 4 of this thesis, only one six-species combination was compared with single-species treatments. Therefore, while there may be positive effects of shredder diversity on leaf processing at other diversity levels, or for other combinations of species, these were not examined.

6.2.1.2. Mechanisms.

6.2.1.2.1. Complementarity effects.

Results from this study have not provided any evidence that complementarity effects are important for driving positive shredder diversity-leaf processing relationships in streams. There was no evidence that the processing rates of single or mixed leaf resources increased with shredder species number in the field (Chapter 3). Moreover, there was no evidence for overyielding in mixed-species assemblages in stream mesocosms (Chapter 4), nor was there a positive relationship between complementarity in leaf diet between shredder species and leaf processing rates (Chapter 5). In general, there is very little evidence in the literature to support the occurrence of complementarity effects among stream detritivores.

To date, only one study using stream detritivores has presented convincing evidence for complementarity effects. Cardinale *et al.* (2002) demonstrated a positive effect of increasing the number of species of filter-feeding caddisfly larvae on total resource consumption. The authors present evidence indicating that species' facilitated each other resource capture through differences in the morphology of their filter-feeding nets, which altered near-bed flow, and increased the resource capture of other species. Cardinale *et al.* (2002) suggest that facilitation through biophysical interactions may be widespread in aquatic systems, because of the common occurrence of current shading, i.e. 'the deceleration of flow from upstream to downstream neighbours'.

While facilitation mediated through the alteration of flow dynamics may be important for relatively sedentary filter feeders, it is less likely to be important for shredders, which tend to be more mobile and can actively track leaf resources (Richardson 1991, Dobson & Hildrew 1992, Rowe & Richardson 2001). In the case of shredders, facilitation is more likely to be mediated through the resource itself, however there is little evidence to support this. Although facilitation has been proposed as a mechanism through which leaf processing has increased with shredder number (Jonsson & Malmqvist 2000), or with particular species combinations (Jonsson *et al.* 2002), only one experiment has provided clear evidence to support this suggestion (Jonsson & Malmqvist 2003).

Jonsson & Malmqvist (2003) tested the effect of the sequential introduction of two shredding stonefly species, *Taeniopteryx nebulosa* and *Protonemura meyeri*, on alder processing rates. Leaf mass loss was significantly greater for the treatments where *Taeniopteryx nebulosa* was introduced after *Protonemura meyeri*, than for all other treatments (i.e. all other combinations of sequential introduction), indicating that *Protonemura meyeri* modified the leaf resource in some way that was beneficial to *Taeniopteryx nebulosa*. The exact nature of the facilitation is unknown, since no behavioural observations were made, however, it is likely that differences in feeding morphologies or feeding behaviour were important.

Bengsston *et al.* (2002) propose a framework for the types of relationships to be expected between biodiversity and ecosystem function, given the major factors that influence species diversity, species abundances and process rates in communities (Section 1.6.2). A positive relationship is expected when there are positive interactions (i.e. facilitation) between species. Given the range of feeding modes represented by species within the shredder functional feeding group, there is certainly potential for positive interactions between species. Therefore, facilitation could be an important mechanism for positive effects of shredder diversity on leaf processing. However, more studies on the occurrence and nature of interactions between shredder species will help to reveal just how widespread facilitation may be among shredders, and therefore, the potential importance of this mechanism in stream detritivore systems.

A positive relationship between biodiversity and ecosystem function is also expected if there is competition between species for limiting resources that can be partitioned (Bengtsson *et al.* 2002, Section 1.6.2). As discussed in Section 1.6.2, there is evidence for resource limitation among shredding detritivores (e.g. Smock *et al.* 1989, Dobson & Hildrew 1992, Rowe & Richardson 2001). Moreover, there are several ways in which leaf litter resources may potentially be partitioned between shredders. One of these is the partitioning of the leaf resource itself, either by partitioning different types of leaf within a pack, or partitioning different parts of the leaf tissue of a single leaf type. Chapter 3 of this thesis provided no evidence that niche-differentiation of this type was important for leaf processing rates in the field, either for mixed or single leaf type resources. However, shredders may also partition the leaf resource spatially, by utilising different microhabitats within leaf packs or utilising different parts of the leaf tissue, or temporally by utilising leaf resources at different times throughout the day, or at different times during the period of leaf fall. While results from Chapter 2 of this thesis revealed a positive influence of shredder richness on leaf processing across natural streams, results from a laboratory experiment (Chapter 4) did not provide any evidence for species richness effects. These results may be reconciled if spatial or temporal partitioning of leaf resources are important mechanisms through which the effects of species richness manifest themselves in the field, since such mechanisms may go undetected in laboratory mesocosms.

The framework presented by Bengsston *et al.* (2002) predicts that niche-differentiation between species will not be an important mechanism for positive biodiversity-function relationships in systems where resources are not limited, or can not be partitioned. Chapter 5 of this thesis clearly demonstrated that there were differences between shredder species in both their leaf preferences, and in their ability to utilise different leaf types when offered no choice, and therefore that resources could potentially be partitioned, at least in terms of leaf type. However, this potential for resource partitioning may not have translated into a niche-differentiation effect during the limited time scale of the field study. Experimental litter bags were deployed in natural streams during mid-November and removed eight weeks later (Section 3.2.2). The field study therefore coincided with the period of peak leaf input into streams, and shredders may not have been resource limited during this time.

For example, Dobson & Hildrew (1992) reported that shredder abundance significantly increased as leaf litter accumulated in experimental leaf traps, in three out of four low-order streams in south-east England, suggesting that shredders were resource limited. However, in the fourth stream, leaf litter retention was naturally high, and there was no increase in shredder abundance with increased leaf accumulation in leaf traps, suggesting that shredders were not resource limited in a stream where leaf litter was abundant. The effects of niche-differentiation between shredder species, may therefore be revealed by a field study performed over a longer time scale, or during a period of minimal leaf input into streams, when shredders are more likely to become resource limited. Moreover, there were large difference in shredder composition and abundance between the stream sites used in Chapter 3 (Appendix D). Therefore, any influence of shredder species richness may have been masked in the field, given the occurrence and abundance of particular species at particular sites, especially *Gammarus pulex*.

Alternatively, niche-differentiation may have been unimportant in natural streams relative to other processes and interactions. The framework of Bengsston *et al.* (2002) predicts that no positive biodiversity-ecosystem function relationship is expected in disturbance-driven systems, or where interference competition dominates, because process rates will be driven by the traits of particular species (i.e. the dominant species). The extent of interference competition in the natural communities studied in Chapter 3 is unknown. However, irregular spates are known to affect invertebrate community structure in streams (Dobson & Frid 1998), and periods of high flow during the study period may have resulted in disturbance of the shredder community. Indeed, the abundance of one shredder species in particular, *Gammarus pulex*, was associated with high leaf mass loss in both field studies of this thesis (Chapter 2 and 3), possibly reflecting the importance of disturbance or interference competition, or both, in structuring the communities examined. The predominance of top-down effects may be another factor that precludes niche partitioning among species (Bengsston *et al.* 2002). Again, the occurrence and strength of predation in the natural invertebrate communities examined in this thesis is unknown. However, the first field study (Chapter 2) did reveal a positive influence of shredder species number on alder processing, and therefore suggests that the natural shredder communities were not completely dominated by disturbance, interference competition or top-down effects.

It is, therefore, unclear why a niche-differentiation effect was not detected in natural shredder communities. Although niche-differentiation between shredder species was tested directly in Chapter 5, any effects of complementarity in shredder diets on leaf processing rates, were clearly outweighed by the effects of particular species. However, Chapter 5 of this thesis represents the only study that has directly tested the niche-differentiation mechanism. Clearly, further study is required to determine the types of niche-partitioning that occur between shredder species, and whether these may drive positive shredder diversity-leaf processing relationships.

6.2.1.2.2. The selection effect.

Evidence from this thesis, and from other studies (Jonsson *et al.* 2002, Jonsson & Malmqvist, in press), has shown that species identity is important for detritus processing in streams. Given the strong influence of particular species on detritus processing rates, the selection effect seems a likely mechanism for driving a positive shredder diversity-leaf processing relationship in streams. That is, that leaf processing rates increase with species number because of the dominance of highly competitive species in high diversity communities. However, so far, there is no evidence from field observations or laboratory experiments to indicate that the selection effect may be an important mechanism in shredder communities.

Selection effects are difficult to demonstrate experimentally in stream detritivore systems for two reasons. First, in order to directly separate selection and complementarity effects, an experimental design is required that replicates every possible species combination, within every diversity level. This represents a major limitation for biodiversity-ecosystem function study in stream detritivore systems, in terms of the practicality of running a great number of mesocosms and collecting a sufficient number of animals to stock them with. This limitation may be overcome in two ways. Either, by using simple experimental designs, to compare single-species treatments with species mixtures (e.g. Chapter 4) or, by examining a very small number of species (e.g. Jonsson & Malmqvist 2000). However, in both of these cases, it is still not possible to separate likely mechanisms, if a positive effect of diversity is observed, because the contribution of individual species, within species mixtures, cannot be separated. Results from Chapter 4 of this thesis showed that there was no overall effect of shredder diversity on leaf processing rates, indicating that neither selection, nor complementarity effects, were occurring. However, it is difficult to determine whether the selection effect may have driven the positive effects of shredder diversity on leaf processing observed in other experiments (Jonsson & Malmqvist, 2000, 2003).

Evidence from field studies suggests that selection effects are not an important mechanism for driving positive diversity-leaf processing relationships in natural shredder communities (Jonsson *et al.* 2001, Huryn *et al.* 2002), and findings from the present thesis support this observation (Chapter 2). The abundance of one species in particular, *Gammarus pulex*, was positively related to leaf mass loss across eighteen natural streams (Chapter 2). Although the occurrence and abundance of *Gammarus pulex* was probably determined to some extent by differences in physico-chemical factors across stream sites, this species was not more likely to occur at high abundances in high shredder diversity communities. A field study by Huryn *et al.* (2002), across seventeen stream sites in Maine, U.S.A., revealed a positive relationship between shredder diversity and leaf mass loss. While leaf mass loss was also positively associated with shredder biomass, there was no evidence that high diversity was related to high shredder biomass. Jonsson *et al.* (2001) reported a positive relationship between shredder species number and leaf mass loss across twenty-three Swedish streams, but did not find any evidence for the presence of dominant species, that may have driven a selection effect.

6.2.2. Wider implications for stream detritivore systems.

The primary drivers of changes in biodiversity in stream systems are; changes in land use, which increase inputs of nutrients, sediment and various pollutants, climate change, and to lesser extent, invasion by exotic species (Richter *et. al.* 1997, Harding *et. al.* 1998, Sala *et. al.* 2000). Sala *et al.* (2000) used global models of climate, vegetation and land use, to estimate changes in the magnitude of these drivers, and the magnitude of biodiversity change itself, between the years 1990 and 2100. Using a ranking system for 'magnitude of change' ranging from small (1) to large (5), they estimated that changes in land use would be maximal for streams resulting in a maximal change in stream biodiversity. Other studies have also indicated that extinction scenarios for stream fauna are likely to be grave (e.g. Richter *et. al.* 1997, Ricciardi & Rasmussen 1999, Dodds 2002). For example, 65% of crayfish, and 67% of unionid mussels are classed as vulnerable, imperilled or extinct in the U.S.A. (Richter *et. al.* 1997). Given the projected scenarios of biodiversity loss in streams, what might be the consequences for stream ecosystem functioning? This ultimately depends on whether there is a relationship between biodiversity and ecosystem functioning in streams, and the shape of any relationship. However, it is difficult to draw any general conclusions from the limited number of experiments that have been performed so far in stream systems

Experimental evidence to support a positive linear relationship (Figure 1.1 b) between shredder diversity and leaf processing has been provided by only one study, that examined a diversity gradient of one to three species (Jonsson & Malmqvist 2000). Another experiment manipulated shredder diversity from one to six species (Jonsson & Malmqvist 2003), and revealed a relationship between diversity and leaf processing consistent with the 'redundant species hypothesis' (Figure 1.1. c). Although field studies have suggested a positive influence of shredder diversity on leaf processing (Jonsson *et al.* 2001, Huryn *et al.* 2002, Chapter 2), they have also revealed that increases in abundance or biomass may be able to compensate for low shredder diversity, therefore also indicating redundancy among shredder species. Therefore, current evidence suggests that decreases in shredder diversity in streams are unlikely to result in a linear decrease in leaf processing rates, since many species may be able to fulfil the functional roles of others.

However, evidence suggests that some species are not redundant, and have particularly strong effects on leaf processing. Strong effects of particular species on an ecosystem process can lead to an idiosyncratic relationship between biodiversity and ecosystem functioning (Section 1.1.2, Figure 1.1 d). Species identity effects have been demonstrated for shredder communities (Ruesink & Srivastava 2001, Jonsson *et al.* 2002, Chapter 4), and for other functional feeding groups in streams including filter feeders, grazers and predators (Jonsson & Malmqvist, in press). When there are species identity effects on an ecosystem process, the consequences of reductions in biodiversity will depend on the species that is lost. For example, evidence from this thesis suggests that *Gammarus pulex* is a particularly important species for leaf processing rates (Chapters 2 and 3) in the streams studied. In the same vein, Ruesink & Srivastava (2001) reported that leaf processing rates were significantly reduced in shredder communities from which the cased caddisfly larva *Lepidostoma unicolor* was removed.

The importance of species identity effects for detritus processing have important consequences for the bioassessment procedures, that are currently in wide use for assessing the impact of pollutants on stream function. The use of bioassessment procedures (e.g. Trent Biological Index, Biological Monitoring Working Party, river invertebrate prediction and classification (RIVPACS)) to evaluate stream function from macroinvertebrate community structure, implies a relationship between structure and function in streams. Further, the use of diversity indices to indicate levels of stream function (e.g. the Shannon-Weiner index), inherently assumes that a reduction in species diversity is related to a reduction in stream function. However, such bioassessment procedures may not give an accurate reflection of levels of stream function, if particular species have large effects on stream processes. A future challenge will be to explore the effects of losing particular individual species on ecosystem processes, and usefully integrate this information into bioassessment procedures. For example, species removal experiments, such as that performed by Ruesink & Srivastava (2001) (Section 6.2.1.1), could be used to examine the effects of losing a range of individual shredder species on detritus processing rates.

The effect of losing a shredder species with a strong influence on leaf processing may depend, however, on the diversity of the community from which it is lost. Although species may appear redundant for leaf processing in the short-term, they may become important as conditions change over time, and additional species are lost i.e. the 'insurance hypothesis' (Yachi & Loreau 1999, Loreau 2000). In this sense, shredder diversity may be important for leaf processing rates over the longer term, as changes in land use and climate alter environmental conditions. A shredder species may be lost from a community when its tolerance to a pollutant (e.g. herbicides, insecticides, detergents) or environmental conditions (e.g. temperature, pH), is exceeded (Metcalfe 1994). Higher shredder diversity communities may be better able to compensate for the loss of a species, because they represent a greater range of tolerance to, or responses to, changing environmental conditions (Yachi & Loreau 1999, Ives *et al.* 2000).

Results from this study provide tentative evidence for the importance of shredder diversity under changing environmental conditions. One way in which environmental conditions may vary in streams, is through changes in the riparian canopy altering leaf litter inputs into streams. For example, logging will result in the replacement of mature trees with early successional species, and therefore a change in the type of leaf resources available to shredders (Golladay *et al.* 1983). The results in Chapter 5 show that shredder species differed in their ability to utilise different leaf resources. Therefore, increased shredder diversity may increase the resilience, or resistance, of leaf processing rates, to changes in leaf inputs. Studies using aquatic microbes have suggested that high biodiversity can act as a buffer against environmental change (e.g. McGrady-Steed *et al.* 1997, Naeem & Li 1997). However, so far, no study has addressed the long-term effects of species diversity, under changing environmental conditions, for stream macroinvertebrate communities. This should be a priority for future study.

The decomposition of allochthonous organic matter by stream detritivores plays a fundamental role in the functioning of headwater streams (Maltby 1996). Detrital pathways are the routes for the major flows of energy and cycling of nutrients in streams (Webster & Benfield 1986, Giller & Malmqvist 1999), and the shredder functional feeding group is known to play an important role in detritus processing (Section 1.6.1). Ultimately, therefore, the effect of reduced rates of leaf processing by shredders on stream function, is the disruption of energy flow and nutrient cycling.

For example, the downstream export of fine particulate organic matter (FPOM), in the form of fragmented leaf material and shredder faeces, may be reduced, having a knock-on effect on other functional feeding groups (i.e. collector-filterers and collector-gatherers), and other trophic levels. Cuffney *et al.* (1990) reported that annual FPOM export was reduced by 66.7% in a stream where most shredders were eliminated, by the application of an insecticide (methoxychlor). Evidence from other studies indicates that changes in FPOM production can affect collector populations (Cummins *et al.* 1973, Richardson & Neill 1991, Grant 1996). For example, Grant (1996) reported that a decrease in FPOM production reduced the growth of the collector species *Chironomus riparius*. Richardson & Neill (1991) found that densities of collectors increased in response to elevated input rates of detritus into artificial stream channels. Therefore, reductions in leaf processing by shredder species, could potentially effect the survival and reproduction of collector populations, which may in turn effect organisms at higher trophic levels, such as predatory invertebrates and fish populations. However, further studies are required to examine these potential effects of reduced leaf processing rates by shredders.

6.3. Comparison of findings in stream detritivore systems with other ecosystem types.

A survey of 91 tests of hypotheses, about the effect of biodiversity on ecosystem function, reported that 43 (47%) demonstrated a positive biodiversity - ecosystem function relationship, while 10 (11%) showed a negative relationship and 38 (42%) showed no effect, or inconsistent effects, of diversity (Schläpfer & Schmid 1999). Out of the 91 tests used to compile this survey, only eight were from aquatic systems, and these were represented by two microbial microcosm studies (McGrady-Steed *et al.* 1997, Naeem & Li 1997) and one study using species of zooplankton (Norberg 1998 in Schläpfer & Schmid 1999). Clearly it is difficult to draw any general comparisons between aquatic systems and other ecosystem types, based on such sparse evidence. However, the literature on aquatic systems, and specifically for stream detritivore systems (Table 6.1), has grown since this survey was compiled, allowing some tentative comparisons to be made.

Experimental plant assemblages represent the large majority of biodiversity – ecosystem function studies (Section 1.2). Positive relationships between plant diversity and a range of ecosystem processes have commonly been observed in such studies. Data compiled by Schläpfer & Schmid (1999) indicates that positive effects of plant diversity on ecosystem processes were reported for 57% of tests, inconsistent or no effects for 37%, and the remainder (6%) showed negative relationships. Similar overall patterns have also been observed, from steam detritivore studies, to date. While 60% of studies have demonstrated positive effects of macroinvertebrate diversity on resource consumption, the remainder has reported no effect, but no negative effects of diversity have so far been revealed (Table 6.1).

The preponderance of positive diversity effects, observed in both plant and stream detritivore systems are perhaps not surprising, given that positive effects of diversity on ecosystem processes are expected in systems where there are positive interactions between species, and/or competition for a limiting resource that can be partitioned (Bengtsson *et al.* 2002). There is evidence that positive interactions can occur between species, both for plant and stream detritivore systems. For example, water sharing via hydraulic lift (Caldwell *et al.* 1998) and nutrient sharing via mycorrhizal networks (Read 1997) in plants, and increased delivery of resources to neighbouring species via alterations in near-bed flow in stream filter feeders (Cardinale *et al.* 2002). Moreover, productivity in terrestrial plant communities is known to be limited by several factors including water, light and various nutrients (Begon *et al.* 1990). Evidence suggests that stream detritivore communities also experience resource limitation (e.g. Smock *et al.* 1989, Dobson & Hildrew 1992, Rowe & Richardson 2001). Further, there is potential for resource partitioning in plant (see Fridley 2001) and stream detritivore (see Section 1.6.2) communities, based on the different ways in which resources are utilised by different species.

However, a closer examination of the types of studies that have reported positive diversity effects, reveals that there may be differences between the patterns observed in plant and stream detritivore systems, and particularly, in the mechanisms driving positive diversity effects. Three out of six of the positive species diversity – ecosystem function relationships reported for stream detritivore systems are based on correlative field data (Table 6.1). Only three out the remaining seven experimental studies reported positive diversity effects (Table 6.1), representing only 43% of experiments, compared with 57% of experiments in plant systems. In contrast, species identity effects were reported for four out of the five studies (80%) in which they were examined, and composition effects were reported for three out of four studies (75%) (Table 6.1). Therefore, species identity and composition effects appear to be more common than positive species diversity effects, for experimental studies in stream detritivore systems.

Apart from studies that have explicitly tested for species identity (e.g. Symstad *et al.* 1998) or composition effects (e.g. Tilman *et al.* 1997a, Hooper & Vitousek 1997), such effects have been rarely been reported for experimental plant assemblages (but see Tilman *et al.* 2001, Hector *et al.* 1999). Reasons for this apparent contrast between stream detritivore and plant systems may stem from differences in experimental designs, and the numbers of species used to construct diversity gradients. Diversity has been manipulated across very low numbers of species in stream detritivore systems, typically one to three, due to practical limitations (see Section 6.2.1.2.2). Experimental designs have replicated all species combinations, at all diversity levels, allowing species identity and species composition effects to be detected. At such low levels of diversity, and across such a narrow range of species, strong effects of particular species, or species combinations, are most likely to manifest themselves as idiosyncratic responses. However, diversity in plant systems has usually been manipulated across a much wider range (typically from one, up to anything between nine and thirty-two species). Further, experimental designs in plant systems have usually assigned species randomly to replicates within each diversity level. Given the wider range of diversity, and the experimental approach used in many plant studies, any strong effects of particular species, or species combinations, are likely to manifest themselves as a positive relationship between biodiversity and ecosystem function, through the selection effect (Section 1.4.1). Schläpfer & Schmid (1999) reported that positive effects of biodiversity on ecosystem processes were often associated with randomised species composition designs, and also with studies that manipulated diversity across a relatively wide range.

Table 6.1. Effects of biodiversity, species identity and composition on resource consumption in stream detritivore studies (sorted by study method and then chronologically).

Reference	Study method	Functional feeding group	Diversity gradient	Diversity effect	Species identity effect	Species composition effect
Jonsson *et al.* 2001	Correlative field data	Shredder	1 - 11	Yes (+)	Not examined	Not examined
Huryn *et al.* 2002	Correlative field data	Shredder	0 – 6[a]	Yes (+)	Not examined	Not examined
Chapter 2	Correlative field data	Shredder	2 - 20	Yes (+)	Yes	No
Jonsson & Malmqvist 2000	Community construction	Shredder	1 - 3	Yes (+)	No	No
Cardinale *et al.* 2002	Community construction	Collector-filterer	1 - 3	Yes (+)	Not examined	Not examined
Jonsson *et al.* 2002	Community construction	Shredder	1 - 3	No	Yes	Yes
Jonsson & Malmqvist 2003	Community construction	Shredder	1, 3, 4, 6	Yes (+)	Not examined	Not examined
Jonsson & Malmqvist in press	Community construction	Collecter-filterer	1 - 3	No	Yes	Yes
Jonsson & Malmqvist in press	Community construction	Grazer	1 - 3	No	Yes	Yes
Chapter 4	Community construction	Shredder	1, 6	No	Yes	Not examined

[a] mean number of shredder taxa per litterbag. (+) indicates positive effects of biodiversity on resource consumption.

The diversity range examined in stream detritivore experiments has been limited for practical reasons (Section 6.2.1.2.2), however, field studies have examined biodiversity effects on ecosystem processes across much wider ranges of diversity (see Table 6.1). Evidence from these studies indicates that the selection effect mechanism is not important for driving the positive effects of shredder diversity on leaf processing in natural streams (Section 6.2.1.2.2). There are very few studies using natural communities, from other ecosystem types, with which to compare patterns in stream detritivore systems. Plant species diversity was found to positively effect total plant cover and nitrogen uptake in an undisturbed grassland in Minnesota (Tilman *et al.* 1996). However, the authors do not address whether the positive diversity effect was driven by the presence of dominant species in high diversity communities.

One further study, from a marine system, reported a positive relationship between the number of sediment dwelling invertebrate species and the flux of ammonia nitrogen to the water column, for three different natural marine communities (Emmerson *et al.* 2001). Results revealed that particular dominant species contributed disproportionately to ammonia nitrogen production at each of the three sites. However, similarly to results from Chapter 2, species with a strong effect on the ecosystem process in question, were present across the range of species richness. This last point is an important one, because the selection effect has been criticised as a legitimate mechanism on the basis that natural communities do not assemble, or disassemble, randomly, and therefore species with strong effects on an ecosystem processes are not more likely to be present in high diversity communities (Section 1.5.2.1). Evidence from both marine and stream systems would, at present, seem to support this.

The effect of diversity on ecosystem processes has also been addressed in soil decomposer systems. Evidence from the limited number of studies, that have examined the effects of soil decomposer diversity on decomposition processes, suggests that positive effects are rare compared with plant systems. A review of soil decomposer studies revealed that five out of eleven experiments reported positive effects of decomposer diversity on an ecosystem process (Mikola *et al.* 2002). Further, species identity or composition effects, were detected in all six experiments that examined them. The overall patterns from soil decomposer experiments therefore appear to reflect those observed from stream detritivore experiments.

This may simply reflect the fact that most studies in soil decomposer systems have also been conducted across a narrow range of diversity (typically from one, up to a maximum of five species). However, there are similarities between soil and stream decomposer systems that may result in similar mechanisms influencing the detritivore diversity-decomposition relationship. For example, soils (Giller 1996) and streams (Dobson & Frid 1998, Finn 2001) are both heterogeneous environments where resource patches are spatially and temporally variable, which in turn affects the distribution and abundance of detritivores (Sulkava & Huhta 1998, Giller & Malmqvist 1998). Such patchiness may in some way influence the biodiversity-ecosystem function relationship in such systems, though the mechanisms are not known (Mikola *et al.* 2002).

Moreover, decomposition processes are influenced by interacting organisms from different trophic groups (bacteria, fungi, macroinvertebrates) in both stream (Maltby 1996, Section 1.6.1) and soil (Mikola *et al.* 2002) systems. However, while the roles of different detritivore trophic groups, and their interactions, are relatively well characterised for stream systems (e.g. Kaushik & Hynes 1971, Cummins *et al.* 1973, Webster & Benfield 1986, Gessner *et al.* 1999, Graça 2001), the roles of individual trophic groups, and their interactions, in soil systems are poorly understood (Mikola *et al.* 2002). Therefore, in stream detritivore experiments, groups of species can be directly linked to ecosystem processes (e.g. shredders are clearly linked with the fragmentation of leaf litter). However, the considerable lack of knowledge about the functional roles of individual decomposer species in soil detritivore systems presents a difficulty for linking species to particular ecosystem processes. In soil detritivore experiments, therefore, the practical inability to identify and separate complex multi-trophic interactions may be an additional reason for the lack of positive biodiversity-function relationships observed.

Few studies have examined explicitly the biodiversity-ecosystem functioning relationship for marine systems. Studies to date have focused on the effects of marine invertebrate diversity on various ecosystem processes and properties including; flux of nutrients to the water column (Emmerson & Raffaelli 2000, Emmerson *et al.* 2001), epiphyte grazing, plant and grazer biomass accumulation (Duffy *et al.* 2001), and invasion resistance (Stachowicz *et al.* 1999). Overall, these studies provide little evidence for positive biodiversity-ecosystem functioning relationships in marine systems. However, such studies are subject to similar practical limitations as stream detritivore experiments

(Section 6.2.1.2.2), and therefore designs have typically involved a narrow range of diversity (from one to three), with every species composition replicated within each diversity level. As for stream detritivore experiments, species identity and composition effects have been reported from marine systems more commonly than positive effects of species diversity (e.g. Duffy *et al.* 2001, Emmerson & Raffaelli 2000). One study did report a positive effect of increasing the diversity of sessile marine invertebrates on the invasion resistance of communities (Stachowicz *et al.* 1999). The authors suggest that the more complete utilisation of space in higher diversity communities reduced resource availability, and therefore, decreased the success of invading species. While there was a significant negative linear relationship between species diversity and 1) the percentage of unoccupied space and 2) the percentage of invaders surviving, the authors did not examine the relative importance of species identity and species composition for invasion resistance.

There is potential for complementarity between marine invertebrates, as for stream detritivores. For example, different species of sediment-dwelling invertebrates show differentiation in the depth and shapes of the burrows that they make (Emmerson & Raffaelli 2000), while species of crustacean grazer exhibit different grazing behaviours (Duffy *et al.* 2001). In contrast to stream detritivore systems, some evidence for complementarity effects has been revealed for marine invertebrate communities. Overyielding is the most stringent and unambiguous test for complementarity effects (see Section 1.5.1), and Emmerson *et al.* (2001) reported that overyielding occurred in just under 25% of the treatments that contained mixtures of invertebrate species. Moreover, the proportion of treatments showing overyielding increased with species number.

Aquatic systems, in general, are vastly under-represented compared with terrestrial systems, in terms of biodiversity-ecosystem function study. Emmerson & Huxham (2002) have suggested that the re-examination of published and unpublished data may prove a valuable tool for assessing biodiversity effects in marine benthic systems, since there is a wealth of literature which has not previously been considered from the biodiversity-ecosystem function perspective. For example, synthesis of data from fifteen studies, that presented information on nutrient fluxes and marine benthic community structure, revealed a positive linear relationship between NH_4 flux and species richness (Emmerson & Huxham 2002). Although cross-study comparisons are subject to limitations (i.e. variability due to unquantified or uncontrolled factors), the same approach could also be applied to stream detritivore systems, to extend current knowledge based on evidence from existing literature.

While the re-analysis of existing data may provide insights, novel research is also required to extend our knowledge to other aspects of biodiversity - ecosystem function relationships in stream detritivore systems. For example, the relationship between functional group diversity and ecosystem function has been explored for plant assemblages (e.g. Hooper & Vitousek 1997, Tilman *et al.* 1997a), soil decomposer systems (e.g. Wardle *et al.* 1997a, Bradford *et al.* 2002) and benthic marine systems (Emmerson & Raffaelli 2000). So far, studies in stream detritivore systems have focused on manipulating species diversity within a single functional feeding group. Species have been used as the basic unit of biodiversity in most studies, across most ecosystem types. However, biodiversity at other levels of taxonomic resolution (e.g. genotype, genus, family, class), or diversity of habitat patches within heterogeneous environments (e.g. different substrate patches on stream beds), may also be important for ecosystem function (Giller *et al.*, in press), both in streams and in other types of ecosystem. Moreover, the effect of biodiversity on an array of ecosystem processes and properties, remains unexplored in stream detritivore systems. For example, on aspects of elemental cycling (e.g. nitrogen transformations), physical structuring (e.g. sedimentation, bioturbation), and on ecosystem properties such as the stability of processes, invasion resistance and trophic structure (see Giller *et al.*, in press). These unexamined areas represent future challenges for biodiversity-ecosystem function research in stream detritivore systems.

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Appendix A.

Environmental data collected across eighteen stream sites for Field Study 1 (Chapter 2). Temperature (°C), dissolved oxygen (% saturation), flow rate (m/s), and conductivity (µS/cm) are mean values. Stream order was assigned using the Strahler Method (Dobson & Frid 1998). Canopy cover was estimated using a visual judgement. River names in parentheses indicate that the site used was a tributary of the river name given.

Site name	River name	Temperature (°C)	Dissolved oxygen (% saturation)	Flow rate (m/s)	Conductivity (µS/cm)	pH	Stream order	Canopy cover
Stone	Maltby Dike	8.2	98	0.36	849	7.7	2	30
Greystones	Porter Brook	5.8	96	0.22	295	7.7	2	100
Lindrick Dale	Anston Brook	7.0	81	0.30	926	7.4	3	90
Barlow Trout Farm	Barlow Brook	5.8	82	0.14	423	7.3	3	98
Smeekly Wood	Barow Brook	5.7	75	0.31	395	7.8	2	98
Hillhouses	(River Rother)	5.5	94	0.58	312	7.5	2	96
Highlightly Farm	Barlow Brook	6.0	86	0.15	306	7.5	3	90
Charlton Brook	Hall Brook Dike	7.3	84	0.30	243	7.0	1	90
Crowdecote	River Dove	6.8	93	0.78	345	7.6	3	40
Cranemoor	(River Dove)	7.5	90	0.21	495	7.2	1	15
Strines	Strines Dike	5.1	96	0.42	592	4.7	3	90
Oughtibridge	(River Don)	7.8	95	0.34	292	7.2	1	60
Netherloads	(River Hipper)	6.2	86	0.28	248	7.2	1	90
Lowmill	(River Deame)	7.7	82	0.34	692	7.2	3	90
Holehouse	(River Etherow)	6.6	85	0.24	158	6.8	1	60
Berrymoor	(River Dove)	7.6	80	0.17	545	7.4	2	60
Brockhurst	River Amber	6.1	86	0.69	262	7.9	2	98
Barlow Brook	Barlow Brook	5.7	80	0.14	413	7.5	3	90

Appendix B.

Summary of biotic data collected across eighteen stream sites for Field Study 1 (Chapter 2). River names in parentheses indicate that the site used was a tributary of the river name given.

Site name	River name	Macroinvertebrate species richness			Macroinvertebrate abundance			Shredder biomass
		Total	Shredder	Non-shredder	Total	Shredder	Non-shredder	(g, wet weight)
Stone	Maltby Dike	21	2	19	6200	3961	2239	37.91
Greystones	Porter Brook	40	13	27	1749	759	990	2.39
Lindrick Dale	Anston Brook	27	5	22	3182	2568	614	20.41
Barlow Trout Farm	Barlow Brook	47	13	34	1117	130	987	0.19
Smeekly Wood	Barow Brook	50	16	34	1002	597	405	0.61
Hillhouses	(River Rother)	46	13	33	2779	335	2444	1.50
Highlightly Farm	Barlow Brook	42	11	31	1299	304	995	0.27
Charlton Brook	Hall Brook Dike	40	9	31	1299	613	686	1.00
Crowdecote	River Dove	15	5	10	320	17	303	0.05
Cranemoor	(River Dove)	59	11	48	7514	1949	5565	10.96
Strines	Strines Dike	19	11	8	293	274	19	0.14
Oughtibridge	(River Don)	46	17	29	1838	580	1258	2.50
Netherloads	(River Hipper)	44	10	34	777	93	684	0.56
Lowmill	(River Dearne)	34	8	26	1916	316	1600	1.72
Holehouse	(River Etherow)	48	20	28	1417	603	814	1.88
Berrymoor	(River Dove)	58	18	40	3768	2139	1629	3.70
Brockhurst	River Amber	49	17	32	1438	298	1140	0.30
Barlow Brook	Barlow Brook	44	11	33	1421	136	1285	0.36

Appendix C.

Macroinvertebrate species found at each site for Field Study 1 (Chapter 2). Site names are abbreviated as follows: Stone = Sto, Greystones = Gre, Lindrick Dale = Lkd, Barlow Trout Farm = Btf, Smeekly Wood = Smw, Hillhouses = Hil, Highlightly Farm = HiF, Charlton Brook = Chb, Crowdecote = Cro, Cranemoor = Cra, Strines = Str, Oughtibridge = Oug, Netherloads = Net, Lowmill = Low, Holehouse = Hol, Berrymoor = Ber, Brockhurst = Bro, Barlow Brook = Bab. Numbers indicate species presence and total abundance found in eight kick samples. For Coleoptera, (A) = indicates adult stage and (L) indicates larval stage. Names in parentheses indicate a sub-genus.

	Site																	
Taxon name	Sto	Gre	Lkd	Btf	Smw	Hil	Hif	Chb	Cro	Cra	Str	Oug	Net	Low	Hol	Ber	Bro	Bab
Shredders																		
Amphipoda																		
Gammarus pulex (L.)	3013	371	2414	0	68	234	1	195	7	1627	0	176	35	129	211	221	13	2
Diptera																		
Tipula (*Savtshenkia*)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Tipula (*Yamatapula*)	0	0	1	1	1	3	0	0	0	22	0	2	0	0	0	5	0	0
Isopoda																		
Asellus aquaticus (L.)	882	7	151	0	0	3	0	0	4	0	2	0	0	18	0	0	0	1
Plecoptera																		
Amphinemura sulcicollis (Stephens)	0	1	0	4	19	1	0	0	0	0	133	5	0	0	1	2	25	0
Brachyptera risi (Morton)	0	1	0	4	70	1	1	0	1	0	0	90	1	0	3	1	40	0
Capnia bifrons (Newman)	0	0	0	4	0	0	11	0	0	0	0	0	0	0	0	37	0	5
Leuctra fusca (Linné)	0	0	0	8	0	1	3	0	0	0	0	0	0	0	0	2	0	0
Leuctra hippopus (Kempny)	0	21	0	39	85	5	114	110	0	45	13	134	24	36	31	832	62	30
Leuctra nigra (Olivier)	0	11	0	1	52	0	0	107	0	0	0	39	0	0	40	2	5	0
Nemoura avicularis Morton	0	2	0	25	1	15	22	0	0	6	0	1	0	11	0	25	6	46
Nemoura cambrica (Stephens)	0	187	0	0	12	16	0	157	0	51	3	38	2	87	98	885	11	0
Nemoura erratica Claassen	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	57	0	0
Nemurella picteti Klapálek	0	0	0	0	0	0	0	0	0	0	23	0	2	0	1	0	0	0
Protonemura meyeri (Pictet)	0	0	0	0	0	0	0	0	0	0	13	11	0	0	6	0	11	0
Protonemura montana Kimmins	0	0	0	0	16	0	0	0	0	0	0	22	0	0	0	0	2	0
Protonemura montana Kimmins	0	0	0	0	16	0	0	0	0	0	0	22	0	0	0	0	2	0

Appendix C (continued)

	Site																	
Taxon name	Sto	Gre	Lkd	Btf	Smw	Hil	Hif	Chb	Cro	Cra	Str	Oug	Net	Low	Hol	Ber	Bro	Bab
Shredders (continued)																		
Plecoptera (continued)																		
Protonemura praecox (Morton)	0	0	0	0	20	0	0	0	0	0	78	15	0	0	51	0	59	0
Trichoptera																		
Adicella reducta (McLachlan)	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0
Agepetus spp.	0	0	0	0	1	0	0	2	0	0	0	1	0	0	0	1	1	0
Athripsodes sp.	0	0	0	0	0	18	0	0	0	0	0	0	0	0	0	0	0	13
Halesus digitatus (Schrank)	0	1	0	0	1	0	12	0	4	0	0	0	0	0	0	0	0	28
Halesus radiatus (Curtis)	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Lepidostoma hirtum (Fabr.)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
Leptoceridae spp. (1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Leptoceridae spp. (2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Leptoceridae spp. (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Limnephilidae spp. (1)	0	5	0	6	78	33	4	23	1	138	0	17	10	28	13	16	21	1
Limnephilidae spp. (2)	0	0	0	24	2	0	124	0	0	47	0	0	2	1	18	19	30	1
Limnephilidae spp. (3)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Limnephilidae spp. (4)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Limnephilidae spp. (5)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Micropterna sequax McLachlan	0	0	1	0	0	0	0	0	0	5	0	1	0	0	0	0	0	0
Odontocerum albicorne (Scopoli)	0	0	0	7	3	0	0	7	0	0	0	5	0	0	3	0	0	0
Potamophylax cingulatus (Stephens)	0	1	0	0	0	0	0	0	0	2	2	0	0	0	1	2	0	0
Potamophylax latipennis (Curtis)	0	15	1	0	1	3	0	8	0	2	0	19	15	0	30	4	4	1
Potamophylax rotundipennis (Brauer)	0	0	0	1	0	0	0	5	0	0	2	4	0	0	20	0	2	0
Sericostoma personatum (Spence)	0	12	0	6	1	0	11	1	0	3	0	0	1	6	2	27	5	8
Non-shredders																		
Diptera																		
Berdenelli spp.	7	1	10	2	2	13	7	6	1	37	0	14	10	9	1	38	5	8
Cheilotrichia spp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0

Appendix C (continued)

Taxon name	Sto	Gre	Lkd	Btf	Smw	Hil	Hif	Chb	Cro	Cra	Str	Oug	Net	Low	Hol	Ber	Bro	Bab
Non-shredders																		
Diptera (continued)																		
Chelifera spp.	0	1	0	3	2	13	15	1	1	11	0	3	3	6	0	1	1	7
Chironmidae spp.	476	206	6	478	76	992	601	251	59	873	0	340	339	398	17	217	119	624
Copropsychoda spp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Culicoides spp.	6	4	1	7	1	7	1	5	0	46	0	1	0	3	2	10	0	2
Cyclorrapha spp.	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0
Diptera spp. (1)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Diptera spp. (2)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Dixa spp.	0	0	0	0	3	2	0	3	0	3	0	4	1	0	0	0	0	2
Eloephila spp.	0	0	0	0	7	7	2	11	0	2	0	3	5	5	3	4	1	2
Forcipomyia spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0
Hemerodrominae spp. (1)	3	1	1	0	1	26	6	1	0	0	4	10	7	0	0	0	10	4
Hemerodrominae spp. (2)	1	1	1	11	1	0	1	0	1	16	0	0	0	8	0	1	0	12
Limnophora spp.	9	0	2	2	0	3	0	0	0	3	0	0	0	0	0	0	0	2
Limonidae spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Muscidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Nematocera spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Nevermannia lundistromi (Enderlein)	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0	0	1	0
Pedicia spp.	0	4	0	12	3	26	21	19	18	23	6	5	30	31	14	11	1	12
Prodiamesinae spp.	49	5	0	3	0	13	0	7	0	11	0	18	3	6	1	3	0	12
Prosimulium spp.	789	205	17	39	14	329	71	2	11	430	1	85	9	280	6	157	46	60
Pseudolimnophora spp.	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Psychoda spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Psychodidae spp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Psychodidae spp. (2)	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0
Ptychoptera lacustre Meigen	0	0	0	0	0	13	0	8	0	0	0	0	0	0	1	1	0	0
Rhagionidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Spligona spp.	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0

Appendix C (continued)

	Site																	
Taxon name	Sto	Gre	Lkd	Btf	Smw	Hil	Hif	Chb	Cro	Cra	Str	Oug	Net	Low	Hol	Ber	Bro	Bab
Non-shredders (continued)																		
Neuroptera																		
Sialis fuliginosa Pictet	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0
Sialis lutaria (L.)	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Trichoptera																		
Diplectrona felix McLachlan	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Drusus annulatus Stephens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hydropschye instabilis (Curtis)	59	69	167	4	12	7	1	46	0	272	0	159	0	3	130	151	39	27
Lype reducta (Hagen)	0	0	0	0	6	0	1	0	0	0	0	0	0	0	0	0	0	0
Philopotamus montanus (Donovan)	0	0	0	2	0	0	0	0	0	2	0	0	0	0	1	27	0	0
Plectronemia conspersa (Curtis)	0	6	0	3	3	1	0	6	0	14	0	1	17	1	3	15	6	0
Rhyacophila dorsalis (Curtis)	0	18	0	7	0	18	6	1	0	14	2	24	22	0	12	17	28	3
Ryhacophila obliterata McLachlan	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	1	0	0
Mollusca																		
Ancylus fluviatilis Müll	1	0	0	31	0	1	6	1	0	15	0	1	0	3	0	21	0	4
Gastropoda spp. (1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lymneae spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	0	0	0
Planorbis laevis Alder	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Planorbus contortus (L.)	0	0	3	0	0	0	0	0	0	6	0	0	0	0	0	0	1	0
Potamopyrgus jenkinsi (Smith)	14	0	9	24	0	325	1	109	0	2525	0	29	0	134	0	52	0	55
Pysa fontinalis (L.)	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Segmentina complanata (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7
Sphaerium corneum (L.)	1	0	1	1	1	254	0	0	2	6	0	0	11	5	1	11	1	4
Unionidae spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0
Valvata cristata Müll	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Zonitoides spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Succinea spp.	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	10	0	0

Appendix C (continued)

	Site																	
Taxon name	Sto	Gre	Lkd	Btf	Smw	Hil	Hif	Chb	Cro	Cra	Str	Oug	Net	Low	Hol	Ber	Bro	Bab
Non-shredders (continued)																		
Coleoptera																		
Agabus spp. (l)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Coleoptera spp. (1) (A)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Coleoptera spp. (2) (A)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Elmis aenea (A) (Müller)	0	3	5	8	0	24	0	0	0	57	1	21	0	1	1	3	54	0
Elmis aenea (L)	0	11	152	65	7	83	11	3	0	143	0	35	0	23	1	15	15	15
Elodes spp. (L)	0	0	0	0	9	3	1	1	0	80	0	5	0	2	5	19	3	0
Helophorus spp. (L)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hydraenidae spp. (L)	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0
Hydraenidae spp. (L)	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Limnius volckmari (A) (Panzer)	0	11	0	26	4	0	8	8	0	37	0	11	1	1	0	3	29	3
Limnius volckmari (L)	0	0	0	8	0	5	1	0	0	0	0	2	0	1	1	4	5	4
Platambus spp. (L)	0	0	0	1	2	0	0	0	0	12	0	0	6	3	0	0	1	4
Potamonectes griseostriatus (A) (Deager)	0	0	1	0	1	0	0	0	0	12	0	0	0	0	0	0	2	0
Arachnida																		
Halacaridae spp. (1)	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	1	0
Halacaridae spp. (2)	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	5	2	0
Halacaridae spp. (3)	5	0	3	1	0	0	4	1	0	14	0	0	1	0	0	0	0	1
Halacaridae spp. (4)	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Halacaridae spp. (5)	0	0	0	0	2	0	0	0	0	20	0	0	0	1	0	0	0	0
Halacaridae spp. (6)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Halacaridae spp. (7)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hydrachnellae spp. (1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Hydrachnellae spp. (2)	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Hydrachnellae spp. (3)	0	0	0	1	2	0	0	0	0	0	1	0	1	0	0	0	0	0
Hydrachnellae spp. (4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hydrachnellae spp. (5)	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
Hydrachnellae spp. (6)	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0

Appendix C (continued)

	Site																
Taxon name	Sto	Gre	Lkd	Btf	Smw	Hil	Hif	Chb	Cro	Cra	Str	Oug	Net	Low	Hol	Ber	Bro	Bab
Non-shredders (continued)																		
Oligochaetae																		
Oligochaetae spp. (1)	47	2	1	39	4	126	18	8	2	2	0	1	6	39	3	3	0	14
Oligochaetae spp. (2)	0	1	0	0	0	0	1	0	0	4	0	1	1	0	1	1	0	0
Oligochaetae spp. (3)	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Hirunidea																		
Batracobdella paludosa (Carena)	72	1	16	1	0	0	0	0	0	2	0	0	0	0	0	0	0	0
Glossiphona complanata (L.)	21	3	5	1	1	0	0	0	0	6	0	1	2	0	0	0	0	0
Helobdella stagnalis (L.)	9	0	2	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Decapoda																		
Austropotamobus pallipes (Lereboulet)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Plecoptera																		
Chloroperla torrentium (Pictet)	0	2	0	0	22	0	2	0	0	0	0	1	4	0	0	5	1	0
Dinocras cephalotes (Curtis)	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Isoperla grammatica (Poda)	0	1	0	3	16	0	7	20	0	3	0	33	8	0	38	17	171	0
Perlodes microcephala (Pictet)	0	0	0	0	5	0	0	0	0	0	0	0	0	0	19	0	0	0
Plecoptera spp. (1)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Plecoptera spp. (2)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Taeniopteryx nebulosa (L.) Aubert	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Ephemeroptera																		
Baetis rhodani (Pictet)	735	307	209	153	259	99	127	68	205	801	3	447	174	617	32	738	318	342
Caenis horaria (L.)	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Ecdyonurus dispar (Curtis)	0	102	0	23	27	11	29	0	0	0	0	0	3	0	24	25	98	3
Ecdyonurus torrentis Kimmins	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0
Ephemera danica Müller	0	0	0	4	0	4	2	0	0	0	0	0	0	11	8	1	5	3
Paraleptophlebia submarginata (Stephens)	0	5	0	7	1	29	3	0	0	12	0	0	1	2	0	29	0	42
Rhithrogena semicolorata (Curtis)	0	142	0	15	73	2	38	91	3	22	0	0	7	0	556	3	171	1

Appendix D.

Shredder species found at each site for Field Study 2 (Chapter 3). Numbers indicate species presence and total abundance found in nine kick samples. Names in parentheses indicate a sub-genus.

	Site							
Taxon name	Stone	Lindrick Dale	Strines	Crowdecote	Outibridge	Berrymoor	Brockhurst	Holehouse
Amphipoda								
Gammarus pulex (L.)	5757	3362	0	10	234	263	12	169
Diptera								
Tipula spp.	0	1	0	0	0	0	0	1
Tipula (*Yamatapula*)	1	1	0	0	0	3	1	0
Isopoda								
Asellus aquaticus (L.)	231	107	0	0	0	2	0	1
Plecoptera								
Amphinemura sulcicollis (Stephens)	0	0	165	0	2	0	99	1
Brachyptera risi (Morton)	0	0	0	0	88	0	32	67
Capnia bifrons (Newman)	0	0	0	0	0	12	0	0
Capnia vidua Klapálek	0	0	3	0	0	0	0	0
Leuctra fusca (Linné)	0	0	0	0	0	2	0	0
Leuctra hippopus (Kempny)	0	0	76	3	14	187	56	145
Leuctra nigra (Olivier)	0	0	3	0	10	0	4	259
Nemoura avicularis Morton	0	0	0	2	0	1	8	0
Nemoura cambrica (Stephens)	0	0	0	0	13	315	30	174
Nemoura erratica Claassen	0	0	0	0	0	6	5	0
Nemurella picteti Klapálek	0	0	100	0	0	0	0	8
Protonemura meyeri (Pictet)	0	0	0	0	0	0	4	0
Protonemura montana Kimmins	0	0	0	0	7	0	0	0
Protonemura praecox (Morton)	0	0	140	3	42	0	27	91

Appendix D (continued)

	Site							
Taxon name	Stone	Lindrick Dale	Strines	Crowdecote	Outibridge	Berrymoor	Brockhurst	Holehouse
Trichoptera								
Adicella reducta (McLachlan)	0	0	0	0	0	0	0	4
Chaetopteryx villosa Fabricus	0	0	0	0	0	0	0	2
Halesus digitatus (Schrank)	0	0	6	1	0	0	0	0
Lepidostoma hirtum (Fabr.)	0	0	0	0	0	1	0	4
Limnephilidae spp. (1)	0	1	0	9	16	105	45	46
Limnephilidae spp. (2)	0	0	0	1	0	0	3	1
Limniphilus auricula Curtis	0	0	0	0	0	0	0	1
Microptema sequax McLachlan	0	4	0	0	0	0	0	0
Odontocerum albicorne (Scopoli)	0	0	0	0	1	0	1	8
Potamophylax cingulatus (Stephens)	0	0	0	1	0	7	1	1
Potamophylax latipennis (Curtis)	0	0	0	0	9	27	5	13
Potamophylax rotundipennis (Brauer)	0	0	0	0	3	2	0	28
Sericostoma personatum (Spence)	0	0	0	0	1	29	3	0
Total species number	3	6	7	8	13	15	17	20
Total abundance	5512	3018	420	26	387	962	332	905

Appendix E.

Environmental data collected across eight stream sites for Field Study 2 (Chapter 3). Temperature (°C), dissolved oxygen (mg/L), flow rate (m/s), and conductivity (µS/cm) are mean values calculated from four measurements over the study period. Stream names in brackets indicate that the site used was a tributary of the river name given.

Site name	River name	Temperature (°C)	Dissolved oxygen (mg/L)	Flow rate (m/s)	Conductivity (µS/cm)	pH
Stone	Maltby Dike	8.58	9.8	0.82	714	7.78
Lindrick Dale	Anston Brook	7.30	10.2	0.64	740	7.58
Strines	Strines Dike	5.74	12.8	0.55	706	4.70
Crowdecote	River Dove	6.96	11.7	0.68	328	7.14
Oughtibridge	(River Don)	7.90	12.0	0.61	222	7.41
Berrymoor	(River Etherow)	5.98	12.2	0.50	401	7.36
Brockhurst	(River Dove)	6.76	11.4	0.76	216	7.54
Holehouse	River Amber	7.12	10.6	0.44	111	6.10

Appendix F.

Values of complementarity calculated for each shredder species pair using three different indices, Schoener's Dietary Overlap Index (NO), Euclidean distance (Ed) and Sørenson's Similarity Coefficient (SSC) and two types of consumption rate data from Experiment 1 (Chapter 5); 'no choice' and 'choice' data. Species pairs are presented in order of the least to the most complementary, according to Schoener's Dietary Overlap Index (NO), using 'no choice data'.

	'No choice' data			'Choice' data		
Species pair	DO	Ed	SSC	DO	Ed	SSC
Sericostoma personatum - Potamophylax latipennis	0.10	11.59	0.10	0.08	29.03	0.29
Leuctra hippopus – Sericostoma personatum	0.12	11.44	0.12	0.11	26.11	0.28
Protonemura praecox – Potamophylax latipennis	0.13	13.25	0.13	0.13	22.62	0.23
Gammarus pulex – Nemoura avicularis	0.13	12.21	0.13	0.13	26.73	0.27
Leuctra hippopus – Potamophylax latipennis	0.15	14.79	0.15	0.13	15.47	0.14
Sericostoma personatum – Nemoura cambrica	0.16	14.53	0.16	0.14	32.10	0.32
Leuctra hippopus – Nemoura cambrica	0.16	18.61	0.16	0.16	13.32	0.11
Protonemura praecox – Leuctra hippopus	0.16	16.13	0.16	0.18	15.10	0.16
Nemoura cambrica – Potamophylax latipennis	0.17	15.50	0.17	0.19	8.34	0.08
Leuctra hippopus – Nemoura avicularis	0.17	17.78	0.17	0.19	21.15	0.22
Protonemura praecox – Sericostoma personatum	0.17	17.51	0.17	0.20	29.23	0.24
Gammarus pulex – Leuctra hippopus	0.20	22.79	0.20	0.22	16.92	0.18
Potamophylax latipennis – Nemoura avicularis	0.20	22.67	0.20	0.23	24.46	0.19
Nemoura cambrica – Nemoura avicularis	0.22	22.25	0.14	0.24	28.18	0.27
Gammarus pulex – Sericostoma personatum	0.24	23.02	0.24	0.27	21.54	0.30
Asellus aquaticus – Nemoura cambrica	0.25	26.36	0.25	0.27	33.26	0.32
Asellus aquaticus – Potamophylax latipennis	0.25	26.69	0.25	0.28	33.15	0.33
Gammarus pulex – Potamophylax latipennis	0.30	31.67	0.30	0.29	14.24	0.13
Asellus aquaticus – Protonemura praecox	0.30	31.45	0.30	0.29	13.78	0.13
Asellus aquaticus – Nemoura avicularis	0.32	31.56	0.32	0.32	21.47	0.19
Gammarus pulex – Nemoura cambrica	0.33	32.03	0.33	0.32	15.03	0.13
Asellus aquaticus – Leuctra hippopus	0.38	37.66	0.38	0.33	28.22	0.29
Gammarus pulex – Asellus aquaticus	0.42	41.89	0.42	0.39	40.24	0.39