Density and reproduction in native and invasive *Linaria vulgaris* populations at multiple spatial scales.

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Abstract

Comparing invasive plants in their native and invasive ranges can answer questions about invasion mechanisms and inform management options. However, few studies have considered how density varies with spatial scale or how individual fitness is affected by conspecific density at different spatial scales. A census was carried out of 15 native UK populations of the perennial herb *Linaria vulgaris* Miller (Plantaginaceae), and of seven invasive populations from a climatically matched area of Alaska. There was no difference in density between native and invasive populations when compared at spatial scales of 0.0625, 0.5, 1 or 4 m^2, or when density was measured as a mean field of each population. However, invasive populations covered a larger area, so density was greater at broad spatial scales. The effect of conspecific density on the height and reproduction of ramets varied with the spatial scale and between ranges. Invasive ramets were shorter than native ramets, and therefore produced fewer mature fruit. However, this was more than compensated for by the greater number of viable black seed in invasive fruit than native fruit. One of the reasons for this was the presence of the seed feeding weevil *Rhinusa antirrhini* in over half of the native, but none of the invasive, fruit. The majority of seed was estimated to fall within 1 m of maternal plants when surrounded with vegetation, but seed travelled further in an unvegetated area. Germination rates were very low in both the field and laboratory. The thesis ends with a description of the biology of *L. vulgaris*. This work demonstrates that invasion and escape from natural enemies can occur at a broad spatial scale, without increased density and vigour at a fine spatial scale.

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1.1 ABSTRACT

Density is spatial scale dependent. The effects of conspecific density on individual fitness will vary with different processes and at different spatial scales. Individual density effects can sum to density dependence within populations. Considering spatial scaling is particularly important when studying exotic plant invasions, for which there are varying definitions emphasising density, dominance and/or impact in the introduced range. Some question whether plant invasions should be considered as distinct from the colonisation process of native plants. Understanding density patterns across both spatial and temporal scales of a plant invasion may clarify definitions and improve understanding of the mechanisms of invasion. There has been growing recognition of the value of comparing density patterns, plant traits, environmental traits and demographic processes between the native and introduced ranges. Difference in the biotic or abiotic environment might drive change in plant traits that affect competition and fecundity, or there may be novel interactions between pre-existing plant traits and the new environment. This may then result in a different emergent density pattern at one or more spatial scales in the introduced compared with the native range. This thesis compares density at fine to medium spatial scales, as well as ramet height and sexual reproductive output, between

populations of the perennial herb *Linaria vulgaris* Miller (Plantaginaceae) in climatically matched areas of its native and invasive range.

1.2 INTRODUCTION

Invasions form large scale replicated experiments and provide insights into ecological and evolutionary processes (Elton, 1958, Sakai et al., 2001, Callaway and Maron, 2006, Sax et al., 2007). Considering the current and likely future environmental and economic impacts of invasive species (Pimental et al., 2000, Walther et al., 2009, Vilà et al., 2011), research is also vital to inform prevention and control efforts (Hulme, 2006, Buckley, 2008). Both understanding and managing the dynamics of invasions involves measuring their density. However, individuals are usually distributed non-randomly and density is spatial scale dependent, so that individuals will experience different local scale densities to the mean field density of the population (Watt, 1947, Kunin, 1997, Gaston et al., 1999, Gunton and Kunin, 2007). The effect of conspecific density on different processes affecting individual fitness and population dynamics will also vary with spatial scale (Addicott et al., 1987, Lortie et al., 2005, Gunton and Kunin, 2007, Gunton and Kunin, 2009). This means that considering patterns and processes at multiple spatial scales is important when studying various aspects of invasion (Pauchard et al., 2003, Pauchard and Shea, 2006, Milbau et al., 2009). This review looks at the importance of spatial scale when measuring the density of plants and the effects of conspecific density on individuals and population processes. This approach is then applied to plant invasions, where an assumption of greater density and vigour in the introduced compared to the native range underpins some of the definitions of invasives and has led to various invasion hypotheses. A greater consideration of spatial scale would be helpful in understanding the various stages and possible mechanisms of plant invasions.

1.3 SPATIAL SCALE AND DENSITY

1.3.1 Spatial scale in ecology

There has been growing recognition of the importance of spatial scale in ecological research (O'Neill, 1989, Wiens, 1989, Levin, 1992, Schneider, 2001). Considerations of spatial scale are integral to pattern and process whether focusing on ecosystems, communities, species, populations or individuals (Addicott et al., 1987, Wiens, 1989, Dungan et al., 2002). Two different senses in which scale can be used are ‘extent’ and ‘grain’ (Wiens, 1989). Grain is the units of observation, so is the lower limit of a study. Extent is the overall area or population to be described, so is the upper limit of observations. No patterns can be detected below the grain of a study and generalisations cannot be made beyond the extent of a study without assuming uniformity as extent increases (Wiens, 1989). If total sampling effort is fixed, increasing your ability to detect broad scale patterns by expanding the extent of a study usually involves enlarging the grain, so costing fine scale resolution and *vice versa*. Changing the scale of measurement means the variance of that variable will change. As extent is broadened the variance between the fine grain samples will usually increase as greater heterogeneity is encountered (Wiens, 1989). The scale of ecological neighbourhoods around an individual can differ between processes and species, so studying the interactions between species can be very sensitive to scaling (Wiens, 1989). Issues of spatial scale have been seen as problematic for ecologists (Levin, 1992). However, multi scale experiments (Lortie et al., 2005, Sandel and Smith, 2009) and considering spatial scale in observational work (Pauchard et al., 2003, Lamarque et al., 2012) can allow the detection of complicated patterns and is seen as having the potential to unify ecology (Levin, 1992, Schneider, 2001).

1.3.2 Density measurement and density effects.

Ecologists measure density for different reasons and in different ways. One way of thinking about density is as a property of a particular species or population in a particular area, with the aim being to compare species or parts of ranges (Damuth, 1981, Gaston et al., 1999). Another reason for measuring density is to consider the impact of density on individual fitness, and to investigate whether and how these density effects have a role in population regulation (Carrete et al., 2008). Density is defined as individuals per unit area, making it scale dependent and not a fixed attribute of a population (Mayor and Schaefer, 2005, Gunton, 2007). Individuals are not usually randomly distributed, but are clustered to form patches within patches with increasing spatial scale (Watt, 1947, Purves and Law, 2002, Hartley et al., 2004). This means that if density is measured in small plots and then extrapolated to broader spatial scales, density at this broader scale will tend to be overestimated. This is because small plots can be biased towards areas of homogenous habitat and will usually miss areas with few or no individuals (Pautasso and Weisberg, 2008). However, measuring density only at a broad spatial scale does not take into account how an individual experiences local density (Turkington and Harper, 1979, Silander and Pacala, 1985, Kunin, 1997).

When considering density as used for comparisons between species and populations in a particular area, far more attention has been paid to the census methods than to choosing the area within which to count individuals (Gaston et al., 1999). However, the area chosen will have a large impact on both the density value and its interpretation (Haila, 1988, Gaston et al., 1999, Girvetz and Greco, 2007). ‘Crude’ density measures cover an arbitrary area, while ‘ecological’ density is measured only using the areas of habitat that the organism uses (Gaston et al., 1999). Crude density measures will tend to be lower than ecological density measures, as they will include inappropriate habitat. Studies with the smallest extent tend to be based in areas of the species’ range with greater abundance (Smallwood and Schonewald, 1996) and do not tend to include ‘true zeros’ - areas of appropriate habitat where the species is absent (Pautasso and Weisberg, 2008, Zuur et al., 2009). For example, these biases mean that population density estimates for mammalian carnivores tend to decline with increasing spatial extent of study (Smallwood and Schonewald, 1996), and that the abundance-body size relationship for mammals may not be as negative as claimed (Blackburn and Gaston, 1996). However, within patches of habitat, it is also possible for density to be relatively uniform, due to processes such as competition, and so remain constant across a range of scales. Density may increase with increasing areas of habitat because of resource concentration and lower effectiveness of natural enemies (Matter, 2000, Mayor and Schaefer, 2005).

Another use of density measurement is to consider the impact of density on individuals and populations (Gunton and Kunin, 2009). Usually only conspecific density is considered, although Goldberg and colleagues (2001) have argued for consideration of the whole plant community. Positive density effects have been found on fruit production (Elam et al., 2007, Spigler and Chang, 2008, Jones and Comita, 2010, Feldman and Morris, 2011) and seed production (Kunin, 1993, Kunin, 1997, Wagenius, 2006, Klank et al., 2010), although no density effect (Mustajärvi et al., 2001) and negative density effects (Meekins and McCarthy, 2000, Maguire et al., 2011) on fecundity are also found. Varying effects of conspecific density are also found on non-reproductive fitness components, such as seedling emergence (Goldberg et al., 2001), seedling mortality (Suzuki et al., 2003), growth (Goldberg et al., 2001, Sletvold, 2005) and survival (Sletvold, 2005, Pujol and McKey, 2006, Gunton and Kunin, 2007, Feldman and Morris, 2011). Mechanisms impacting on individual fitness where there can be density effects include plant herbivory (Gunton and Kunin, 2007, Maguire et al., 2011), seed or fruit herbivory (Ǻgren et al., 2008, Jones and Comita, 2010, Klank et al., 2010), pollinator visitation (Kunin, 1997, Mustajärvi et al., 2001, Klank et al., 2010, Feldman and Morris, 2011), quality of pollinator visits (Kunin, 1993), and pollen receipt (Groom, 1998, Wagenius, 2006). One explanation for the variation in detection, strength and direction of density effects among studies is that the relationships between density and performance, at one particular spatial scale, will often be non-linear

(Goldberg et al., 2001, Gunton and Kunin, 2007), and so depend on the range of densities included in the study. For example, flower production and relative growth rate were greatest at intermediate density values in an experimental study using a wide range of densities (Gunton and Kunin, 2007). Variation in density effects between studies could also be to do with variation in the spatial scale at which density is recorded (Gunton, 2007).

Under the mean field assumption, individuals are expected to experience others in proportion to the mean density for each species over the whole plot. However, because of patchiness, individuals are expected to experience more intra-specific and less inter-specific competition than would be expected from their relative densities (Murrell et al., 2001, Stoll and Prati, 2001). Each individual in a population will have a different surrounding pattern of conspecific density from fine to broad spatial scales, before eventually converging on the mean field density at the widest extent of the population. Ecologists are encouraged to take a plant’s eye view (Turkington and Harper, 1979) and consider local neighbourhoods around individuals (Antonovics and Levin, 1980, Silander and Pacala, 1985). However, the size of the neighbourhood impacting upon the individual will vary with the species and process in question (Addicott et al., 1987, Holland et al., 2004, Gunton and Kunin, 2009). For example, the survival of *Silene latifolia* in a field experiment was best explained by conspecific density measured within 0.28 m, but the seed mass per plant was most strongly related to density when measured within 11 m (Gunton and Kunin, 2009). This also occurs at the level of a population’s response to environmental variables, so the abundance of long-horned beetles responded most strongly to the proportion of forest-cover at different spatial scales for different species (Holland et al., 2004).

Density is a deceptively simple term. Factors that need to be defined clearly and possibly uncoupled from a consideration of density (Ghazoul and Shaanker, 2004), are population size (Cappuccino, 2004, Wagenius, 2006), nearest neighbour distance (Kunin, 1992, Kunin, 1993, Wagenius, 2006), spacing (Kunin, 1997, Mustajärvi et al., 2001), patch size (Groom, 1998), population area (Lamont et al., 1993), isolation (Silander, 1978, Steffan-Dewenter and Tscharntke, 1999, Wagenius, 2006) and connectivity (Ǻgren et al., 2008). An explicit consideration of spatial scale is needed to consider these different aspects of population pattern and hierarchy, and investigating these is easier for experimental compared with observational studies (Gunton, 2007).

Density and population size may or may not be interchangeable depending on the circumstances (Ǻgren, 1996, Elam et al., 2007). Population size is identical to density measured at the spatial extent that encompasses the population with the largest extent. Individuals or processes might be insensitive to the relative amount of clumping of individuals within this total area. Difficulties might arise from the way a population is defined, commonly as being separated by a certain distance without individuals. For example, within a 500 m radius area, two clumped areas of plant growth each containing 50 plants and separated by 100 m distance without any individuals would be considered as two separate populations and 50 would be used as the population size of each. The same spatial extent, containing 100 plants which are not separated by 100 m distance without individuals, would be considered as one population and 100 used as the population size. The appropriate way to investigate and analyse such situations depends on whether the process in question is spatial scale insensitive, or whether the process is actually responding to density at a broad spatial scale. It is difficult to uncouple these two possibilities. For example, flower production of a forest herb was negatively affected by conspecific density at fine scales (1 m), but the positive effect of total population size may or may not be about density at broad scales (Ǻgren et al., 2008). The threshold effect in population size influencing maternal fitness found in a study of the invasive wild radish (*Raphanus sativus*), could be simply about number of individuals, or it could be scale dependent as larger numbers cover a greater area (Elam et al., 2007).

Some studies looking at the effect of density on individuals are measuring density as a mean field in the same way as for comparing different species or parts of species ranges (Johnson et al., 2004, Kolb, 2005). A population is defined in a particular way and then the number of individuals divided by the area that the population covers. The result of measuring density only in this way, is that the spatial scale used has varied between the different populations used in the study. Kolb (2005) found that seed production was positively related with population size due to limited pollinator visitation, but not with population mean field density. However, here pollinator visitation might still be considered to be ‘responding’ to density at a broad spatial scale, rather than number, so that a density effect may have been found if density had been calculated using the same area for each population. Other studies have measured fine scale density in circles or annuli focused around individuals, but also used the variable spatial scale population mean field density (Spigler and Chang, 2008, Klank et al., 2010). It may be more appropriate to use the spatial extent of the population covering the most area as the area for broad scale density calculation for each of the populations in the study. Using individual focused density and considering a wide range of spatial scales offers more potential for understanding density effects (Sletvold, 2005, Wagenius, 2006, Gunton and Kunin, 2007, Gunton and Kunin, 2009).

Different components making up an individual's fitness can have density effects in different directions (Gunton and Kunin, 2007, Feldman and Morris, 2011). Fecundity is often found to decline with decreased local density (Silander, 1978, Cappuccino, 2004, Feldman and Morris, 2011), but at the same time herbivore damage may decrease (Silander, 1978) or survival increase (Feldman and Morris, 2011). Experimental studies on *Vincetoxicum hirundinaria* and *V. nigrum* have found the opposite effect, with increased seed (Maguire et al., 2011) or fruit production (Ǻgren et al., 2008) at low density, but also increased foliar (Maguire et al., 2011) or fruit herbivory (Ǻgren et al., 2008). Different fitness components and mechanisms will also vary in the spatial scale at which they are most sensitive to density (Gunton and Kunin, 2007). The density of conspecifics at distances between 1 and 4 m from individuals of *Sabatia angularis* had a positive effect on fruit set, but density at less than 1 m distance had a negative effect on seed set (Spigler and Chang, 2008). This meant that the overall reproductive success was negatively associated with density at less than 1 m scale, positively associated with density at 1 – 4 m scale, and negatively associated with mean field population density (Spigler and Chang, 2008).

Within the same fitness component or mechanism, the strength and sometimes the direction of density effects can change across spatial scales (Gunton and Kunin, 2007), with components varying in their sensitivity to spatial scale (Gunton and Kunin, 2009). For example, the proportion of plants affected by mammalian herbivores had opposing quadratic responses to conspecific density at fine and broad spatial scales; with intermediate densities at fine scale being most attacked, while intermediate densities at broad scale being least attacked (Gunton and Kunin, 2007). The degree, direction and spatial scale of density effects and density dependence can also vary within one species across life cycle stages (Rees and Paynter, 1997, Goldberg et al., 2001, Sletvold, 2005).

1.3.3 Spatial scaling and density dependence

Individual fitness-density relationships can sum to population regulating density dependence (Antonovics and Levin, 1980, Murdoch, 1994, Sletvold, 2005, Feldman and Morris, 2011), although the role of density dependence in regulating natural populations has been questioned (Berryman et al., 2002). Detecting classical density dependence requires a long time series, so comparisons of different populations across space are often used instead (Walde and Murdoch, 1988, Cappuccino, 1992, Hails and Crawley, 1992). In order to have a regulating effect on population density, this spatial density dependence has to bring about temporal density dependence (Hails and

Crawley, 1992). Difficulties with detecting density dependence may be related to investigating at the wrong spatial scale (Ray and Hastings, 1996), not considering spatial variation (Schmitt and Holbrook, 2007) and problems with getting a sufficient sample size at larger spatial scales (Hails and Crawley, 1992). The ability to detect population regulating density dependence might depend on matching the scale of study to the scale of population mixing (Ray and Hastings, 1996). Indeed, in insect studies Ray and Hastings (1996) found that choosing an inappropriate spatial scale can be as much of a difficulty when trying to detect density dependence as a short time series and low test power.

1.4 SPATIAL SCALE, DENSITY AND DENSITY EFFECTS IN PLANT INVASIONS

1.4.1 Definitions, stages and scales of invasion

A large source of confusion in the study of invasions is due to differences in definitions of invasive species and in the understanding of terminology (Kolar and Lodge, 2001, Shea and Chesson, 2002). Some definitions of invasion consider that an invasive species must be an exotic that overcomes a geographic barrier to establish in a new range (Richardson et al., 2000, Colautti and MacIsaac, 2004, Wilson et al., 2009). However, others include the colonisation and dominance of nearby habitats in the definition (Davis and Thompson, 2000, Valéry et al., 2009), and emphasise the similarity in ecological processes between native and exotic colonisers (Davis and Thompson, 2000, Meiners, 2007, Valéry et al., 2009). This has led to calls for the end of invasion ecology as a separate discipline (Davis et al., 2001, Valéry et al., 2013). Davis and Thompson (2000) distinguish between different types of colonisers and define invasives as being only those colonisers that have a negative impact, although this means that the definition is linked to the qualities of the recipient community (Valéry et al., 2008). Valéry and colleagues (2008, 2013) argue that a definition should be based on the essence of the phenomenon itself, rather than on its consequences. They consider the defining process of invasion to be a species acquiring a competitive advantage when natural obstacles are removed. This competitive advantage then allows rapid spread and the species to become ‘dominant’ in terms of biomass or density (Valéry et al., 2008). One consequence of this definition is that it uncouples the need for an exotic invasive to be denser in its invasive compared with its native range; it only needs to be ‘dominant’ in the new environment. However, for Lamarque and colleagues (2012) a defining characteristics of an invasive is that it is denser than in the native range.

One of the contributing factors to this variety of definitions may be a failure to distinguish between different stages of an invasion (Kolar and Lodge, 2001, Dietz and Edwards, 2006). Also contributing to the confusion, and bound up with the stage of an invasion, is the spatial scale at which an invasion is considered and defined. Valéry and colleagues (2008) do not define dominance in terms of spatial scale, but a species could be dominant at a fine spatial scale while not at a broader landscape scale and *vice versa*. Colautti and MacIsaac (2004) suggest a neutral stage-based terminology where an exotic might pass through various filters via two possible routes towards stage V where it is at high fine and broad spatial scale density

(Figure 1). Although they do not explicitly discuss spatial scale, Colautti and MacIsaac are essentially considering the invasion process at two conceptual spatial scales (Figure 1). An introduced species which is localized and rare could become locally dominant at a fine spatial scale (stage IVb) before dispersing at a broader scale to reach stage V (Figure 1). Alternatively, it could first become widespread at a broad spatial scale (stage IVa), followed by ‘gap filling’ to dominate at a finer spatial scale (stage V).

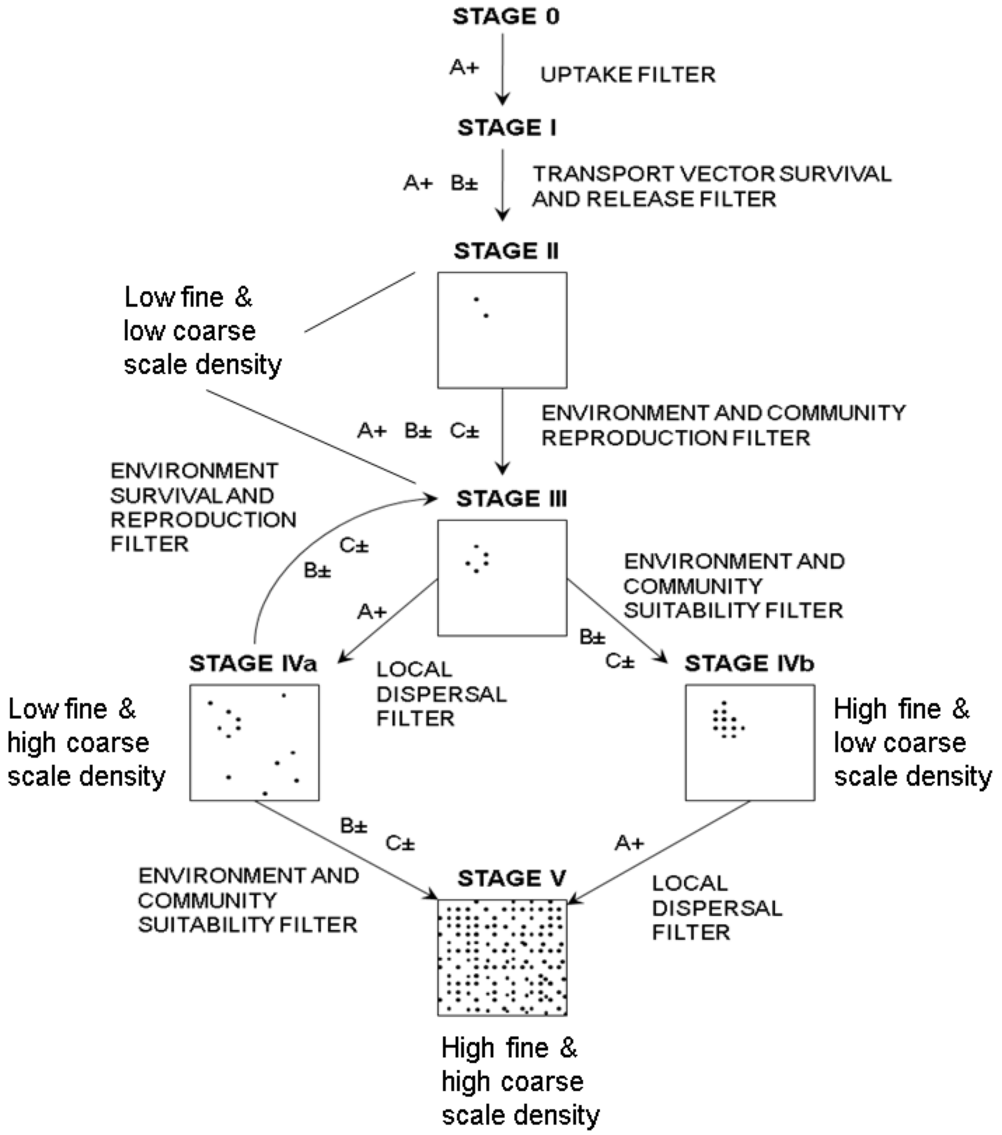

Figure 1. A stage based neutral terminology for the invasion process, adapted from Colautti and MacIsaac (2004) with example distributions. Potential invaders begin in a donor region (Stage 0) and pass through filters to reach other stages. There are three classes of determinants that have positive or negative effects on the probability that a potential invader will pass through a filter: (A) propagule pressure; (B) physio-chemical requirements of the potential invader; and (C) community interactions. Reproduced with permission from John Wiley and Sons.

Interestingly, Colautti and MacIsaac (2004) consider only a widespread species (stages IVa and V) to be an ‘invasive’ and not one at high local densities (stage IVb). However, a land manager focused on a smaller spatial scale is likely to consider an introduced species at stage IVb to already be invasive, as it may be having an impact on native species. At this fine spatial scale a species would seem to have fulfilled the dominance criterion of Valéry and colleagues (2008), although at a broader spatial scale it is not dominant in the ecosystem.

The use of Colautti and MacIsaac’s stages is likely to create more clarity and it helps to consider which filters a species must pass through to reach the next stages. However, there is still the possibility of confusion, depending on exactly which spatial scales are being considered in place of the two conceptual scales as the total extent and fine scale grain. These stages are points along a continuum, so the actual density pattern of an exotic species is likely to vary continuously with spatial scale and with different regions from within the entire range. If an invasion is to be labelled as stage IV or V for example, then it is also important to define the actual spatial extent and the size of the fine scale grain that this label is being applied to.

Heger and colleagues (2013) have argued that different fields of research will generate different viewpoints about the definition of invasives, and that it is not possible or even desirable to have a uniform definition of invasion. If this is to be the case, it will be important to recognise that there are likely to be different patterns and processes occurring at different spatial scales and to be clear about the spatial extent and grain being described.

Uncoupling the change in pattern from the impact at different scales in the new environment is also likely to be helpful (Ricciardi and Cohen, 2007), because the relationship between density and impact is not necessarily linear (Yokomizo et al., 2009) and the types of impact will vary with spatial scale. In the next section I examine different approaches that have been taken to study pattern and process in plant invasions.

1.4.2 Comparing native with invasive species and the native with the invasive range

Much of the research into invasive species has focused on understanding whether invasive plants are more likely to have particular traits compared with their native neighbours and/or related but non invasive species (Rejmánek and Richardson, 1996, Radford and Cousens, 2000, Prinzing et al., 2002, Meiners, 2007, Jogesh et al., 2008, van Kleunen et al., 2010, Palacio-López and Gianoli, 2011). One of the aims has been to improve prediction of likely invaders (Heger and Trepl, 2003, Lambdon and Hulme, 2006). While there is some evidence that certain reproductive traits and abundance of plants in the native range are associated with invasiveness (Hayes and Barry, 2008, van Kleunen et al., 2010), there has been discussion as to how successful this has been and how much research into traits tells us (Heger and Trepl, 2003, Moles et al., 2008, Thompson and Davis, 2011, van Kleunen et al., 2011). A second strand of research has been to compare the invasibility of environments with different characteristics to determine if some are more likely to be invaded than others (Crawley, 1987, Tilman, 1997, Levine and D'Antonio, 1999, Levine, 2000, Fine, 2002, Ohlemüller et al., 2006, Milbau et al., 2009). These two approaches can be combined in the study of the relationship between the traits of the invader and those of the invaded ecosystem (Heger and Trepl, 2003, Moles et al., 2008, Erfmeier and Bruelheide, 2010, Hierro et al., 2013, Mata et al., 2013).

A fourth approach to the study of invasions is to compare patterns and processes of invasions over time (Heger and Trepl, 2003, Colautti and MacIsaac, 2004, Dietz and Edwards, 2006, Hawkes, 2007). Most research on invasions is carried out on plants in areas where they are already both widespread and locally dominant (Colautti & MacIsaac's stage V) (Simons, 2003, Hierro et al., 2005). However, understanding what contributes to successful uptake (stages 0 to I), transport (stages I to II) and establishment (stages II to III) could help with prevention (Mack and Lonsdale, 2001, Lockwood et al., 2005, Barney, 2006, Jongejans et al., 2007). Comparing propagule pressure and interaction of species traits with the environment in instances of successful compared with failed invasions could be particularly illuminating (Simons, 2003, Zenni and Nuñez, 2013). These failed instances of invasion could be from different species or from populations of the same species that has successfully invaded at a different time or place. However, studying these earlier stages of invasion can be more difficult (Zenni and Nuñez, 2013). In the context of Colautti and MacIsaac's (2004) framework, these 'failed invasions' include species that have stalled at various earlier stages, so if conditions altered it might be possible for them to move between stages and increase in density.

Until recently most of these four approaches to invasive research were carried out only in the invasive range, with any comparisons being between invasive and non-invasive species (Hierro et al., 2005). However, there has been growing recognition of the importance of the native range in invasion ecology research (Hinz and Schwarzlaender, 2004, Hierro et al., 2005, Guo, 2006). Comparing both the density, and the interaction of traits and environment affecting that density, can indicate whether density is being moulded by the same processes in both ranges (Hierro et al., 2005). Four aspects that may have changed between the native and exotic range include the abiotic environment, competition with neighbours, pollination and herbivory (Hierro et al., 2005). Zenni and Nuñez (2013) consider it unimportant to know about failed invasions when comparing species in their native and invasive ranges. However, studying populations that have failed or stalled at certain stages in the introduced range and comparing with the native range might reveal common barriers limiting population spread.

Various invasion hypotheses have been put forward to explain the higher densities of plants in their invasive ranges (Blossey and Notzold, 1995, Callaway and Aschehoug, 2000, Keane and Crawley, 2002, Dickson et al., 2012, Hufbauer et al., 2012). However, only in the last five to ten years have there been a reasonable number of studies examining whether or not populations of species really are denser in their introduced compared with the native range (Table 1). While many comparisons of individual species do confirm a greater density in the introduced range, some have found no difference and one a decrease in density range (Table 1). A meta-analysis by Parker and colleagues (2013) found that invasive plants (as recognised by local dominance and impact) were moderately likely to be more abundant in their invasive range, although there was a great deal of variability. One explanation for these differences is that some species may be at earlier stages of invasion. This raises the issue of whether these comparisons and invasion hypotheses should only cover plants already recognised as invasive, or whether they should include all introduced exotics that may or may not progress to become invasive. Indeed, when Firn and colleagues (2011) compared the cover of 26 herbaceous species in 1 m^2 quadrats in their native and introduced (rather than only invasive) ranges, they found that most did not have increased cover in the introduced range. The argument starts to become circular if an invasive is to be defined as a species that is denser in the invasive compared with the native range (Lamarque et al., 2012). Instead, highly invasive species may be locally dominant and/or widespread in both their native and invasive range, so that abundance at home predicts abundance away (Firn et al., 2011, Parker et al., 2013).

Another explanation for variation in the density difference seen between studies and species is that many of the studies comparing density have been carried out at only one spatial scale (Table 1). Most commonly this has been of 1 m^2 quadrats (Table 1). Many used different spatial scales in different sized populations or in different ranges (Lonsdale and Segura, 1987, Sheppard et al., 1990, Woodburn and Sheppard, 1996, Paynter et al., 2003, Jakobs et al., 2004, Herrera et al., 2011, Alba and Hufbauer, 2012). Even if no density difference is found at the 1 m^2 scale, one may still be found at a broader or finer spatial scale. This is because of the way in which empty space at the edge of populations or between clumps is often treated in surveys (section 1.3.2). In addition to, or instead of, a difference in mean density between the native and exotic range, there may be a difference in variance of density and in the patterns of this variance at different spatial scales (Buckley et al., 2003). This suggests that rather than comparing a single spatial scale between ranges, more information about invasion stages and processes can be gained by comparing the pattern of density across spatial scales in the native and exotic range. This will show which stage an invasion is in (Colautti and MacIsaac, 2004), while if density is greater at a certain spatial scale in the invasive compared with the native range, then this approach can also point to particular barriers having been removed and the possible mechanisms involved in this invasion.

Table 1. Continued on the next page. Density comparisons between the native and introduced ranges of plants and the resolution of measurement. Also see unpublished data reported by Hinz and Schwarzlaender (2004).

Species	Reference	Higher (+), no difference or lower (-) density in introduced range	Spatial scale
Acer negundo	Lamarque et al., 2012	+	Plotless density estimator at medium scales and presence or absence within forests of differing sizes.
Acer platanoides		No difference	
Achillea millefollium	Beckmann et al., 2009	+	1 m^2 and 0.0707 m^2
Acroptilon repens	Callaway et al., 2012	+ cover	1 m^2
Buddleja davidii	Ebeling et al., 2008	No difference	Mean field
Carduus nutans	Sheppard et al., 1990, Woodburn and Sheppard, 1996	+ for seedlings and flowering individuals	0.5 m^2 native, 0.25 m^2 invasive
Cenaturea melitensis	Moroney and Rundel 2013	+ and no difference for different regions of invasive range	0.2 m^2
Cirsium arvense	Cripps et al., 2010	No difference	1 m^2
Cytisus scoparius	Paynter et al., 2003	+	Varied

Table 1 continued.

Species	Reference	Higher (+), no difference or lower (-) density in introduced range	Spatial scale
Fallopia japonica	Maurel et al., 2013	No difference	1 m^2
Genista monspessulana	Herrera et al., 2011	+	Varied
Heliotropium europaeum	Sheppard et al., 1996	+	1 m^2
Hieracium pilosella	Beckmann et al., 2009	+	1 m^2 and 0.0707 m^2
Hypericum perforatum	Beckmann et al., 2009	+	1 m^2 and 0.0707 m^2
	Vilà et al., 2005	+	Mean field
Lythrum salicaria	Edwards et al., 1998	+	0.5 m^2
	Bastlová-Hanzélyová 2001	+	10 m^2
Mimosa pigra	Lonsdale and Segura, 1987	-	25 m^2 or 4 m^2
Rhododendron ponticum	Erfmeier and Bruelheide, 2004	+ for seedlings, no difference for adult plants	1 m^2
Solidago gigantea	Jakobs et al., 2004	+	1 m^2 or 0.25 m^2
Verbascum thapsus	Alba and Hufbauer 2012	+	Varied

1.4.3 Invasion mechanisms at different stages

Along with an observed increased density or dominance in a new ecosystem, there can also be observations of increased growth (Erfmeier and Bruelheide, 2004), height (Lonsdale and Segura, 1987, Prati and Bossdorf, 2002, Hawkes, 2007), survival (Vilà et al., 2005), sexual (Lonsdale and Segura, 1987, Edwards et al., 1998, Buckley et al., 2003, Hawkes, 2007, Herrera et al., 2011) and vegetative (Beckmann et al., 2009) reproductive output and seedling recruitment (Erfmeier and Bruelheide, 2004) compared with the native range. Some field comparisons of particular plant species have found that individuals are taller in the invasive range (Lonsdale and Segura, 1987, Bastlová-Hanzélyová, 2001, Prati and Bossdorf, 2002, Jakobs et al., 2004, Ebeling et al., 2008, Herrera et al., 2011), while other field and flora comparisons have found no difference in heights between ranges (Edwards et al., 1998, Thébaud and Simberloff, 2001, Paynter et al., 2003, Beckmann et al., 2009, Cripps et al., 2010). A quantitative meta-analysis indicates that introduced plant species do tend to be larger compared with where they are native (Hawkes, 2007). However, Bayesian meta-analysis by Parker and colleagues (2013) found that only the world’s most invasive plants were strongly likely to be larger where invasive, and that this result could be an artefact of differing methodology between ranges. Invasive populations for some plant species have even been found to be shorter than in parts of their native range (Erfmeier and Bruelheide, 2004, Vilà et al., 2005).

Components of sexual reproduction found to be increased in the invasive range of some plant species include a greater proportion of the population flowering (Beckmann et al., 2009), larger inflorescences (Prati and Bossdorf, 2002, Ebeling et al., 2008), increased fruit set (Lonsdale and Segura, 1987), heavier or larger seed (Buckley et al., 2003, Ebeling et al., 2008) and more seed per fruit (Lonsdale and Segura, 1987, Edwards et al., 1998, Herrera et al., 2011). There is also evidence that allocation to vegetative reproduction can be greater, with the numbers of stolons per plant and the stolon to biomass ratio greater in the invasive ranges of three clonal plants (Beckmann et al., 2009). However, there have also been findings of no difference in fruit set and seed size or mass between ranges (Prati and Bossdorf, 2002, Buckley et al., 2003, Erfmeier and Bruelheide, 2004) and fewer fruits per plant in the invasive range (Herrera et al., 2011). A meta-analysis found that plants in the invasive range generally did allocate more towards reproduction than conspecifics in the native range (Hawkes, 2007). However, two global comparisons of seed mass between the native and invasive range had conflicting results (Daws et al., 2007, Mason et al., 2008).

These trait changes can be proximate causes of an increased density and competitive ability. One set of hypotheses consider this competitive advantage to be caused by post-introduction change in plant traits associated with decreased investment in anti-herbivore resistance and an increased investment in competitive ability. The Enemy Release hypothesis considers that this occurs through phenotypic plasticity (Keane and Crawley, 2002, Wolfe, 2002). However, the Evolution of Increased Competitive Ability (EICA) hypothesis is that this change in traits occurs through selection (Blossey and Notzold, 1995). In both cases, the ultimate cause of an increased competitive ability is considered to be an absence or reduction in specialist herbivory in the new environment compared with native competitors (Cripps et al., 2006, Hawkes, 2007).

Common garden and field experiments have found evidence both for selection (Maron et al., 2004, Qin et al., 2013) and for plasticity (Willis et al., 1999, Franks et al., 2008, Alba et al., 2011) of competitive traits. The distinction between trait change through selection and trait change through phenotypic plasticity may not always be straightforward because phenotypic plasticity can itself be selected for (Bradshaw 1965, Chun, 2011). While there is evidence that genetic differentiation does occur in the invasive range (Bossdorf et al., 2005), meta-analysis suggests that traits usually do not change in the way predicted by the EICA hypothesis (Felker-Quinn et al., 2013). There is also doubt about the importance of change in herbivory as an invasion mechanism and the role of specialist and generalist herbivores (Agrawal and Kotanen, 2003, Dawson et al., 2009, Heard and Sax, 2013). A quantitative meta-analysis showed that exotics suffer less herbivory than their native congeners and also that damage is marginally greater for plants in their native compared with their exotic range (Liu and Stiling, 2006). There is also evidence that more invasive exotics suffer less herbivory than less invasive exotics (Carpenter and Cappuccino, 2005). This was because of lower generalist herbivory on the more invasive exotics, perhaps because of better or novel deterrents (Jogesh et al., 2008). However, an experiment and other meta-analyses suggest that exotic plants may be similarly or even more impacted by herbivory and disease than neighbouring native plants (Agrawal and Kotanen, 2003, Parker et al., 2006, Parker and Gilbert, 2007, Chun et al., 2010). The conflict between the findings of these community studies that compare native and invasive plants, and the findings of biogeographical studies that compare ranges (Wolfe, 2002, Liu and Stiling, 2006), could have a number of explanations, including that the net effect of natural enemies may not be equal in the native and invasive ranges (Colautti et al., 2004). Characteristics that increase fitness compared with conspecifics in the native range may not translate into increased fitness compared with competitors in the introduced range (Colautti et al., 2004).

Where there is a release from natural enemies, this has not always been found to translate into the predicted increased performance or competitive ability (Edwards et al., 2007, Chun et al., 2010, Cripps et al., 2010). Indeed, reduced competition in the new environment can result in trait change for reduced competitive ability (Bossdorf et al., 2004), so it may be more appropriate to refer to trait changes that allow exploitation of the new environment, rather than necessarily trait changes that result in an increase in competitive ability. A release from specialist flower and seed predators may have a direct impact on fecundity (Edwards et al., 1998, Prati and Bossdorf, 2002), rather than acting through selection for decreased herbivore resistance (Blossey and Notzold, 1995). Random genetic drift (Fennell et al., 2010) recombination (Lavergne and Molofsky, 2007) and hybridisation (Ellstrand and Schierenbeck, 2000) may also contribute to post-invasion trait change.

Another set of explanations for invasion emphasise the pre-existing traits of the exotic in combination with the new biotic and/or abiotic environment. The root exudates of *Centaruea diffusa* have much stronger negative effects on new neighbours in the invasive range than on neighbours from its native range (Callaway and Aschehoug, 2000). There is evidence that some exotics are able to begin growth earlier in the spring than natives (Dickson et al., 2012). It is also possible that in successful invasions the subset of the native phenotypes that were transported were those that were pre-adapted to the new environment and were more likely to be invasive (Bossdorf et al., 2008). Pre-invasion selection may have occurred so that exotics are already adapted to anthropogenically disturbed environments (Hufbauer et al., 2012). Horticulture may result in selection for phenotypes that are larger or have other traits providing a greater competitive ability compared with native relatives (Kitajima et al., 2006, Ross and Auge, 2008).

All of these trait changes or pre-existing traits may act to allow exotics to take more advantage of niche space created by an increased supply or a decreased uptake in environmental resources; most commonly due to disturbance (Davis et al., 2000, Mata et al., 2013). In disturbed ecosystems an invasive might be more limited by dispersal barriers than by competition from native species (MacDougall and Turkington, 2005). Human altered habitats may be more easily invaded, and with increased global transport overcoming long distance dispersal barriers, this can result in the global homogenisation of floras (La Sorte et al., 2007, Hufbauer et al., 2012). This means that the biotic and sometimes abiotic conditions then become increasingly similar to the native conditions of a potential invader and so facilitate further invasions (Parker et al., 2006, Hierro et al., 2013). In this situation it can become difficult to determine which invasions are driving change in ecosystems, and which are merely passengers and indicators of other changes such as eutrophication and altered disturbance regimes

(MacDougall and Turkington, 2005, HilleRisLambers et al., 2010). Thompson and Davis (2011) argue that there are simply global species ‘winners’ and ‘losers’ depending on their adaptations to human altered environments, with disturbance occurring to the same extent in both the native and introduced ranges of species. If this is the case, then density would be expected to be the same in both ranges. The frequency, intensity or scale of disturbance would need to alter for higher density to occur in the introduced range (Hierro et al., 2006). However, there is evidence that the level of disturbance can be the same in both ranges, but with stronger effects in the introduced compared with the native range (Hierro et al., 2006). This might be because of the influence of other differences between ranges, such as the escape from native range soil pathogens (Hierro et al., 2006).

If a change in density has been observed between the native and invasive range, then a difference in plant traits or environmental variables between ranges might point towards possible invasion mechanisms. For example, if plants are taller in the introduced compared with the native range then this might point towards species investing more in direct competition with neighbouring species. Increased dispersal opportunities in the new environment and increased seedling establishment due to greater disturbance might explain why a species is becoming more widespread at a landscape scale in comparison with the native range.

The different invasion mechanisms described above may act in combination and play a role at different stages of an invasion (Dietz and Edwards, 2006, Qin et al., 2013). The variation in evidence for changes in traits and processes between the native and exotic ranges may be because species are at different stages of invasion and because a variety of different invasion mechanisms are operating in different species. The resulting density pattern across spatial scales will be influenced by the grain of environmental heterogeneity, which determines where it is possible for an exotic to invade depending on its physio-chemical requirements and will also influence the community interactions (Colautti and MacIsaac, 2004). The density pattern will also depend on propagule output and dispersal as influenced by the invader's traits and the environment (Colautti and MacIsaac, 2004). Although Colautti and MacIsaac only refer to dispersal when density patterns move from localised to widespread (Figure 1), the degree of dispersal at different distances is important in influencing density at a variety of spatial scales. Dispersal and establishment over short distances influences local density and allows local gap filling from stage IVa to stage V and stage III to IVb. Dispersal and establishment over longer distances allows the exotic to become more widespread at a larger scale from stages III to IVa and stages IVb to V.

Propagule pressure includes both the number of propagules (usually seeds) in an individual 'release event' and the frequency of these events over time (Lockwood et al., 2005). Lockwood and colleagues (2005) consider that the influence of propagule pressure swamps the effects of other influences on establishment. Greater sexual or vegetative reproductive output will clearly increase dispersal and establishment ability (Mason et al., 2008). However, in addition to changes in the number of seeds or new ramets initiated (Mason et al., 2008, Beckmann et al., 2009), there may be a difference compared with the native range in the average distance travelled by a seed or in the inter-ramet distance. This is because both can be influenced by the density or the height of conspecifics and other surrounding vegetation (Nadeau et al., 1991, Marchetto et al., 2010, Benot et al., 2013). There may also be a difference in the number of rarer long distance dispersal events of propagules, for example if there is greater opportunity for human-mediated transport within the invasive range (Lonsdale and Lane, 1994, Mack and Lonsdale, 2001, Wichmann et al., 2009, von der Lippe et al., 2013). An exotic’s seedling or ramet establishment may also be made more likely in its invasive range compared with its native range if there is a different disturbance regime, although disturbance may not promote invasion if it causes an equal amount of mortality to the exotic (Buckley et al., 2007). The fraction of *Echium plantagineum* seedlings establishing was greater in invasive than in native range populations, even though there was no difference in seed production between ranges (Grigulis et al., 2001). This was thought to be due to lower levels of competition in the invasive range (Grigulis et al., 2001). However, survival of these seedlings to flowering was lower in the invasive compared with the native range, probably because of the drier climate in the invasive range (Grigulis et al., 2001). Differences in reproductive output, dispersal distance, seed germination, seedling or ramet establishment and then survival, as influenced by the biotic and abiotic environment, could all result in a different density pattern across spatial scales in comparison with the native range.

1.4.4 Density effects and density dependence in plant invasions

The density of an invasive will feed back in different ways at different spatial scales to affect intra and inter-specific competition and facilitation, with effects on herbivory (Maguire et al., 2011), pollination (St Denis and Cappuccino, 2004), fecundity (Meekins and McCarthy, 2000, Cappuccino, 2004, Davis et al., 2004, Elam et al., 2007), dispersal (Marchetto et al., 2010), growth (Meekins and McCarthy, 2000, Garren and Strauss, 2009) and seedling survival (Garren and Strauss, 2009). The density of an invasive can therefore influence invasion mechanisms (Taylor and Hastings, 2005) and can also alter the underlying abiotic and biotic environment (Buckley et al., 2007, Vilà et al., 2011). Density at fine spatial scales provides most information about the interaction with native species (Pauchard et al., 2003). An invasive at high fine scale density may be having a large impact on native vegetation (a ‘pushing out’ invasive), while one at lower fine scale density that is widespread at a broad spatial scale may have little impact on native vegetation (a ‘fitting in’ invasive) (Cronk and Fuller, 2001). The competitive strategy of an invasive may change over time and with varying conditions (MacDougall and Turkington, 2004, Hawkes, 2007).

Turning to intra-specific competition, a component Allee effect is where there is a positive relationship between conspecific numbers or density and any component of individual fitness (Stephens et al., 1999). This can lead to a demographic Allee effect where overall fitness has a positive relationship with density (Stephens et al., 1999, Taylor and Hastings, 2005). In a ‘strong’ demographic Allee effect negative growth rate occurs when the population density falls beneath an Allee threshold (Taylor and Hastings, 2005). Allee effects in plants are often caused by a lack of pollen donors and pollinators in small and/or sparse populations (Davis et al., 2004, Elam et al., 2007), so exotics that are self-fertile or able to reproduce vegetatively may have an advantage in establishing if introduced at low numbers (van Kleunen et al., 2007). Allee effects might also operate through competition with native species, so that there may be a critical density at a fine spatial scale when an invasive is able to outcompete other species and become dominant within fine scale patches (Cappuccino, 2004). Cappuccino (2004) established that higher seed set by individuals of *Vincetoxicum rossicum* in denser patches was not because of differences in pollinator visitation and suggested that it was caused by reduced inter-specific competition. However, Elam and colleagues (2007) point out that higher pollen load size or pollen quality may have increased seed set, rather than reduced inter-specific competition.

Component Allee effects (positive density effects) may not translate into a demographic Allee effect (positive density dependence) if fitness is affected by other processes where there are negative density effects (Stephens et al., 1999, Kanarek et al., 2013). The existence of positive or negative density dependence within a population, and the spatial scale over which it operates, depends on the combination of the component positive and negative density effects on individual fitness (Kanarek et al., 2013). The effect of conspecific density on processes affecting fitness, such as pollination or herbivory, are likely to operate at different strengths and sometimes in different directions at different spatial scales (Gunton and Kunin, 2007, Gunton and Kunin, 2009). Taylor and Hasting’s (2005) review of Allee effects in invasions does not consider the spatial scale over which an

Allee effect might operate or the effect of density across spatial scales on the progress of an invasion. However, the presence and strength of Allee effects have the potential to mould spatial distributions, because they can prevent establishment and limit movement through invasion stages (Figure 1).

When environmental stochasticity is the more important factor in initial population survival, then the number of releases of an exotic species should explain invasion success (Taylor and Hastings, 2005). However, if Allee effects have a greater influence on population persistence, then the size of individual releases will be a better predictor of establishment (Taylor and Hastings, 2005). Including stochasticity and interactions of individuals with their immediate neighbours, rather than using mean field density, in a reaction diffusion model shows how even very small founding populations can establish (Kanarek et al., 2013).

The spatial pattern across scales is also important for subsequent movement through invasion stages (Colautti and MacIsaac, 2004). Differing density patterns at medium to broad spatial scales will have differing rates of spread into unoccupied areas. This is due to the physical distribution in the landscape affecting how propagules reach different areas, the threshold and spatial scale of Allee effects and the ability of managers to detect and control patches (Lewis and Kareiva, 1993, Emry et al., 2011). Leaving many small patches untreated may result in the greatest spread (Emry et al., 2011) as these will have a larger edge to area ratio and will be adjacent to uninvaded areas. This means small satellite patches may have a greater role than large central patches in expanding the overall range into new areas at landscape spatial scales and can also result in infilling between patches when viewed at medium spatial scales (Moody and Mack, 1988, Colautti and MacIsaac, 2004).

However, if these smaller and more isolated patches are limited by Allee effects then it may be more effective to target larger and more central patches for control (Cappuccino, 2004). Allee effects can slow invasion (Kot et al., 1996, Tobin et al., 2007), but there is a risk that initial lag times can result in underestimating the potential for later spread rates (Hastings, 1996). Decisions about targeting control will depend on the pattern of the invasion across spatial scales, the relationship between density and types of impact (Yokomizo et al., 2009) and the manager's aims with respect to preventing spread into new areas and reducing density at particular spatial scales. Allee effects can be exploited or created for management (Tobin et al., 2011), but compensatory density effects can reduce the effectiveness of biological control (Garren and Strauss, 2009).

1.5 STUDY SPECIES AND THESIS STRUCTURE

Pauchard and colleagues (2003) studied the perennial invasive herb *Linaria vulgaris* Miller (Plantaginaceae) at three discrete spatial scales in West Yellowstone, Montana & Wyoming. They recorded the location of patches in a 20 x 10 km area, the shape and area of patches in five 50 x 100 m plots within this area and the density and height of ramets in 0.2 x 0.5 m quadrats at the centre and edge of randomly selected patches. The pattern found at the landscape scale, with patches aggregated in newly invaded areas, but more dispersed in highly invaded areas, corresponds with the invasion stages described by Colautti and MacIsaac (2004) (Figure 1). At fine spatial scales, density and height was higher in quadrats at the centre than the edge of patches (Pauchard et al., 2003). Pauchard and colleagues (2003) interpreted this as expanding populations that can displace native vegetation, although Lehnhoff and colleagues (2008, 2009) found both expansion and contraction of *L. vulgaris* patches from one year to the next in different environments. *L. vulgaris* was one of the earliest documented plant invasions to North America (Mack, 2003) and is recorded as naturalised in all mainland US states and Canadian provinces and territories except Nunavut (Saner et al., 1995, USDA, 2010, Brouillet et al., 2013). There is some evidence that *L. vulgaris* is expanding into more natural environments and at higher elevations (Pauchard et al., 2003, Sutton et al., 2007, Pauchard et al., 2009). However, there has been no comparison of density or of plant traits between populations in the native (Eurasia) and invasive (North America) ranges of *L. vulgaris*. This thesis takes the approach recommended by Hierro and colleagues (2005) by comparing populations of *L. vulgaris* in the UK with populations in a climatically matched area of Alaska, where its range is currently expanding (AKEPIC, 2013).

Most comparative studies between native and invasive ranges have been of species that only reproduce sexually (although see Beckmann et al., 2009). However, vegetative reproduction can have consequences for fine scale density patterns and inter and intra-specific interactions (Benot et al., 2013). Clonal integration has been linked to invasive success because ramets in unfavourable patches can be supported by the rest of the clone (Song et al., 2013). *L. vulgaris* reproduces both through self-incompatible sexual reproduction (Arnold, 1982, Docherty, 1982, Clements and Cavers,

1990) and initiating new ramets from lateral roots (Bakshi and Coupland, 1960, Charlton, 1966, 1967, Nadeau et al., 1991).

L. vulgaris is also interesting for comparative study because in the native range it supports a number of specialist herbivores (Kock, 1966). Some species have been accidentally or deliberately introduced as biological control to parts of the invasive range (Harris, 1961, Saner, 1991, McClay, 1992, Volenberg et al., 1999, MacKinnon et al., 2005, Sing et al., 2005, Wilson et al., 2005, MacKinnon et al., 2007, Egan and Irwin, 2008, Turner and De Clerk-Floate, 2008), or are currently being assessed for introduction (Barnewall, 2011, Toševski et al., 2011b, Montana Agricultural Experiment Station and Extension Service, 2013, Andre Gassmann, personal communication). Comparison of populations with and without particular herbivores may be informative about the role of enemy release in invasions and the possible use of biological control. A wide range of processes, including competition, pollination, herbivory, seed resourcing, seed dispersal and vegetative reproduction, potentially affect the individual fitness and population dynamics of *L. vulgaris*. All these processes also have the potential to both be affected by ramet density and to impact on density at multiple spatial scales.

This study treats density as spatial scale dependent and considers any differences in density between ranges and pattern across scales as an emergent property of the interplay between the environment, plant traits and density. Chapter 2 examines whether *L. vulgaris* populations in an area of the invasive range are denser than populations in a climatically matched area of its native range. Rather than choosing a fixed spatial scale, a complete census of the positions of ramets in randomly chosen populations allows density to be compared at a variety of fine to medium spatial scales. It also allows density to be measured and compared between ranges in different ways: as the numbers of ramets within quadrats of different sizes (here called ‘grid density’), as the number of ramets surrounding focal ramets within different distances (‘ramet focused density’) and as the total number of ramets within the area covered by the population (‘mean field density’). Comparisons are also made at a broader spatial scale of the area covered by populations and the recorded number of populations in both study areas. These results are then considered in the context of differing definitions of invasives and stages of invasion.

Difference in plant traits may influence the density pattern seen in both ranges, so Chapter 3 examines whether ramets in the invasive populations are taller, more likely to flower and whether they produce more fruit and viable seed than ramets in the native populations. The underlying influence of any difference between ranges in the biotic and abiotic environment is considered, including the effect of the seed feeding weevil *Rhinusa antirrhini* Paykull (Curculionidae). Possible effects of conspecific density on an individual’s height and sexual reproductive output are also investigated using ramet focused density at different spatial scales.

Dispersal and recruitment are important to the resulting density pattern across spatial scales. Chapter 4 tests how *L. vulgaris* seed dispersal distances are affected by different vegetation environments. The relative role of sexual versus vegetative reproduction in maintaining populations and establishing new populations is investigated by looking at seed germination rates, shoot growth from root fragments and root connections between ramets in natural populations.

Most studies of *L. vulgaris* have been carried out in the invasive range, so chapter 5 includes information drawn from earlier chapters and other work as part of a Biological Flora of the British Isles for *L. vulgaris.* Chapter 6 discusses the findings of this thesis and considers the implications for the management of *L. vulgaris* and directions for future research.

Chapter 2. Comparison of the density of native UK and invasive Alaskan *Linaria vulgaris* Miller populations.

2.1 ABSTRACT

Density varies with spatial scale, however most comparisons of density between native and invasive ranges consider only one spatial scale. This chapter compares the density of the perennial herb *Linaria vulgaris* Miller (Plantaginaceae) in randomly selected populations from climatically matched areas of the UK (native range) and Southeast Alaska (invasive range). The position of every *L. vulgaris* ramet was recorded in fifteen UK populations and seven Alaskan populations. This allowed density to be compared between the ranges at a variety of spatial scales and also using different types of density measurement. For quadrats at fine spatial scales that contained *L. vulgaris,* there was no difference in density between the UK and Alaskan populations. There was also no difference in the mean field density of populations between the UK and Alaska. However, Alaskan populations had more fine scale quadrats without ramets compared with the UK populations studied in 2008, but not compared with UK populations studied in 2009. The Alaskan populations covered larger areas than the UK populations. The larger population areas meant that ramets within the invasive range experienced higher surrounding conspecific densities at medium spatial scales compared with ramets in the native range. Records and surveys also indicated that there are more *L. vulgaris* populations at a landscape scale within the Alaskan study area than within the UK study

areas. These results suggest that *L. vulgaris* traits influencing fine spatial scale density have not altered in response to the novel invasive range environment. However, *L. vulgaris* may have been better able to disperse and establish both a greater number and larger populations in this part of the invasive range.

2.2 INTRODUCTION

Measuring density is fundamental to both managing (Yokomizo et al., 2009, Delmas et al., 2011, Tobin et al., 2011) and understanding the dynamics of alien invasive plants (Sakai et al., 2001, Shea and Chesson, 2002). Most definitions of invasive species involve some consideration of density, whether the definition focuses only on dispersal ability and 'dominance' in a new environment (Richardson et al., 2000, Valéry et al., 2008), or also includes their impacts (Davis and Thompson, 2000). Hypotheses of invasion mechanisms such as Enemy Release (Keane and Crawley, 2002, Liu and Stiling, 2006), Evolution of Increased Competitive Ability (Blossey and Notzold, 1995) and Novel Weapons (Callaway and Aschehoug, 2000) are based on the assumption that alien invasive plants reach higher densities in the novel environment compared with their native range (Crawley, 1987, Noble, 1989). However, until recently, relatively few studies of invasive plants have included the native range (Hinz and Schwarzlaender, 2004). Comparing the native with the invasive range is important to establish to what extent density patterns differ between ranges (Hierro et al., 2005, Lamarque et al., 2012). It can also indicate which processes might have changed to enable invasion, compared with species that are currently only established or introduced (Hierro et al., 2005, Guo, 2006). Comparing the demography of native and invasive populations can inform management plans (Ramula et al., 2008).

Field comparisons of density between native and invasive ranges have had mixed results, with some studies finding no difference between ranges, or even a lower density in the invasive range (Table 1). A study of 26 herbaceous introduced species found that most did not have a greater cover within 1 m^2 plots in their introduced compared with their native range (Firn et al., 2011). A meta-analysis by Parker and colleagues (2013) found that invasive plants were moderately likely to be more abundant in their invasive range, but that there was a large variability between species. Understanding these differences between species and studies can be helped by considering both spatial scale (Pauchard and Shea, 2006) and invasion stages (Colautti and MacIsaac, 2004, Dietz and Edwards, 2006, Hawkes, 2007). Density is defined as individuals, ramets or biomass per unit area, making it a scale dependent and emergent property of a population, rather than a fixed attribute (Wiens, 1989, Gunton, 2007, Gunton and Kunin, 2009). For example, populations in two study areas could have the same density at a broad scale, but differing clustering patterns at fine spatial scales. Alternatively, two study areas could have the same mean density at fine spatial scales, but with individuals covering a different extent of the broad spatial scale.

These differing density patterns across spatial scales can indicate what ‘stage’ (Colautti and MacIsaac, 2004) or ‘phase’ (Dietz and Edwards, 2006) an invasion is in. Both Colautti and MacIsaac’s (2004), and Dietz and

Edward’s (2006) frameworks describing the invasion process might benefit from a more explicit consideration of density and scale. For example, two areas with the same broad scale density, but differing fine scale density, could correspond to Colautti and MacIsaac’s (2004) stages IVa and IVb (Figure 1). Two areas with differing broad scale density but the same fine scale density might correspond to stages IVb and V (Figure 1). The density pattern seen reflects underlying scale dependent processes such as dispersal, environmental constraints and inter and intra-specific competition (Pauchard and Shea, 2006), with these processes changing in importance as the invasion progresses (Colautti and MacIsaac, 2004, Dietz and Edwards, 2006). The degree and type of any impact of the invasive on both the biotic and abiotic environment will also depend in part on this density pattern across spatial scales (Pauchard and Shea, 2006). The invasive species might only have a significant impact on native species when it reaches high fine scale density, with any ‘transformer’ effects (Richardson et al., 2000) on the environment occurring when the invasive reaches high density at both fine and broad spatial scales. Management can benefit from awareness of the spatial pattern of an invasive plant across spatial scales and the likely processes involved (Moody and Mack, 1988, Collingham et al., 2000, Emry et al., 2011).

Despite this, most studies comparing density between ranges use just one spatial scale, most commonly 1 m^2 (Sheppard et al., 1996, Edwards et al., 1998, Bastlová-Hanzélyová, 2001, Erfmeier and Bruelheide, 2004, Cripps et al., 2010, Maurel et al., 2013), or occasionally two spatial scales (Beckmann et al., 2009, Lamarque et al., 2012). Other studies have occurred at one spatial scale within any one population, but with the spatial scale varying between ranges or populations by using different quadrat sizes (Lonsdale and Segura, 1987, Jakobs et al., 2004), or by using mean field density, where the population number is divided by the area covered (Paynter et al., 2003, Ebeling et al., 2008, Herrera et al., 2011). An additional approach to using areas of fixed size or the mean field density, is to measure the density environment as experienced by an individual within the population. This involves measuring the density within a certain distance of an individual (Turkington and Harper, 1979, Gunton and Kunin, 2007, 2009). Although overlapping circles surrounding individuals in a population will be non-independent, this can be useful for investigating how conspecific density at differing spatial scales influences individual fitness. Measuring the density at varying spatial scales surrounding many individuals can build a picture of the range of density environments experienced within that population.

L. vulgaris is a perennial herb native to Europe and invasive in North America that reproduces both clonally and by self-incompatible seed production (Saner et al., 1995). Although it is known for invading anthropogenically disturbed areas (Coupland et al., 1963, Darwent et al., 1975), Pauchard and colleagues (2003) found that it was also capable of expansion into high elevation naturally disturbed habitats. While Pauchard and colleague’s (2003) study was carried out at landscape, stand and patch scales, no studies have characterised and compared fine to medium scale density between invasive and native range populations.

This study focuses on whether there are any differences in density at fine to medium spatial scales between climatically matched native (UK) and invasive (Alaskan) *L. vulgaris* populations. Here, ‘fine’ spatial scale is used to refer to areas of 4 m^2 or smaller, with ‘medium’ spatial scale to 515 m^2 (a circle with a radius of 12.8 m) and then ‘landscape’ spatial scale referring to larger areas. The spatial scales examined are of ramet density within areas from 0.0314 m^2 to 515 m^2, with statistical analysis at fine spatial scales. A complete census of ramet positions within twelve UK native and seven Alaskan invasive study populations allows the density pattern to be understood across fine to medium spatial scales. There is also a comparison of *L. vulgaris* population number along transects and within the spatial extent of three 0.5 degree grid squares. This approach also allows the comparison of three methods of measuring and presenting density; here called ‘grid’, ‘mean field’ and ‘ramet focused’.

This chapter addresses the following hypotheses:

Populations of *L. vulgaris* will be at higher density at fine and medium spatial scales in the invasive compared with the native range.

Individual *L. vulgaris* ramets will experience higher conspecific density at fine and medium spatial scales in the invasive compared with the native range.

2.3 METHODS

2.3.1 Fieldwork

2.3.1.1 Region selection

The UK part of the study was carried out in the 0.5 degree grid squares with the centres 51.75 °N, 0.25 °E (south Essex) and 53.75 °N, 1.25 °W (west Yorkshire), allowing repeat research visits and providing contrasting landscapes. The invasive range grid square was chosen by matching the climate of western North American grid squares with the two UK grid squares, by using a principle components analysis of a 1961–1990 monthly climate means dataset (Intergovernmental Panel on Climate Change, 2008). The climatically closest grid square that had records of *L. vulgaris* and was accessible for research was in Haines, Alaska, with a central point of 59.25 °N, 135.25 °W. See Appendix A for further details.

The earliest records of *L. vulgaris* in Alaska are from the 1960s (Clemson, 1961, Hultén, 1968). Currently the main concentrations are centred on the towns of Anchorage, Fairbanks and Haines, with scattered records in the Yukon and across the coast and interior to 67.25 °N on the Dalton Highway (AKEPIC, 2013). Most records are from below 500 m elevation on disturbed roadsides, urban and garden areas, although there are some records for fields and trails (AKEPIC, 2013). Although *L. vulgaris* has not yet been recorded in the Arctic-Alpine ecogeographic region in the north and west of Alaska (AKEPIC, 2013), it is native in areas with similar climate as analysed by the CLIMEX matching program (Carlson et al., 2008). Most records of *L. vulgaris* in Alaska are since the year 2000, and although much of this will be due to increased recording, there are reports of recent new occurrences in some areas and increasing densities in established areas (AKEPIC, 2013). *L. vulgaris* has been assigned an invasiveness ranking in Alaska of 69 out of a possible 100, based on ecological impacts, plant attributes, distribution and feasibility of control measures (Carlson et al., 2008).

A 2005 survey found that Haines has 14 of 26 invasive plants that are, or are considered likely, to become very invasive in South East Alaska (Lamb and Shephard, 2007). The earliest written record of *L. vulgaris* in Haines is from 1978 (Williams, 1978). In 2010 *L. vulgaris* was present on most roadsides on the Haines peninsula and was also common on other disturbed ground and in gardens, but had not been found in undisturbed natural areas or foot trails (AKEPIC, 2010 and personal observation).

2.3.1.2 Site selection

Records of *L vulgaris* within the UK 0.5 degree grid squares were obtained from the Botanical Society of the British Isles Vascular Plants Database (2007), with some additional records collected in 2007 (Ken Adams, personal communication). A random selection was made from records that were at 1 km or 100 m precision made since 1987. The kilometre or 100 m grid squares of the selected records were searched for *L. vulgaris* populations in June 2008 by two people walking together, up to a maximum search time of four hours. The search started in any area that matched any description in the record, and then moved on to linear features before searching open areas. This resulted in eight sites in the UK that were safe for fieldwork and where research access was granted (Figure 2 & Table 2). Only one site was in the Yorkshire grid square compared with seven in Essex (Table 2). This is because there were fewer Yorkshire records, fewer populations were found from these records and because a greater number than in Essex could not be accessed because they were on railway land.

Records of *L. vulgaris* in Alaska were obtained from the Alaska Exotic Plants Clearing House (AKEPIC, 2010). Records within 100 m of each other were amalgamated. Records from the Skagway area of the grid square were removed because the local climate differed significantly (Nowacki et al., 2001, Parker, 2001). Records were again randomly selected and searched for *L. vulgaris*, resulting in seven Alaskan sites that were safe for field work (Figure 3 & Table 2). The Alaskan records had been recorded at a higher resolution than the UK records, so a Global Positioning System (Garmin eTrex Venture, Garmin Europe Ltd, SO40 9LR) was used to identify the site and a search strategy and time limit was not needed.

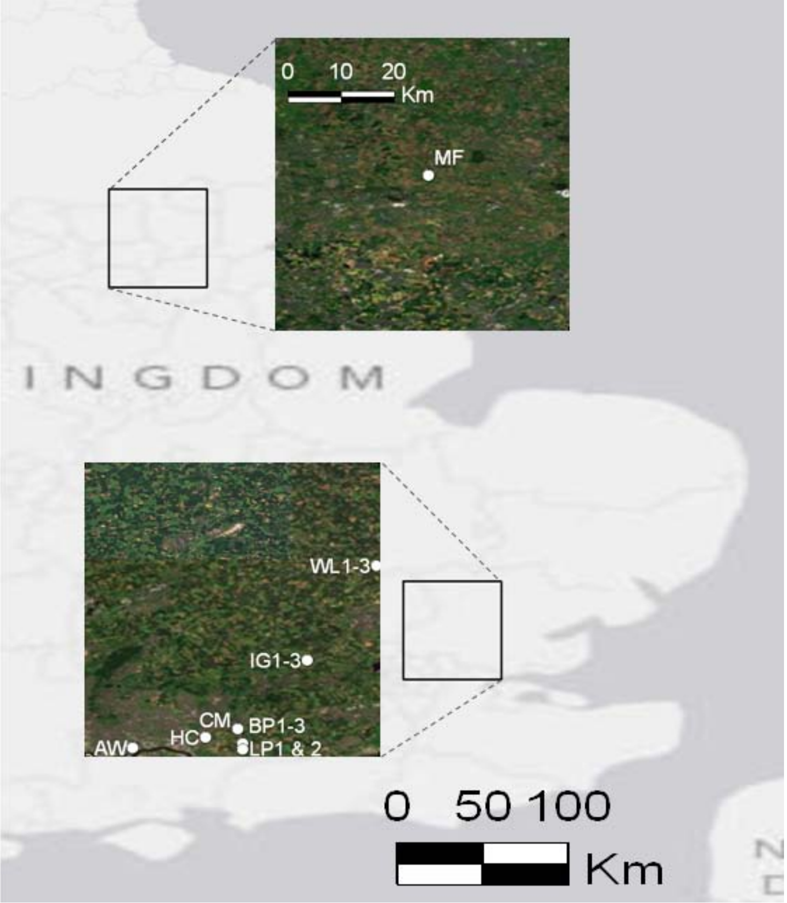

Figure 2. *L. vulgaris* study populations within 0.5 degree grid squares in Yorkshire and Essex. Created in Esri ArcMapTM 10.0 with the Esri and DeLorme basemap and with 1999 Millennium Map aerial photography supplied by ESRI and sourced from Get Mapping Plc: www.getmapping.com, RG27 8NW.

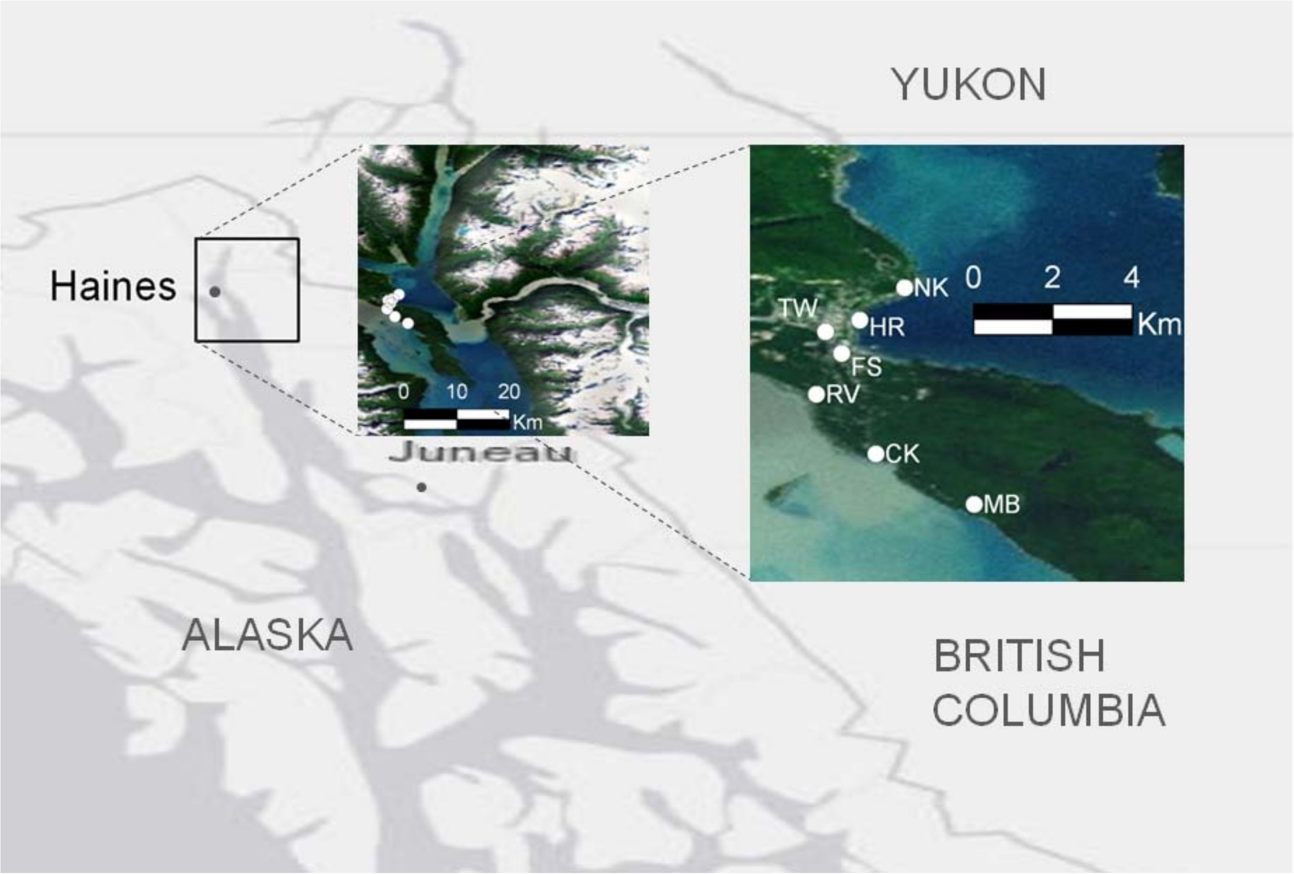

Figure 3. *L. vulgaris* study populations within a 0.5 degree grid square in Southeast Alaska. Created in Esri ArcMapTM 10.0 with the Esri and DeLorme basemap and i-cubed eSAT imagery supplied by ESRI.

Table 2. Continued on the next page. *L. vulgaris* populations surveyed in Autumn 2008 and/or 2009 in the UK and Autumn 2010 in Alaska (AK). [a] Part of the MF 2008 population was surveyed in Spring 2008. [b] Only part of the FS population was surveyed. Table B1 contains further details about the population sizes and other plant species.

Region	Population	Latitude and longitude	Description	Ramets alive in Autumn.
UK	AW	N 51.515° E 0.081°	Unshaded and disturbed brown-field site.	67 in 2008 0 in 2009
	BP1	N 51.522° E 0.267°	Shaded and disturbed sand bank by footpath.	355 in 2008 523 in 2009
	BP2	N 51.522° E 0.266°	Partly shaded ditch edge by footpath.	NA in 2008 131 in 2009
	BP3	N 51.522° E 0.266°	Unshaded grassland. Grazed by rabbits (*Oryctolagus cuniculus*).	NA in 2008 320 in 2009
	CM	N 51.548° E 0.260°	Partly shaded south facing alcove in hedgerow. Grazed by rabbits.	182 in 2008 79 in 2009
	HC	N 51.532° E 0.205°	Partly shaded south facing hedgerow.	123 in 2008 200 in 2009
	IG1	N 51.663° E 0.379°	Partly shaded in arable field margin by railway line.	7 in 2008 0 in 2009
	IG2	N 51.663° E 0.379°	Partly shaded bank by railway line. Appeared after spoil from railway works.	0 in 2008 3 in 2009
	IG3	N 51.662° E 0.377°	Unshaded arable field margin by railway line. Appeared after spoil from railway works.	0 in 2008 653 in 2009
	LP1	N 51.512° E 0.270°	Unshaded grass and herbs next to footpath. Burned in 2009.	264 in 2008 356 in 2009
	LP2	N 51.512° E 0.268°	Shaded footpath edge. Burned in 2009.	42 in 2008 0 in 2009
	MF	N 53.765° W 1.239°	Unshaded bank of rubble and shaded and partly shaded grassland near railway line. Disturbed by railway works.	517 in 2008 [a] 301 in 2009
	WL1	N 51.824° E 0.496°	Partly shaded minor roadside hedgerow. Occasionally cut.	132 in 2008 93 in 2009

Table 2 continued.

Region	Population	Latitude and longitude	Description	Ramets alive in Autumn.
UK	WL2	N 51.824° E 0.496°	Shaded minor roadside hedgerow. Occasionally cut.	NA in 2008 86 in 2009
	WL3	N 51.824° E 0.496°	Unshaded grass margin between footpath and ditch. Occasionally cut.	NA in 2008 470 in 2009
AK	CK	N 59.204° W 135.435°	Low grass and herbs on a promontory between a gravel roadside pull in and the estuary. Disturbed. Unshaded.	1779
	FS	N 59.227° W 135.443°	Tall grass and herbs with occasional shrubs and patches of rubble between a minor road and a ruined building. Unshaded.	629 [b]
	HR	N 59.235° W 135.439°	Population is on both sides of a harbour breakwater among sparse vegetation and rubble. Unshaded.	651
	MB	N 59.193° W 135.413°	Gravel and bank of a drainage ditch at the edge of a driveway. Partly shaded.	229
	NK	N 59.242° W 135.428°	Gravel roadside pull in with sparse vegetation. Recently disturbed with new gravel and machinery. Unshaded.	138
	RV	N 59.218° W 135.448°	Grass and herbs and a grass bank between wetland and road. Very high tides reach the edge of the population and it is likely to be occasionally submerged. Footpath though the patch and disturbance in the area from digging by Brown bears (*Ursus arctos*). Partly shaded.	1035
	TW	N 59.232° W 135.446°	Grass and herb verge between pavement and ditch. Occasionally cut. Partly shaded.	344

2.3.1.3 Population surveys

Patches of *L. vulgaris* were defined as separate populations if there was a distance of more than 25.6 m between ramets. This distance was used because it was the greatest radius used to calculate ramet focused density. Some of the UK sites had several populations. Recording took place in September–October 2008 and 2009 for fifteen UK populations and late August–October 2010 for seven Alaskan populations (Table 2). The 2008 survey was on the nine UK populations AW, BP1, CM, HC, IG1, LP1, LP2, MF and WL1 (Table 2). Two sections of the MF population could only be recorded in April and June 2008 rather than in autumn 2008. Population IG1 had died, population AW had been destroyed and population LP2 had been burned before the 2009 survey (Table 2). Six additional populations (BP2, BP3, IG2, IG3, WL2 and WL3) were included in the 2009 survey. IG2 and IG3 were new populations established since the 2008 survey after spoil from rail side works fell onto the field boundary. Further details about the study populations are in Appendix B.

A baseline was defined along the longest axis of the population area and the population was surveyed on a 0.25 m^2 celled grid, marked out with steel 6 ” (15 cm) nails or plastic markers. A 0.5 x 0.5 m quadrat was used across the grid to record the x and y position of every *L. vulgaris* ramet to the nearest cm. Where possible the recorder stood outside of the population boundary to avoid trampling. Tags were used to mark any ramets that were on the very edge of quadrats to prevent any repeat sampling as successive rows were recorded. The HR population was on both sides of a breakwater with a road between, so two baselines with grids were used. The NK population consisted of sparse clusters of *L. vulgaris*, so three baselines were used, with compass and tape measure used to keep them parallel or at 90 degrees to the initial baseline. Vegetation in populations HC, IG2 and IG3 made it impossible across most of the population to set up and record to a 0.25 m grid. Instead, as these populations were narrow, x and y positions were taken straight from the baseline. Obstacles meant that the positions of 98 UK 2008 ramets (out of 1343), 71 UK 2009 ramets (out of 3215) and 21 Alaskan ramets (out of 4805) could only be recorded approximately.

2.3.1.4 Population characteristics

Soil samples were taken from eight UK 2009 populations and six Alaskan populations in 2010. Separate soil samples were not taken from BP2, IG2, WL2 and WL3 because funding was limited and these were assumed to have a similar soil type as the sampled populations within the same site. Population BP1 was on a sand bank so was sampled separately from grassland populations BP2 and BP3. A soil sample was not taken from the Alaskan population MB because all the substrate was gravel. Samples were analysed for the proportions of clay, sand and silt particles, pH, field moisture content, organic content and Ca, K, Mg, Mn, Na, P and S content. Alaskan soil samples were analysed by Laurie Wilson at the University of Alaska Fairbanks (Palmer Research Center, 1509 S. Trunk Rd., Palmer, AK 99645). UK soil samples were analysed by François Bochereau at Forest Research (Alice Holt Lodge, Farnham, Surrey, UK GU10 4LH). Further details about the soil analysis are in Appendix C.

The vegetation height in the centre of each 0.5 x 0.5 m quadrat was recorded to the nearest 5 cm up to 50 cm and then to the nearest 10 cm. Four outlying vegetation heights of 2 and 3 m in population HC were bounded at 1 m, because it was the height of surrounding plants growing from within the quadrat that was of interest, rather than the canopy height of neighbouring woody plants. The percentage of unvegetated ground in each quadrat was estimated in the categories ≤ 5 %, 6 – 25 %, 26 – 50 %, 51 – 75 %, 76 – 95 % or > 95 % unvegetated ground. Plant taxa that occurred in most quadrats, were dominant in a few quadrats or that were shading the site were identified at least to genus. The amount of shading of the population or sections of the population was recorded as shaded where there was a canopy over *L. vulgaris* ramets, partly shaded if ramets are shaded for part of the day, or unshaded. Signs of disturbance were also recorded.

For analyses in Chapter 3 that included vegetation height and cover, quadrats that had missing values were replaced in various ways, as follows. A fire at the time of the 2009 recording in the LP population meant that the median vegetation height from 2008 had to be used. Railway work just before the 2009 recording in the MF population crushed vegetation for half of the population. These missing values were replaced with the median vegetation height recorded in 2010, because 2008 vegetation heights had been much higher than observed across the rest of the MF population during 2009. Occasional missing values for vegetation height and vegetation cover were replaced with the neighbouring quadrat values, having studied photographs taken during fieldwork to check that this was appropriate.

2.3.1.5 Landscape scale comparison

The intensity, purpose and practice of historical recording of *L. vulgaris* populations differs between the Alaskan and UK grid squares, making it difficult to compare the population number at the landscape scale. A walked survey for *L. vulgaris* populations was carried out along 1.5 km (59.213° N, 135.438° W to 59.224° N, 135.446° W) of a minor road in Haines. This road had not been included in a 2007 roadside survey of *L. vulgaris* (Arhangelsky, 2007). The same length was walked in August 2011 along 1.5 km of footpaths across Belhus Woods Country Park, UK (51.520° N, 0.255° E to 51.512° N, 0.274° E), where there were *L. vulgaris* population records within the Park, but not on the walked route. Roadsides in the Haines area are mainly loose gravel. An environment in the UK with a similar substrate and level of disturbance are railway sides and embankments. A 10 km section of track was selected between1 km East of Brentwood station (51.638° N, 0.341° E) and 2.6 km before Chelmsford station (51.715° N, 0.455° E), having excluded 1 km either side of Ingatestone station. Another 10 km of track was selected in East Yorkshire between 1 km East of South Milford station (53.780° N, 1.234° W) and 1.9 km before Selby station (53.778° N, 1.086° W). It was not possible to survey railway sides by foot, so surveys were carried out from trains at the peak of *L. vulgaris* flowering in August 2011, with the location of flowering populations recorded up to an estimated 5 m from the trackside. The journey was made four times so that each side could be surveyed twice by one observer. Track near stations were excluded so that the train would be travelling at a similar speed throughout the survey.

2.3.2 Statistical analysis

Three types of density measurements were compared during analysis: these were called ‘grid density’, ‘mean field density’ and ‘ramet focused density’. Population characteristics were also compared to identify whether biotic and abiotic conditions differed significantly between the UK and Alaska.

2.3.2.1 Grid density analysis

The map of ramets for each population was overlaid with rectangular grids forming squares of sides 0.25 x 0.25 m (0.0625 m^2), 0.5 x 0.5 m (0.25 m^2), 1 x 1 m (1 m^2) and 2 x 2 m (4 m^2). The population boundary was defined at each scale by excluding from the dataset any corner and edge squares not containing *L. vulgaris*, but retaining empty squares if there were *L. vulgaris* containing squares on both sides of the empty square at any point on either the same column or row. Any difference between the ranges was investigated by comparing generalised linear models and generalised linear mixed effect models using the package glmmADMB (Skaug et al., 2012) in R 2.15.2 (R Core Team, 2012). Four models were compared at each spatial scale. Two included region (UK or AK) as a fixed effect, but with and without population as a random effect. Two contained no fixed effects, but with population or population nested within region as random effects. Model comparison was based on Akaike’s Information Criterion (AIC) (Burnham and Anderson, 2002). The finest spatial scale data was zero-inflated, so two sets of analyses were carried out. At each spatial scale, the number of ramets in only the squares containing *L. vulgaris* was modelled using a truncated negative binomial distribution for the errors. For the 0.0625 m^2 and 0.25 m^2 spatial scale, there was also an analysis of the presence or absence of *L. vulgaris* in squares, with the errors modelled using a binomial distribution and a logit link. There were too few squares without ramets for presence/absence analysis at the 1 m^2 and 4 m^2 scale.

2.3.2.2 Mean field density and population area analysis

The ‘mean field density’ of each population was the total number of ramets divided by the area within the population boundary as defined above for the 0.0625 m^2 spatial scale squares. Wilcoxon rank sum tests were used to compare the mean field densities and areas of UK 2008 and 2009 populations with Alaskan populations. Figures were created using the R package Lattice (Sarkar, 2008).

2.3.2.3 Ramet focused density analysis

The mapping of all ramet positions also allowed the calculation of ‘ramet focused density’ – the density within a circle of a certain radius around each ramet. The number of ramets (including the focal ramet) per m^2 was calculated within 0.1 m, 0.2 m, 0.4 m, 0.8 m, 1.6 m, 3.2 m, 6.4 m and 12.8 m radii of each ramet. The density within 25.6 m of every ramet is also shown in descriptive figures, but not used in further analysis in Chapter 3. This is because for the UK populations IG1, IG2, IG3, LP1, LP2 and MF and Alaskan populations CK, FS, HR, RV and TW there were either further patches of *L. vulgaris* or appropriate habitat for *L. vulgaris* within 25.6 m that were not possible to survey. For the other populations there were no further *L. vulgaris* ramets up to 25.6 m from the outermost ramets.

The FS population survey ended at 16 m on the x baseline because the whole population was too large to completely survey within the available time. Only ramets further than 6.4 m from the unsurveyed section were used as focal ramets. Ramets within 6.4 m of the unsurveyed section were recorded only to provide the ramet focused density measurements of focal ramets. The ramet focused density calculations for focal ramets where part of the surrounding 12.8 m radius circle fell in the unsurveyed section were adjusted to remove that segment. The IG populations could not be surveyed beyond 1.6 m y from the baseline because of the railway line, where there could have been further *L. vulgaris* ramets. Again, circles surrounding ramets that extended beyond 1.6 m y had a segment removed for the ramet focused density calculations.

‘Ramet focused density’ is non-independent because the density environment at a particular spatial scale is usually shared by neighbouring ramets, so Standard Errors of the means or 95 % Confidence Intervals of the means cannot be calculated. However, only using the ramets within a population whose density environment at a particular spatial scale does not overlap would have biased analysis towards ramets that were less clumped at that spatial scale.

2.3.2.4 Population characteristics analysis

Hierarchical cluster analysis using hclust in R 2.12.2 (R Development Core Team, 2011) was used to check to what extent Alaskan and UK 2009 populations group separately for their soil characteristics. Textural, chemical elements and pH were included both separately and in combination. A chi-square test was used to test if the numbers of Alaskan quadrats in the six bare ground classes differed significantly from what would be expected if they were in the same proportions as the UK 2009 quadrats. Logged vegetation height was compared between UK 2009 and Alaska with a generalised least square and general linear mixed effects models using the functions gls and lme from the package nlme (Pinheiro et al., 2011) in R 2.12.2 (R Development Core Team, 2011). Four models were compared: region as a fixed effect and population as a random effect, only region as a fixed effect, only population as a random effect and population nested within region as a random effect. Comparison of models with different random effects structures and the same fixed effects was done using Restricted Maximum Likelihood (REML). Comparison of models with the same random effects structure and nested fixed effects used Maximum Likelihood (ML). The natural log of vegetation height plus one was used to achieve homogeneity of variance and normality of residuals.

2.4 RESULTS

2.4.1 Population characteristics

Cluster analysis of soil chemical and textural properties together did not separate the UK 2009 and Alaskan populations (Figure 4). However, when only soil texture is considered, all of the Alaskan populations group with the UK BP and LP sites because of their high sand and low clay content (Figure 5 and Tables C1 & C2). There was no difference in grouping whether a complete or single linkage method was used. The relative proportion of Alaskan quadrats across the unvegetated ground categories differed from the proportions of the UK 2009 quadrats ($\chi_2 = 13971$, d.f. = 4, $p < 0.001$). A smaller proportion of the Alaskan quadrats had less than 5 % bare ground and a higher proportion had a large amount of bare ground compared with the UK 2009 quadrats (Figure 6). UK vegetation was taller than Alaskan vegetation, with a UK 2009 mean vegetation height of 25.71 cm ± 1.32 S. E. mean and an Alaskan mean of 13.28 cm ± 0.44 S. E mean (Figure 7). Including region as a fixed effect in a model of logged vegetation height, with population as a random effect, was marginally more likely than a model with population alone (Likelihood ratio = 4.12, d.f. = 1, p = 0.042, method = ML), with a difference of 2.12 AIC units (Table 3).

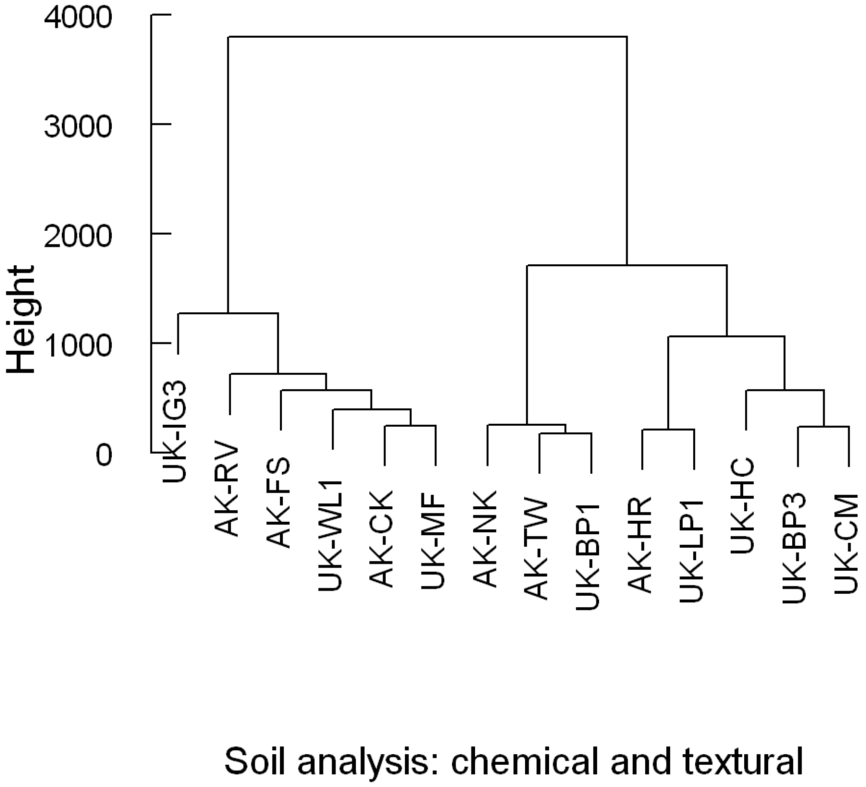

Figure 4. Hierarchical cluster analysis of soil texture, pH, loss on ignition and chemical elements P, K, Ca, Na, Mn, Mg and S for UK and Alaskan *L. vulgaris* population soil samples.

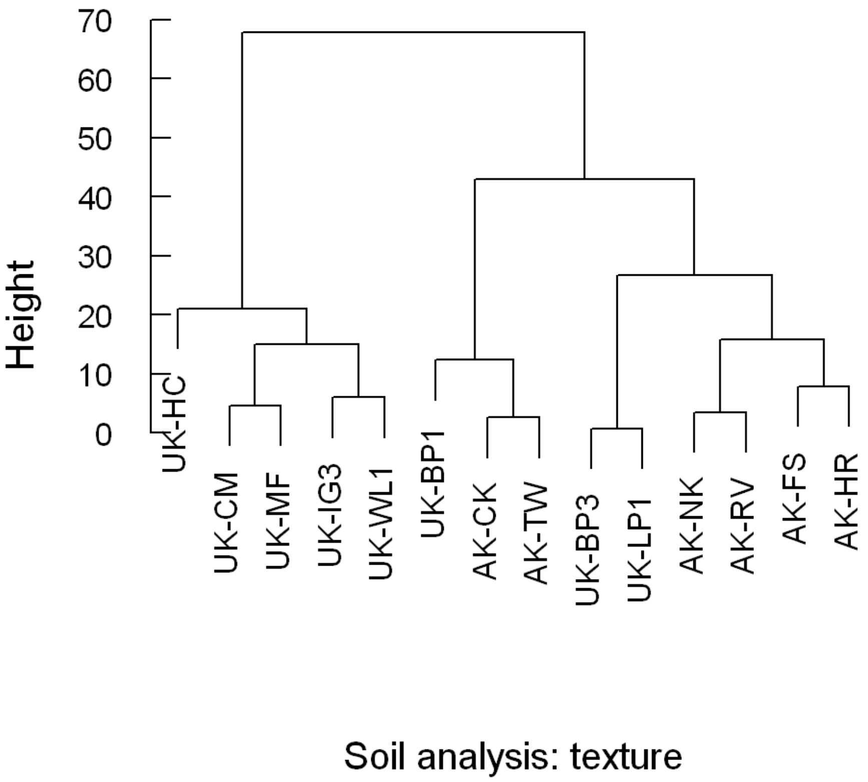

Figure 5. Hierarchical cluster analysis of soil texture for UK and Alaskan *L. vulgaris* population soil samples.

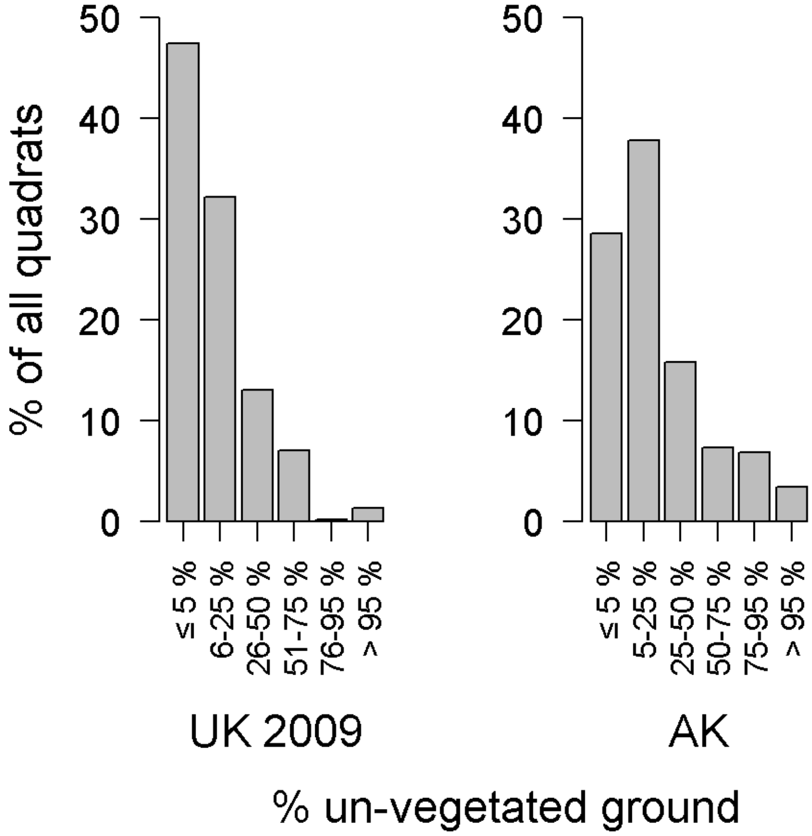

Figure 6. Proportion of quadrats in UK 2009 and Alaskan (AK) *L. vulgaris* populations in six classes of the amount of unvegetated ground within the 0.5 x 0.5 m quadrats.

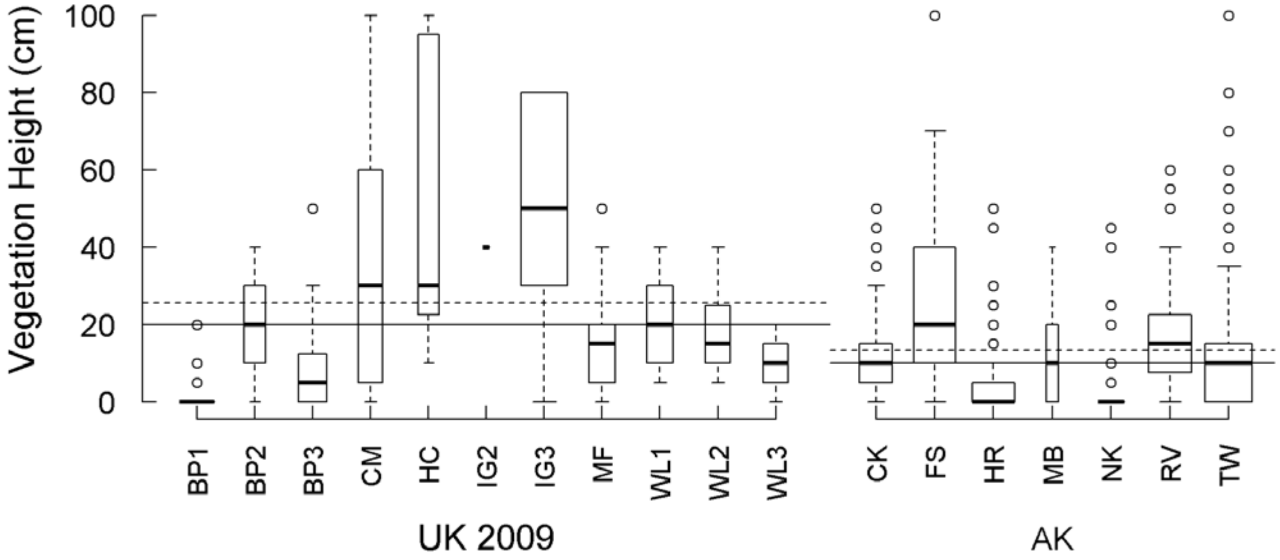

Figure 7. Boxplot of vegetation height in the centre of 0.5 x 0.5 m quadrats across UK 2009 and AK *L. vulgaris* populations, including quadrats without *L. vulgaris* ramets. Solid lines are the medians and dashed lines the means. Box widths are proportional to the square root of the number of quadrats surveyed in each population. There are also two outliers of 120 cm in population TW and one outlier of 160 cm in population RV that are not shown.

Table 3 Mixed effects models and a generalised least square model of Ln+1 vegetation height measured in a 0.5 m x 0.5 m grid across *L. vulgaris* populations in the UK 2009 and Alaska (region). Comparisons of models with the same fixed components, but different random components, should be done using AIC from models fitted using Restricted Maximum Likelihood (REML). Comparison of models with different fixed components, but the same random components, should be done using AIC from models fitted using Maximum Likelihood (ML).

Fixed components	Random components	AIC (REML)	AIC (ML)
Region	**Population**	***6295.27***	**6294.24**
Region	NA	*7060.29*	
NA	Population	6297.40	6296.36
NA	Region/Population	6297.94	

2.4.2 Density comparison

2.4.2.1 Grid density

There was no difference in *L. vulgaris* ramet number between UK 2008 and Alaska (Table 4) or between UK 2009 and Alaska (Table 5) when comparing grid squares of sizes 0.0625 m^2 (0.25 m grid), 0.25 m^2 (0.5 m grid), 1 m^2 (1 m grid) or 4 m^2 (2 m grid) that contained *L. vulgaris*. Density differs at the level of the population, but not between regions, because models with population nested in region or with region as a fixed effect are equivalent to models with population alone (Table 4 &Table 5). The maximum densities are slightly higher in Alaska at very fine grid sizes, but this is likely to be a sampling effect because Alaskan populations covered a larger area and so had more squares than UK populations (Table 6).

A larger proportion of the 0.0625 m^2 and 0.25 m^2 squares from the UK populations recorded in 2008 contained at least one *L. vulgaris* ramet compared with the Alaskan populations (Table 7). However, for the UK 2009 populations, the AIC of the models with population as a random effect where region is and is not included as a fixed effect, are within two points (Table 8). The p-values of likelihood ratio tests between these models are borderline, but indicate that there is not a significant decrease in log likelihood when region as a fixed effect is dropped from the model with population as a random effect (0.0625 m^2 spatial scale change in deviance = 3.72, d.f. = 1, $p = 0.0538$; 0.25 m^2 spatial scale change in deviance = 3.32, d.f. = 1, $p = 0.0684$). This means that the simpler model containing only population as a random effect should be preferred. There is a large difference in the predicted occupancy for the UK 2009 squares between models that have country as a fixed effect, but with and without the population structure as a random effect (Table 8). This occurs because the UK 2009 populations have a high variation in the proportion of empty squares within the population (10 to 92 % for 0.0625 m^2 squares). For example, UK populations BP1 and IG3 have a patchy population structure with a large proportion of empty squares (Figures B2, B3 & B12), while populations BP2 and WL3 have very few empty squares (Figures B4 & B21).

Table 4. Models of *L. vulgaris* ramet number in grids of varying spatial scales across nine UK 2008 and seven Alaskan populations. Squares without ramets were excluded and errors were modelled using a truncated negative binomial distribution. The Minimum Adequate Model at each spatial scale is in bold. The 1 m^2 and 4 m^2 models do not include population IG1 because it has only one square at these scales.

Grid size	Fixed component	Random component	AIC
0.0625 m^2	Region	Population	7716.42
0.0625 m^2	Region	NA	7850.50
0.0625 m^2	**NA**	**Population**	**7716.20**
0.0625 m^2	NA	Region/Population	7718.20
0.25 m^2	Region	Population	5071.56
0.25 m^2	Region	NA	5164.36
0.25 m^2	**NA**	**Population**	**5069.56**
0.25 m^2	NA	Region/Population	5071.56
1 m^2	Region	Population	2937.54
1 m^2	Region	NA	2991.10
1 m^2	**NA**	**Population**	**2936.50**
1 m^2	NA	Region/Population	2938.50
4 m^2	Region	Population	1550.89
4 m^2	Region	NA	1597.84
4 m^2	**NA**	**Population**	**1550.07**
4 m^2	NA	Region/Population	1552.07

Table 5. Models of *L. vulgaris* ramet number in grids of varying spatial scales across 12 UK 2009 and seven Alaskan populations. Squares without ramets were excluded and errors were modelled using a truncated negative binomial distribution. The Minimum Adequate Model at each spatial scale is in bold.

Grid size	Fixed component	Random component	AIC
0.0625 m^2	Region	Population	9673.20
0.0625 m^2	Region	NA	9868.60
0.0625 m^2	**NA**	**Population**	**9672.04**
0.0625 m^2	NA	Region/Population	9674.04
0.25 m^2	Region	Population	6475.74
0.25 m^2	Region	NA	6618.94
0.25 m^2	**NA**	**Population**	**6473.76**
0.25 m^2	NA	Region/Population	6475.76
1 m^2	Region	Population	3946.62
1 m^2	Region	NA	4058.80
1 m^2	**NA**	**Population**	**3944.68**
1 m^2	NA	Region/Population	3946.68
4 m^2	Region	Population	2165.56
4 m^2	Region	NA	2234.96
4 m^2	**NA**	**Population**	**2163.76**
4 m^2	NA	Region/Population	2165.76

Table 6. Mean and range of ramet density from squares formed from grids of four sizes across nine UK 2008, 12 UK 2009 and seven Alaskan (AK) *L. vulgaris* populations. All squares without ramets were excluded.

Grid square size	UK 2008	UK 2009	AK
0.0625 m^2	45.01 (16 – 256)	45.75 (16 - 304)	51.83 (16 - 512)
	562 squares	1072 squares	1455 squares
0.25 m^2	26.90 (4-140)	24.49 (4 - 200)	28.41 (4 - 248)
	247 squares	527 squares	655 squares
1 m^2	16.99 (1-94)	12.11 (1 - 134)	15.00 (1 - 144)
	97 squares	266 squares	312 squares
4 m^2	10.51 (0.75-38)	6.82 (0.25 - 76)	8.34 (0.25 - 55.75)
	39 squares	118 squares	139 squares

Table 7. Models of presence or absence of *L. vulgaris* in grid squares of different spatial scales across nine 2008 UK populations and seven Alaskan (AK) populations. Squares beyond the population boundary were excluded. Errors were modelled using a binomial distribution. Models are compared at each spatial scale using Akaike's Information Criterion (AIC) and the Minimum Adequate Model is in bold.

Grid size	Fixed component	Random component	AIC	Probability of ramet presence in a square
0.0625 m^2	**Region**	**Population**	**7268.26**	**UK = 0.67 AK = 0.24**
0.0625 m^2	Region	NA	8832.88	UK = 0.52 AK = 0.20
0.0625 m^2	NA	Population	7273.80	0.47
0.0625 m^2	NA	Region/Population	7273.22	0.45
0.25 m^2	**Region**	**Population**	**2388.70**	**UK = 0.92 AK = 0.47**
0.25 m^2	Region	NA	2948.74	UK = 0.75 AK = 0.32
0.25 m^2	NA	Population	2394.08	0.78
0.25 m^2	NA	Region/Population	2393.62	0.76

Table 8. Models of presence or absence of *L. vulgaris* in grid squares of different spatial scales across 12 2009 UK populations and seven Alaskan populations. Squares beyond the population boundary were excluded. Errors were modelled using a binomial distribution. Models are compared at each spatial scale using Akaike's Information Criterion (AIC) and the Minimum Adequate Model is in bold.

Grid size	Fixed component	Random component	AIC	Probability of ramet presence in a square
0.0625 m^2	Region	Population	9977.98	UK = 0.54 AK = 0.24
0.0625 m^2	Region	NA	12528.48	UK = 0.21 AK = 0.20
0.0625 m^2	**NA**	**Population**	**9979.70**	**0.42**
0.0625 m^2	NA	Region/Population	9981.34	0.40
0.25 m^2	Region	Population	3609.98	UK = 0.83 AK = 0.47
0.25 m^2	Region	NA	4456.88	UK = 0.37 AK = 0.32
0.25 m^2	**NA**	**Population**	**3611.30**	**0.71**
0.25 m^2	NA	Region/Population	3613.10	0.70

2.4.2.2 Mean field density and population area

The mean field density of UK 2008, UK 2009 and Alaskan populations lie in the same range (Figure 8). There was no difference in mean field density, when area is calculated from the population boundary placed around squares of 0.0625 m^2, between UK 2008 and Alaskan populations (Wilcoxon rank sum test, W = 45, $p > 0.05$), or between UK 2009 and Alaskan populations (Wilcoxon rank sum test, W = 53, $p > 0.05$). However, many of the Alaskan populations covered a larger area than the UK populations

(Figure 8). The mean of the Alaskan population areas was significantly larger than the mean of the UK 2008 population areas (Wilcoxon rank sum test, W = 5, $p < 0.005$) and the mean of UK 2009 population areas (Wilcoxon rank sum test, W = 18, $p < 0.05$).

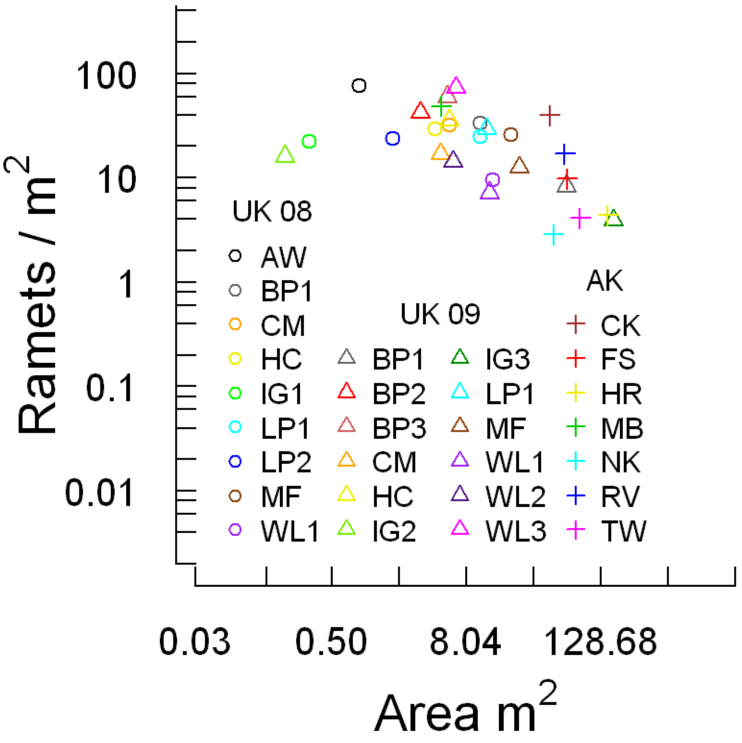

Figure 8. Mean field density of *L. vulgaris* ramets in UK 2008, UK 2009 and Alaskan populations. The area is calculated from within the population boundary as defined for the 0.0625 m^2 (25 x 25 cm) square density calculations. The area axis corresponds to the areas of circles of differing radii around ramets that are used in the ramet focused density figures.

2.4.2.3 Ramet focused density

The density surrounding ramets declines with increasing spatial scale, demonstrating a clustering pattern at fine spatial scales (Figure 9). The means of the densities surrounding Alaskan ramets are slightly greater than the means of the densities surrounding UK 2008 and UK 2009 ramets at all spatial scales (Figure 9a). This is also true if the mean is calculated from the population means, rather than from all individual ramets (Figure 9b). The medians of the densities surrounding all Alaskan ramets are also slightly higher than the medians of the densities surrounding the UK ramets, except when measured within 0.1 m where the Alaskan and UK 2009 median is identical at 95.49 ramets / m^2 (three ramets) (Figure 10). However, at fine spatial scales the difference between Alaskan and UK 2009 mean densities is similar to the difference between UK 2009 and 2008 mean densities.

The UK density means and medians begin to decline more sharply as the circle radius becomes larger than 0.8 m (Figure 10). However, the Alaskan mean and median densities maintain a similar trajectory across 1.6 m, 3.2 m and 6.4 m distances (Figure 10). The higher mean density surrounding Alaskan ramets at these broader scales is largely caused by populations CK and RV (Figure 11c), whose shape, large area and high population number results in a larger number of ramets having higher surrounding densities at broader scales compared with other populations. The other Alaskan population mean densities are within the range of the UK populations across all spatial scales. Alaskan outliers at the < 0.1 m scale reach to densities just below 800 ramets / m^2, compared with below 600 ramets / m^2 for UK 2009 and below 400 ramets / m^2 for UK 2008. This is likely to be a sample size effect, as there were more Alaskan than UK ramets.

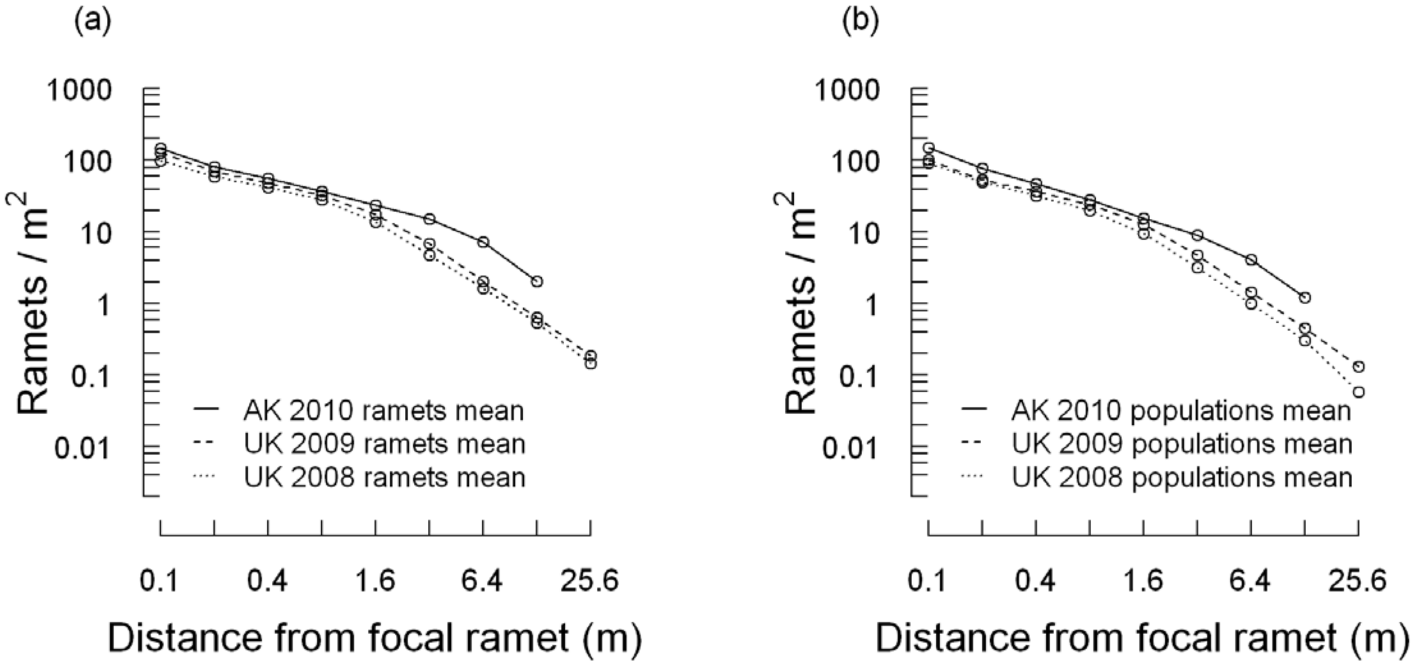

Figure 9. Means of *L. vulgaris* ramet density within circles of varying radii surrounding ramets from UK populations in 2008 and 2009, and in Alaskan populations in 2010. In (a) the mean is calculated from densities surrounding all the ramets and in (b) the mean is calculated from the population means of the ramet focused density. Distance is the radii of circles surrounding focal ramets, within which ramet focused density is calculated.

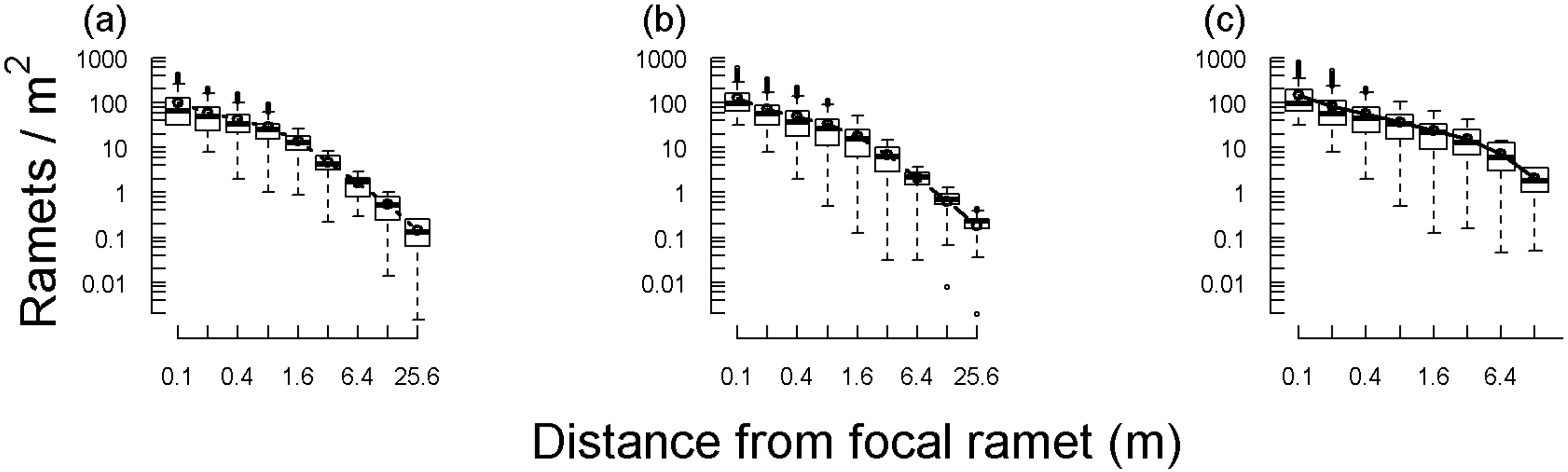

Figure 10. Boxplots and means of densities within circles of varying radii surrounding *L. vulgaris* ramets in (a) all UK 2008 populations, (b) all UK 2009 populations and (c) all Alaskan populations. The Alaskan < 25.6 m spatial scale is not included because only densities in two populations could be accurately measured at that scale.

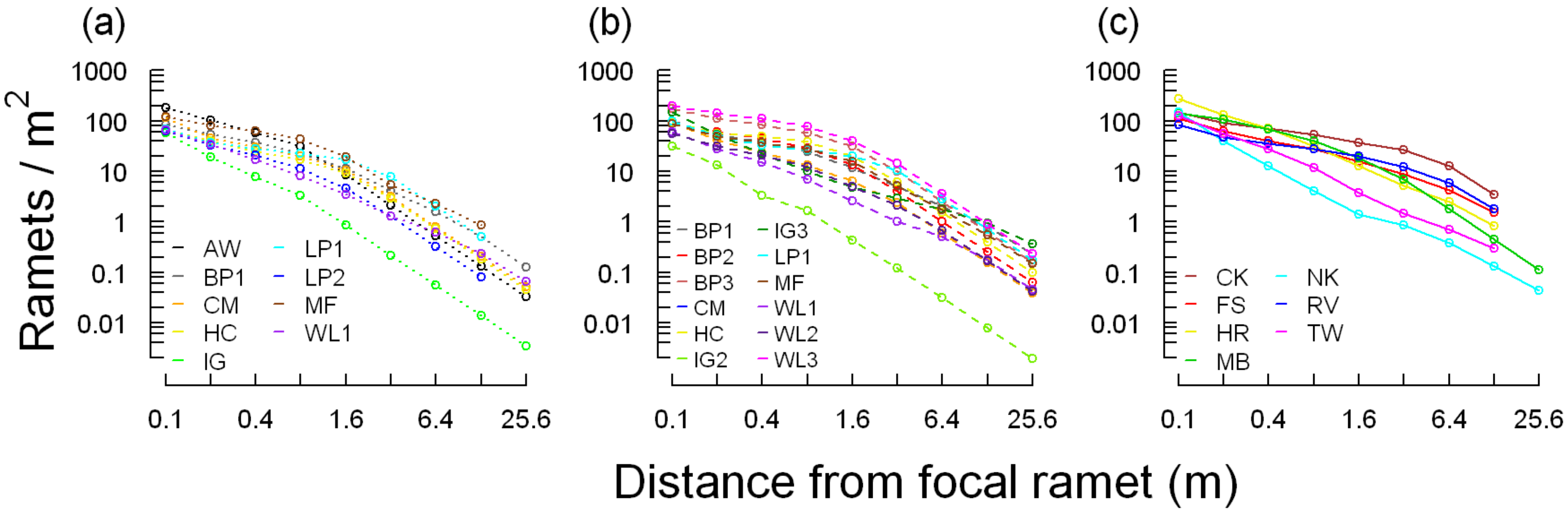

Figure 11. Population means of the densities within circles of varying radii surrounding *L. vulgaris* ramets from (a) UK 2008 populations, (b) UK 2009 populations and (c) Alaskan populations.

2.4.2.4 Landscape scale comparison

There were 277 *L. vulgaris* records from the Alaskan Haines grid square to the end of 2012 (Figure 12) (AKEPIC, 2013). Six of these records had a precision of within 100 m and the remaining records had a precision of 30 m or less. The oldest record from within the grid square was from 2005. All records are from low to medium intensity developed land (Multi-Resolution Land Characterization Consortium, 2001), with the majority of records from roadsides and parking areas (AKEPIC, 2013). All but 14 of these records included details about disturbance at the site, with the most common disturbance form being the importation of aggregates during road or railway maintenance (AKEPIC, 2013). Other disturbance types included mowing, trampling, aggregate extraction and mechanical tree or brush cutting (AKEPIC, 2013). Only two sites were recorded as affected by the non-anthropogenic disturbance of streams and landslides (AKEPIC, 2013).

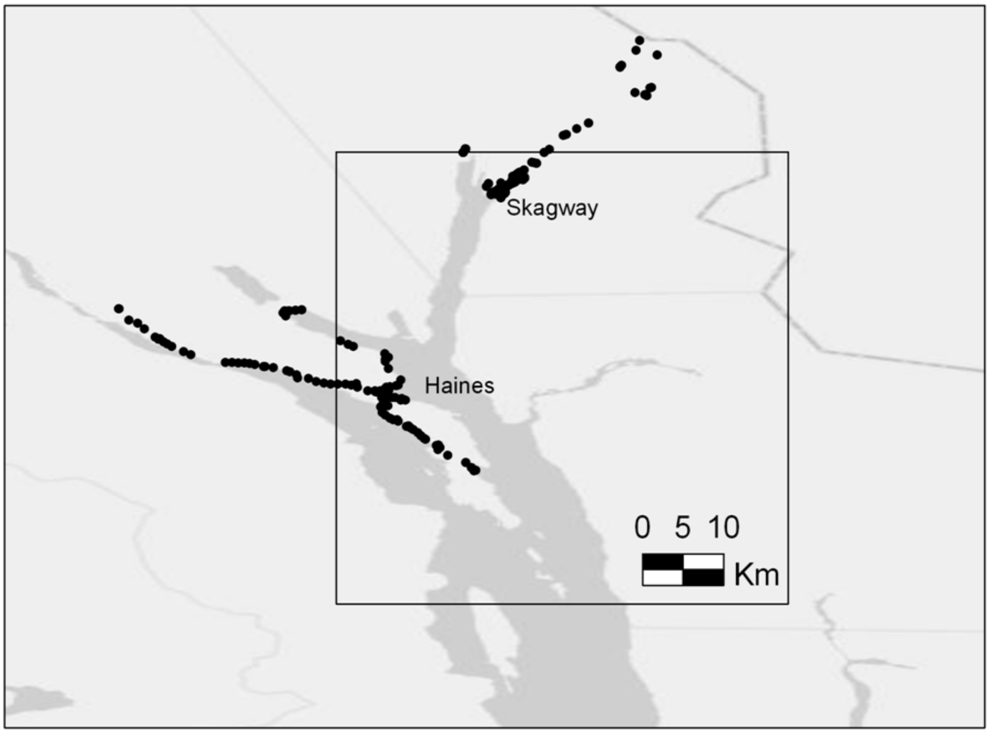

Figure 12. *L. vulgaris* records from the Alaska Exotic Plant Information Clearinghouse to the end of 2012 around Haines in Southeast Alaska. There were 277 records within the 0.5 degree grid study square, with the earliest record from 2005. Created in Esri ArcMapTM 10.0 with the Esri and DeLorme basemap.

There were 285 records of *L. vulgaris* in the Essex grid square between 1987 and 2012 (Figure 13). Precision varied between 100 m and 10,000 m, with most records at 1000 m (Botanical Society of the British Isles, 2013). Variation in precision means that the areas covered by some records overlapped and results in 217 independent record areas. There were also some records with the same grid reference and precision, however, many of these had descriptions indicating that these were independently recorded populations rather than duplicates. This makes the likely number of separate populations recorded in the Essex grid squares to be 242. There were 107 independent record areas from a total of 227 records in the Yorkshire grid square between 1987 and 2012. Precision varied between 1000 m and 10,000 m (Botanical Society of the British Isles, 2013). Unlike the Essex square, most duplication in the Yorkshire dataset was from records entering from different sources, but originating from the same population recording (Kevin Walker, personal communication). There were 22 populations of *L. vulgaris* on the 1.5 km of surveyed road in Alaska, but no populations were found in the 1.5 km walked survey in the UK. There were 11 flowering populations recorded on the 10 km Essex railway survey and seven flowering populations on the 10 km East Yorkshire railway survey.

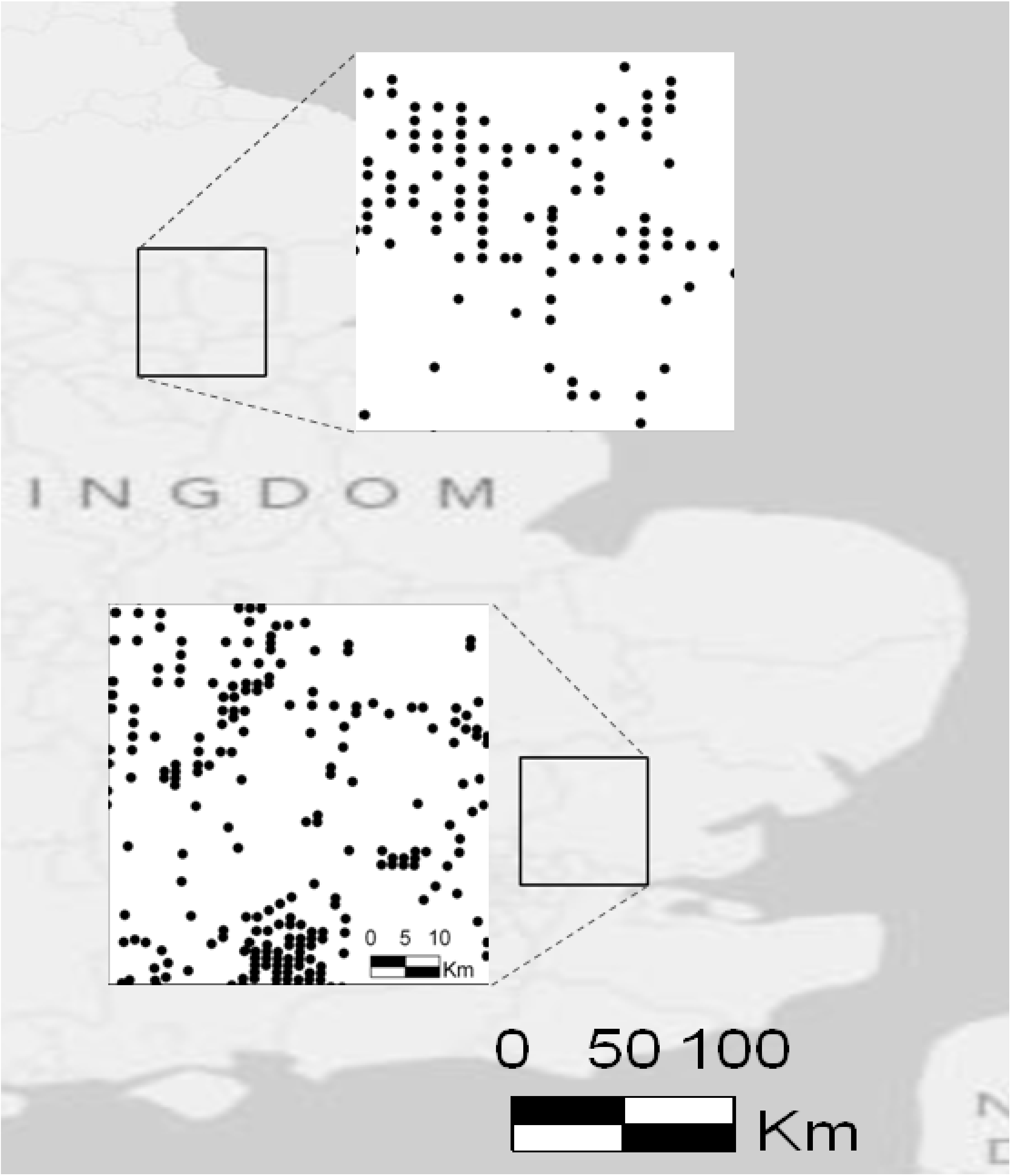

Figure 13. *L. vulgaris* records from the Botanical Society of the British Isles vascular plants database 1987-2012 in the Essex and Yorkshire 0.5 degree grid squares. Accounting for duplication, there are 242 recorded populations in the Essex grid square and 107 recorded populations in the Yorkshire grid square. Created in Esri ArcMapTM 10.0 with the Esri and DeLorme basemap.

2.5 DISCUSSION

2.5.1 Density across spatial scales and density measurement

This study adds to the growing evidence that plants are not always at higher densities in their invasive compared with their native range (Ebeling et al., 2008, Cripps et al., 2010, Firn et al., 2011, Maurel et al., 2013, Parker et al., 2013). Indeed, Firn and colleagues (2011) argue that increased abundance in the invasive range may be the exception rather than the rule. However, here I could only examine a very restricted part of the native and invasive range. It is possible that the density of *L. vulgaris* in the Haines region is lower than across the rest of the North American invasive range. Other studies of invasive *L. vulgaris* populations using quadrat based densities report smaller ranges and higher mean densities than found in the Alaskan populations at the same spatial scale (Clements and Cavers, 1990, Repath, 2005, Lehnhoff, 2008). In Montana, a clearcut site had a mean of 96 (56 Standard Deviation) and a riparian site a mean of 256 (126 S. D.) ramets / m^2 in randomly placed 0.0625 m^2 quadrats (Lehnhoff, 2008). Two sites in Yellowstone National Park had a higher mean of 28 stems / m^2 and a smaller range of 5 to 56 stems / m^2 at the 1 m^2 scale than the Alaskan populations (Repath, 2005) (Table 6). Five sites in Ontario had a range of 57-160 ramets / m^2 with a quadrat size of 0.25 m^2 (Clements and Cavers, 1990). Although Clements and Cavers did not report the mean, this range lies outside the Alaskan populations' mean of 28.41 ramets / m^2 from 0.25 m^2 grids (Table 6). Mean densities from 0.1 m^2 quadrats placed in the centre (approximately 180 ramets / m^2) and interior (approximately 130 ramets / m^2) of large populations in the West Yellowstone area are much higher than the

Alaskan 0.0625 m^2 and 0.25 m^2 means (Pauchard et al., 2003). The Alaskan mean densities at these very fine spatial scales are more similar to the approximately 45 ramets / m^2 mean density found from quadrats placed at the edge of the West Yellowstone populations (Pauchard et al., 2003).

These other studies could simply indicate a higher density in these areas of the invasive range compared with Alaskan populations. However, these studies are on very few populations and are carried out in a restricted geographical range, with three being from the Yellowstone area (Pauchard et al., 2003, Repath, 2005, Lehnhoff, 2008). There is also a risk that study populations chosen arbitrarily are biased towards areas of high abundance (Smallwood and Schonewald, 1996), so these studies may not reflect the true range of densities of *L. vulgaris* in the invasive range. More importantly, here density was measured across the whole area of each population, including edges. The large sample size used here, both within and between populations, results in a fuller description of the range of densities at fine spatial scales within this part of the invasive range. Considering only the mean density can be limiting when comparing populations and ranges. Two populations could have the same mean field or mean density of sample quadrats at a particular scale, but a differing variance in density because of a differing spatial structure (Gunton and Kunin, 2007). In the case of invasive plants this could result in differing impacts on native vegetation. Where single figure comparisons are needed, the median density from sampled quadrats might be a more robust comparison between populations.

Some studies comparing the native and invasive ranges of plants do not detail how populations were selected and which areas of a population were sampled (Lonsdale and Segura, 1987, Edwards et al., 1998, Bastlová-Hanzélyová, 2001). Some of the sampling techniques used either deliberately bias or have the potential to bias towards larger populations with continuous coverage and/or towards the centre of populations (Sheppard et al., 1996, Erfmeier and Bruelheide, 2004, Cripps et al., 2010, Herrera et al., 2011). This means that the complete spatial pattern of a plant species, including isolated individuals and satellite patches, may not be considered. This is important because it limits the comparison of pattern between the native and invasive range and of any possible changes in underlying processes. Lack of knowledge about spatial pattern and density could have implications for how an invasion is managed (Moody and Mack, 1988, Marchetto et al., 2010, Emry et al., 2011, Tobin et al., 2011).

Studies on *L. vulgaris* where the mean field density can be calculated have values lying outside of the range found in the UK and Alaskan populations (Nadeau et al., 1991, Stout et al., 1998) (Figure 8). A site established in a barley crop in Canada had a mean field density of 539 stems / m^2 over an area of approximately 0.13 m^2 (Nadeau et al., 1991), while a UK meadow had 0.007 plants / m^2 over an area of 40,000 m^2 (Stout et al., 2000). Mean field density values can vary greatly depending on decisions about the spatial extent and shape used to calculate population area (Haila, 1988), with outlying individuals and patches having a large influence on mean field density. Nadeau and colleague's (1991) study, where *L. vulgaris* root pieces were planted in a barley crop and on fallow land, illustrates a disadvantage with using mean field density. In both 1988 and 1989 there were more shoots and the diameter of the population was greater on the fallow land than in the barley crop. There was more clustering on the fallow land than barley and a frequency plot of number of shoots as a function of distance from the centre of plots shows that local scale densities were much higher on fallow land than barley (Nadeau et al., 1991). However, density was reported as mean field density, with 539 shoots / m^2 in 1988 and 95 shoots / m^2 in 1989 on barley compared with around 247 shoots / m^2 for both years on fallow land (Nadeau et al., 1991). If mean field density figures are considered alone, this suggests that *L. vulgaris* was more successful growing in the barley crop the first year and then switched in the following year. However, the area covered had simply increased in the barley crop between years, but there was still a higher local density and a greater total area covered on the fallow land.

The variation in density with spatial scale and between different measurement techniques is largely due to the extent to which areas without individuals are included in sampling (Mayor and Schaefer, 2005). Fine spatial scale sampling focused in areas with clusters of individuals will result in a higher mean than if density is recorded using a larger sampling unit (Wiens, 1989). This effect of clumping can be seen in the ramet focused density figures, where density declines with increasing area around the focal ramet (Figures 9 – 11). A completely uniform density pattern across spatial scales would result in a horizontal line in figures 9 – 11. One result of this is that the shape of *L. vulgaris* populations increasingly affects density recording as spatial scale increases, until the point when the scale encompasses the whole population. The registration and shape of the grid or the spacing and shape of sample quadrats also matters, because it will vary the amount of non-occupied space captured at population edges and between clusters in the population interior (Fortin, 1999, Dungan et al., 2002).

At fine spatial scales there was more non-occupied space within the population boundaries of the Alaskan populations than the UK 2008 populations. This is because of the clustering pattern of *L. vulgaris* and because the Alaskan populations were larger. However, some of the UK 2009 populations also displayed a similar pattern to the Alaskan populations, with empty areas between patches. The difference in results between the UK 2008 and 2009 populations suggests that this may be a characteristic at the population rather than regional level. More populations would need to be sampled to be sure whether a genuine difference occurs between regions. It is interesting to note that it was the IG3 population that contributed most to the high proportion of empty squares in the UK 2009 datasets. This was a new population established over a large area after disturbance from railway side works. As such it may have more in common with the characteristics of the Alaskan populations that occupy large fairly recently disturbed areas, than with most of the UK populations.

The ramet focused density plots (Figures 9 - 11) show that some of the Alaskan populations’ mean densities declined at a slower rate with increasing spatial scale, indicating that more of these populations’ ramets were further from an edge. This is caused partly by the larger areas covered and partly by the population shapes; with more of the Alaskan populations being a circular shape rather than along a linear feature. This study focuses on fine scale density, so conclusions about *L. vulgaris* density at broader population and landscape scales need to be cautious due to the lack of replication.

It is difficult to compare the UK and Alaskan records because they have been collected using different methods for different purposes (AKEPIC, 2013, Botanical Society of the British Isles, 2013). Whilst there is likely to be under recording in both regions, there has been a greater intensity of recent recording in the Haines square and at a greater precision compared with the UK (AKEPIC, 2013, Botanical Society of the British Isles, 2013). 76 of the Haines records are from 2005 and 2007 road surveys where recording took place every ¼ mile (402 m) (Arhangelsky, 2007, Lamb and Shephard, 2007). In contrast, in the UK grid squares there are differences in recording effort between areas (Botanical Society of the British Isles, 2013). Allowing for duplication in the UK dataset, there are fewer recorded populations in the UK than the Alaskan grid squares (section 2.4.2.4). Most of the Haines grid square is sea, ice or high elevation coniferous forest (Figure 3, Multi-Resolution Land Characterization Consortium, 2001). If the area is restricted to habitat suitable for *L. vulgaris*, then there does appear to be a higher density of populations in disturbed habitat around the town of Haines than in the UK. This is also indicated by the population surveys, as flowering populations on disturbed railway line sides in the UK were few and widely spaced, while on the only un-surveyed major road in Haines *L. vulgaris* was nearly continuous (personal observation).

2.5.2 Stages, definitions and impacts of invasion

In Colautti and MacIsaac's (2004) stage based definition of invasion (Figure 1), the actual spatial scales and density are not defined. This means that placing an invasion at a particular stage depends on the interpretation of 'dominant' and the particular local and regional spatial scales of interest. An invasive species could be considered widespread and dominant at a certain spatial extent, while at broader spatial scales it could be localized and dominant. This appears to be the situation with *L. vulgaris* in Alaska. If only the immediate Haines region is considered, then *L. vulgaris* invasion can be categorised as stage V: widespread and dominant. At the broader spatial extent of the 0.5 degree grid square, *L. vulgaris* in Haines could be categorized as stage IVb: localized and dominant. The same is true when zooming out to a spatial extent encompassing Alaska, the Yukon and British Columbia, because *L. vulgaris* is currently predominantly restricted to anthropogenically disturbed areas (AKEPIC, 2013).

Colautti and MacIsaac's (2004) stages recognise the different processes and timings involved in the aspect of becoming dominant at fine spatial scales and in the aspect of dispersing and establishing across a landscape. Colautti and MacIsaac (2004) do not define their stage IVb (localised but dominant) as invasive; a species is only considered invasive once it has become widespread (stages IVa or V). This seems to uncouple the definition of an invasive from being denser in the invasive range than the native range. A species could be in stage IVa and actually have a lower density at fine spatial scales than in the native range. However, it would be considered invasive because it has become widespread in the invasive range, even if it had a similar distribution across its native range. In contrast, Lamarque and colleagues (2012) argue that a species cannot be considered invasive if there is no difference in density compared with the native range. As their research on the density of two exotic maple trees took place at several spatial scales, presumably they are referring to increased density at any spatial scale (Lamarque et al., 2012). This raises the issue of whether the degree of impact should be considered as part of the definition of an invasive species (Davis and Thompson, 2000), rather than a mechanistic definition (Valéry et al., 2008).

The degree of impact may be uncoupled from the degree to which density has changed compared with the native range. A species could be at the same fine scale density in the native and invasive range, but have a stronger competitive impact on surrounding species in the new range due to novel interactions (Callaway and Aschehoug, 2000, Callaway et al., 2012). Impact does not necessarily strongly correlate with invasiveness and density (Ricciardi and Cohen, 2007), but also depends on the characteristics of the native community (Crawley, 1987, Levine and D'Antonio, 1999, Li and Stevens, 2011). Where impact does correlate with density, the relationship may be non-linear (Yokomizo et al., 2009). In the disturbed habitats around Haines, it is not clear whether *L. vulgaris* has been a passenger or a driver of change (MacDougall and Turkington, 2005, HilleRisLambers et al., 2010). Experimental studies, or observational work in environments where *L. vulgaris* is a more recent arrival, would help to determine the potential for impact on native species and ability to invade less disturbed habitats (Pauchard et al., 2009).

2.5.3 Implications for invasion mechanisms

These results suggest that the novel environment is having no plastic or selective impact on *L. vulgaris* traits that influence density at fine spatial scales (Leifso et al., 2012). Similarly, any ‘circumstantial’ mechanisms of invasion not based on trait change, such as repeated introductions or trait novelty (Callaway and Aschehoug, 2000, Marrs et al., 2008), have also not altered fine scale density (Leifso et al., 2012). The range of biotic and abiotic micro-environments experienced by *L. vulgaris* ramets may simply be very similar between the UK and Alaska. Certainly, populations in both ranges are in disturbed and human altered habitats (Hufbauer et al., 2012, Hierro et al., 2013). Alaskan communities contained many European and widespread species (La Sorte et al., 2007), of which several were shared with the UK population communities (Table B1). Alternatively, environmental differences may exist between ranges, but not that impact the mean and range of density at fine spatial scales. Physiological and morphological traits relating to fine spatial scale density, such as the spacing of new ramets along a rhizome, may be relatively insensitive to selection or plasticity.

The larger population area of some of the Alaskan populations could be partly due to a different landscape structure, perhaps with the UK having a finer grain for changes in vegetation or man-made structures (Wiens, 1989). Some of the UK and Alaskan populations were constrained on some edges. However, in most cases, in both the UK and Alaskan populations there was no obvious barrier to population spread in at least one direction. It is possible that disturbance allowing population establishment tends to be at a finer grain in the UK than in Alaska, resulting in smaller initial population sizes. However, when railway works resulted in spoil being deposited over a 48 x 5 m area, the IG3 population was able to establish at high density over the whole area of the disturbance within one year. In contrast, the Alaskan NK population had also been established after recent disturbance over a large area, but individuals were at a lower density across both the population area and at fine spatial scales compared with the IG3 population (Figures B25 & B12). This difference could be caused by differing propagule pressure and resource availability between the populations (Lockwood et al., 2005, Mata et al., 2013), but also indicates that Alaskan ramets have not fundamentally changed from UK ramets in an ability to establish and reach high local densities.

The indication of a higher number of populations in disturbed habitat in the Haines area compared with the UK, suggests that *L. vulgaris* in Alaska is better able to disperse and establish in new areas. This could be due to increased propagule pressure and opportunities for long distance dispersal (Lockwood et al., 2005, Mason et al., 2008, Herrera et al., 2011) and/or a greater disturbance area and frequency creating more resource ‘windows of opportunity’ (Davis et al., 2000). This might be combined with a possible greater ability of *L. vulgaris* compared with native species to rapidly exploit these new resources (Funk and Vitousek, 2007, Dickson et al., 2012).

Although no difference has been found between the native and invasive populations in fine scale density, *L. vulgaris* could still be more vigorous and have a greater reproductive output in the invasive range. Chapter 3 examines whether there is any difference in height and reproductive traits between the UK and Alaskan *L. vulgaris* populations. Any trait differences found might partially explain the larger number of populations in disturbed Alaskan habitat compared with the UK. Dispersal ability, seed viability and conditions for germination are important in the establishment of new populations. Chapter 4 examines seed dispersal distances in different habitats, seed germination and the role of sexual versus clonal reproduction in maintaining populations.

Chapter 3. Comparison of the height and sexual reproduction of UK native and Alaskan invasive *Linaria vulgaris* Miller populations.

3.1 ABSTRACT

Invasive plants are expected to be more vigorous and to have greater fecundity than conspecifics in the native range. This chapter compares the height, flowering, fruit and seed production of *Linaria vulgaris* Miller (Plantaginaceae) ramets from 12 UK (native) populations and seven Alaskan (invasive) populations from climatically matched areas. Contrary to expectations, invasive ramets were shorter than native ramets. Alaskan ramets were more likely to flower than UK ramets at a given height, but because Alaskan ramets were shorter, the proportion of UK and Alaskan ramets that flowered was similar. The taller heights resulted in mature UK ramets producing more fruit than the Alaskan ramets, but there was no difference between the regions in the ratio of mature fruit to failed flowers and fruit per ramet. However, Alaskan fruit were more likely to contain viable seed and had a greater number of viable seed than UK fruit, even though UK fruit were larger. This greater seed production of Alaskan fruit counteracted the reduced fruit number per ramet, so that Alaskan ramets were predicted to produce more seed than UK ramets. The seed predator *Rhinusa antirrhini* Paykull (Curculionidae) was present in more than half of the UK fruit, but was not found in any of the sampled Alaskan fruit. *R. antirrhini* presence

decreased the number of viable seed in UK fruit. However, UK fruit unpredated by *R. antirrhini* were still less likely than Alaskan fruit to have viable seed, and if seed was present had fewer seed. The greater seed production of Alaskan ramets may be contributing to the higher density at broad spatial scales (section 2.4.2). However, it is not known whether *L. vulgaris* is seed limited in this part of the invasive range, or whether site availability and conditions for seedling establishment are of greater importance.

3.2 INTRODUCTION

Two important themes in invasion ecology research have been to examine the characteristics of invasive species (Noble, 1989, Rejmánek and Richardson, 1996, Williamson and Fitter, 1996) and the invasibility of communities (Crawley, 1987, Tilman, 1997, Fine, 2002, Ohlemüller et al., 2006). However, the identification of universal invasive traits has been limited (Thompson et al., 1995, Hayes and Barry, 2008, Thompson and Davis, 2011, although see Pandit et al., 2011) and studies on whether certain communities are more resistant to invasion than others also show mixed results (Levine and D'Antonio, 1999). More recently there has been growing emphasis on comparing conspecific populations in the invasive and exotic range (Hinz and Schwarzlaender, 2004, Hierro et al., 2005, Guo, 2006, Ramula et al., 2008). This aims to identify changes that may have enabled invasion and also allows an examination of the relationship between the particular traits of the invader and the novel environment (Heger and Trepl, 2003, Mata et al., 2013). Observed trait differences could be due to phenotypic plasticity (Williams et al., 1995, Parker et al., 2003, Ebeling et al., 2011), or result from post-introduction genetic change such as adaptive selection (Maron et al., 2004, Hierro et al., 2009, Felker-Quinn et al., 2013, Kumschick et al., 2013) or hybridisation (Ellstrand and Schierenbeck, 2000).

Expected changes include a greater vigour and fecundity of individuals in the invasive compared to the native range (Crawley, 1987, Noble, 1989, Stastny et al., 2005). Some field comparisons of particular plant species have found that individuals are taller in the invasive range (Lonsdale and Segura, 1987, Bastlová-Hanzélyová, 2001, Prati and Bossdorf, 2002, Jakobs et al., 2004, Ebeling et al., 2008, Herrera et al., 2011), while other field and flora comparisons have found no difference in heights between ranges (Edwards et al., 1998, Thébaud and Simberloff, 2001, Paynter et al., 2003, Beckmann et al., 2009, Cripps et al., 2010). A quantitative meta-analysis indicates that introduced plant species tend to be larger compared with where they are native (Hawkes, 2007). However, Bayesian meta-analysis by Parker and colleagues (2013) found that only the world’s most invasive plants were strongly likely to be larger where invasive, and that this result could be an artefact of differing methodology between ranges. Invasive populations for some plant species have even been found to be shorter than in parts of their native range (Erfmeier and Bruelheide, 2004, Vilà et al., 2005).

Components of sexual reproduction found to be increased in the invasive range of some plant species include a greater proportion of the population flowering (Beckmann et al., 2009), larger inflorescences (Prati and Bossdorf, 2002, Ebeling et al., 2008), increased fruit set (Lonsdale and

Segura, 1987), heavier or larger seed (Buckley et al., 2003, Ebeling et al., 2008) and more seed per fruit (Lonsdale and Segura, 1987, Edwards et al., 1998, Herrera et al., 2011). There is also evidence of increased seedling recruitment (Erfmeier and Bruelheide, 2004) and increased vegetative reproduction (Beckmann et al., 2009). However, for some species, certain components of reproduction such as fruit set and seed size showed no difference between ranges (Prati and Bossdorf, 2002, Erfmeier and Bruelheide, 2004) or were reduced in the invasive range (Herrera et al., 2011). A meta-analysis found that plants in the invasive range generally allocated more towards reproduction than conspecifics in the native range (Hawkes, 2007). However, two global comparisons of seed mass between the native and invasive range had conflicting results (Daws et al., 2007, Mason et al., 2008).

Observed trait changes have led to various hypotheses for invasion mechanisms. A particular focus has been the evidence for decreased or absent specialist herbivory in the invasive range (Edwards et al., 1998, Cripps et al., 2006, Hawkes, 2007, Cripps et al., 2010). The Enemy Release hypothesis suggests this escape from specialist herbivores provides exotics with a direct competitive advantage over native species (Keane and Crawley, 2002, Wolfe, 2002). The Evolution of Increased Competitive Ability (EICA) hypothesis argues that this operates through selection, rather than plasticity, with selection for decreased herbivore defence and increased investment in competition (Blossey and Notzold, 1995). Common garden and field experiments have found evidence both for selection (Maron et al., 2004, Qin et al., 2013) and for plasticity (Willis et al., 1999, Franks et al., 2008, Alba et al., 2011). However, a release from enemies has not always been found to translate into the predicted increased competitive ability (Edwards et al., 2007, Cripps et al., 2010). Indeed, reduced competition in the new environment could result in reduced competitive ability (Bossdorf et al., 2004). A meta-analysis suggests that while evolution does occur in the invasive range, traits usually do not change in the way predicted by the EICA hypothesis (Felker-Quinn et al., 2013).

Alternatively, or in addition to the impact of the invasive range environment, genetic change within parts of the native range might pre-adapt populations to the invaded ecosystem (Bossdorf et al., 2008, Jenkins and Keller, 2011, Hufbauer et al., 2012). This could include an increased capacity for phenotypic plasticity (Chun, 2011). For example, horticultural demands could result in the selection of phenotypes for invasion that are larger and have greater reproductive allocation (Crawley et al., 1996, Ross and Auge, 2008). Founder effects and genetic drift can also play a strong role in differentiating invasive populations from conspecific native populations (Fennell et al., 2010).

Traits may not need to alter from the native range in order to play an important role in invasion; novel interactions in the invasive range may be sufficient (Callaway and Aschehoug, 2000, Callaway et al., 2012). Of particular importance may be ‘invasion windows’ that are created by a fluctuating availability of resources; most commonly caused by disturbance (Davis et al., 2000, Mata et al., 2013). Invaders might be more able to take advantage of these windows than natives if, for example, the invader uses resources more efficiently (Funk and Vitousek, 2007), begins growth earlier in the season (Dickson et al., 2012) or has a higher propagule pressure (Lockwood et al., 2005).

These various mechanisms for invasion need not be mutually exclusive (Qin et al., 2013) and may play a role at differing stages of the invasion process (Dietz and Edwards, 2006). Finding out which, if any, traits have changed between the native and invasive range of an introduced species might point to different drivers and mechanisms of invasion. This might partially explain the invasion stage that has been reached (Colautti and MacIsaac, 2004) and any differences in density compared with the native range at different spatial scales. The previous chapter compared the density of native and invasive populations of *L. vulgaris* in climatically matched areas of the UK and Alaska. At spatial scales up to 4 m^2 there was no difference in density between UK native and Alaskan invasive range *L. vulgaris* populations (section 2.4.2.1). However, invasive range populations tended to cover a larger area and there were more populations in disturbed areas of the invasive study area than in the native study areas (sections 2.4.2.2 & 2.4.2.4). This chapter addresses the following hypotheses:

L. vulgaris ramets in the invasive range populations will be taller, more likely to flower, and will produce more fruit and seed than in the native range populations.

This chapter also addresses the question of what influences the height and sexual reproduction of *L. vulgaris* ramets in both ranges. In particular:

> at what spatial scale(s) does conspecific density affect an individual ramet’s height and sexual reproductive output?

have *L. vulgaris* ramets in the invasive range populations escaped their specialist seed feeder *Rhinusa antirrhini* Paykull (Curculionidae).

3.3 METHODS

3.3.1 *L. vulgaris* sexual reproduction and insect herbivores

L. vulgaris is self-incompatible (Docherty, 1982) and flowers June – October in the UK. Legitimate pollination visits are mainly from long and intermediate tongued *Bombus* species (Stout et al., 2000, Newman and Thomson, 2005a, Burkle et al., 2007). Primary and secondary nectar robbing was frequent in both UK and North American populations, but had little impact on fecundity (Stout et al., 2000, Newman and Thomson, 2005a, Burkle et al., 2007). Ants are attracted to robbed flowers, which may protect against flower and seed herbivory from the beetle *Brachypterolus pulicarius* L. (Kateridae) and weevil *R. antirrhini* (Newman and Thomson, 2005b). The two celled fruit mature September – November in the UK and seed dehisce passively from slits in the apex. In addition to disc shaped black seeds, *L. vulgaris* also produces distinct grey seeds, which are less viable and thought to be caused by incomplete seed resourcing (Arnold, 1982, Clements and Cavers, 1990).

B. pulicarius adults feed on *L. vulgaris* vegetative tips, buds and flowers, and oviposit into buds from June (Kock, 1966, Wilson et al., 2005). The larvae feed on pollen, anthers and ovaries before leaving the flowers and pupating in the soil over winter (Kock, 1966). There is disagreement as to whether the later instar larvae of *B. pulicarius* will also feed on immature seed (McClay, 1992, Wilson et al., 2005).

R. antirrhini adults feed on developing *L. vulgaris* buds, leaves and stems from May (Kock, 1966), with some also referring to *Rhinusa* sp. feeding on flowers and pollen (Arnold, 1982). Eggs are laid into immature *L. vulgaris* fruit from August, with the fruit developing an internal and external spur at the oviposition site (Kock, 1966). Seed close to the egg and spur swell (Kock, 1966). The larvae feed on seed and then pupate within the fruit, inside cells made from cemented seed and fruit fragments (Kock, 1966). The adults emerge in the late autumn, feed and then overwinter in litter, or occasionally remain and overwinter within the fruit (Kock, 1966, Wilson et al., 2005). Adults emerge from the apex of mature open fruit (Kock, 1966), although the separate biotype on invasive *L. dalmatica* (L.) Miller (Dalmation toadflax) in Canada have also been observed making exit holes in the side of mature fruit (Turner and De Clerk-Floate, 2008, Hernández-Vera et al., 2010). *R. neta* Germar has a similar life history to *R. antirrhini* (Wilson et al., 2005), but is non gall-forming and its distribution is thought to be restricted to Central and Southern Europe and hot summer sites within the invasive range of *L. vulgaris* (Harris and Gassmann, 1998).

B. pulicarius, *R. antirrhini* and *R. neta* are established in North America (Sing et al., 2005, De Clerck-Floate and Cárcamo, 2011, Douglas et al., 2013). *R. antirrhini* has been observed in Alaska (Michael Rasy and Steven Seefeldt, personal communication), but the status of *B. pulicarius* and *R. neta* in the state is unknown.

3.3.2 Fieldwork

3.3.2.1 Population selection and surveying

Climatic matching was used to identify a 0.5 degree grid square in Alaska that was similar to two UK 0.5 degree grid squares (Appendix A). *L. vulgaris* populations within these squares were randomly selected from records, resulting in 12 UK populations that were surveyed in autumn 2009 and seven Alaskan populations surveyed in autumn 2010. The position of every ramet in each population was recorded to the nearest cm. The vegetation height and the proportion of unvegetated ground were recorded from every 0.5 x 0.5 m quadrat in a grid across each population. The dominant plant taxa and whether the population was shaded, partly shaded or unshaded were also noted. Soil samples from six of the Alaskan populations and eight of the UK populations were analysed for soil texture, pH and for Ca, K, Mg, Mn, Na, P and S content (Appendix C). Further details about population selection and surveying are in section 2.3.1.

3.3.2.2 Recording height and reproductive structures

Recording took place in September-October 2009 for UK populations and late August-October 2010 for Alaskan populations. The order of recording as far as possible followed the relative fruiting maturity of the populations. The height of the longest stem of every ramet in the population was recorded to the nearest centimetre. Height was not recorded for 62 UK ramets and for one Alaskan ramet. This was either because their stems were broken, or because they could not be reached, although in this case their location was recorded at least approximately. These ramets were excluded from analysis, although they were used to calculate the ramet focused density environment of other ramets. This left 3152 UK ramets and 4684 Alaskan ramets.

Ramets were recorded as flowering if there was evidence of reproductive structures having been present during that year. The number of inflorescences and the number and type of each of the reproductive structures were recorded, starting from the base of the lowest inflorescence and working upwards. Reproductive structures were categorised as: bud (green or purple with no petals visible), dead bud (black or dark brown and soft), unopened flower (petals visible but not the palette), open flower (petals fully open with visible palette), dead flower (dead petals, may develop into new fruit), new fruit (green or purple fruit 5 mm or less in length with style present), closed adult fruit (fruit greater than 5 mm length, or less than 5 mm length that are light brown with no style), opening adult fruit (as closed adult fruit, but with a crack at the apex or side of the fruit that is less than 1 mm width and not likely to be caused by herbivory), open fruit (as closed adult fruit, but with a greater than 1 mm width opening that is not likely to be caused by herbivory), dead fruit (soft and blackened or dark brown fruit of greater than 5 mm length), scar (structures of less than 5 mm length which are soft and dark brown or black, or where only the pedicel remains).

For every ramet with opening fruit at the point of survey, the most basal opening fruit on the most basal inflorescence was collected. Populations that on their first survey still had ramets flowering and/or some new fruit still to mature were visited again in October, when the most basal opening fruit was again collected from all flowering plants. Populations where there was only a single fruit collection period were HC, LP, MF, HR and MB. Where a ramet had opening fruit available during both collection periods, only the earliest collected fruit was used.

Where possible the length and width of the fruit was recorded to the nearest 1 mm. The presence of any holes from herbivory or external spurs caused by egg laying was also noted. The fruit was then broken open for seed counting and internal spurs were recorded along with any other evidence of seed predation such as the exuviae of Chalcid parasitoid wasps (de Vere Graham, 1969), or evidence of pupation of *R. antirrhini*. The number of *R. antirrhini* adults, pupae and larvae were recorded in each fruit. Seeds were distinguished from any seed fragments as being 1 mm or greater in diameter and with an outline where deviations from a perfect circle did not cross the centre point. The number of ‘black’ and ‘grey’ seeds were counted in each fruit (Clements and Cavers, 1990). Clements and Cavers (1990) reported that grey seeds had been pollinated, but were incompletely filled and had very low viability. This study focuses on the presence and impact of the seed feeder *R. antirrhini* in UK and Alaskan *L. vulgaris* populations, although the foliage feeder *C. lunula* and flower feeder *B. pulicarius* were also observed in the UK population LP in 2009.

3.3.3 Statistical analysis

General and generalized linear mixed effects models were fitted using R 2.12.2 (R Development Core Team, 2011) and 2.15.2 (R Core Team, 2012), with model selection and comparison based on Akaike’s Information Criterion

(AIC) (Burnham and Anderson, 2002). Colinearity between explanatory variables was checked using the package AED and explanatory variables were not used if colinearity was greater than 0.5 (Zuur, 2010). The protocol for model simplification was to start with models including all biologically meaningful explanatory variables and two way interactions and to first find the most appropriate variance structure and random structure (Zuur et al., 2009). All models used random intercepts of the populations. The optimal fixed structure was then found by first dropping any interaction terms before dropping main terms (Zuur et al., 2009). Where AIC values rose slightly on dropping a term, a Likelihood Ratio test was used to compare models (Zuur et al., 2009). Model validation was carried out by inspecting plots of normalized residuals and model fits (Zuur et al., 2009). Figures were created using the package Lattice (Sarkar, 2008).

3.3.3.1 Ramet height analysis

General linear mixed models with normal errors were fitted using the function lme from the package nlme (Pinheiro et al., 2011) in R 2.15.2 (R Core Team, 2012). Height was logged to provide homogeneity of residual variance and a correlation structure was included that allowed variance to differ between countries (Zuur et al., 2009). Minimum adequate models were found by dropping down from a full model containing the fixed effects: region, vegetation height bounded at 1 m, shading, surrounding ramet density measured within either 0.1 m, 0.2 m, 0.4 m, 0.8 m, 1.6 m, 3.2 m, 6.4 m or 12.8 m, polynomial terms for vegetation height and density, and the two-way interactions between region, vegetation height and ramet density. Ground cover categories could not be included as the models would not converge. Comparison of models with the same random effects structure and different fixed effects used Maximum Likelihood (ML), with the final minimum adequate model presented using Restricted Maximum Likelihood (REML) (Zuur et al., 2009). This process was then repeated in two separate analyses containing first just the UK and then just the Alaskan populations. The same process was also carried out to check whether using population number, population area or mean field density as fixed effects provided models with a lower AIC than using ramet focused density within 6.4 and 12.8 m.

3.3.3.2 Flowering analysis

Generalized linear mixed models with binomial errors were fitted using the function lmer from the package lme4 (Bates et al., 2011) in R 2.12.2 (R Development Core Team, 2011). Using a logit link and random intercepts of the populations produced models with the lowest AIC. The minimum adequate models were found by dropping down from a full model containing the fixed effects: region, Ln (natural log) ramet height, difference between ramet height and vegetation height, surrounding ramet density measured within either 0.1 m, 0.2 m, 0.4 m, 0.8 m, 1.6 m, 3.2 m, 6.4 m or 12.8 m, shading and all two-way interactions. Using the difference between ramet height and vegetation height, rather than vegetation height alone, made more biological sense and produced models with lower AIC values. The correlation between Ln ramet height and the difference from vegetation height was 0.390. Unlike in the height analysis, shading was used as a binary category by combining the shaded and partly shaded populations and comparing these with unshaded populations, as this produced models with a lower AIC.

3.3.3.3 Fruit analysis

Analysis of the number of adult fruit (adult closed, opening or open fruit) on each ramet used only ‘mature’ ramets: those whose fruit production was reasonably complete at the time of survey. These were the subset of ramets where at least 85 % of the total reproductive structures (excluding dead flowers) were mature fruit, unpollinated or aborted fruit, dead buds or dead fruit, rather than alive buds, flowers or new fruit. Dead flowers were excluded from the total because it was not possible to tell if these had been pollinated and might develop into fruit. The UK populations MF and IG2 were excluded from analysis as they contained only one mature ramet each. The Alaskan population FS was also excluded because all the mature ramets were too close to the un-surveyed section of the population for accurate flowering density measurements. This left 647 mature ramets for analysis; 210 UK ramets from ten populations and 437 Alaskan ramets from six populations.

Generalized linear mixed models of the number of adult fruit per ramet were fitted with negative binomial errors using the function glmmadmb from package glmmADMB (Hilbe, 2007, Fournier et al., 2012, Skaug et al., 2012) in R 2.12.2 (R Development Core Team, 2011). Using a log link function and population as a random effect produced models with the lowest AIC. The overdispersion parameter varied between 1.42 and 1.54 and using zero-inflated models did not reduce this. The minimum adequate models were found by dropping down from a full model containing the fixed effects: region, Ln ramet height, either Ln vegetation height bounded at 1 m or the difference between ramet height and vegetation height, density of surrounding flowering ramets at one of the eight spatial scales, polynomial terms and all two-way interactions.

The proportion of adult fruit versus failed reproductive structures (dead buds or dead, unpollinated or aborted fruit appearing as scars or dead fruit) on mature UK and Alaskan ramets were compared by fitting generalised linear mixed effects models with and without region as a fixed effect. These models were fitted using the function lmer from the package lme4 with binomial errors, a logit link function and population as a random intercept (Bates et al., 2011).

3.3.3.4 Seed analysis

Populations MB, MF and WL2 did not produce any opening fruit during the survey periods. The numbers and percentages of fruit with seed and *R. antirrhini* attack are given for the 438 collected opening fruit that were each from a separate ramet. However, fruit were removed from statistical analysis where ramet focused density was unknown (FS population), from populations where only one or two fruit were collected (BP3, IG2 and IG3), where fruit number on the ramet was unknown (largely because of the fire affecting some of the LP population ramets) or where fruit size was unknown.

This left 308 opening fruit for analysis, with 87 UK fruit from seven populations and 301 Alaskan fruit from five populations.

Analysis of the black seed number per fruit used the function glmmadmb from package glmmADMB (Fournier et al., 2012, Skaug et al., 2012) in R 2.15.2 (R Development Core Team, 2011). Data were zero-inflated, so hurdle models were used; first by fitting the presence and absence of seed using binomial errors and a complementary log-log link, then by fitting the number of seed in fruit where seed was present using truncated negative binomial errors and a log link (Zuur et al., 2009, Skaug et al., 2012, Zuur et al., 2012). Minimum adequate models were found by dropping down from a full model containing the fixed effects: region, Ln ramet height, number of adult fruit on the ramet, fruit volume, density of surrounding flowering ramets at one of the eight spatial scales, the presence or absence of *R. antirrhini* and all two-way interactions.

These analyses of black seed presence and number were then repeated for: a) UK fruit alone without the region effect, b) Alaskan fruit alone without the region effect and c) both Alaskan and UK fruit without *R. antirrhini*. The total (black and less viable grey) seed presence and number were also analysed for the combined Alaskan and UK fruit without *R. antirrhini* to check whether reductions in black seed were replaced by grey seed. The ratio of black to grey seed within each fruit were too overdispersed for analysis, because the quasibinomial error family cannot be used in generalised linear mixed effects models.

3.4 RESULTS

3.4.1 Ramet height results

Contrary to expectation, Alaskan ramets were shorter than UK ramets (Figure 14). Region is included in each of the Minimum Adequate Models for density measured at different spatial scales, which also include population shading and vegetation height (Table D1). The mean Alaskan ramet height was 13.3 cm ± 0.149 S. E. (median 11 cm) and the mean UK ramet height was 24.5 cm ± 0.458 S. E (median 16 cm). Ramets shorter than 10 cm make up 44 % of all the Alaskan ramets, compared with 31 % of the UK ramets. However, the proportion of ramets between 10 and 40 cm were similar between the two countries. There were no Alaskan ramets taller than 65 cm, but 8 % of the UK ramets were taller than 65 cm, with some UK ramets growing to 180 cm. The Minimum Adequate Model where conspecific ramet focused density was measured within 1.6 m has the lowest AIC (Table 9). At this spatial scale there is a humped relationship between ramet height and density. Ramet height also has a humped relationship with vegetation height (Table 9). There is an interaction between region and vegetation height, because vegetation heights differ between regions (section 2.4.1). Ramets are tallest in partly shaded areas of populations, although shading is partly confounded with population.

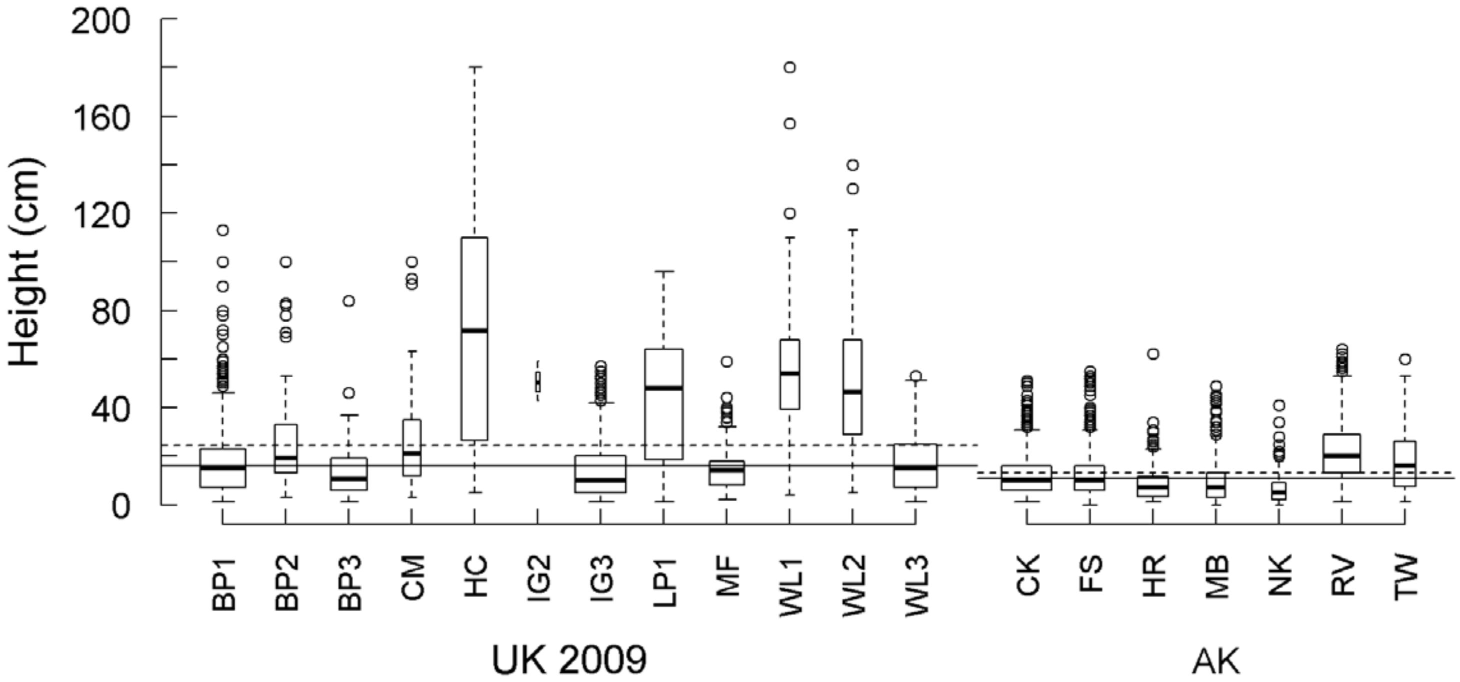

Figure 14. Ramet heights in UK and Alaskan *L. vulgaris* populations. The dashed line is the mean height calculated from all ramets in each region and the solid line is the median height calculated from all ramets in each region.

Table 9. Fixed effects of the minimum adequate model of *L. vulgaris* Ln ramet height with the surrounding ramet density measured within 1.6 m. Populations are modelled as random intercepts and have a standard deviation of 0.560. The model was selected using AIC, but p-values are given for reference. Models for density at other spatial scales are in Table D1.

Fixed effects	Estimate	S.E.	t-value	p-value
Intercept (UK, partly shaded)	2.79	0.146	19.10	< 0.001
Region AK	-0.703	0.273	-2.36	0.0307
Shaded	-0.331	0.105	-3.14	0.0017
Unshaded	-0.449	0.111	-4.04	< 0.001
Vegetation height	0.0204	0.00168	12.11	< 0.001
Vegetation height^2	-0.000168	1.52×10^{-5}	-11.09	< 0.001
Ramet density within 1.6 m	0.0229	0.00219	10.48	< 0.001
Ramet density within 1.6 m^2	-0.000268	3.62×10^{-5}	-7.41	< 0.001
Region AK : Vegetation height	0.00648	0.00120	5.42	< 0.001

However, the presence of interactions in these combined models shows that UK and Alaskan populations have different relationships between ramet height and the fixed effects (Table D1). This means that including both UK and Alaskan populations in the same model is constraining the shape of these different relationships (Figure D2). In separate analyses of UK and Alaskan populations, density at fine spatial scales in the UK does not include a polynomial term (Table D2). Population shading is also excluded from the Alaskan models (Table D3). With density within 1.6 m held at the median, Alaskan ramet heights increase with vegetation height, however UK ramet heights increase until vegetation height is approximately 60 cm and then decline (Figure 15). There is also an interaction between ramet density and vegetation height, which varies between regions and with spatial scale (Tables D2 & D3).

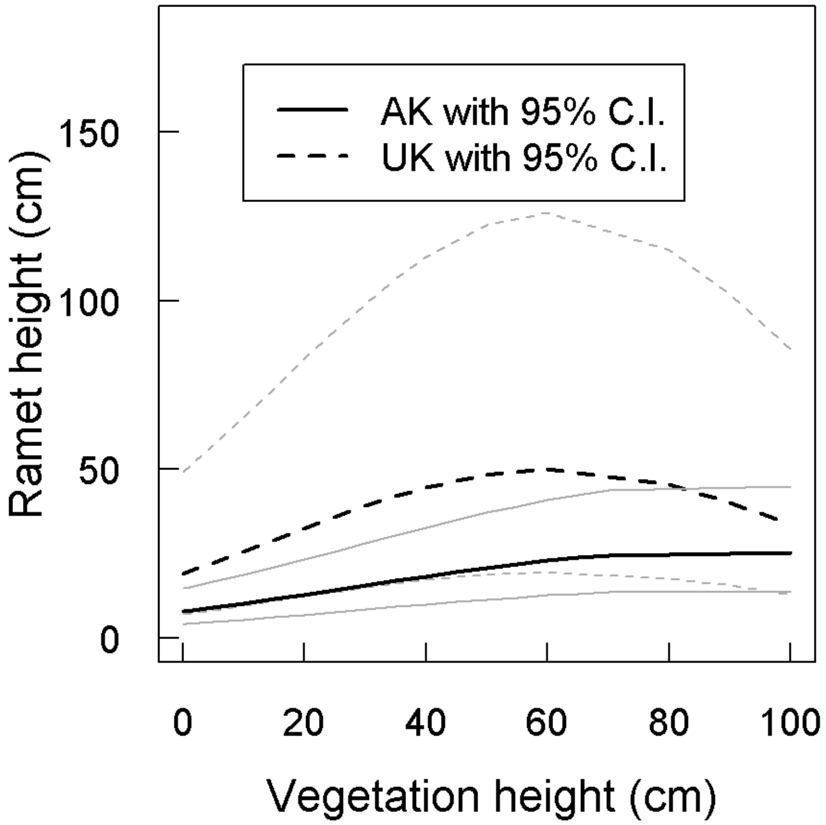

Figure 15. Predicted mean ramet height with surrounding vegetation height for UK and Alaskan *L. vulgaris* ramets. Predictions are from separate general linear models for UK and Alaskan populations, where population is modelled as a random intercept. The surrounding lines are the 95 % Confidence Intervals for the populations. The surrounding ramet density is held at 173 ramets within 1.6 m (20 ramets / m^2). The UK model includes the amount of shading and the mean line is for partly shaded populations.

In contrast to when UK and Alaskan populations are analysed together, the separate UK and Alaskan minimum adequate models with the lowest AIC are for when density is measured within 12.8 m (Figure D3). The AIC of models that instead of ramet focused density used either population number (UK = 7487.43, AK = 9200.80), population area (UK = 7483.92, AK = 9197.39) or the mean field density (UK = 7485.24, AK = 9195.91) were higher than the minimum adequate models using density within 12.8 m (UK = 7360.17, AK = 9083.33). The relationship between height and ramet density varies across the spatial scale at which density is measured and between regions (Figure 16). These predictions differ from the combined UK and Alaska analysis (Figure D2). At 10 cm vegetation height the relationship between UK ramet height and ramet density is positive at the < 0.1, < 0.2, < 0.4 and < 1.6 m spatial scales, but there is no relationship at the < 0.8 m spatial scale (Figure 16). From the < 3.2 m spatial scale, many of the UK populations are encompassed by the circles that density is calculated within, so that all the ramets within a population have the same density value. The relationship between Alaskan ramet height and ramet density is weaker and quadratic; moving from a slightly negative relationship at very fine spatial scales towards a slightly positive plateauing relationship at broader spatial scales.

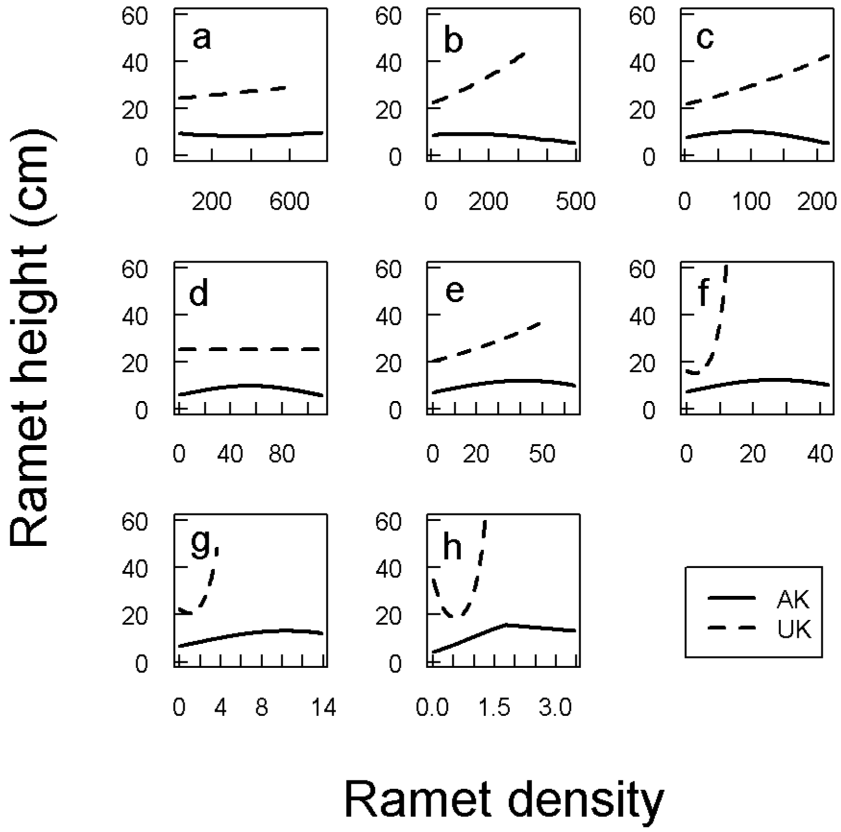

Figure 16. UK and Alaskan *L. vulgaris* mean ramet height predictions from Minimum Adequate Models with surrounding ramet density within a) 0.1 m b) 0.2 m c) 0.4 m d) 0.8 m e) 1.6 m f) 3.2 m g) 6.4 m h) 12.8 m. The UK and Alaskan populations have been analysed separately and the UK mean is for partly shaded populations. The vegetation height has been held at the median of 10 cm. When the vegetation height is 50 cm UK and Alaskan ramet heights decline with density at < 0.1 and < 0.2 m spatial scales.

3.4.1.1 Identical height models with differing spatial scales of density

In addition to the minimum adequate models at each spatial scale, maximal models were also compared containing the same fixed effects, but with density measured at different spatial scales. When UK and Alaskan populations are analysed together then density measured within 0.8 m, 1.6 m and 12.8 m have a lower AIC compared with the models with density at other spatial scales (Figure 17), indicating that variation in density measured at these three spatial scales better explains variation in ramet height. However, when UK and Alaskan populations are analysed separately, the UK models where density is measured within 0.8 and 1.6 m have much higher relative AIC values compared with other spatial scales. The lower AIC values seen in the combined analysis for the models with density measured within 0.8 and 1.6 m are because of the Alaskan populations. Indeed, density within 0.8 m was dropped when finding the UK minimum adequate models (Table D2). AIC values are lowest at the < 12.8 m spatial scale because most of the density values are confounded with the population.

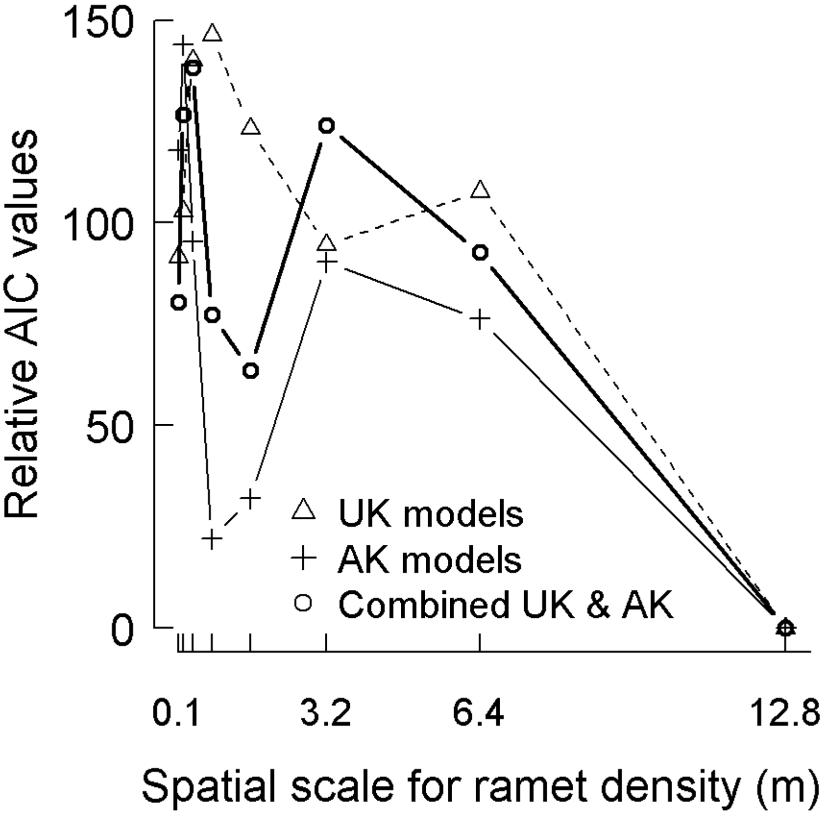

Figure 17. Comparison of relative Akaike's Information Criterion values across maximal models of *L. vulgaris* Ln ramet height, where conspecific ramet density has been measured around ramets within 0.1 m, 0.2 m, 0.4 m, 0.8 m, 1.6 m, 3.2 m, 6.4 m and 12.8 m. Models using these different spatial scales are compared within analysis of UK populations, Alaskan populations and for combined analysis of both UK and Alaskan populations. For each of the three sets of analyses, the model with the lowest AIC was for the < 12.8 m spatial scale and the AIC values at other spatial scales are shown relative to this. The models all contain the fixed effects: shading, vegetation height, vegetation height^2, ramet density, ramet density^2 and two way interactions, with the addition of region for the combined analysis. Population was modelled as random intercepts. Figure D3 shows a comparison of minimum adequate models.

3.4.2 Flowering results

17.39 % of the UK 2009 ramets and 22.97 % of the Alaskan ramets flowered. There was a wide variation between populations in the proportion of ramets that flowered (Tables D4 & D5). The flowering probability of an individual ramet is influenced by region, ramet height, ramet density, shading and the difference between ramet height and vegetation height (Table 10). The minimum adequate model where surrounding ramet density was measured within 3.2 m had the lowest AIC (Table D6).

The probability of flowering increases with ramet height (Figure 18) and in unshaded populations. Alaskan ramets were more likely to flower at a given height than UK ramets. In shaded or partly shaded populations a 12 cm tall Alaskan ramet in the same height of vegetation with the median surrounding density (12 ramets / m^2) had a 7.28 % predicted probability of flowering while a 12 cm tall UK ramet had a 3.23 % probability of flowering. If unshaded, the flowering probability increases to 23.78% for Alaskan ramets and 11.72 % for UK ramets. However, Alaskan ramets were shorter than UK ramets, so the median height of Alaskan ramets (11 cm) and the median height of UK ramets (16 cm) had a similar predicted probability of flowering in shaded or partly shaded populations (4.68 % and 5.85 %). The predicted probability of flowering is 16.32 % for an 11 cm unshaded Alaskan ramet and 19.83 % for a 16 cm unshaded UK ramet.

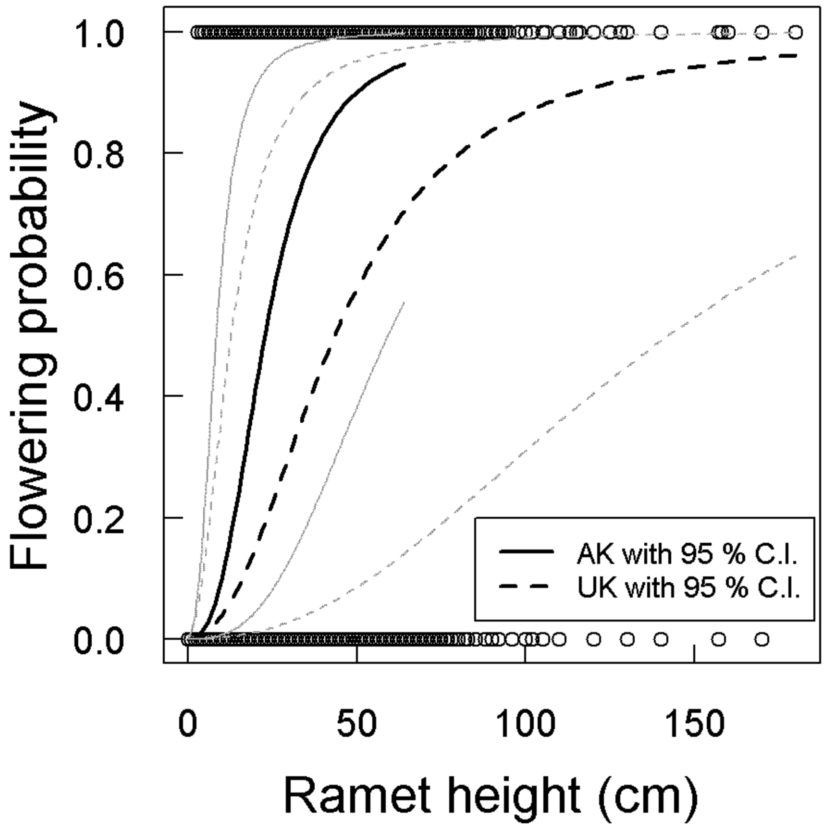

Figure 18. Predicted flowering probability with *L. vulgaris* ramet height in shaded or partly shaded populations when ramet density within < 3.2 m of the focal ramet is set at 12 ramets / m^2 and vegetation height is the same as ramet height. Thick lines are the mean predictions for Alaskan and UK ramets and thin lines are the surrounding 95 % Confidence Intervals of the populations. These predictions are from a generalized linear mixed effects model with binomial errors, a logit link and random population intercepts.

The probability of flowering increases as a ramet approaches the height of, and then overtops, surrounding vegetation (Figure 19). For example, an 11 cm tall Alaskan ramet at 12 ramets / m^2 density and 100 cm vegetation height has a 0.25 % probability of flowering, while if the vegetation height is

0 cm the ramet has a 8.50 % probability of flowering. The probability of flowering also increases with increasing ramet density, but with high variation between the populations (Figure 20). An 11 cm tall Alaskan *L. vulgaris* ramet growing in the same height of vegetation has a 2.8 % probability of flowering when surrounded by the lowest observed density of 0.16 ramets / m^2 within 3.2 m, but this increases to a 30.98 % probability of flowering at the greatest observed density of 42.21 ramets / m^2. There is a positive interaction between ramet height and ramet density, so that for tall ramets the effect of ramet density on flowering is stronger and vice versa (Table 10). There is also a positive interaction between ramets reaching or being taller than the surrounding vegetation and ramet density (Table 10). In the models for density within 1.6 m and at finer scales, there is an interaction between region and density (Table D6). This means that the relationship between density and flowering probability continues to be positive for Alaskan ramets, but in the UK the relationship becomes flat or slightly negative.

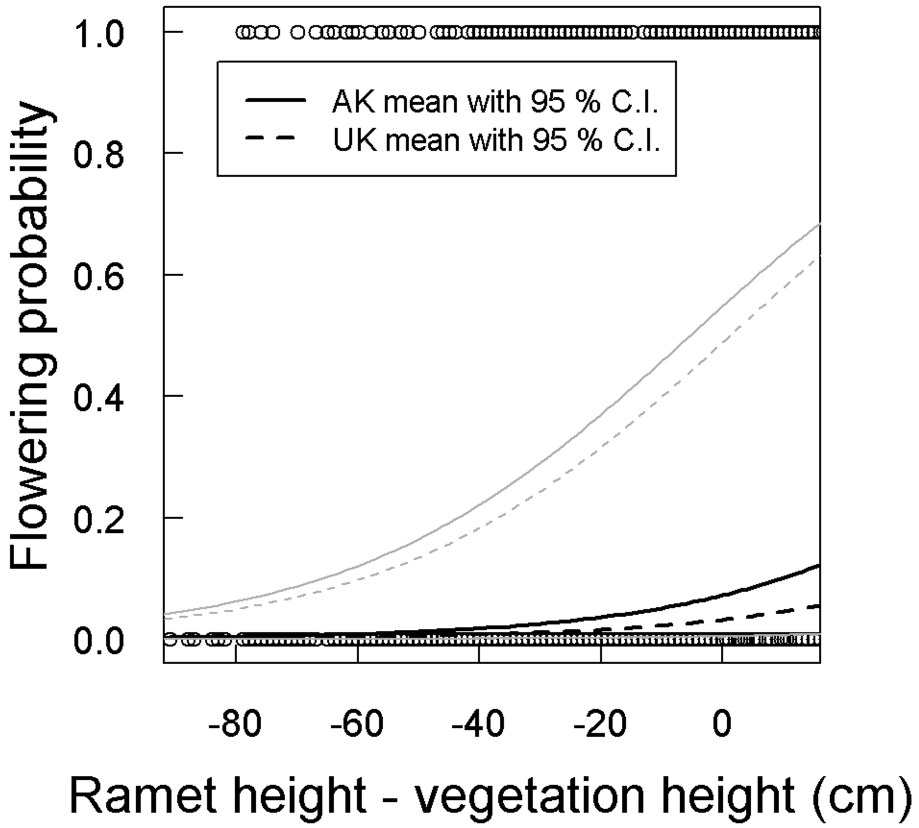

Figure 19. Predicted flowering probability of *L. vulgaris* as the difference between the ramet height and vegetation height reduces until the ramet becomes taller than the surrounding vegetation (positive difference). Here the ramet height has been fixed at 12 cm, so - 80 is equivalent to a vegetation height of 92 cm. Thick lines are the mean flowering probability for Alaskan and UK ramets and thin lines are the surrounding 95 % Confidence Intervals for the populations. These predictions are for shaded or partly shaded populations and conspecific ramet density has been fixed at 12 ramets / m^2 within 3.2 m of the ramet. Predictions are from a generalized linear mixed effects model with binomial errors, a logit link and random population intercepts.

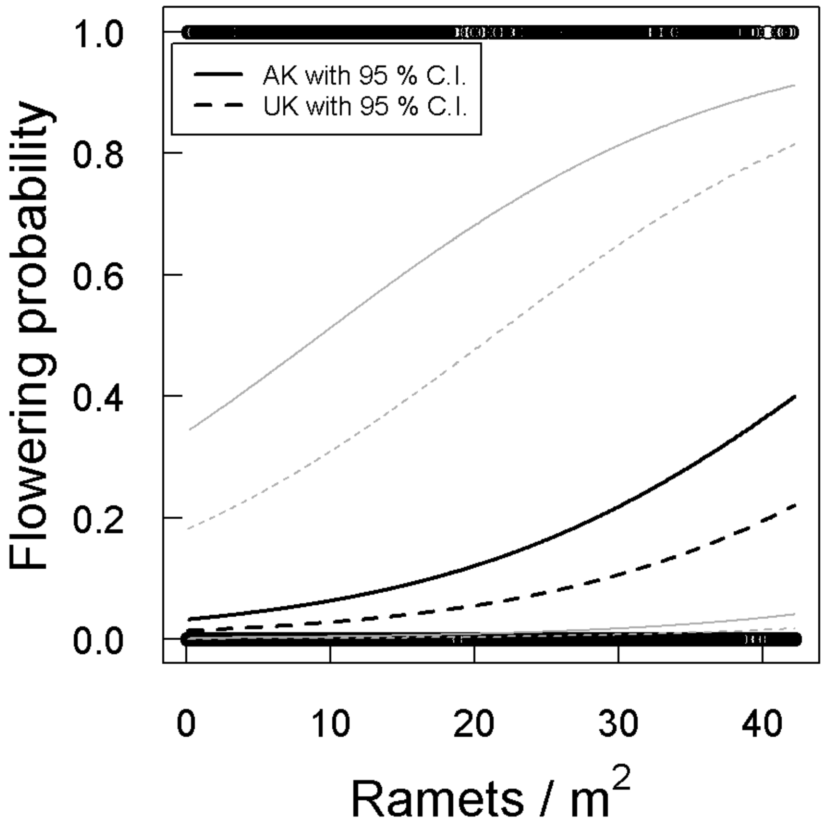

Figure 20. Predicted flowering probability of an *L. vulgaris* ramet with increasing conspecific ramet density within 3.2 m. Predictions are for shaded and partly shaded ramets and the ramet height and vegetation height are set at 12 cm. Thick lines are the mean predictions for Alaskan and UK ramets and the thin lines are the 95 % Confidence Intervals of the populations. Predictions are from a generalized linear mixed effects model with binomial errors, a logit link and random population intercepts.

Table 10. Fixed effects of the Minimum Adequate Model for *L. vulgaris* ramet flowering probability with surrounding flowering ramet *L. vulgaris* density within 3.2 m. Generalized linear mixed effects model using lmer (lme4) with binomial errors, logit link function and 19 Populations as random intercepts with a standard deviation of 1.366. N = 7899 ramets. The model was selected using AIC, but p-values are given for reference. Models for density at other spatial scales are in Table D6.

	Estimate	S.E.	z-value	p-value
Intercept (UK, some shading)	-7.99	0.689	-11.60	< 0.001
Region AK	-0.623	0.847	-0.736	0.462
Ln ramet height	1.46	0.159	9.18	< 0.001
Vegetation height difference	0.0171	0.00381	4.49	< 0.001
Density at < 3.2 m scale	-0.109	0.0296	-3.70	< 0.001
Unshaded	1.38	0.508	2.72	0.00663
Region AK : Ln ramet height	0.577	0.187	3.09	0.00120
Ln ramet height: Density	0.0703	0.0104	6.78	< 0.001
Veg. height difference: Density	0.00160	0.000353	4.54	< 0.001

3.4.3 Fruit results

Mature Alaskan ramets produced fewer adult fruit than mature UK ramets. The mean number of fruit produced by mature Alaskan ramets was 4.98 ± 0.270 S. E. (median = 4) while the mean number of fruit produced by mature UK ramets was 8.38 ± 0.618 S. E. (median = 6). 18.45 % (81 of 437) of the mature Alaskan and 14.76 % (31 of 210) of the mature UK ramets produced no adult fruit. However, this difference between the regions was dropped from a generalised linear model when ramet height and flowering ramet density measured within 0.8 m, 1.6 m, 3.2 m or 6.4 m of the ramet were included, with population as a random intercept (Table D7). When flowering ramet density is measured at very fine spatial scales (within 0.1 m, 0.2 m or 0.4 m) the effect of region is kept in the models (Table D7), although no difference had been found in flowering densities between Alaska and the UK.

The density of flowering ramets measured within 1.6 m and 3.2 m of the focal ramets provided the minimum adequate models with the lowest AIC (Table D7), so the model using density within 3.2 m is given as an example (Table 11). Fruit production increases with ramet height until a threshold around 1 m (Figure 21) and increases slightly as the surrounding flowering ramet density increases (Figure 22). The effect of ramet height on fruit production is the same for UK and Alaskan ramets as there were no interactions with region (Table 11). Vegetation height or the difference between ramet height and vegetation height was dropped from all the models.

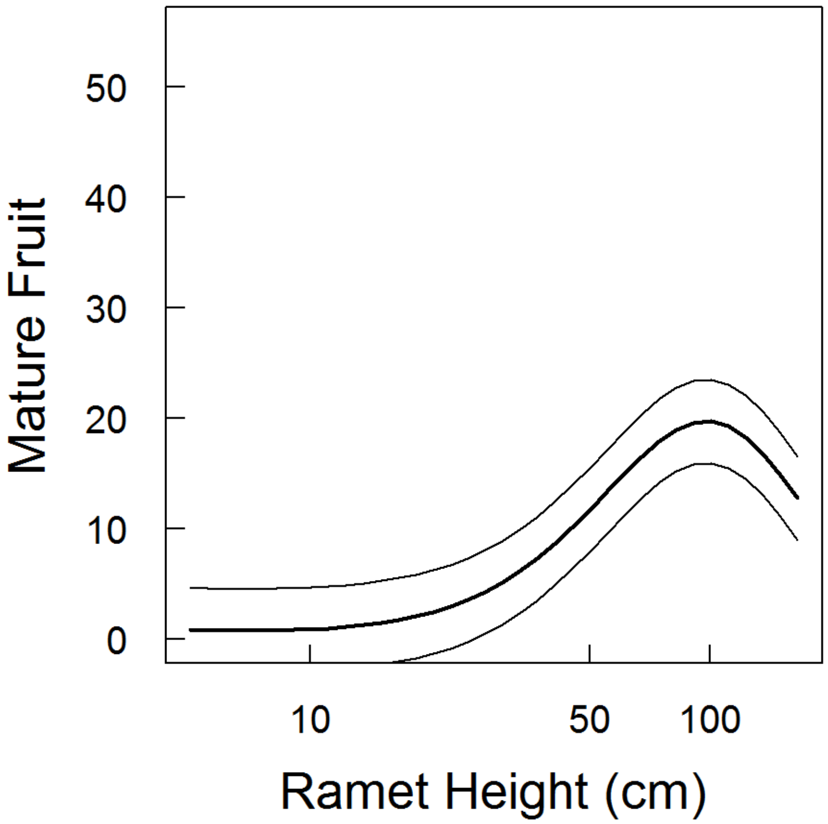

Figure 21. Predicted relationship between *L. vulgaris* fruit production and ramet height for a Minimum Adequate Model including flowering density measured < 3.2 m from the ramet. Flowering density is held at the median of 2.89 ramets / m^2. Surrounding lines are the 95 % Confidence Intervals of the 16 random population intercepts.

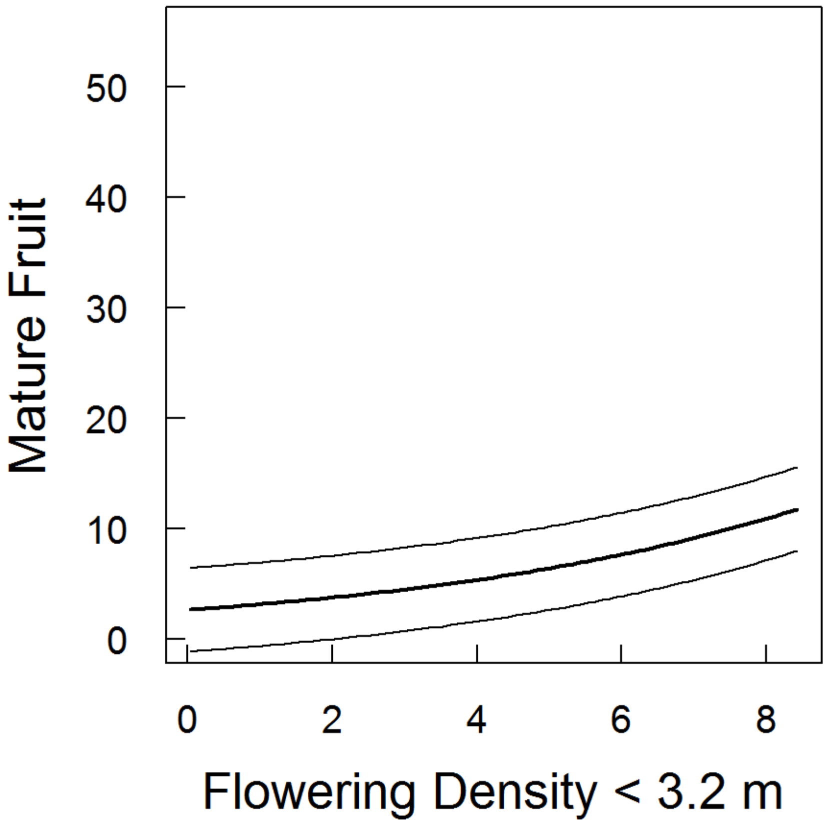

Figure 22. Predicted relationship between *L. vulgaris* fruit production and surrounding flowering ramet density within < 3.2 m, for a Minimum Adequate Model also including ramet height. Ramet height is held at the median of 27 cm. Surrounding lines are the 95 % Confidence Intervals of the 16 random population intercepts.

Fruit production increases with increasing density of flowering ramets when measured at the < 0.8 m, < 1.6 m, < 3.2 m and < 6.4 m spatial scales, but there is no relationship at the < 12.8 m spatial scale (Table D7). At fine spatial scales (< 0.1 m, < 0.2 m and < 0.4 m) the relationship between fruit production and flowering density depends on ramet height, and at the < 0.2 m scale also on region (Table D7). A 50 cm tall ramet is predicted to have increased fruit production with increasing flowering density at all the fine spatial scales. However, the interaction between region and flowering density within < 0.2 m means that at the median height of flowering ramets (27 cm), UK ramets are predicted to increase fruit production with increasing density, but there is a slightly negative effect for Alaskan ramets. Below a ramet height of 10 cm the relationship between surrounding flowering density at fine scales and mature fruit becomes flat or slightly negative. The 14 mature ramets below 10 cm height were all Alaskan and half produced fruit.

There was no difference between the UK and Alaska in the proportion of flowering structures (adult fruit plus failed structures) on mature ramets that were adult fruit (AIC with region = 3011.10, AIC without region = 3011.84). The mean proportion of flowering structures that were adult fruit on each mature ramet was 0.663 ± 0.0151 S. E. Out of a total of 647 mature ramets, 81 Alaskan and 29 UK ramets produced no adult fruit, and 224 Alaskan and 47 UK ramets produced only adult fruit.

Table 11. Fixed effects of a generalized linear mixed effects model of *L. vulgaris* adult fruit production with negative binomial errors, a log link and 16 populations as random intercepts. The negative binomial dispersion parameter is 1.54. Models for flowering density at other spatial scales are in Table D7.

Fixed effects	Estimate	S.E.	z-value	p-value
Intercept	7.00	4.08	1.71	0.0865
Ln ramet height	-9.33	3.58	-2.6	0.00925
Ln ramet height^2	3.42	1.02	3.35	< 0.001
Ln ramet height^3	-0.350	0.0951	-3.68	< 0.001
Flowering ramet density within 3.2 m	0.162	0.0341	5.17	< 0.001

3.4.4 Seed results

Alaskan fruit were more likely to have black seed present and to have a greater number of black seed than UK fruit (Table 12 & Figure D4). 90.27 % (334) of the Alaskan fruit had black seed, compared with 50.00 % (84) of the UK fruit. The mean black seed number was 47.61 ± 2.41 S. E. for Alaskan fruit and 7.71 ± 1.54 S. E. for UK fruit. Excluding the fruit with no black seed, the mean black seed number was 57.74 ± 2.52 S. E. for Alaskan fruit and 15.42 ± 2.85 S. E. for UK fruit.

There were no *R. antirrhini* or evidence of *R. antirrhini* found in Alaskan fruit, but 53.57 % (90) of the UK fruit contained *R. antirrhini*. Of the UK populations where more than two fruit were collected, all had *R. antirrhini* present (Table D8). The mean black seed number for the UK fruit with *R. antirrhini* was 3.22 ± 0.64 S. E. The mean black seed number for the UK fruit without *R. antirrhini* was 12.50 ± 3.14 S. E, which was still fewer than the Alaskan fruit. If the fruit without black seed are excluded, then the mean black seed for UK fruit with *R. antirrhini* was 6.74 ± 1.13 S. E and without *R. antirrhini* was 23.78 ± 5.42 S. E. 47.78 % (43) of the UK fruit with *R. antirrhini* contained black seed and 52.56 % (41) of the UK fruit without *R. antirrhini* contained black seed. Region remains as a fixed factor in models of both black seed presence and black seed number (Table 12), showing that *R. antirrhini* seed predation is not the only factor causing the reduced seed presence and number in the UK compared with Alaska. This is confirmed by analysis comparing the Alaskan fruit with just the UK fruit without *R. antirrhini* (Table D9).

38.10 % of the UK fruit with no black seed and 44.45 % of the Alaskan fruit with no black seed contained incompletely filled grey seed instead (Table 13). A higher percentage of the UK than the Alaskan fruit contained no seed or only grey seed (Table 13), while a higher percentage of the Alaskan fruit than the UK fruit contained a mixture of black and grey or only black seed (Table 13). However, the lower black seed presence and number in UK fruit without *R. antirrhini* compared with Alaskan fruit is because of a lower total seed production, not because more of the UK seed is grey. This is shown by analysis of the total (black and grey) seed presence and number of Alaskan and the UK fruit without *R. antirrhini* (Table D10).

When the UK and Alaskan fruit were analysed together, larger fruit were both more likely to have black seed present and to have a greater number of black seed (Table 12). Black seed was also more likely to be present when there were more other adult fruit on the same ramet at the time of collection (Table 12). The surrounding density of flowering ramets did not affect black seed presence or absence (Table 12). However, flowering ramet density at some spatial scales was included in models of black seed number (Table D11). This was because the flowering ramet density interacted with region or *R. antirrhini* presence. A simpler model of black seed number obtained by dropping main effects from a model without interactions is shown in table 12 to demonstrate the difference in black seed number between regions. When the two regions were analysed separately, flowering density at all spatial scales was dropped from both the black seed presence and black seed number models (Table 14 & Table 15).

In these separate region analyses, both UK and Alaskan black seed presence continued to be more likely with increasing fruit size (Table 14 & Table 15). UK Ln fruit size (mean = 5.23 ± 0.0643 S. E) was significantly larger than Alaskan Ln fruit size (mean = 4.70 ± 0.0491 S. E.) (Wilcox rank sum test = 17698, location difference = 0.446, $p < 0.001$). However, black seed presence was more likely in Alaska than in the UK for the same fruit size, and the larger fruit size in the UK did not compensate for the reduced probability of black seed presence. The large standard deviation for UK populations was caused by the outlying UK population BP2, where all fruit had black seed present. Alaskan black seed presence increased in probability as the number of other adult fruit on the ramet increased, in addition to the fruit size (Table 14). However, for the UK fruit, the probability of black seed presence increased with ramet height interacting with fruit size (Table 15). *R. antirrhini* presence was not included in the UK black seed presence model, because dropping it caused a non-significant decrease in likelihood (Change in deviance = 3.19, d.f. = 1, $p = 0.0739$). However, the sample size for the UK black seed presence model was small. For just the fruit with black seed present, the number of black seed in Alaskan fruit simply increased with fruit size (Table 14), while the number of black seeds in UK fruit was affected only by *R. antirrhini* presence or absence (Table 15).

The higher black seed production per Alaskan fruit outweighs the lower fruit production per Alaskan ramet when estimating black seed production per ramet in comparison with the UK. The Alaskan median of four fruit per ramet, multiplied by the Alaskan median of 29 black seed per fruit, gives an estimate of 116 black seed per Alaskan ramet. Using the Alaskan mean of

46 black seed per fruit gives an estimate of 230 black seed per Alaskan ramet. The UK median of six fruit per ramet, multiplied by the UK mean of nine black seed per fruit, gives an estimate of 54 black seed per UK ramet. The UK median black seed number was zero.

Table 12. A model of black seed presence and absence in UK and Alaskan (AK) fruit, followed by a model of the number of black seeds where present in UK and Alaskan fruit. The seed presence model uses binomial errors with complementary log-log link and has 388 observations with 12 populations as random intercepts. The seed number model uses truncated negative binomial errors with a log link and has 307 observations with ten populations as random intercepts. The seed number model shown here was obtained by dropping down from the main effects only without considering interactions. This is in order to demonstrate the difference between the regions, because the Minimum Adequate Model included two-way interactions (Table D11).

Model	Variable	Estimate	S. E. estimate	Z-value	p-value
Black seed presence UK & AK	Intercept	-3.18	0.638	-4.98	< 0.001
	Region: AK	1.59	0.322	4.93	< 0.001
	Adult fruit	0.0291	0.0124	2.35	0.019
	Ln fruit size	0.489	0.107	4.57	< 0.001
	R. antirrhini present	-0.879	0.369	-2.38	0.017
Black seed number UK & AK	Intercept	-3.44	0.484	-7.11	< 0.001
	Region: AK	1.28	0.402	3.18	0.0015
	Ln fruit size	1.207	0.0724	16.7	< 0.001
	R. antirrhini present	-1.69	0.361	-4.69	< 0.001

Table 13. Number of lowest opening fruit collected from the UK and Alaska (AK) containing no seed, incompletely filled grey seed and/or viable black seed. Herbivory evidence in addition to the presence of *R. antirrhini* includes holes, frass or *R. antirrhini* parasitoid exuviae. 168 UK fruit and 370 Alaskan fruit were collected, but only 87 of the UK and 301 of the Alaskan fruit were used in statistical analysis (see section 3.3.3.4).

	Black seed present	Black seed absent	Any seed absent	Only grey seed present	Both black and grey seed present	Only black seed present
UK total 168	84	84	52 (30.95 %)	32 (19.05 %)	13 (7.74 %)	71 (42.26 %)
Herbivory evidence 100	47	53	34	19	9	38
Containing *R. antirrhini* 90	43	47	30	17	8	35
AK total 370	334	36	20 (5.41 %)	16 (4.32 %)	55 (14.86 %)	279 (75.41 %)
Herbivory evidence 3	3	0	0	0	0	3

Table 14. Models of black seed presence or absence in Alaskan (AK) fruit and black seed number in Alaskan fruit where black seed is present. The seed presence model uses binomial errors with a complementary log-log link and has 301 observations with five populations as random intercepts. The seed number model uses truncated negative binomial errors with a log link and has 270 observations with five populations as random intercepts.

Model	Variable	Estimate	S. E. estimate	Z-value	p-value
AK Black seed presence	Intercept	-1.62	0.572	-2.84	0.0046
	Adult fruit	0.0450	0.0222	2.03	0.0426
	Ln fruit size	0.476	0.116	4.10	< 0.001
AK Black seed number	Intercept	-2.41	0.340	-7.12	< 0.001
	Ln fruit size	1.26	0.0686	18.3	< 0.001

Table 15. Models of black seed presence in UK fruit and black seed number in UK fruit where black seed is present. The seed presence model uses binomial errors with a complementary log-log link and has 87 observations with seven populations as random intercepts. The seed number model uses truncated negative binomial errors with a log link and has 37 observations with five populations as random intercepts.

Model	Variable	Estimate	S. E. estimate	Z-value	p-value
UK Black seed presence	Intercept	34.23	20.06	1.71	0.088
	Ln ramet height	-8.77	4.75	-1.85	0.065
	Ln fruit size	-7.40	3.77	-1.96	0.050
	Ln ramet height: Ln fruit size	1.85	0.888	2.08	0.037
UK Black seed number	Intercept	2.91	0.405	7.19	< 0.001
	R. antirrhini presence	-1.65	0.508	-3.26	0.0011

3.5 DISCUSSION

3.5.1 Reduced height in the invasive range

Contrary to expectations of increased vigour and the Evolution of Increased Competitive Ability hypothesis (Blossey and Notzold, 1995, Stastny et al., 2005, Blumenthal and Hufbauer, 2007), invasive *L. vulgaris* ramets were shorter than native ramets. This difference consisted of both a slightly higher proportion of very small ramets in the Alaskan populations compared to the UK, and also the absence of the very tall ramets found in some UK populations. One other field study (Erfmeier and Bruelheide, 2004) and two common garden experiments (van Kleunen and Schmid, 2003, Bossdorf et al., 2004) on other plant species have also found reduced heights in the invasive range or in plants of invasive origin. However, no other studies have reported heights of *L. vulgaris* in the rest of the invasive range, so it is unclear to what extent the shorter ramet heights are particular to the Haines region.

The surrounding vegetation in the Alaskan populations is shorter than in the UK populations (section 2.4.1). *L. vulgaris* has less need to invest in height because a competitive advantage depends on the surrounding height strategies of competitors, rather than an individual's absolute height (Falster and Westoby, 2003). Increased ramet height requires greater investment in growing and maintaining the stem, and so could be at the expense of lateral spread of the clone (Huber and Wiggerman, 1997). Maintaining the same height rather than overtopping neighbouring vegetation can also be a strategy to avoid wind stress (Nagashima and Hikosaka, 2011). Although the Haines area was climatically matched with the UK grid squares, the analysis gave equal weight to the ten climatic variables and the winter and spring temperatures were a poorer match than other climatic variables (Appendix A). Actual weather station data shows a colder winter, later spring and lower summer maximum temperatures for the Haines area in 2010 compared with Essex and Yorkshire in 2009 (Table A3). This shorter and cooler growing season is likely to be contributing to shorter vegetation and *L. vulgaris* ramet heights (Kollmann and Bañuelos, 2004), although Haines does have one hour twenty minutes more daylight at mid-summer than Essex, and fifty-five minutes more than Yorkshire (National Oceanic and Atmospheric Administration, 2013). Moles and colleagues (2009) found that precipitation in the wettest month was more important than temperature in predicting maximum species heights across latitude, with taller heights where there was greatest precipitation. However, over 30 years, Haines had more wet days and higher precipitation in the summer and autumn, and fewer wet days but with slightly higher precipitation in the winter and spring than in Essex (Table A3). Haines had unusually high rainfall in 2010 compared with the 30 year mean and the UK (Table A3 & Figure A4), but this was concentrated in the late autumn of 2010 and so is unlikely to have affected final ramet heights.

Region remains an explanatory factor in models containing vegetation height, suggesting there are additional differences between the regions that are influencing ramet height. Many of the UK populations showed similar height distributions to Alaskan populations, with certain UK populations having some very tall ramets (Figure 14). The large variation in height between UK populations suggests that *L. vulgaris* has a high potential for phenotypic plasticity in response to different local environmental conditions. In addition to the climatic difference between the two regions, there may simply be more variation in local conditions between the UK populations than between the Alaskan populations. One of these conditions could be the degree of shading because change in the red: far red ratio of light from an overhead canopy and surrounding vegetation can result in adoption of a shade avoidance strategy, which includes stem elongation (Smith, 1982, Ballaré et al., 1990, Franklin, 2008). However, the height model including both the UK and Alaskan ramets predicts that it is the partly-shaded ramets that will be taller, not the completely shaded ramets. When UK and Alaskan ramets are analysed separately, shading is only important in the UK models. Rather than being only about the degree of shading, this may instead be pointing to the presence of a hedgerow or fencing to provide physical support. The UK populations BP1, BP2, CM, HC, WL1 and WL2 had ramets taller than 1 m and had woody vegetation and/or fencing that were not present in any of the Alaskan populations. No ramets grew beyond 1 m unsupported (personal observation).

A related factor is that many of the UK populations were also likely to have had a warmer microclimate than the surroundings, with ramets growing on the South side of sheltering vegetation (CM, HC, WL1, WL2) or banks (BP1, MF). Most of the other UK populations also had some protection from the wind (BP2, IG2, IG3, LP1), with only two populations (BP3 and WL3) reasonably exposed. In contrast, most of the Alaskan populations (CK, FS, HR, NK) were exposed or only slightly protected by nearby vegetation (MB, TW), with only one population on a South facing slope (RV).

The higher proportion of very small ramets in Alaskan populations and the taller ramets in UK populations may also indicate differences in the age-structure between the ranges. Alaskan populations may be recruiting more throughout the year and or having greater survival within the year of young ramets. However, there is no evidence that this has led to increased local densities in Alaskan populations (section 2.4.2.1). Older populations may contain older clones with a larger root biomass more able to resource early and tall shoot growth. The ages of the UK and Alaskan populations are unknown; Alaskan populations had been established for at least three years (AKEPIC, 2010), but the UK records were at too broad a spatial scale to be sure that the same population was being referred to (Botanical Society of the British Isles, 2007). However, it is noticeable that the new UK population IG3 had a high proportion of small ramets (Figure 14). In addition to shorter vegetation heights, Alaskan populations also had a higher proportion of areas with very low vegetation cover compared with the UK populations (section 2.4.1). This might indicate more disturbance, resulting in lower levels of competition, but could also indicate lower levels of resources in general. More frequent and intense disturbance might mean that the Alaskan populations have been established for fewer years than the UK populations. However, disturbance also occurred in the UK and caused both the destruction and initiation of some populations. More evidence is needed about the relative intensity, frequency and scale of disturbance in both ranges. The lower competition for light and the possible lower competition for nutrients and physical space in Alaska might result in the selection for reduced competitive ability and smaller ramets (Bossdorf et al., 2004).

Rather than a plastic or post-invasion selective response to a differing environment (Bossdorf et al., 2005, Davidson et al., 2011), an alternative explanation for the shorter invasive ramets is a pre-invasion genetic difference between the UK populations and the source material for the populations in the Haines region (Hufbauer et al., 2012). *L. vulgaris* was introduced to North America before 1700 as a garden plant and continued to be used in horticulture during the 20th century (Saner, 1991, Mack, 2003). It was among the earliest plants recorded to have become naturalised, and in the 18th Century became the earliest documented plant invasion in North America (Mack, 2003). The native source(s) of material for the Haines *L. vulgaris* populations is unknown, although it is likely to have arrived via the Yukon where there are records from the early 1900s (AKEPIC, 2013). The location and historical importance of Haines as a transport hub makes it likely that the area was one of the earliest naturalisations of *L. vulgaris* into Alaska (Arhangelsky, 2007, AKEPIC, 2013). High levels of genetic variation have been found within and between Western North American populations of *L. vulgaris,* suggesting multiple introductions from the native range (Ward et al., 2009b). However, no population genetic studies have been carried out on Alaskan or native European *L. vulgaris.* Given the range of heights of the UK ramets, the difference in ramet heights between ranges seems most likely to be a plastic response.

3.5.2 Conspecific density at different spatial scales

The relationship between density measured at different spatial scales and ramet height differs between the UK and Alaska (Figure 16). The models with the lowest AIC when UK and Alaskan populations are analysed separately are those where density is measured at the largest scale within 12.8 m (Tables D2 & D3). This could be because density at this scale is confounded with environmental conditions affecting height at the population level, with multiple ramets having the same density value. The Alaskan population CK has higher density at the < 12.8 m scale than the other populations and so is having a large impact on the shape of the relationship. The shape of the curve for the UK populations at < 3.2, < 6.4 and < 12.8 m is being strongly affected by population LP, where most ramets were taller than the UK median and all the ramets had the same density value at these spatial scales. However, density within 12.8 m was better in explaining deviance in height than the population number, area or the mean field density. This spatial scale is probably combining aspects of the population level impact on ramet height and the effect of a ramet being in the edge or interior of populations.

There is a difference between the UK and Alaskan populations in how well density measured within 0.8 and 1.6 m explains height deviance compared with density measured at other spatial scales (Figures 17 & D3). This might be because the generally larger populations in Alaska (section 2.4.2.2) result in more variation in density at this spatial scale between ramets that are towards the centre or towards the edge of Alaskan populations. It could also be that stronger effects, such as shading, are obscuring the impact of density at this spatial scale in the UK. There is a difference between the strength of evidence for inclusion of a variable in a model and the strength of the relationship with the dependent variable. This can be seen at the fine spatial scales, where models using density within 0.1 m have a lower AIC than those at < 0.2 and < 0.4 m scales (Figure D3). However, the relationship between the Alaskan ramet heights and density within 0.1 m is almost flat when vegetation height is 10cm, while UK ramet heights only increase slightly with density (Figure 16). Higher densities at very fine spatial scales in the UK probably reflect older and better resourced clones that are more likely to both produce more ramet shoots and taller stems. When the surrounding vegetation height is 50 cm the relationship between ramet height and conspecific density within 0.1 and 0.2 m becomes negative, which may reflect within genet trade-offs.

The tallest Alaskan heights are predicted at intermediate densities for most spatial scales (Figure 16), as was found for growth rates and survival in Gunton and Kunin’s (2007) experimental *Silene vulgaris* populations. Initial increases in height with density could be associated with being in a well resourced site and towards the centre of a longer established patch. The decline of height at greater densities may be because of local competition for nutrients and/or clones investing in producing multiple new shoots rather than tall stems. The broader spatial scale measurements include density surrounding the ramet at fine spatial scales, so decline in height with higher broad scale densities will also include processes occurring at local scales.

The interaction between density and other variables can also alter with spatial scale. This is demonstrated by the effect of the density of surrounding flowering ramets on the fruit production of ramets. The positive relationship between flowering ramet density at spatial scales from < 0.8 to < 6.4 m and fruit production may be because denser flowering patches are likely to both be better resourced and attract more pollinators with genetically distinct pollen (Table D7). At finer spatial scales the effect of density on fruit production interacts with ramet height (Table D7). For tall ramets, the surrounding flowering ramet density at these finer spatial scales continues to have a positive effect on fruit production. However, as ramets become shorter the relationship becomes flatter. A negative impact of density at fine spatial scales and positive impacts at broader spatial scales on sexual reproduction has been found in *Sabatia angularis* (Spigler and Chang, 2008) and suggests competition at fine spatial scales, but facilitation of sexual reproduction at broader spatial scales. In this case, for tall *L. vulgaris* ramets, density appears to be having a greater facilitating effect on fruit production than any possible competitive effects at fine scales. The fruit production of shorter ramets may be more affected by competition at fine spatial scales than tall ramets. Experimental work might help to check whether this is an artefact of these models and to disentangle different density effects and covariates. The differences across spatial scale in the effect of density between regions and also in interaction with other variables, shows that the spatial scale at which conspecific density is measured can have an impact on what conclusions are made (Lortie et al., 2005). It also shows that different processes impacting fitness are likely to be occurring at different spatial scales.

3.5.3 Differences in sexual reproduction between regions

The proportion of ramets flowering are similar between the UK and Alaska, showing that it is ramet height relative to neighbours, rather than absolute height, which is important in determining flowering. The shorter Alaskan ramet heights do result in a smaller number of fruit being produced by mature Alaskan compared with mature UK ramets. However, this lower fruit number per ramet is more than countered by the greater presence and number of viable seed in the Alaskan compared with the UK mature fruit. This is contrary to findings from a global analysis of seed production between native and invasive ranges of invasive plants (Mason et al., 2008).

The native and invasive populations studied here were from a restricted area of the geographical range. However, comparisons with the limited number of other studies suggests that seed production per fruit may reflect a real difference between ranges, rather than being unique to these areas of the UK and Alaska. A large Southern UK population had a similar mean and distribution of seed production per fruit to that found here, with a mean of 5.47 ± 0.965 S. E. seed per fruit and with 54 % of the 140 sampled fruit empty (Stout et al., 2000, Jane Stout, personal communication). Mean seed per unpredated fruit was 13.1 ±10.3 S. E. at the end of July and 54.1 ± 21.1 S. E. in October for one Italian population, and 27.7 ±15.8 S. E. in October for another Italian population (Nepi et al., 2003). Most Western North American studies report mean seed per fruit consistent with these Alaskan invasive populations. Five populations in Ontario with the flower and seed predators *B. pulicarius* and *R. antirrhini* had 40.2 mean seed in fruit only containing black seed and 32.0 mean seed in fruit containing both black and grey seed (Clements and Cavers, 1990). A population in Colorado with unknown seed predator status had 88.4 ± 4.6 S. E., 90.7 ± 7.16 S. E. and 100.9 ± 8.1 S. E. mean seed per fruit over three years (Burkle et al., 2007).

Two populations predated by *R. antirrhini* in Montana had 22 and 50 mean seed per fruit (Lehnhoff, 2008). However, a New York population with *R. antirrhini* was similar to the UK populations, with a mean of 4.3 ± 2.9 S. E. seed per fruit and a range of 0 - 93 seed per unpredated fruit and 0 - 11 seed in the 78 % of fruit that had been predated (Arnold, 1982).

The Montana populations also demonstrate the high variability possible in seed production between populations and years, with ‘minimal’ seed production in two Montana populations, and no seed production in four populations for one year (Repath, 2005, Lehnhoff, 2008). As the comparison here between the UK and Alaskan populations is based only on one year in each range, the difference might be due to variation in seed production between years, rather than a consistent difference between ranges. However, fruit collected to the same protocol from UK populations surveyed in 2008 (not presented here) have a similarly low 8.08 ± 1.12 S. E. mean black seed per fruit, with 51.66 % fruit without black seed. In addition to variation between populations and years, *L. vulgaris* has a long flowering season that results in the seed output from a single population varying as the autumn progresses (Arnold, 1982). This is likely to be a consequence of varying abiotic and biotic conditions during the periods when flowers were pollinated and when seeds were resourced and predated (Arnold, 1982). This means that if seed is collected only over a few days, then any difference between regions might be a consequence of environmental conditions. The sampling protocol used here, with fruit from the longer flowering populations collected in both September and October will have helped to make the seed production results in both regions more representative.

However, it is possible that the long flowering period and the timing of surveys may have affected estimates of mature fruit production. The greater mean fruit production of UK compared with Alaskan ramets was calculated from ramets that had mostly completed flowering (85 % of reproductive structures were mature fruit or had failed) by early to mid - October. It was important to measure production only from mature ramets and also not to wait until very late in the year, because fruit from ramets that matured early sometimes falls off the stem and different structures become hard to distinguish as they decompose. However, this does mean that ramets that still had a large proportion of flowers late in the season were excluded from this estimate. In Alaska these flowers were unlikely to be pollinated and to mature seed before the first heavy snowfall. However, depending on the weather, UK ramets may be able to ripen seed into November. It is possible that these ramets that were excluded from calculations include not just ramets that initiated flowering later, but also those with extended flowering periods and therefore potentially larger than average flower and mature fruit production. Therefore, in some years the mean UK fruit production per ramet may be slightly higher than estimated here, which could partly mitigate for the lower seed production found per UK fruit. The reason for greater fruit production per UK ramet is because UK ramets were taller than Alaskan ramets and produced more flowers overall, rather than a higher proportion of flowers developing to mature fruit in the UK.

Three possible causes of lower seed counts in the UK are greater herbivory, pollen limitation and resource limitation compared with Alaska (Arnold, 1982). *R. antirrhini* presence as a cause of black seed absence was removed from the UK model. However, the sample size for the UK is relatively low and the p-value was borderline at the 0.05 level in the test for whether deviance increased significantly when *R. antirrhini* was removed from the model. While the relative importance of *R. antirrhini* in producing a greater proportion of empty fruit in the UK is unclear, *R. antirrhini* predation does contribute to the lower number of black seed found in UK fruit compared with Alaskan fruit. Seed predation by *R. antirrhini* was not the only cause of the lower seed presence and number in UK fruit, because the non-predated UK fruit were also more likely to have no or fewer seed than Alaskan fruit. It is possible that *R. antirrhini* adults had already emerged from these UK fruit, but this is unlikely because the fruit collected were those where the apex had just cracked with no more than a 1 mm gap. There were no exit holes in the side of apparently unpredated fruit (Turner and De Clerk-Floate, 2008).

The flower feeder *B. pulicarius* was observed in the UK population LP1 . *B. pulicarius* was not observed in Alaskan populations and was listed as absent from Alaska in 1991 (McNamara). However, the survey period in both regions only just overlapped with the usual period of *B. pulicarius* activity (Kock, 1966). The main effect of *B. pulicarius* feeding is to delay flowering and reduce fruit set by destroying flowers (Kock, 1966, McClay, 1992). Kock (1966) notes that *B. pulicarius* larva would often leave some of the ovules within an ovary intact, so it is possible that some flowers predated by *B. pulicarius* are able to mature and be fertilised, but with reduced seed output. If *B. pulicarius* was present in the UK populations, but not Alaskan populations, then this might explain the lower seed set in UK fruit without

R. antirrhini, although not the larger number of fruit without any seed. However, the proportion of mature fruit to failed reproductive structures per ramet did not differ between the UK and Alaska. This suggests that *B. pulicarius*, if present only in the UK, was not causing any difference between the regions, or only affected early flowering ramets.

Another contributor to reduced seed number per fruit in the UK might be lower rates of pollination compared with Alaska. A population of *L. vulgaris* studied in Colorado was not pollen limited (Irwin and Maloof, 2002), with another North American study finding that one *Bombus* spp. visit transferred more than enough outcross pollen to fertilize all ovules (Arnold, 1982). However, Arnold (1982) also suggested in his study that a lack of pollinator visits at one point in the year did have a corresponding impact on seed set. Nearly half of the ovaries of *L. vulgaris* flowers studied by Arnold (1982) did not enlarge, which could be caused by pollen limitation and/or early seed abortion. It might be that visitation rates by pollinators are lower in the UK than in Alaska and/or that the smaller population sizes and fewer numbers of populations at a landscape scale in the UK (sections 2.4.2.2 and 2.4.2.4) results in a smaller pool of genetically distinct pollen. Feeding by adult *R. antirrhini* and *B. pulicarius* (if present) on anthers, pollen and flowers will reduce male fitness in addition to female fitness (Arnold, 1982).

However, if pollen availability and/or transfer were lower in the UK, this again would be expected to have also reduced the proportion of fruit set per ramet in the UK compared with Alaska, which was not seen. A lack of pollination also does not explain the mature fruit found without seed, as unfertilized carpels would not enlarge. The positive effect found here of flowering ramet density at all spatial scales on UK and Alaskan fruit production may be due to correlations with other characteristics, rather than increased rates of pollination with increasing density. These include better resources and older and/or taller ramets occurring in larger populations and towards the centre of patches at all spatial scales. Individual ramets in less favourable parts of the population could be affected by periods of inadequate resources, resulting in early post-fertilization abortion of seed.

Clements and Cavers (1990) found that most of the seasonal variability in viable seed production was due to variation in resource availability, rather than predation or inefficient pollination. Inadequate resourcing can result in incompletely filled grey rather than viable black seed (Clements and Cavers, 1990). However, Wilson and colleagues (2005) interpret grey seed as resulting from *B. pulicarius* feeding. While *B. pulicarius* feeding does result in reduced seed weights and viability (Nadeau and King, 1991, McClay, 1992), reduced seed weights were also found in *L. vulgaris* plants attacked by the root mining moths *E. serratella* and *E. intermediella* (Saner, 1991, Saner and Müller-Schärer, 1994). This suggests that herbivory is reducing the available resources for seed production and resulting in grey seeds, rather than being a direct effect of seed feeding. Therefore grey seeds that occurred in both the UK and Alaska might be a consequence of herbivory or simply a direct lack of resources at particular points in the season during seed maturation.

However, the production of these grey seeds again does not explain the reduced black seed presence and number found in UK ramets. The total (black and grey) seed presence and number was also lower in UK fruit, rather than there being a greater proportion of grey seeds in the UK compared with Alaska. In addition to resulting in incompletely filled grey seed, restriction of resources (caused by change in weather, competition and/or herbivory) might result in post-fertilization seed abortion (Arnold, 1982, Burd, 1994, Stout et al., 2002). This could explain the lower total (black and grey) seed number in UK fruit and the greater number of mature fruit without any seed. Abortion of some seed and fertilised fruit might function to focus limited resources into producing viable seed (Stephenson, 1981). Several of the Essex populations were affected by low rainfall in late August and September 2009 (Table A4), with surrounding vegetation dying back, although most *L. vulgaris* ramets survived (personal observation).

Here, the release from seed feeders in the invasive range is one of the factors resulting in increased seed production compared with the native range. This raises the possibility of the use of biological control. *R. antirrhini*, acting in combination with *B. pulicarius,* has reduced *L. vulgaris* seed production in some North American populations (Harris, 1961, Wilson et al., 2005), and is now being deliberately spread as a biological control agent (Turner and De Clerk-Floate, 2008). Powell and colleagues (1994) stated that *R. antirrhini* ‘does not do well’ where there are extreme cold winter temperatures. However, *R. antirrhini* were found in Fairbanks, Alaska, in 2006 (Michael Rasy and Steven Seefeldt, personal communication) and seed feeding weevils (species unknown) were collected from populations in Anchorage in 2002 (Matthew Carlson, personal communication). However, Sing and colleagues (2005) argue that the density reductions in *L. vulgaris* seen in Canada are only correlative with, rather than caused by, the accidental introduction of *R. antirrhini* and *B. pulicarius*. If populations are not seed limited then the greater number of populations seen at the Alaskan landscape scale compared with the UK may be because of a greater number of establishment sites (Grigulis et al., 2001, Jongejans et al., 2007). If this is the case, then land management to reduce ‘invasion windows’, or targeted control in certain areas to reduce dispersal, may be of more value or needed as well as a biological control programme to reduce general seed output (Davis et al., 2000, Buckley et al., 2007).

The findings of this study are in contrast to those predicted by the Enemy Release and the Evolution of Increased Competitive Ability Hypotheses, where release from insects is predicted to result in increased growth and greater competitiveness (Blossey and Notzold, 1995, Keane and Crawley, 2002). Here, release from a seed feeder contributes directly to increased seed production, rather than greater vigour. This study demonstrates that a plant does not need to become more vigorous than in its native range to be invasive (Bossdorf et al., 2004). Allocation of resources towards increased height would not be an advantage amongst the shorter vegetation and reduced growing season in Alaska. Instead, an introduced plant needs to adjust allocation of resources to compete effectively with the native or other neighbouring invasive plants in the new range, whether by direct competition or by being able to take advantage of resource windows (Davis et al., 2000, MacDougall and Turkington, 2004). This can include becoming shorter than in the native range (Vilà et al., 2005). A common garden experiment would be needed to determine whether the difference found here between ranges is the result of a phenotypically plastic response, or if there has been selection for reduced height and compensatory increased seed production per fruit in Alaska (Bossdorf et al., 2004, Bossdorf et al., 2005, Ebeling et al., 2011). However, as it is not known whether or not UK or Alaskan populations are seed limited (Egan and Irwin, 2008), the relative importance of this increased seed production in explaining invasion in Alaska is unclear. In the next chapter I examine patterns of *L. vulgaris* seed dispersal, rates of seed germination and the role of vegetative reproduction in the maintenance of populations.

Chapter 4. Seed dispersal, germination and vegetative reproduction of *Linaria vulgaris* Miller.

4.1 ABSTRACT

Density patterns can be affected by dispersal and establishment, which includes both seed dispersal and vegetative reproduction. Seed dispersal distances, germination rates and the vegetative reproduction of *Linaria vulgaris* Miller (Plantaginaceae) were investigated. For seven *L. vulgaris* plants surrounded by vegetation, half of the seed estimated to fall within 1.85 m had been deposited by 0.28 to 0.97 m from the plants (0.58 m mean). However, seed travelled further from four maternal plants that were not surrounded by vegetation, with half of the seed estimated to fall within 0.85 to 1.38 m of the plants (1.18 m mean). In a germination trial of 256 UK *L. vulgaris* seeds in conditions mimicking a UK spring, only three seed germinated (1.17 %). The three germinated seed were black, rather than incompletely filled grey seed, and had received a previous cold treatment at 5 °C for seven days. The germination of a sample of UK seed sown outdoors varied with the maternal plant, suggesting variability in seed resourcing. Both trials indicated that a short period at low temperature might be required to initiate germination. 15 of 40 (37.5 %) 10 cm *L. vulgaris* root fragments transplanted to a meadow initiated shoots at various times within 12 weeks of transplantation. However, there was low shoot survival. Both seeds and root fragments could produce multiple shoots. Excavation of sections of two UK *L. vulgaris* populations suggest established populations

are largely maintained by vegetative rather than sexual reproduction. However, seed dispersal will be important for establishing satellite patches and new populations. Both this long distance seed dispersal, and the establishment of seedlings and of new ramets from root fragments, is more likely in environments with shorter and sparser vegetation.

4.2 INTRODUCTION

Seed dispersal, seed germination and vegetative reproduction can contribute to the emergent density pattern of plant populations (Nathan and Muller-Landau, 2000, Bullock et al., 2002, Seabloom et al., 2005, Benot et al., 2013). Differences between the native and invasive range in seed dispersal parameters (Jongejans et al., 2008a), seedling recruitment (Hierro et al., 2009) and the balance between sexual and vegetative reproduction (Beckmann et al., 2009), may contribute to any observed differences between ranges in density patterns across spatial scales. *Linaria vulgaris* Miller (Plantaginaceae) has the same range of densities at fine spatial scales in UK and Alaskan study populations (sections 2.4.2.1 and 2.4.2.3). This may be because of similarity between the ranges in processes affecting dispersal and establishment of *L. vulgaris* at fine spatial scales (Firn et al., 2011). At broader spatial scales the Alaskan populations are larger and there are more populations in the Alaskan study area than in the UK (sections 2.4.2.2 and 2.4.2.4). One contributor to this difference may be the greater seed production found in Alaskan compared with UK fruit (section 3.4.4) (Williams et al., 2010, Herrera et al., 2011, although see Mason et al., 2008). The greater number of seed in itself increases the chances of long distance dispersal events. However, this might also be contributed to by increased opportunities for dispersal and/or improved establishment of seed or root fragments in Alaska. It is also possible that the larger population sizes are caused by increased dispersal and/or establishment of new seedlings or ramets at the edges of populations.

Field data on seed dispersal are used to inform and parameterise models of invasive plant spread (Kot et al., 1996, Jongejans et al., 2008a, Jongejans et al., 2008b, Caplat et al., 2012). However, these models do not usually take into account the impact that surrounding vegetation might have both on the mean distance travelled by seed and the shape of seed deposition (Thiede and Augspurger, 1996, Marchetto et al., 2010). Surrounding vegetation usually reduces the distance that a seed travels, both by directly blocking seeds, and also by reducing wind velocity and increasing turbulence (Bullock and Moy, 2004, Cousens et al., 2008). However, in some circumstances the presence of surrounding vegetation could increase long distance dispersal, as uplift in forested areas is known to cause very long distance dispersal (Nathan et al., 2002). The prevailing wind direction also has a strong effect on the deposition pattern of wind dispersed seed (Bullock and Clarke, 2000). A Canadian study of the seed dispersal around patches of *L. vulgaris* in a barley crop found a negative exponential pattern of dispersal and estimated that 96 % of seed was deposited within 0.5 m (Nadeau and King, 1991). However, there have been no studies of *L. vulgaris* seed dispersal within the native range, or consideration of the possible impact of the presence or absence of surrounding vegetation on the dispersal pattern.

Once deposited, seed viability and the abiotic and biotic conditions for successful germination and establishment are a filter for determining the number of populations that establish at a broad spatial scale (Colautti and MacIsaac, 2004). Particularly low germination rates have been observed for Canadian *L. vulgaris* under field conditions (Lewis, 1954, Nadeau and King, 1991). Laboratory germination studies also found relatively low rates of germination of Canadian and Baltic *L. vulgaris* seed (Clements and Cavers, 1990, Nadeau and King, 1991, Necajeva and Ievinsh, 2008), although Lewis (1954) reported 74 and 88 % germination for Canadian seed from two years when pre-chilled. To my knowledge there have been no germination studies on UK *L. vulgaris* seed. Previous germination studies of *L. vulgaris* were carried out at higher temperatures than mean spring temperatures in the UK and Southeast Alaska (Lewis, 1954, Clements and Cavers, 1990, Nadeau and King, 1991, Necajeva and Ievinsh, 2008). There is also conflicting evidence as to whether cold stratification at 5 °C is important for breaking dormancy (Lewis, 1954, Ellis et al., 1985, Nadeau and King, 1991, Necajeva and Probert, 2011) or is unnecessary (Clements and Cavers, 1990, Necajeva and Ievinsh, 2008).

The relative importance of sexual compared with vegetative reproduction for the maintenance of existing and establishment of new populations is also unclear. Ward and colleagues (2009b) found high levels of genetic diversity within Western North American invasive *L. vulgaris* populations and suggest that populations are being maintained mainly by sexual rather than vegetative reproduction. However, Egan and Irwin (2008) found no seedlings in plots within established populations in Colorado, despite a high seed input. Transplanted *L. vulgaris* produce new shoots in similar patterns to that of wild populations (Nadeau et al., 1991) and very northerly populations are thought to be maintained by vegetative reproduction because most fruit has insufficient time to mature (Staniforth and Scott, 1991).

Here, studies of seed dispersal, germination, ramet growth and the root connections in UK populations are used to address the following questions:

What is the seed dispersal pattern around an individual of *L. vulgaris* and what influence do surrounding vegetation types (grassland, hedgerow and ploughed field) have on this pattern?

What percentage of *L. vulgaris* seeds germinate in spring conditions and is previous cold stratification required? Can seed germinate in summer conditions?

What percentage of *L. vulgaris* root sections produce new ramets?

What percentage of the spring cohort in UK populations are new seedlings compared with clonal ramets and what are the typical distances between successive ramets from the same clone?

4.3 METHODS

4.3.1 Seed dispersal

Twenty 2nd year *L. vulgaris* plants from Mires Beck Nursery (Mires Beck Nursery, Low Mill Lane, North Cave, Brough, East Ridings of Yorkshire, HU15 2NR) were potted on into 0.21 m diameter and 0.2 m depth terracotta pots using peat-free compost on 26th June 2008 and then overwintered in a cold frame at the University of Leeds Experimental Gardens. These individuals originated from stock plants grown from seeds collected from a Yorkshire roadside population (54.073° N, 0.711° W). Seeds collected from these stock plants had been sown on 5th April 2007. Each pot originated from one seedling and plants had been kept outside.

In August 2009, twelve of the pots were selected based on having upright stems without many open fruit. Four of the pots each were randomly assigned to a unvegetated harrowed field (53.865° N, 1.335° W), a meadow with grasses and herbs approximately 0.6 m tall between lines of young trees in an agroforestry plot and 1 m from a 1.8 m tall hawthorn hedgerow amongst grasses and herbs approximately 0.5 m tall besides the agroforestry plot (53.865° N, 1.329° W) (Figure 23). Maternal plants that were placed in the meadow had maximum stem heights between 0.70 and 0.87 m (mean 0.77 m). Maternal plants at the hedgerow had maximum stem heights of between 0.69 and 0.79 m (mean 0.73 m). Maternal plants in the field had maximum stem heights of between 0.55 and 0.78 m (mean 0.66 m). Most of the fruit of the meadow and hedgerow plants was either overtopping or level with the top of surrounding vegetation. Pots were placed at least nine metres apart and dug approximately 0.15 m into the ground.

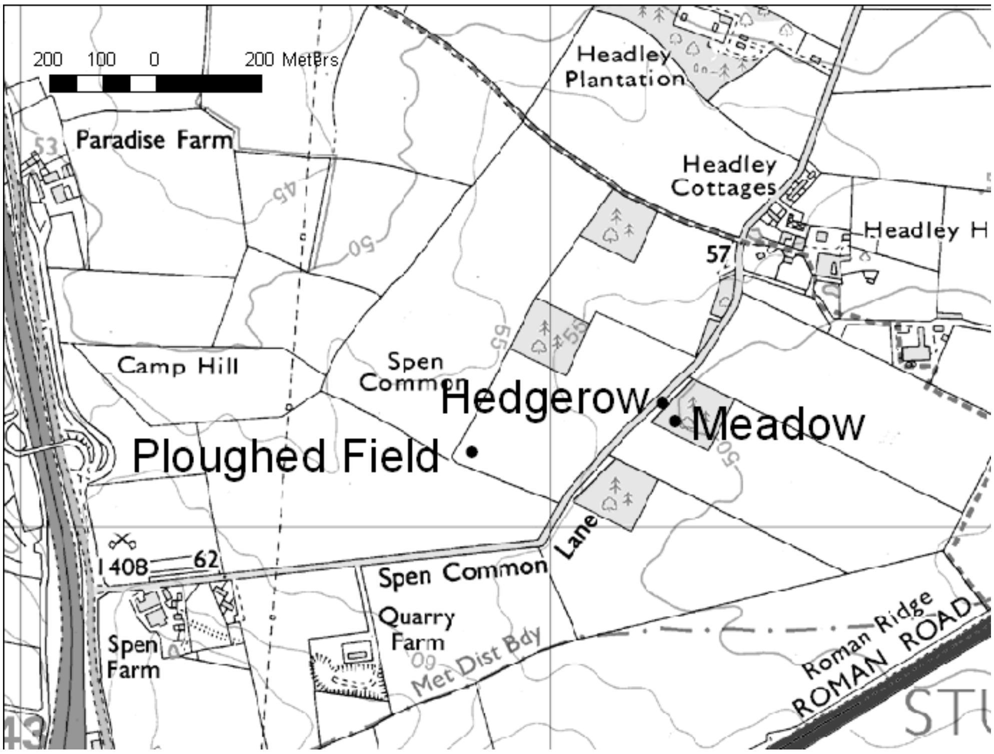

Figure 23. Seed dispersal experiment sites at the University of Leeds farm. ©Crown Copyright/database right 2012. An Ordnance Survey/EDINA supplied service.

Plastic 90 mm diameter petri dishes were weighted with soil and taped shut. A thin layer of Agralan Insect Barrier Glue was smeared over the lid of the petri dish to form a sticky seed trap (Bullock et al., 2006) (Agralan Ltd. The Old Brickyard, Ashton Keynes, Swindon, Wiltshire SN6 6QR). This was done at the field site just before placing to avoid collecting any stray seeds. Traps were placed in the four directions 60, 150, 240 and 330 degrees around each *L. vulgaris* pot (Figure 24). The direction was chosen to accommodate the 60 to 240 degree hedgerow line and no traps were placed at 330 degrees at the hedgerow. One trap was placed with the centre at 0.23 m from the centre of the pot, two along the circumference of the circle at

0.46 m from the centre of the pot, four at 0.92 m and eight at 1.85 m. Considering the 0.09 m diameter of the traps, these were the distances that allowed the placement of traps to form a segment with an angle of approximately 22.5 degrees around each pot. This would provide data for four distances within 2 m, for a quarter of the possible directions that seed might leave the parent plant. The traps were pushed down to ground level amongst the vegetation. Trampling of surrounding vegetation was avoided as far as possible by walking only between the four angles and around the outside of the circle. Traps were put into position on the 29th, 30th and 31st of August and 1st September 2009.

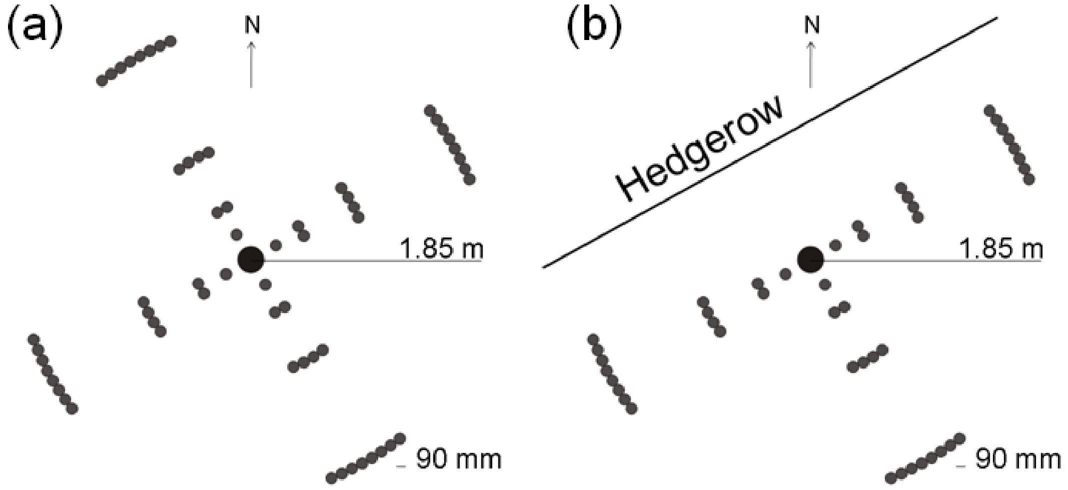

Figure 24. a) Layout of seed traps at 60 º,150 º, 240 º and 330 º, and at 0.23 m, 0.46 m, 0.92 m and 1.85 m from the centre of the maternal *L. vulgaris* plants in the field and the meadow. b) Layout of seed traps at the hedgerow.

L. vulgaris seeds on traps were counted *in situ* three weeks later on the 19th, 20th and 21st September 2009, following the order that the traps had been placed. The majority of seeds found in the traps were black, although occasional incompletely filled grey seeds were also included in the total number. The direction and length of flowering stems that leaned over the edge of the pot were recorded. The area around the pots out to 5 m was checked for *L. vulgaris* seedlings the following spring.

The seed densities found at 0.23, 0.46, 0.92 and 1.85 m distance from each maternal plant were interpolated to estimate seed densities at other distances with monotonic Hermite splines using the Fritsch-Carlson method in the function splinefun in R 2.12.2 (Fritsch and Carlson, 1980, R Development Core Team, 2011). Monotonic interpolation maintains either the increase or decrease between two data points; non-monotonic functions would allow the seed density curve to decrease and then increase between data points or *vice versa*. The same method was also used to fit curves of seed densities with increasing area around the maternal plant, with the density at 0 distance assumed to be the same as at 0.23 m. The area under these curves of seed density with increasing area is an estimate of the number of seeds deposited, so integration was used to estimate cumulative seed number with increasing radius from the maternal plant.

The increasing seed trap area over the four sampled distances to form four segments with an angle of 22.5° allows comparison of direction and distance travelled of the trapped seed. The percentages of seed trapped in the different directions were compared with the expected percentage if all directions were equally likely (25 % in the field and meadow and 33.33 % at the hedgerow). Adding the vectors of each trapped seed gives a mean direction of seed travel for the three environments.

An estimate was also made of the potential maximum seed output from each maternal plant during the three weeks. The seed was counted from three mature closed or opening fruit from each of seven unused plants with the same origin as the maternal plants. Most seeds from fruit open on 1st September were lost during transportation, so the number of new fruit that opened between the 1st and 20th September were used to estimate the potential seed release. The number of open fruit (with the crack at the apex greater than 1 mm) on each of the maternal plants on the 1st September was taken from the number of open fruit on each on the 20th September. The number of seed that could potentially have been shed by each maternal plant was estimated by multiplying this fruit number by the median seed number of 96.

4.3.2 Seed germination

4.3.2.1 Growth cabinet trial

In June 2010 two seeds were taken from each of 128 seed samples that had been collected from opening fruit in five UK populations in September and October 2009 (BP2, HC, IG3, LP1, WL1) (section 2.3.1.3). Seed had been stored from November 2009 at 15 °C and 15 % relative humidity. Each sample was the total of either black or grey seeds from the whole or half of one fruit. Eight seeds were placed in each of 32 90 mm diameter plastic petri dishes, containing one filter paper disc (Sartorius Stedim 87 g/m^2 grade 292). The 32 dishes were divided into pairs, so that the two seeds from the same fruit sample were split across the paired dishes. For 14 of the dish pairs there was one seed each from the populations BP2, HC, WL1 or IG3 and five seeds from LP1, while one pair of dishes had six and one pair eight seeds from the LP population. The filter papers were moistened with distilled water and the dishes covered with clear plastic film followed by the petri dish lid. One of each pair of dishes was placed in the dark at a constant temperature of 5 °C for seven days, with the others in the dark at a constant temperature of 20 °C in a growth cabinet (Microclima, MC1750HE, Snijder Scientific, Tilburg, Holland) for seven days. Then on 17th June the dishes that had been at 5 ºC were also transferred to the growth cabinet, which was set to 60 % humidity with a 14 hour day and temperatures between 5 and 11 °C. Temperatures changed gradually during the 24 hours between a high of 11 °C at midday and a low of 5 °C at midnight. On 25th June 2010 temperatures were increased by 5 °C so that at midday they were reaching 16 °C and at midnight reaching 10 °C. The filter paper was kept damp with distilled water as needed.

4.3.2.2 Experimental gardens trial

Seed was collected from seven maternal ramets in a population at Wigan Flashes (53.524° N, 2.616° W) on 21st and 22nd September 2007 and were stored at room temperature. 375 seeds were sown into a 1:1 peat and sand mixture in 7 cm square and 7 cm deep pots on the 29th May 2008. Each of the 24 pots contained 16 seed from the same maternal ramet (apart from two containing only ten and 13 seed). There were two pots each for seed from five of the ramets, four pots for seed from the sixth ramet and ten pots for seed from the seventh ramet. Pots were blocked across two trays so that an equal number of pots from the same maternal ramet were in each tray. Pots were randomly positioned within each tray. Trays were placed in open cold frames at the University of Leeds Experimental Gardens and watered as needed during hot weather.

4.3.3 Ramet growth

On the 13th April 2011 forty 10 cm lengths of lateral roots were cut from four year old *L. vulgaris* plants of Yorkshire origin grown in compost in cold frames at the University of Leeds Experimental Gardens. Roots were cut so that they included a node where shoots might initiate and any existing shoots were cut off. Roots weighed between 0.19 and 1.94 g. Roots were kept in compost and transplanted the following day to a meadow in an agroforestry plot at the University of Leeds farm (53.869° N, 1.329° W). The meadow had been cut to approximately 5 cm height. Roots were buried 2 m apart in 15 x 10 cm excavated plots at a depth of 5 cm and were then watered. The presence and height of any shoots was checked after four, eight and 12 weeks. The meadow was cut to approximately 10 cm between eight and 12 weeks.

4.3.4 Ramet connections

In April 2011 the position and height of all ramets was plotted using 0.5 x 0.5 m quadrats within sections of the populations BP1 and IG3 (Table 2). Ramets in these sections were excavated to see if their root systems were connected or unconnected with surrounding ramets. Many ramets had lateral spreading roots, but for many it was not possible to confirm whether or not these were connected with other ramets. Ramets that were confirmed as unconnected were examined for the presence or absence of broken sections of thicker roots that would be likely to be from previous years and also for the distinctive cotyledons or cotyledon scars to determine whether they were seedlings. The BP1 population section was an 11 x 1.5 m transect. It was more difficult to successfully dig up and record root connections in the IG3 population, so only two 1 x 0.5 m sections were used. The distances between these connected ramets were calculated and then compared with the nearest neighbour distances from other UK and Alaskan populations (Table 2) Calculations were also made of the distance between the location of ramets in UK populations in 2009 and the nearest ramet from 2008 to those points. Figures were produced using the packages spatstat and lattice in R 2.12.2 (Baddeley and Turner, 2005, Sarkar, 2008, R Development Core Team, 2011).

4.4 RESULTS

4.4.1 Seed dispersal results

The pattern of seed deposition with distance varied among both individual maternal *L. vulgaris* plants and vegetation environments, with broadly three different shapes (Figure 25). Five plants in all three vegetation environments had peaks in seed density at 0.46 m, while three plants in the meadow and hedgerow had a decline in density between 0.23 m and 0.46 m. Three plants in the unvegetated field had flatter distributions of seed; one with slightly increasing seed density over distance and two with maximum densities at 0.92 m. On one of the hedgerow plants no fruit opened during the three weeks. Most of the seed released from the plants placed in the meadow and hedgerow was estimated to fall within 1 m (Figure 26, Table 16). In the meadow half of the seed estimated to be deposited within 1.85 m fell within 0.35, 0.55, 0.60 or 0.70 m of the four maternal plants. For the three hedgerow plants half of the seed had been deposited by 0.28, 0.59 and 0.97 m. However, seed travelled further from the plants in the unvegetated field, with half the seed deposited by 0.85, 1.18, 1.31 and 1.38 m (Figure 26). The calculation of potential seed output for each plant was inaccurate, with some of the estimates of seed deposited within 1.85 m greater than the estimate of total seed output (Table 17), so could not be used to estimate the percentage of seed travelling beyond 1.85 m.

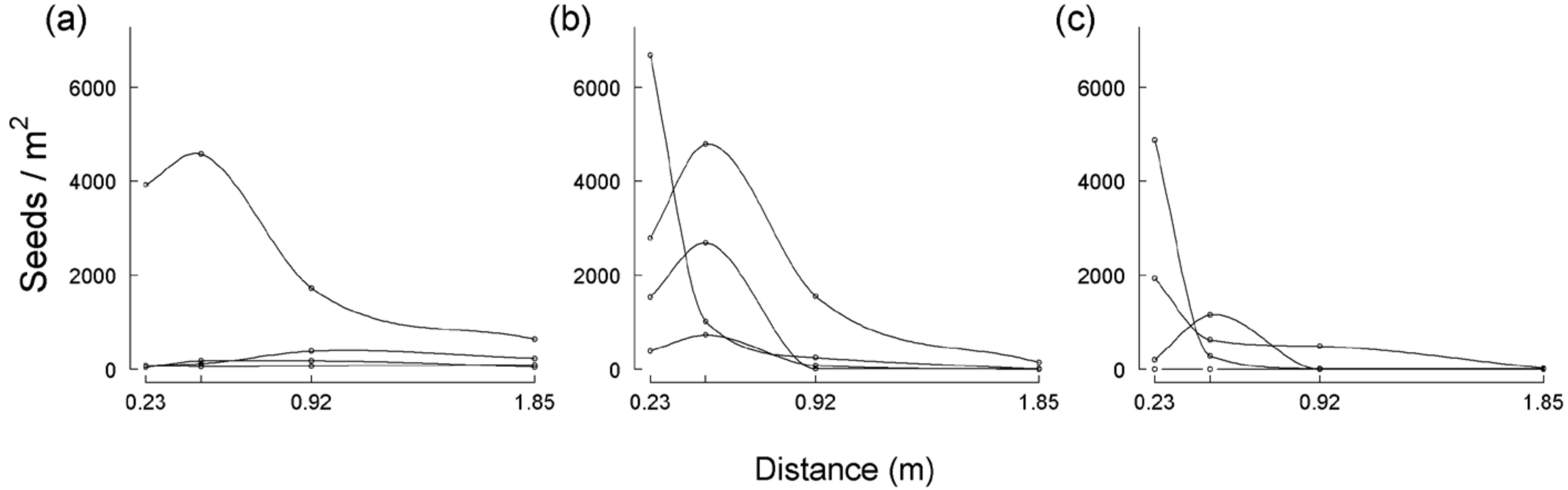

Figure 25. *L. vulgaris* seed density at four distances from the centre of 12 pots of *L. vulgaris* placed in a) unvegetated field b) meadow and c) hedgerow habitat for three weeks in September. The field pots and meadow pots were surrounded by four 0.09 m diameter traps at 0.23 m, eight traps at 0.46 m, 16 traps at 0.92 m and 32 traps at 1.85 m distances. The hedgerow pots had three traps at 0.23 m, six traps at 0.46 m, 12 traps at 0.92 m and 24 traps at 1.85 m distance, as there were no traps at 150 degrees direction from the pot. Seed densities at intermediate distances have been interpolated using a monotone Hermite spline.

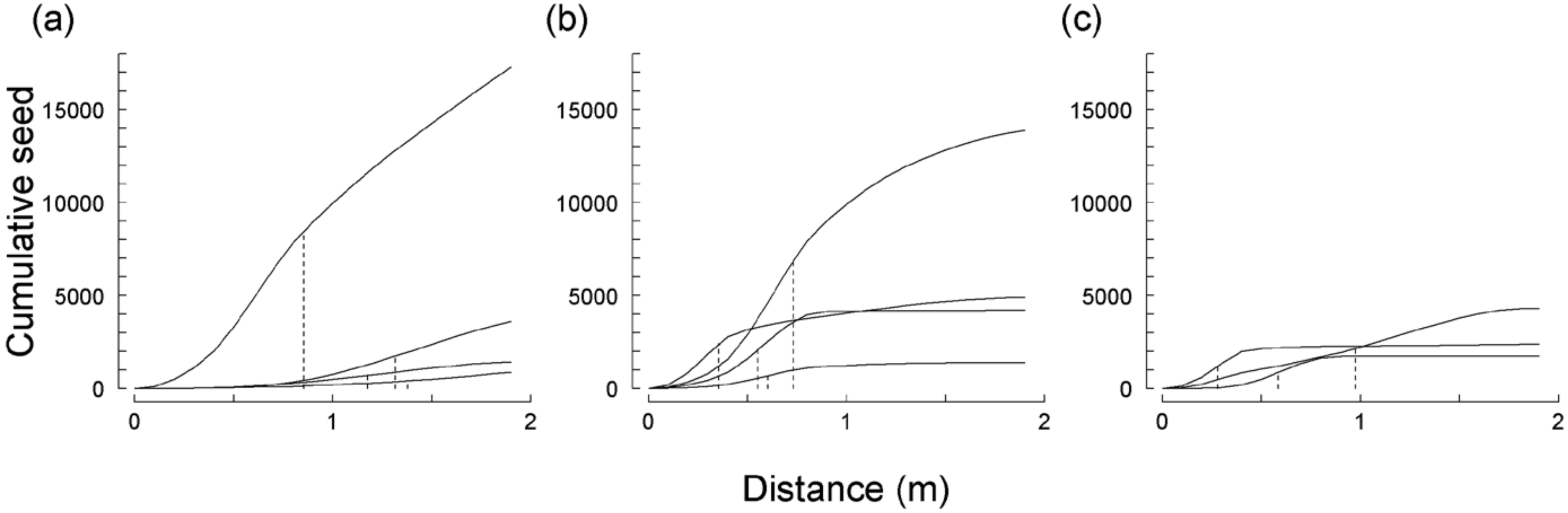

Figure 26. Estimated cumulative seed number surrounding 12 *L. vulgaris* pots placed in a) an unvegetated field b) a meadow and c) a hedgerow environment for three weeks in September. Distance is the radius of the circle around each pot. Seed numbers are estimated from seed traps placed at 0.23, 0.46, 0.92 and 1.85 m from the pots by integrating the curves of seed density against area. One of the hedgerow pots produced no open fruit during the three weeks. Dashed lines show the circle radius within which 50 % of the seed fell, out of the estimated seed to fall within 1.85 m.

Table 16. Estimated *L. vulgaris* seed numbers deposited within 0.5, 1 and 1.85 m from 11 maternal plants in an unvegetated field, meadow and by a hedgerow. Seed numbers were estimated by integrating curves of seed density against area around the maternal plants from seed traps at 0.23, 0.46, 0.92 and 1.85 m. The seed density at the pot centre was assumed to be the same as the seed density at 0.23 m.

Maternal plant environment	Seed within 0.5 m (as % of seed within 1.85 m)	Seed within 1 m (as % of seed within 1.85 m)	Seed within 1.85 m
Field	82 (5.78 %)	498 (35.25 %)	1414
Field	3326 (19.62 %)	9965 (58.77 %)	16957
Field	75 (2.16 %)	766 (22.06 %)	3475
Field	55 (6.60 %)	202 (24.32 %)	829
Meadow	430 (31.14 %)	1246 (90.30 %)	1380
Meadow	1625 (38.64 %)	4159 (98.93 %)	4204
Meadow	3170 (64.99 %)	4059 (83.23 %)	4877
Meadow	2915 (21.08 %)	9917 (71.74 %)	13824
Hedgerow	2137 (90.00 %)	2275 (95.80 %)	2374
Hedgerow	504 (29.16 %)	1728 (100 %)	1728
Hedgerow	1041 (24.05 %)	2241 (51.77 %)	4329

Table 17. The potential seed output of each plant over the three weeks was estimated from the number of new open fruit and the median seed number of fruit. Seed numbers were estimated by integrating curves of seed density against area around the maternal plants from seed traps at 0.23, 0.46, 0.92 and 1.85 m.

Maternal plant environment	Potential seed output	Estimated seed within 1.85 m as % of potential seed output
Field	8320	17 %
Field	22568	75 %
Field	20384	17 %
Field	4992	17 %
Meadow	15184	9 %
Meadow	32344	13 %
Meadow	11856	41 %
Meadow	18616	74 %
Hedgerow	3536	67 %
Hedgerow	1352	128 %
Hedgerow	3224	134 %

There was an uneven distribution of seed in the four directions in the field (Chi sq = 42.5, d.f. = 3, $p < 0.001$), meadow (Chi sq = 54.52, d.f. = 3, $p < 0.001$) and hedgerow (Chi sq = 10.51, d.f. = 2, $p < 0.01$). 54.79 % of the seed trapped in the field were in seed traps at 60° from the maternal plant and the mean direction as calculated from the trapped seed was 62°

(Figure 27a). 51.65 % of seed trapped in the meadow was at 60 degrees and the mean direction was 79° (Figure 27b). However, at the hedgerow site, the mean direction of seed dispersal was 201°, with a higher percentage of seed in traps at 240° (46.69 %) than expected, and a lower percentage than expected at a 90° angle to the hedgerow at 150° (20.23 %) (Figure 27c). In the field and meadow there is a shift in bias from 330° to 60° with increasing distance (Figure 27a & b). *L. vulgaris* seed was also observed being blown across the surface of the ploughed field. No *L. vulgaris* seedlings were found surrounding the maternal plants in any of the three environments the following year.

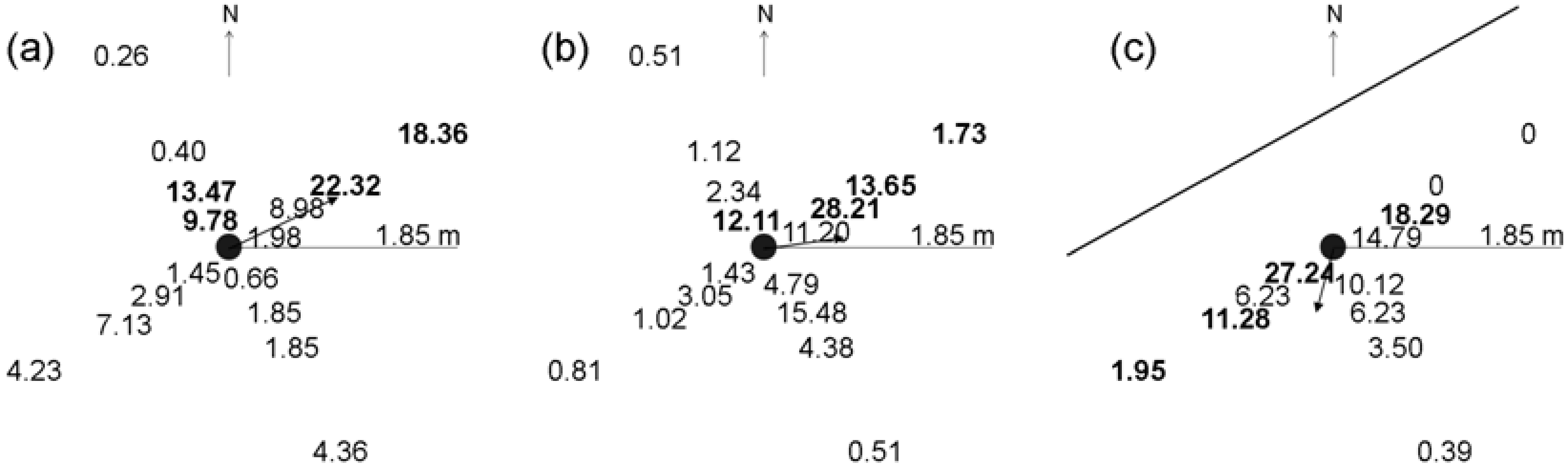

Figure 27. Percentage of *L. vulgaris* seeds in traps at 60°, 150°, 240° and 330° and 0.23 m, 0.46 m, 0.92 m and 1.85 m from maternal plants a) in an unvegetated field b) in a meadow and c) by a hedgerow. Arrows show the mean direction and distance travelled from all of the seeds trapped in each environment. In the unvegetated field the mean direction of the trapped seed was 62° and the mean distance was 0.95 m. In the meadow the mean direction was 79° and the mean distance was 0.52 m. At the hedgerow the mean direction was 201° and the mean distance was 0.44 m.

4.4.2 Seed germination results

4.4.2.1 Growth cabinet trial

Only three of the 256 seeds (1.17 %) germinated after 13 days in the growth cabinet. The remaining seeds had not germinated after 21 days. The three seedlings were from black seeds that had received the cold treatment. Two of the seedlings were from separate fruit in population BP2, but the population of the third seedling was unknown because the dish labels had been disturbed. 74 seeds had been infected by fungi by the end of the trial.

4.4.2.2 Experimental gardens trial

The seed was sown in late May 2008 and had not germinated after six weeks. However, when they were checked again on 25th October 2008, germination had occurred, with shoot heights between 1 and 64 mm, and with more than one shoot produced per seed (Table 18). Germination varied with parental identity, with seed from four of the maternal plants having no or minimal germination (Table 18). Although the date of first shoot emergence is unknown, germination may have occurred after minimum temperatures at the Experimental Gardens were between 1 and 8 °C for ten nights from 29th September. Previously, temperatures had only been as low as 6 °C on isolated nights (Figure 28).

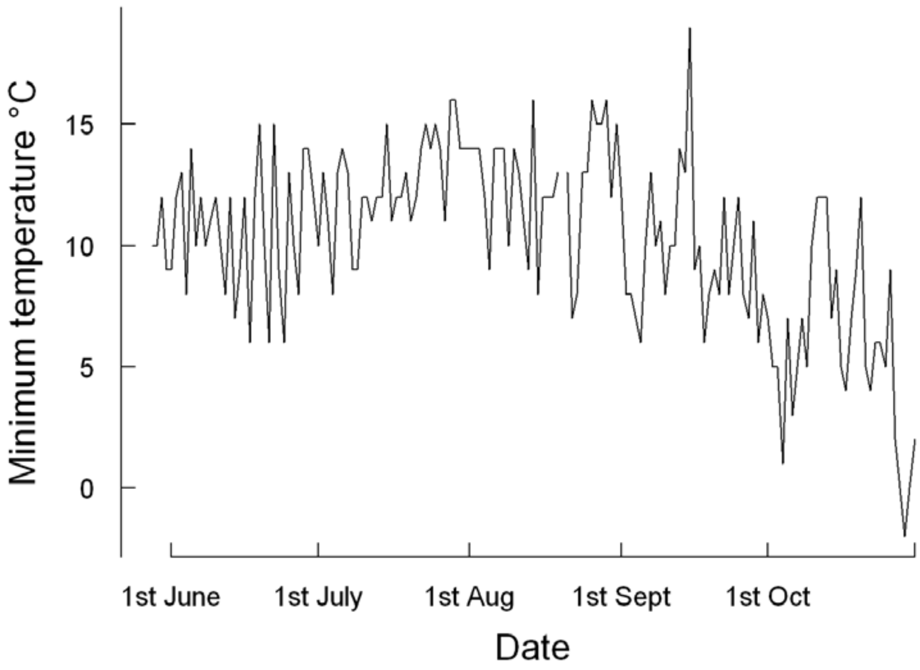

Figure 28. Minimum 24 hour temperatures at the University of Leeds Experimental Gardens during the 2008 *L. vulgaris* seed germination trial.

Table 18. Number of *L. vulgaris* shoots on 25th October 2008 from seeds sown on 29th May 2008 that were collected from seven maternal ramets on 21st and 22nd September 2007. Shoot height varied between 1 and 64 mm. [a] Sown with only 13 seeds. [b] Disturbed by birds. [c] Sown with only 10 seeds.

Maternal ramet	Number of shoots in separate pots, with 16 seeds per pot.									
A	16	31	26	25	21	23	23	30	24	27 [a]
B	3	0 [b]	0	0						
C	19	12								
D	15	4								
E	0	0 [b,c]								
F	0	0								
G	0	0								

4.4.3 Ramet growth results

Fifteen of the forty roots produced shoots at some point within 12 weeks, but there was low survival. No difference was found in original weight between the roots that did and did not produce shoots ($t = 1.59$, d.f. = 19.15, $p = 0.127$). Four weeks after burial nine of the forty roots had produced 12 shoots with heights between 1 and 25 mm. After eight weeks there were five roots with shoots present, because shoots from seven of the roots had died, but three new roots had produced shoots with heights between 2 and

20 mm. After 12 weeks there were six roots with shoots between 2 and 85 mm in height, of which three roots had two or three shoots. Shoots from three of the roots had died between six and twelve weeks, but two new roots had produced shoots and one of the roots where the shoot had previously died had produced further shoots. Only two shoots of the original 12 shoots that were present at four weeks survived to 12 weeks.

4.4.4 Ramet connections results

No cotyledons or cotyledon scars were observed in either population and there was no obvious dichotomy in size or appearance of roots and stems to distinguish between ramets and seedlings. While shoots were found that had separate root systems, most of these stems were growing from sections of roots of a few centimetres in length that appeared to have died back from the previous year. Of the 208 ramets in the BP1 population section, 50 were confirmed to have separate root systems, but most of these appeared to be growing from sections of the previous year’s roots (Figure 29). Two shoots were possible seedlings, based on the shape of roots rather than cotyledon presence. Of the 27 shoots in the first section of population IG3, five were unconnected and were possible seedlings. Of the 49 shoots in the second section of population IG3, three were unconnected and one was a possible seedling. The internode distance between the connected ramets varied between 1 and 30 cm, with a mean distance of 9.24 cm and a median distance of 5.10 cm. However, this may be biased towards shorter distances because it was more difficult to follow and excavate longer root connections.

If multiple ramets at the same location are included in the internode distance calculation the median distance is 0 cm and the mean is 3.31 cm (Figure 30).

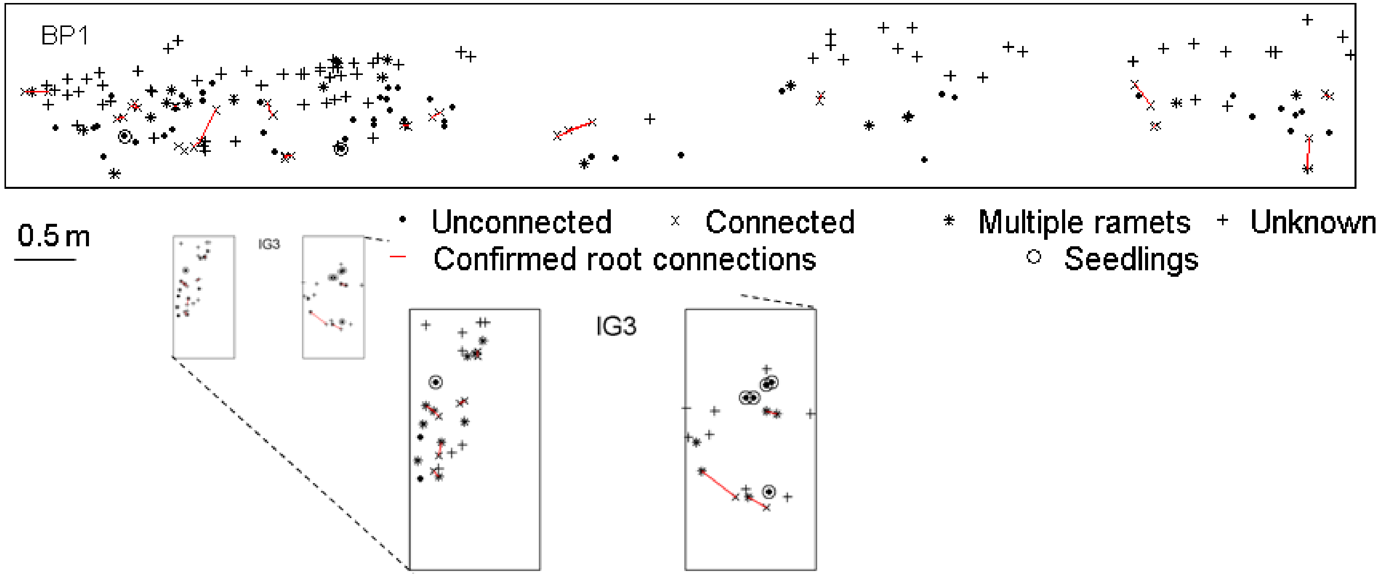

Figure 29. Excavated *L. vulgaris* ramets in a1.5 x 11 m section of population BP1 and two 1 x 0.5 m sections of population IG3. Ramets that were confirmed to be connected by roots are connected by red lines. Ramets that were not connected to other ramets, but that appeared to be growing from sections of the previous year's roots are shown as dots. Plants that were not connected to other ramets and appeared to be seedlings are circled. For the remaining ramets shown as crosses it was not possible to determine whether or not they were connected to other ramets, although most had lateral roots.

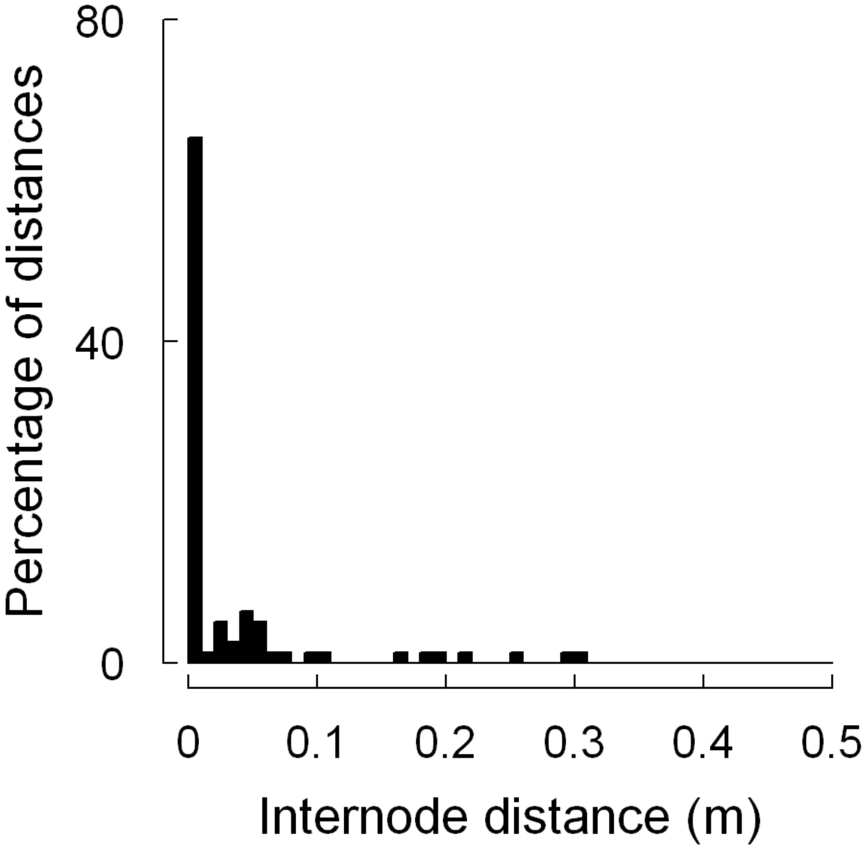

Figure 30. Distances between connected ramets in excavated sections of *L. vulgaris* populations BP1 and IG3.

The median nearest neighbour distances between ramets in UK 2009 populations varied between 0 and 0.14 m (Figure 31) and in Alaskan populations the median nearest neighbour distances were between 0 and 0.06 m (Figure 32). Ten of the populations had maximum nearest neighbour distances within 0.5 m (BP2: 0.25 m, BP3: 0.36 m, CM: 0.37 m, HC: 0.31 m, LP1: 0.37 m, MF: 0.41 m, WL2: 0.35 m, WL3: 0.27 m, CK: 0.45 m and MB: 0.22 m). Nine of the populations contained ramets that were more isolated from neighbours (BP1: 4.49 m, IG2: 0.71 m, IG3: 1.34 m, WL1: 0.78 m, FS:

1.49 m, HR: 2.69 m, NK: 1.27 m and RV: 2.04 m and TW: 0.52 m). The UK populations that were recorded in 2008, 2009 and spring 2010 show a similar spatial pattern between years (Appendix B). Population BP1 had expanded and also developed a satellite patch between 2008 and 2009 (Figures B2 & B3), although it is possible that the satellite patch was missed in 2008. The expanded part of the population and satellite patch are more likely to have been established from seed dispersal. Population HC expanded slightly in spatial extent between 2008 and 2009 (Figures B8 & B9), which could be vegetative and/or sexual reproduction. However, some support for the importance of sexual reproduction in population maintenance is provided by the very small population IG1, which did not produce mature fruit in 2008 and did not survive into 2009 (Figure B10). Figure 33 shows the distances between ramets in UK 2009 populations and their nearest neighbour from the same population in 2008. Given the likely level of precision in recording of ramets between years, this could indicate that many ramets are growing from last year’s root stock in similar positions. However, it cannot be ruled out that the same patterns may also have been produced by predominantly sexual rather than vegetative reproduction.

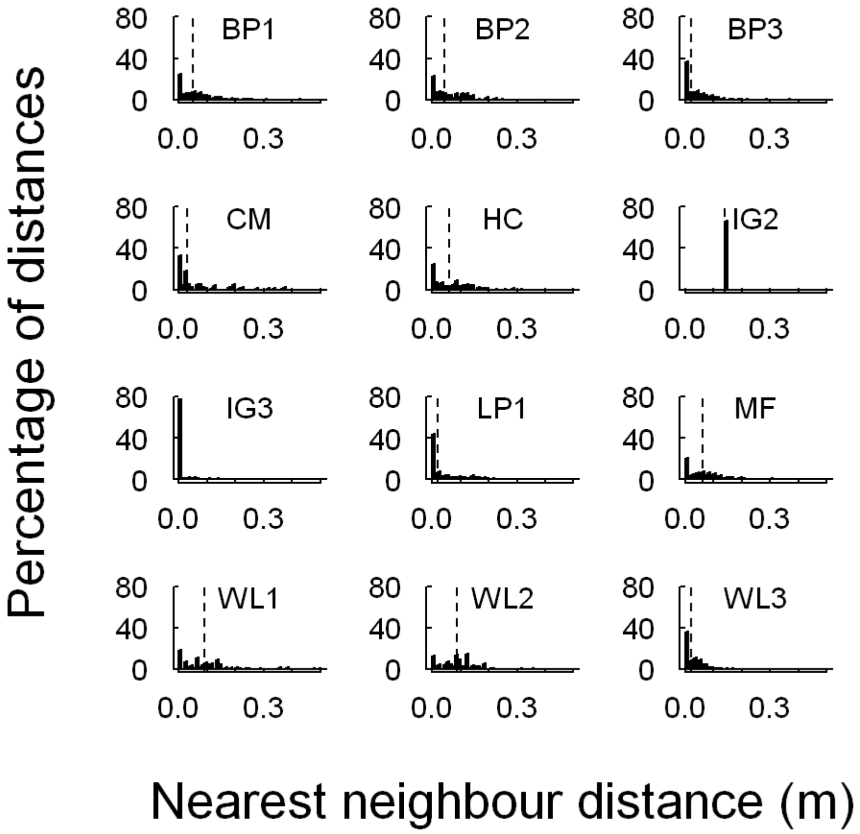

Figure 31. Nearest neighbour distances up to 0.5 m for *L. vulgaris* ramets in UK 2009 populations as a proportion of all the nearest neighbour distances. Dashed lines are the median distances for each population. Four populations had ramets that were further than 0.5 m from a neighbour: BP1 up to 4.49 m, IG2 up to 0.71 m, IG3 up to 1.34 m and WL1 up to 0.78 m.

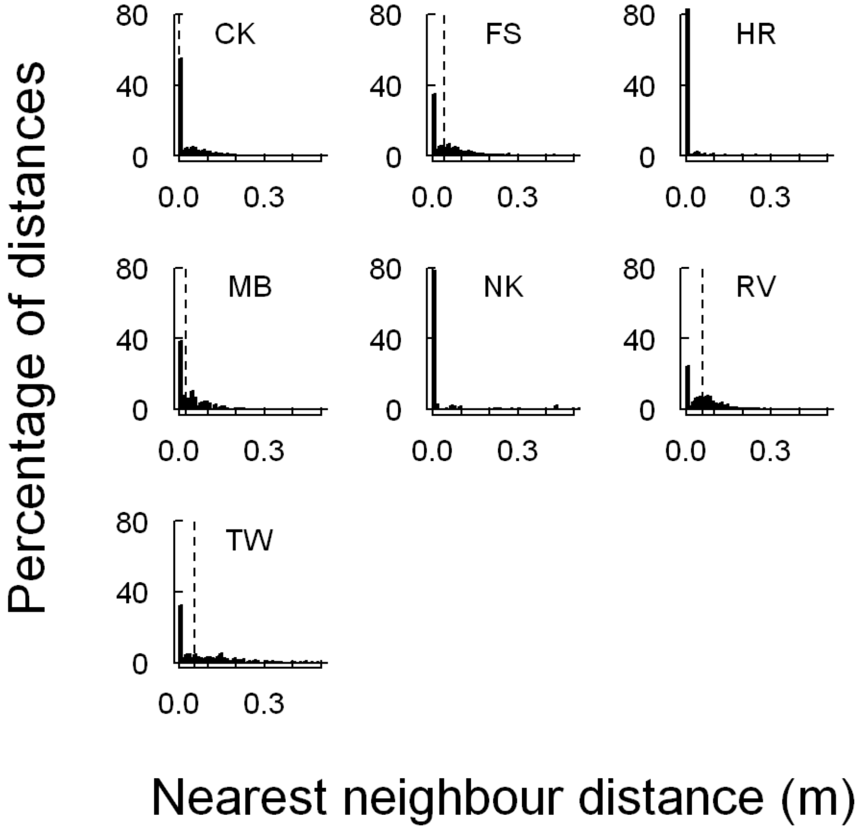

Figure 32. Nearest neighbour distances up to 0.5 m for *L. vulgaris* ramets in Alaskan populations as a proportion of all the nearest neighbour distances. Dashed lines are the median distances for each population. Five populations had ramets that were further than 0.5 m from a neighbour: FS: 1.49 m, HR: 2.69 m, NK: 1.27 m and RV: 2.04 m and TW: 0.52 m

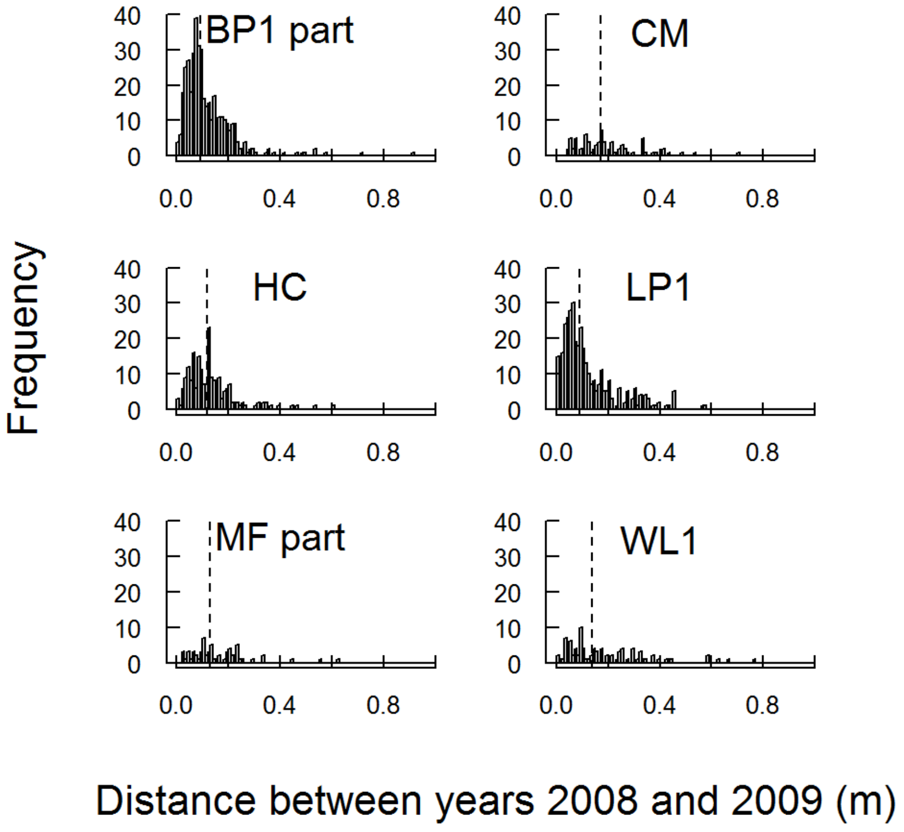

Figure 33. Distance of each autumn 2009 ramet from where the nearest ramet was in autumn 2008 in six UK *L. vulgaris* populations. The dotted line is the median distance of 2009 ramets from 2008 ramets for each population. In 2009 the BP1 population had greatly expanded, so here only the part of the BP1 2009 population is used that overlays the population in 2008. Only the central patch of the MF population is compared because the side sections were only surveyed in spring 2009 rather than autumn.

4.5 DISCUSSION

The spatial pattern of plant populations can be moulded by environmental heterogeneity (Collins and Glenn, 1990, Seabloom et al., 2005), biotic interactions such as competition (Seabloom et al., 2005, Stoll and Bergus, 2005) or natural enemies and demographic processes such as dispersal through seed (Nathan and Muller-Landau, 2000, Bullock et al., 2002, Seidler and Plotkin, 2006) or vegetative reproduction (Benot et al., 2013). The lack of difference in density at fine spatial scales between native and invasive range *L. vulgaris* populations suggests that processes influencing fine scale pattern do not differ between the ranges (section 2.4.2.1). However, the larger population extents and greater number of populations in the invasive range study area indicate that one or more factors influencing broad scale pattern do differ. One of these factors may be the greater viable seed production of the Alaskan populations (section 3.4.4). Here I have examined three important recruitment stages (seed dispersal, seed germination and vegetative reproduction) to understand how they might be influencing fine and broader scale abundance and distribution of *L. vulgaris*.

The dispersal curves show that most of the seed released in vegetated environments will be deposited within 1 m of the maternal plant (Figure 26 & Table 16). Nadeau and King (1991) estimated that 96 % of seed produced by *L. vulgaris* growing amongst barley was deposited within 0.5 m, which is a shorter dispersal kernel than found here. However, Nadeau and King (1991) were measuring distance from the edge of *L. vulgaris* stands rather than from the centre of stands or around individual plants. Results here show a patchy seed distribution immediately around the maternal plant. Seed deposited in the 0.23 m traps will have fallen fairly directly to the ground from fruit at short heights and/or during lower wind speeds. Several of the high seed densities at 0.23 m could be attributed to particular flowering stems leaning over the seed traps. Seed deposited in the 0.46 m traps are likely to have fallen from stems bent over during gusts of wind (Soons and Bullock, 2008). A large proportion of the seed within an individual fruit can be released at the same time in this way, with seed from the same fruit deposited close together (personal observation). This might be a factor in explaining the maintenance of the pattern of clumped distribution at fine spatial scales (section 2.4.2.3), although this patchy distribution of seed around a single flowering ramet will be masked in larger flowering stands of *L. vulgaris*.

In the unvegetated field a greater proportion of the seed is estimated to be deposited beyond 1 m than in the vegetated environments (Figure 26 & Table 16). The shape of the density and cumulative seed number curves also indicates that a greater proportion of seed is likely to be travelling beyond 1.85 m in the unvegetated field compared with the meadow or hedgerow (Figures 25 & 26). Colonisation rates of new locations depend on the shape of the tail of dispersal curves (Kot et al., 1996). However, it is difficult to extrapolate from this study the likely proportion of seed travelling beyond 1.85 m. Measuring and modelling the tail of dispersal curves is notoriously difficult (Nathan and Muller-Landau, 2000) and using unrealistic dispersal curves in models can have a large impact on estimates of rates of spread of invaders (Kot et al., 1996).

Seed has a longer primary dispersal distance in the field because the absence of vegetation is likely to have resulted in higher wind speeds around the fruit and also means that seed will not be trapped (Cousens and Mortimer, 1995, Bullock and Moy, 2004). This has outweighed any greater wind turbulence and gusts expected in vegetated environments that can be important for releasing seed and creating uplift for longer distance travel (Cousens et al., 2008). *L. vulgaris* seeds are likely to be too heavy for uplift to be an important factor.

However, secondary dispersal mechanisms may also be greater in unvegetated environments. *L. vulgaris* seed was observed being blown across the surface of the field. This was also observed across open ground around Alaskan study populations (section 2.3.1). Seed caught in traps in the field would otherwise be likely to have travelled further, before collecting in a depression or at a barrier (Matlack, 1989). These areas where seed has been concentrated might provide a more appropriate micro-environment for germination and establishment (Matlack, 1989). This is an additional explanation for aggregated patterns. It also suggests that satellite populations of *L. vulgaris* are more likely to establish at distances of tens of metres around existing populations in less vegetated environments, both because of greater numbers of seeds reaching new space and the lower competition likely in these environments.

Rare long distance dispersal events are likely to be caused by animal and human mediated dispersal. *L. vulgaris* seed has been observed to be dispersed by ants (Saner et al., 1995). However, the major cause of dispersal to new locations is probably human mediated dispersal of seeds and root fragments in soil and gravel, and of seeds attached to vehicles (Lonsdale and Lane, 1994) and in clothing (Wichmann et al., 2009). The airflow of passing vehicles is likely to cause the release of seeds and also to move seeds across the ground in the same way as was observed with gusts of wind (von der Lippe et al., 2013).

Establishment of new populations from seed depends on the seed being viable and able to germinate at the site where the seed has settled. The failure of any seeds to germinate from three of the maternal plants in the experimental gardens trial is consistent with variation in provisioning of seed between individuals at a particular time (Clements and Cavers, 1990). The likely delay in germination of the seeds until October suggests that low temperatures, or possibly repeated alternation between high and low temperatures (Lewis, 1954), are needed to break dormancy. The three seeds that germinated in the growth cabinet were black rather than grey and had received the cold treatment, but these rates are too low to determine if this is significant. Germination rates from other *L. vulgaris* germination trials show considerable variation and also conflicting evidence on the importance of cold stratification in breaking dormancy. Necajeva and Probert (2011) found that the highest germination rate was 69.7 % after 20 weeks of cold stratification and that this seed could germinate at lower temperatures than seed treated for only four weeks or kept dry. Lewis (1954) reported that the highest germination rates of 74 % and 88 % from two years were obtained after 89 days cold stratification. Nadeau and King (1991) also found significantly higher rates of germination after cold stratification. However, Necajeva and Ievnish (2008) found near identical rates of 32 - 33 %

germination for seed that received a dry cold treatment, a wet cold treatment or that were sown within a week of collection. Clements and Cavers (1990) also report high germination from seed not receiving a cold treatment, with 56.5 % from fruit with only black seed and 27 % from fruit with grey and black seed. *L. vulgaris* seed may be heterogeneous in dormancy breaking requirements, due to conditions experienced by the maternal plant (Necajeva and Probert, 2011). Certainly there can be considerable variation between years, with 53 % germination after eight weeks of cold stratification one year but only 6 % after the same treatment the following year (Nadeau and King, 1991). The lower germination rate found in this growth cabinet trial compared with most previous studies may be caused by both lower seed viability because of the delay before the trial, and also the shorter photoperiod and the lower and fluctuating temperatures compared with the 14.5 to 16 hours of light at 20 to 30 °C of most of the previous studies (Lewis, 1954, Clements and Cavers, 1990, Nadeau and King, 1991, Necajeva and Ievinsh, 2008). The short cold stratification used here is likely to have been inadequate for good germination at the temperatures used of 5 to 16 °C (Necajeva and Probert, 2011). These results are consistent with Necajeva and Probert's (2011) findings of less than 5 % germination at 10 °C for seed after no or four weeks of cold stratification. Most of the fungal infections (also reported by Clements and Cavers, 1990) occurred towards the end of the trial, so are likely to indicate seed unable to germinate at these temperatures, rather than the infection having prevented germination.

The very low germination rate found in the trial is consistent with the absence of seedling establishment around the dispersal study. This might be expected in the meadow and hedgerow environment with high competition for light, but is surprising in the unvegetated field. It is possible that the field may have been too exposed and wet for seed germination and seedling establishment. The location of UK and Alaskan study populations suggests a preference for well drained sites in warmer microclimates with intermediate levels of disturbance (Table B1). However, seed scattered in the Autumn on both cleared and uncleared marked plots adjacent to the MF population also failed to establish seedlings (personal observation), which is consistent with Egan and Irwin’s (2008) findings. However, seedlings did establish in gravel around *L. vulgaris* plants kept at the Experimental Gardens (personal observation). In the first year of Nadeau and King’s (1991) dispersal study, seedlings established around only three out of 14 stands in a fallow field and there was an emergence of only 0.23 % from pre-sown plots. There was no seedling establishment the following year (Nadeau and King, 1991). It is reported that *L. vulgaris* seed can germinate within weeks of release (Necajeva and Ievinsh, 2008), but this was not observed in these UK or Alaskan study populations.

These low seed germination and establishment rates and the results from the study of ramet connections suggest that sexual reproduction is likely to play a minor role in maintaining and expanding existing populations. Most of the BP ramets, and some of the IG3 ramets, were growing from what appeared to be sections of the previous year’s root systems that had partly died back. However, the generality of this root fragmentation and predominance of vegetative reproduction is unknown and might reflect the unusually high sand content and shading of the BP population. The mean distance between connected *L. vulgaris* ramets is relatively long compared with other clonal plants (Benot et al., 2013), resulting in an *L. vulgaris* genet being likely to overlap in space with other *L. vulgaris* genets and species (Benot et al., 2013). A fire in September 2009 that killed most of the above ground parts of ramets in the LP populations resulted in ramet re-growth across the whole population within four weeks (personal observation). The spatial locations of ramets in UK populations are similar although not exactly the same between 2008, 2009 (Figures B1 - B21) and spring 2010 (personal observation), although the same distribution being produced from mainly sexual reproduction cannot be ruled out. In addition to producing shoots on lateral roots, the germination and ramet growth studies show that both seedlings and ramets grown from pieces of root can produce multiple shoots from the same location. Overall this evidence suggests that the clumped patterns seen in both UK and Alaskan populations are a result of vegetative reproduction, rather than restricted seed dispersal.

The high genetic diversity within large Rocky Mountain populations found by Ward and colleagues (2009b), with ramets only twice found to be from the same genet, may reflect the founding of populations by a number of genetically diverse seed (or possibly root fragments), with these diverse genets then maintained by vegetative reproduction. Their distances between samples (varying with population size) may have been larger than the scale of individual genets and was also likely to bias towards ramets on the edge of clumps within the population (Ward et al., 2009b). The relative contribution of sexual and vegetative reproduction to the following year's cohort may vary between populations and years depending on pollinator availability, flower and seed predation, disturbance, the weather and season length (Arnold, 1982, Staniforth and Scott, 1991).

Seed dispersal is likely to be of more importance in founding new *L. vulgaris* populations, although dispersal of root fragments may also play a role. It is unclear whether the new population IG3 was established from seed, root fragments or both after spoil was deposited from railway works. As also found by Nadeau and colleagues (1992), new ramets can grow from short lengths of UK *L. vulgaris* roots, although the poor survival of these ramets suggests that this may not allow sufficient early resource provision to adequately compete when surrounded by other vegetation. Another possibility for the establishment of new populations is from a seed bank, as low germination rates can indicate a risk spreading strategy by waiting for improved germination conditions (Venable and Brown, 1988). Two burial studies reported that *L. vulgaris* seeds could remain viable after five years, but fifteen field studies suggest that in practice *L. vulgaris* has only a transient seed bank (reviewed in Thompson et al., 1997). Egan and Irwin (2008) reported four *L. vulgaris* seedlings emerging in plots from which all vegetation had been cleared before seed release. However, as *L. vulgaris* seed can be blown across unvegetated ground, it is possible that these seedlings originated from plants that were 3 m away, rather than from a seed bank. This absent or at best limited seed bank suggests that the establishment of new *L. vulgaris* populations relies on the dispersal of viable seed or root fragments into an area where there is a resource window (Davis et al., 2000, Mata et al., 2013), usually due to recent disturbance. Vegetative reproduction may then be important in establishing rapidly before the niche is occupied by competitors. The younger ramets of clonal plants, or the ramets in less favourable resource patches, may be supported by other parts of the clone (Pennings and Callaway, 2000). However, Hellström and colleagues (2006) found resource competition between sibling *L. vulgaris* ramets, with damaged ramets not supported by the rest of the clone.

There are some differences between the UK and Alaskan populations that might result in differences in medium to long distance dispersal of both seed and roots. This could partly explain the greater extent and number of populations in the Alaskan study area (sections 2.4.2.2 and 2.4.2.4). Seed dispersal distances might be expected to be longer in the UK because ramets were taller. Seed released from taller ramets will have a longer falling time (Thomson et al., 2011), and if taller than surrounding vegetation will be likely to be exposed to higher wind speeds and less likely to be intercepted by vegetation (Soons et al., 2004). However, the surrounding vegetation in the UK populations is also correspondingly taller, with more of the UK populations growing along or near tall vegetation or fencing that would reduce wind speeds (Table B1), although it could increase turbulence and uplift. A higher proportion of the area of the Alaskan compared with the UK populations has less than 5 % vegetation cover (Figure 6), which could increase seed dispersal distances. The greater number of seed produced by Alaskan ramets (section 3.4.4) means that long distance dispersal events will happen more frequently, so the establishment of new populations is more likely (Lockwood et al., 2005). An important contributing factor is that a greater number of the Alaskan populations are on or near roads. This allows both dispersal on and in the airflow of vehicles (von der Lippe et al., 2013), increased wind dispersal due to lower vegetation at the road edge and increased chance of establishment due to greater disturbance. Records of some new *L. vulgaris* populations in Alaska note that they occur where substrate has been moved and added on and around roads and railways (AKEPIC, 2013). Roads in the Haines area are mainly gravel and the roadsides are periodically disturbed by ditching, grass cutting, snow clearance and a programme of road repairs since 2007 (personal observation, State of Alaska Office of Management and Budget, 2011). This is likely to make the dispersal of seeds and roots to new locations more likely and also creates improved conditions for establishment.

Control of *L. vulgaris* could target individuals and populations in areas with low or little surrounding vegetation, as in these areas seed can both disperse further and establishment is more likely (Marchetto et al., 2010), although there is also the risk of creating further disturbance and a ‘weed shaped hole’ for re-invasion (Buckley et al., 2007). Populations could also be prioritised for control where there is a high potential for human mediated dispersal and/or positioned where there is greater risk of dispersal into conservation priority areas (Moody and Mack, 1988). Control options for *L. vulgaris* may differ depending on whether the priority is to reduce spread or to reduce local population density (Shea et al., 2010). Biological control may only be helpful in reducing spread if it reduces seed production to a level where it limits the number of seed reaching appropriate establishment sites. The relative importance of disturbance and dispersal opportunities for the recruitment of new populations compared with seed production is not yet known.

Chapter 5. Biological Flora of the British Isles: *Linaria vulgaris* Miller (Plantaginaceae).

5.1 ABSTRACT

Linaria vulgaris is a perennial herb native to the British Isles. The species native range is Europe and West Asia and it is invasive in North America and naturalised in several other regions. *L. vulgaris* typically occupies disturbed, open and well drained sites, but it can tolerate some shading and a wide range of soil types and pH. It has a plastic growth form with a wide variation in height, branching and flowering between populations. Reproduction is both by self-incompatible seed production and vegetative shooting from the stem to root transition zone and from lateral roots. Flowers contain nectar in a long spur and are usually open between July and September. Legitimate pollination is primarily by long and intermediate tongued Bumblebee species such as *Bombus hortorum* and *B. pascuorum*. High rates of nectar robbing also occur, but this does not affect seed production. There is a large variation in seed production between fruit, individuals and populations. Mature fruit often contain incompletely filled grey seed instead of, or in addition to, the more viable black seed. Over half of sampled fruit were affected by *Rhinusa antirrhini* seed predation, which reduced the seed number. The disc shaped seed are released passively from September, and amongst vegetation most seed falls within 1 m of the maternal plant. Seed has a heterogeneous response to cold stratification, with a proportion of seed able to germinate immediately on release, but germination rates in the

remainder are improved by cold stratification at 5 °C for 12 or more weeks. Most field studies report only a transient seed bank. Established populations may be maintained largely by vegetative reproduction, which occurs from buds on lateral roots a few cm below the soil surface. Shooting can occur from root fragments as small as 1 cm. *L. vulgaris* supports a number of specialist insect herbivores, many of which are used, or are being evaluated, for biological control in North America.

5.2 DESCRIPTION

The genus *Linaria* (tribe Antirrhineae) contains over 150 Northern hemisphere herbaceous annuals and perennials (Sutton, 1988). The genus has a native range covering Europe, Asia and North Africa, with the highest diversity of species being centred on the Mediterranean (De-Yuan, 1983). *Linaria* has been moved from the Scrophulariaceae family into Plantaginaceae, following molecular analysis showing that Scrophulariaceae *sensu lato* was polyphyletic (Olmstead and Reeves, 1995, Albach et al., 2005). *L. vulgaris* is a perennial herb with an upright (occasionally trailing) and often branched stem. The sessile leaves have entire margins, are linear to narrowly lanceolate and 11 - 75 mm (median = 32 mm, n = 80) in length. They are arranged alternately, but often appear whorled. The zygomorphic cream to yellow flowers have closed lips and nectar in a 12 - 16 mm (median = 13 mm, n= 50) length spur (Figure 34). The upper lip is two lobed and the lower lip three lobed with a yellow to orange palate. The 3 - 11 mm (median = 7 mm, n = 373) length ovoid seed capsules (hereafter called fruit) are two celled. The black to dark-brown seed are disc-shaped with a slightly notched wing and are 1.0 – 2.2 mm diameter (mean = 1.64 mm ± 0.0293 S. E., n = 75) (Figure 35).

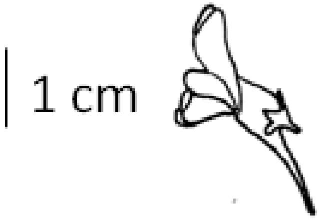

Figure 34. Open *L. vulgaris* flower.

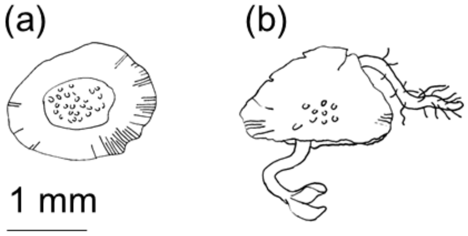

Figure 35. a) *L. vulgaris* seed.
b) Two day old *L. vulgaris* seedling.

5.3 GEOGRAPHICAL AND ALTITUDINAL DISTRIBUTION

In the British Isles *L. vulgaris* is present in 70 % (1967) of 10 km grid squares in Britain, with fewer records in northern Scotland, but it is recorded in only 8.22 % (81) of Irish 10 km squares. The British altitude range is 0 – 360 m (near Alston, Cumberland), but it is found up to about 1,600 m in the Alps (Hultén, 1970). Grime and colleagues (1988) suggest that *L. vulgaris* is probably increasing in the British Isles due to a capacity to exploit artificial habitats. The native range of *L. vulgaris* is across Europe and West Asia (Hultén, 1970). *L. vulgaris* subspecies *chinensis* occurs in China and Korea (Wu and Raven, 1998), and the broad leaved glandless subspecies *acutiloba* occurs in eastern Asia, including China and Mongolia (Hultén, 1970, Wu and

Raven, 1998). As a result of extensive naturalisation in North America, *L. vulgaris* now has a circumpolar boreo-temperate distribution.

L. vulgaris is naturalised in all mainland US states and Canadian provinces and territories except Nunavut (Saner et al., 1995, USDA, 2010, Brouillet et al., 2013). In North America it currently occurs to over 3000 m and to 67.25° N (Pauchard et al., 2003, AKEPIC, 2013). It is also established in Mexico (CONABIO, 2008) and has been recorded in Chile (Reiche, 1911), Jamaica (Hultén, 1970) and Guatemala (Veblen, 1975). *L. vulgaris* is naturalised in New Zealand (Allan Herbarium, 2000) and in Australia, where it is recognised as a weed of the natural environment and agriculture (Randall, 2007). It is naturalised in South Africa (Hultén, 1970, AGIS, 2007) and Swaziland (Hultén, 1970).

5.4 HABITAT

L. vulgaris occurs on dry to slightly moist soils (Biological Records Centre, 2013). The absence from parts of Scotland and Ireland suggests that its distribution is limited by wet conditions. *L. vulgaris* has a preference for open sites, but tolerates partial shading. It is found on a full range of slopes and aspects, although in the Sheffield area it was more abundant on South rather than North facing slopes (Grime et al., 1988). A study of microtopography in a Wisconsin field with a gradient range of 1.5 m showed that *L. vulgaris* was at highest density at intermediate topography, rather than on ridges or in depressions (Zedler and Zedler, 1969).

L. vulgaris is commonly found on loose, well-drained substrates, such as railway ballast and spoil heaps (Grime et al., 1988), but it will occur on a range of soil types and has a wide pH tolerance. Soil samples from eight UK populations had a pH range from 4.40 to 8.03 and organic matter content, as measured by a loss on ignition, was between 3 and 25 % (Table C1). Soil textures were sand, sandy loam, loam and clay loam (Table C1). Grime and colleagues (1988) note occasional occurrences on more acidic soils down to pH 3.5. *L. vulgaris* is found on sites in Europe and North America with high heavy metal concentrations (Long, 1974, Shallari et al., 1998), with some evidence of population differentiation for copper tolerance (Long, 1974).

5.5 COMMUNITIES

L. vulgaris has a competitive-ruderal strategy (Grime et al., 1988). It generally occurs in ruderal early successional communities and usually requires disturbance to establish. Grime and colleagues (1988) note that *L. vulgaris* is restricted to sites with low productivity and moderate disturbance where the growth of more robust perennials is limited. Following disturbance, a new UK population in an area with high propagule pressure established rapidly over the whole area of the disturbance (Figure B12). Other populations declined in abundance or died out over years as grasses became taller and more abundant or the canopy closed (personal observation).

Railway embankments, road verges and brownfield sites are common habitats and *L. vulgaris* has also been found growing on walls (Grime et al., 1988). *L. vulgaris* is a characteristic species of the UK Priority Habitat ‘Open

Mosaic Habitat on Previously Developed Land' (BRIG, 2008). It is an occasional member of the *Papaver rhoeas – Silene noctiflora* (OV16) and *Reseda lutea – Polygonum aviculare* (OV17) weed communities that are characteristic amongst arable crops in south east England (Rodwell et al., 2000). It is an infrequent member of the *Festuca rubra* (SD6e) and *Poa pratensis* (SD6f) sub-communities of *Ammophila arenaria* mobile dunes (Rodwell et al., 2000). *L. vulgaris* occurs infrequently in the *Potentilla reptans* - *Tragopogon pratensis* sub-community of *Avenula pubescens* calcicolous grassland (CG6b) (Rodwell et al., 1992). *L. vulgaris* has also been observed in mesotrophic grasslands, hedgerows and field margins (Table B1). *L. vulgaris* has a clumped distribution due to vegetative reproduction, although newly established populations typically have a lower fine scale density and are less aggregated (Populations IG3 and NK, Figures B12 & B26). Often there are several distinct high density patches within metres or tens of metres that are related to historical disturbances and/or microclimates (Figures B2, B3, B16, B17, B24 & B28).

5.6 RESPONSES TO THE ENVIRONMENT

Where there is physical support from surrounding vegetation or fencing, partial shading results in increased stem height and decreased branching (personal observation). Where there is no physical support or there is full shading ramets are usually stunted and are less likely to flower (personal observation). Populations where the canopy cover increases over years typically exhibit a reduction in population size or die out (personal observation). This also occurs where the height and density of grasses increase (personal observation). Apical grazing, herbivory or cutting usually increases branching. *L. vulgaris* wilts in very strong sunlight and sometimes the upper portion of the stem dies (personal observation). *L. vulgaris* is relatively tolerant of periods of drought during the summer (personal observation). A fast moving grass fire at a UK population (LP1) in September killed most of the above ground stems, but some of these dead stems remained upright with some intact fruit and seed. Shooting from roots occurred rapidly and before re-growth of other species. After four weeks there were twice as many individual ramets as before the fire (356 before, 700 after) and these new ramets were up to 20 cm in height with three of the ramets flowering.

5.7 STRUCTURE AND PHYSIOLOGY

5.7.1 Morphology

The growth form varies with environmental conditions; upright forms dominate, but trailing forms are observed amongst dense vegetation and where vegetation is frequently cut (personal observation). The typical height range of mature stems in the UK has been given as 30 - 80 cm (Clapham et al., 1987), although the mean height of all ramets from 12 UK populations was 24.5 cm ± 0.458 S. E. (median = 16 cm, n = 3152). Stems were found to 1.8 m in partly shaded environments where there was physical support (Figure 14). The base of the stem of taller ramets and ramets from older clones becomes woody. The presence and degree of branching from the base or upper stem is variable and usually increases in response to cutting or herbivory (personal observation). 27.38 % of 3214 UK ramets sampled in 2009 were branched and 17.39 % of the UK ramets flowered, with considerable variation amongst populations in the proportion of ramets that flower (Table D4). The number of inflorescences on 548 flowering UK ramets sampled in autumn 2009 varied between one and 84 (mean = 4.68 ± 0.28 S. E., median = 2, n = 548). The number of flower buds, flowers and fruit on each flowering ramet in the UK varied between one and 1136 (mean = 15.20 ± 2.44 S. E., median = 9, n= 486). The mean number of fruits on 210 UK ramets that had mostly completed flowering was 8.38 ± 0.618 S. E. (median = 6) (section 3.4.3). Flowers have five sepals and five stamens, but one is a much reduced vestigial stamen of < 0.5 mm. One pair of the stamens are approximately 7 mm in length and the other pair are approximately 9 mm in length. The style length is approximately 8 mm and ovary length is approximately 2 mm. Abnormal peloric flowers are relatively common in both native and invasive ranges (Saner et al., 1995, Cubas et al., 1999, personal observation). There are occasional glandular hairs on the upper stem and abaxial leaf surface. There are no stomata on the adaxial leaf surface and there are 89.45 stomata / mm^2 on the abaxial surface (mean, range 54 - 145, n = 20).

The stem to root transition zone is usually 1 - 5 cm below the soil surface and new shoots can initiate from this zone (personal observation) (Figure 36a). In observations on English and Canadian *L. vulgaris*, Charlton (1966, 1967) categorised roots as either short annual roots that do not produce new shoots, or long perennial roots that produce new shoots from buds on the roots. These long roots initially grow horizontally up to 45 cm and then change to vertical growth, sometimes deeper than 1 m (Charlton, 1966). Buds are not formed from the long root tissue itself, but from the base of shorter lateral roots growing from the long root (Charlton, 1966). This usually occurs where the long root begins to change direction to vertical growth and sometimes from the horizontal part of the long root (Charlton, 1966) (Figure 36b). New long roots are usually initiated in the horizontal to vertical growth transition zone or near existing shoots (Charlton, 1967). All roots have the potential to become long roots, but are thought to be inhibited in development by larger long roots (Charlton, 1967). During the peak flowering period, Abrahamson (1979) found that 9 % of total biomass was allocated to flowers, 33 % to leaves, 43 % to the stem and 15 % to below ground parts. Biomass allocation became highly variable later in the season (Abrahamson, 1979).

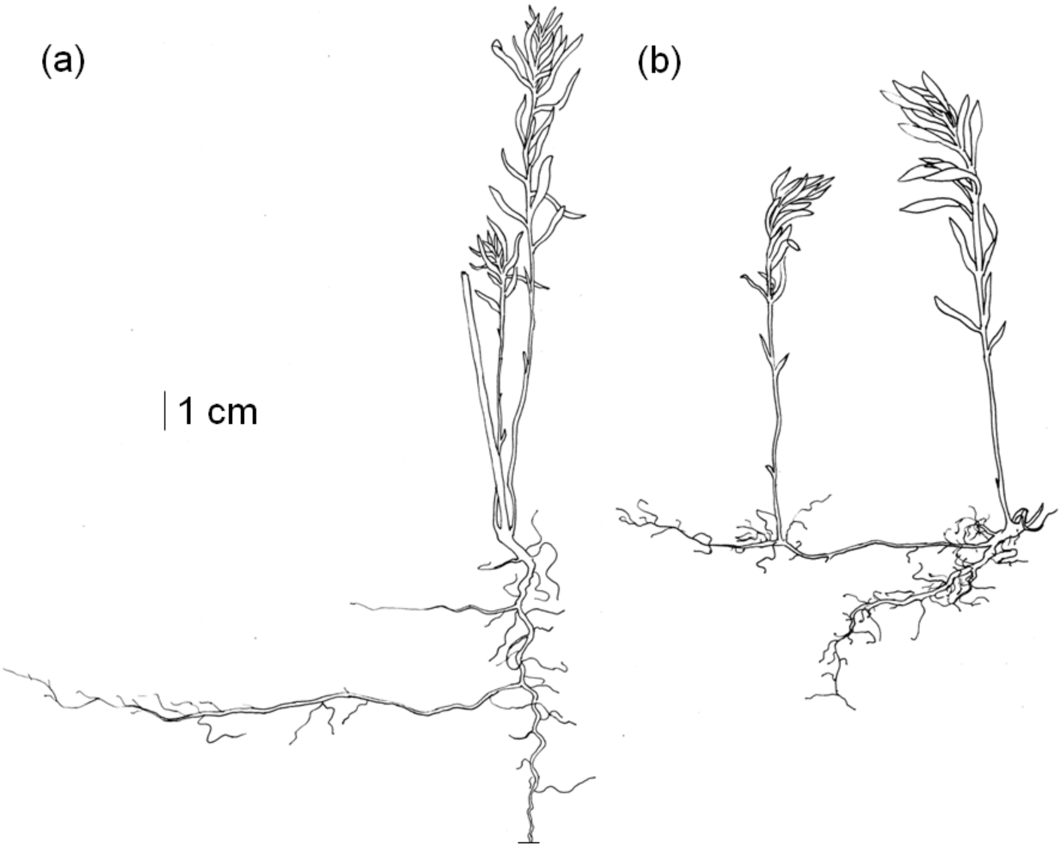

Figure 36. a) *L. vulgaris* ramet in April shooting from the base of a dead stem, with horizontal lateral roots. b) *L. vulgaris* ramets in April shooting from lateral roots.

5.7.2 Mychorriza

L. vulgaris has an association with vesicular-arbuscular mycorrhiza (Pendleton and Smith, 1983).

5.7.3 Perennation: reproduction

L. vulgaris is a hemicryptophyte, as vegetative buds are usually within 5 cm of the soil surface (personal observation). The main tap root overwinters, but smaller roots die back over winter, and in two UK populations most of the previous year's lateral roots connecting ramets had decayed by spring (section 4.4.4). Roots and vegetative buds collected from Northern Japan survived to -7 °C without injury and when they were gradually cold hardened they survived to -15 °C without injury (Noshiro and Sakai, 1979). Vegetative reproduction can start within three weeks of germination (Nadeau et al., 1992, personal observation.). Shooting occurs from buds in the axils of scale leaves on the underground or ground level portion of the stem and from buds on long lateral roots (Charlton, 1966). Groups of one to four buds usually occur on the long root where it changes from horizontal to vertical growth and also on the horizontal part of the long root (Charlton, 1966). Root buds form acropetally along the root (Charlton, 1966). The mean spacing of ramets along intact lateral roots (not including ramets initiating from the stem) in sections of two UK populations was 9.24 cm (range 1 - 30 cm, n = 28 pairs) (section 4.4.4). On fallow land this pattern of shoot initiation can result in the formation of clumps of shoots in a ring around the original ramet (Nadeau et al., 1991), although unlike for *L. dalmatica* the original ramet does not usually die back to leave distinct rings (Lehnhoff, 2008). Shooting is possible from root fragments as short as 1 cm (Nadeau et al., 1991) and is common from fragments of 10 cm (section 4.4.3). Evidence from excavating sections of UK populations (section 4.4.4), and from the lack of seedling establishment within some North American populations (Egan and Irwin, 2008), suggests that established populations may be largely maintained by vegetative reproduction.

5.7.4 Chromosomes

L. vulgaris is diploid with 12 chromosomes (Darlington and Wylie, 1955, Dempsey et al., 1994, Montgomery et al., 1997). Tetraploids produced in the laboratory had a number of differences such as increased flower size and a longer flowering period, but had reduced pollen fertility and reduced fruit and seed set (Tandon and Bali, 1959).

5.7.5 Physiological data

Sibling ramets of *L. vulgaris* are physiologically integrated, at least initially, as 5.7 % of a ^{13}C tracer moved to a sibling ramet (Hellström et al., 2006). However, rather than providing support for damaged ramets, a ramet could compensate better for damage if its sibling ramets were also damaged, indicating within-clone competition for resources (Hellström et al., 2006). There was net ^{13}C flow from ramets where the apex had been removed to undamaged ramets, suggesting that resources are not directed towards a single damaged ramet if there are more viable undamaged ramets within the genet (Hellström et al., 2006).

Bakshi and Coupland (1960) found that very little starch accumulated in the root system at any time. Intranuclear crystalloid inclusions forming layers of tubules in close association with the nucleoli have been found in cells from the leaf, style and ovary of *L. vulgaris* (Ciampolini et al., 1980, Dudek and Hesse, 1980, Bigazzi, 1989). These may have a role in the synthesis, storage and breakdown of storage proteins (Cresti et al., 1983). In root segments in the laboratory, light increased the likelihood of shoot bud initiation and the number of buds per lateral root base, but there was no effect of hormones or changes in carbohydrate level (Charlton, 1965).

5.7.6 Biochemical data

Iridoid glycosides act as deterrants and toxins for generalist herbivores, but attract and stimulate feeding for some specialist herbivores (Bowers, 1991). Antirrhinoside and its derivatives are the major iridoid glycosides (defensive secondary plant metabolites) found in all plant tissues of *L. vulgaris* (Ilieva et al., 1992, Nikolova-Damyanova et al., 1994, Beninger et al., 2009). An antirrhinoside content of 1.05 % ± 0.05 S. D, linarioside of 1.50 % ± 0.03 S. D., 5-O-glucosylantirrhinoside of 0.9 % ± 0.1 and 5-O-allosylantirrhinoside content of 0.50 % ± 0.06 S.D. is reported for above ground tissues of Bulgarian *L. vulgaris* (Nikolova-Damyanova et al., 1994). However, the antirrhinoside content of UK sourced *L. vulgaris* during the flowering period was 9.69 % ± 1.06 S. E. in flowers, 16.97 % ± 0.90 S. E. in buds and 4.92 % ± 0.40 S. E. in roots (Beninger et al., 2009). The distribution of antirrhinoside is consistent with the reproductive strategy, with high concentrations in roots during the period when the plant is only reproducing vegetatively and lower root concentrations during budding and flowering (Beninger et al., 2009). Concentrations in flowers were lower relative to the non-vegetatively reproducing *Antirrhinum majus* (Beninger et al., 2009). When feeding on *L. dalmatica,* the foliar feeding *Calophasia lunula* Hufnagel (Noctuidae) could sequester antirrhinoside (Jamieson and Bowers, 2010).

Flavonoids determine flower colours and may also act as feeding deterrants (Harborne, 1991). The yellow colour of *L. vulgaris* flowers are determined by aurones modified by the presence of several other flavonoids and cinnamic acids (Valdés, 1970). The flavonoid glycoside linarin (acacetin-7-O-beta-D-rutinoside) is present in the flowers of *L. vulgaris* and other species, but not found in the leaves (Valdés, 1970). *L. vulgaris* also contains glycoside 4-O-acetylpectolinarin (also known as linariin) (Smirnova et al., 1974, Nikolova-Damyanova et al., 1994, Scherbakova et al., 2011), which is reported to have growth-regulating activity in *Linaria* (Sergiev et al., 2004). Above ground *L. vulgaris* parts sampled from the Urals and analysed with spectrophotometry had a mean acetylpectolinarin content of 13.2 %, with 18.8 % in the flowers (Scherbakova et al., 2011). However, using thin layer chromatography to examine Bulgarian *L. vulgaris*, Nikolova-Damyanova and colleagues (1994) reported an acetylpectolinarin content of only 1.9 % ± 0.2 S. D.

Linaria vulgaris also contains tricylic quinazoline alkaloids, including vasicine and choline (Harkiss, 1972, Hua et al., 2002). There is uncertainty about the toxicity of *L. vulgaris* to grazing animals, but as most animals will not be primarily feeding on *L. vulgaris* exposure is thought to be relatively low (review and risk assessment in Sing and Peterson, 2011). Both iridoid and flavonoid glyclosides have been used in chemotaxonomic studies of *Linaria* (Valdés, 1970).

5.8 PHENOLOGY

In the British Isles, seedling and ramet shoots emerge March to April and flowering occurs from late June to September, although new buds and flowers have been observed into early November. Seedlings can flower in the first year. Insect herbivores can delay the flowering period (McClay, 1992, Saner and Müller-Schärer, 1994). For 20 infloresences studied in New York, flowers that opened on the 1st day of flowering for a particular inflorescence had a mean lifespan of five days, while flowers opening on the 8th day of an inflorescence flowering had a mean lifespan of 2.5 days (Arnold, 1982). Flowers mature more or less acropetally and fruit mature and release seed from late August to early November (personal observation). There is a large variation in the flowering and fruiting phenology between populations and between individual ramets within populations (Saner et al., 1995, personal observation). Stems die back over winter, with some woody stems remaining erect into the following year (personal observation). Bakshi and Coupland (1960) report a life span for individual roots of up to four years.

5.9 FLORAL AND SEED CHARACTERS

5.9.1 Floral biology

L. vulgaris is an obligate outcrosser due to a single locus gametophytic self-incompatibility system (Docherty, 1982). Legitimate pollination visits, where pollen is brushed on the dorsal side of the pollinator as it probes for nectar, were observed in England from the long tongued *Bombus hortorum* L.

(Apidae) and intermediate tongued *B. pascuorum* Scopoli (Stout et al., 2000). Visits are also reported in Italy from the butterflies *Pieris rapae* L. (Pieridae) and *Colias crocea* Geoffroy (Pieridae) (Nepi et al., 2003). In North America *L. vulgaris* is also pollinated to a lesser extent by small solitary bees and the rufous hummingbird *Selasphorus rufus* Gmelin (Trochilidae) (Burkle et al., 2007, personal observation). On average *Bombus* spp. visited 20 % of the open flowers on each *L. vulgaris* plant (Stout et al., 1998). Unexpectedly, given the complexity of *L. vulgaris* flowers, *Bombus* spp. displayed low floral constancy, with only 75 % of the visits to *L. vulgaris* flowers being followed by a visit to a conspecific flower (Stout et al., 1998).

Nectar is secreted from the nectary below the ovary and collects in the spur (Nepi et al., 2003). Nectar quantity varies considerably between flowers (Stout et al., 2000) and populations, with reported means of 1.0 ± 0.08 µl (Arnold, 1982) and ranges of 2-3 µl and 5-8 µl (Nepi et al., 2003). Arnold (1982) calculated a rate of nectar production at midday of 0.09 ± 0.02 µl per hour, and that a flower drained of nectar could refill the spur in 11 hours. The main sugar is sucrose with small quantities of glucose, fructose and raffinose (Arnold, 1982, Nepi et al., 2003). *L. vulgaris* can actively reabsorb sucrose through spur cells (Nepi et al., 2003). This may be in order to recover energy at the end of the flowering period or to maintain the same concentration of sugar when evaporation occurs (Nepi et al., 2003). There is some evidence for a positive effect of nectar volume on seed set (Nepi et al., 2003).

Primary and secondary nectar robbing, by short tongued *Bombus* species and also the intermediate tongued *B. pascuorum*, was frequent in studies from both native and invasive ranges, but had little impact on fecundity (Stout et al., 2000, Newman and Thomson, 2005a, Burkle et al., 2007). In a study in Southern England, 96 % of open *L. vulgaris* flowers had holes in the corolla and 54 % of closed flowers had also been robbed (Stout et al., 2000). Robbed flowers were more frequently empty of nectar (Stout et al., 2000). If nectar robbers also collect pollen, then they may perform a pollinating role (Stout et al., 2000). In North America, ants are attracted to robbed flowers and may protect against flower and seed herbivory from the beetle *Brachypterolus pulicarius* L. (Kateridae) and weevil *Rhinusa antirrhini* Paykull (Curculionidae) (Newman and Thomson, 2005b). Rather than making holes in the spur, *B. pascuorum* was also observed in Europe visiting closed flowers and probing for nectar between the closed petals from the side of the corolla (Nepi et al., 2003).

5.9.2 Hybrids

Crosses of *L. vulgaris* with *L. repens* (L.) Miller form the fertile hybrid *L.* x *sepium* Allman, which occurs in Europe and North America (Olsson, 1974, Saner et al., 1995, Preston et al., 2002). Hybrids are also formed with the invasive *L. dalmatica* in North America (Ward et al., 2009a). There is also evidence of introgressive hybridisation with other *Linaria* species in the native range (Jancko, 1964).

5.9.3 Seed production and dispersal

L. vulgaris typically produces two distinct seed types: in addition to the black to dark brown seed, grey (also light brown or pale yellow) colour seed also occur in mature fruit. These ‘grey’ seeds are incompletely filled and thought to be caused by a lack of resources (Clements and Cavers, 1990) and can be a result of herbivore feeding elsewhere on the plant (Saner and Müller-Schärer, 1994). Grey seed are significantly lighter than black seed (Wilcox rank sum test = 4464, $p < 0.001$). Black seed weigh 0.012 – 0.28 mg (mean = 0.13 mg ± 0.00658 S. E., n = 75) and grey seed weigh 0.016 – 0.20 mg (mean = 0.075 mg ± 0.00379 S. E., n = 75). Fruit may contain only one seed type or a mixture. 47 (27.98 %) of 168 mature fruit sampled from ten UK populations contained grey seed, including 13 fruit with both black and grey seed. The mean black seed production per mature fruit was 7.71 ± 1.54 S. E. (0 – 131, n = 168), with half of the fruit without black seed (Table 13). 52 (30.95 %) of the sampled fruit contained neither black nor grey seed (Table 13). 90 (53.57 %) of sampled fruit contained the seed feeding weevil *R. antirrhini* and these had a mean black seed number of 3.22 ± 0.64 S. E. (0 – 31) compared with 12.50 ± 3.14 S. E. (0 – 131, n = 78) black seed for unpredated fruit. *R. antirrhini* was not the only cause of fruit with no seed, because 22 (13.09 %) of these fruit did not contain *R. antirrhini*. *R. antirrhini* was found in fruit from eight out of the ten populations, with the two populations where it was not recorded having had only one or two fruit collected (Table D8).

Seed dehisce passively from cracks that occur at the apex when the fruit has matured from a green/purple colour to light brown. Seed is usually released from fruit as stems are blown in the wind, but occasionally whole fruit fall and release seed on the ground (personal observation). When surrounded by vegetation, most seed is deposited within 1 m of the maternal plant, but in unvegetated areas seed travels further and can be blown across the ground and collect in depressions and at barriers (section 4.4.1).

5.9.4 Viability of seeds

Canadian studies report variation in germination rates (35 – 65 %) and viability (37 – 76 %) between populations (Clements and Cavers, 1990), higher germination rates for later collected seed within populations (Clements and Cavers, 1990) and also considerable variation in germination rates between years (Nadeau and King, 1991). Tetrazolium chloride tests found only 40 – 51 % viability soon after collection for seed from a population in Alberta (Nadeau and King, 1991), but there was 95 % viability for seed from the Baltic coast after 20 weeks storage at -20 °C (Necajeva and Probert, 2011). A study where seed was buried and then subsequently disturbed reported that seed could remain viable for more than five years (Roberts, 1986). However, fifteen field studies suggest that in practice *L. vulgaris* has only a transient seed bank persisting for less than one year (reviewed in Thompson et al., 1997). Thompson and colleagues (1997) argue that a single record from a burial study showing a persistent seed bank should not be accepted if it is inconsistent with field studies. *L. vulgaris* seed is heterogeneous in response to cold stratification, with some seed able to germinate immediately after release (Nadeau and King, 1991, Necajeva and Ievinsh, 2008, Necajeva and Probert, 2011). Most studies report that wet stratification at 5 °C increases germination rates (Lewis, 1954, Ellis et al., 1985, Nadeau and King, 1991, Necajeva and Probert, 2011). Necajeva and Probert (2011) found the highest germination rates after 20 weeks of stratification, while Nadeau and King (1991) found no improvement in germination beyond eight weeks of stratification. The base germination temperature (below which germination is zero) of approximately 5 °C after no or only four weeks of wet stratification was reduced to approximately 1 °C after 12 or 20 weeks of wet stratification (Necajeva and Probert, 2011). The time to 50 % germination for Baltic seed was five to 10 days for temperatures of 10 to 35 °C, but increased to 25 days at 5 °C (Necajeva and Probert, 2011). Seed that had not germinated after stratification on wet agar at 5 °C for 20 weeks had a lower viability of approximately 85 % compared with ungerminated seed that had been stored dry at -20 °C (Necajeva and Probert, 2011). In a previous study, Necajeva and Ievinsh (2008) found no difference in germination rates (32 - 33 %) a week after collection, after cold dry storage or after cold wet storage. There was also no significant effect of Giberellic acid treatment (43 and 59 %) (Necajeva and Ievinsh, 2008). Alternating temperatures and repeated wetting and drying can also help to break dormancy (Lewis, 1954). Seed is unable to germinate in the dark (Lewis, 1954) and is reported to not produce seedlings when buried greater than 2 cm below the soil surface (Nadeau and King, 1991). Germination is significantly inhibited by sodium chloride concentrations of 50 mM (6 % germination rate) and seed does not recover after rinsing with distilled water (Necajeva and Ievinsh, 2008). ‘Grey’ seed are incompletely filled and less viable with < 10 % germination reported (Clements and Cavers, 1990).

5.9.5 Seedling morphology

The cotyledons of seedlings are initially similar to the first leaves of ramets (Figure 37a), but then become increasingly spade shaped during development (Figure 37b & c). In a North American trial, in the first few weeks of growth seedlings had higher shoot biomass accumulation compared with ramets grown from root fragments, but the roots of the ramets were ten times as long as those of the seedlings (Nadeau et al., 1992). However, the number of shoots produced were similar between ramets and seedlings (Nadeau et al., 1992).

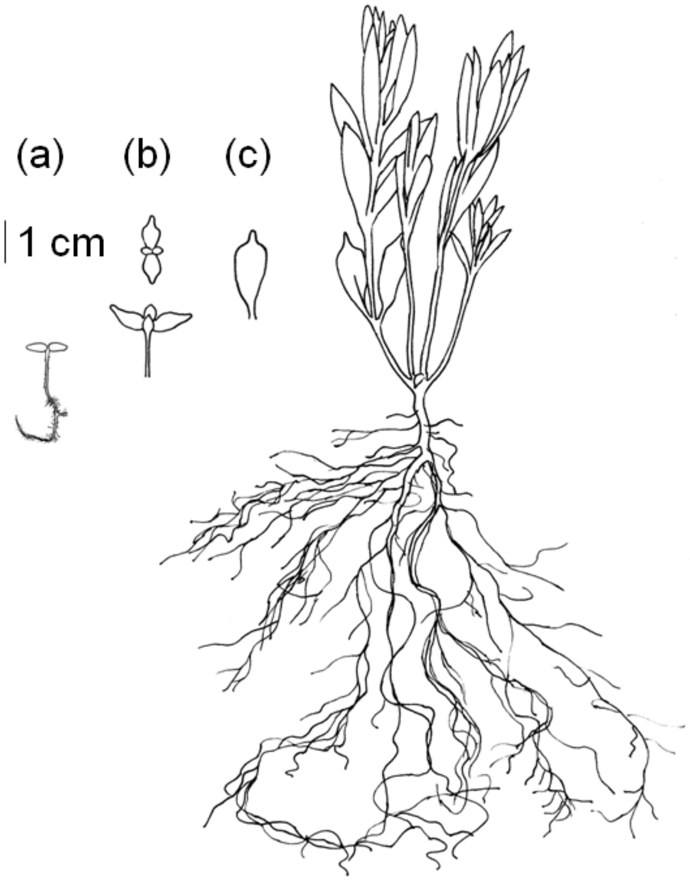

Figure 37. a) One week old *L. vulgaris* seedling b) Two week old *L. vulgaris* seedling cotyledons c) Six week old *L. vulgaris* cotyledon and seedling.

5.10 HERBIVORY AND DISEASE

5.10.1 Animal feeders

Specialist insect herbivores known to be present in Great Britain include: the foliage feeding moth *C. lunula* (McClay and Hughes, 1995), the stem mining weevil *Mecinus janthinus* Germar (Curculionidae) (Van Hezewijk et al., 2010, Toševski et al., 2011a), the root mining weevil *Rhinusa linariae* Panzer (Curculionidae) (Kock, 1966), the flower feeding beetle *B. pulicarius* (Kock, 1966, McClay, 1992, MacKinnon et al., 2005), the flower and fruit feeding moth *Eupithecia linariata* (Geometridae) Denis & Schiffermüller (Kock, 1966) and the flower and seed feeding weevil *R. antirrhini* (Kock, 1966, Sing et al., 2005, Caldara et al., 2010, Hernández-Vera et al., 2010). In North America different biotypes of *R. antirrhini* have been discovered that preferentially feed on *L. vulgaris* or *L. dalmatica* (Hernández-Vera et al., 2010).

Specialist insect herbivores present in Europe, but not recorded in Britain, include: the stem galling weevil *R. pilosa* Gyllenhal (Kock, 1966, Barnewall, 2011), the seed feeding weevil *R. neta* Germar (Caldara et al., 2010, Hernández-Vera, 2011) and the root mining moths *Eteobalea serratella* Treitschke (Cosmopterigidae) and *E. intermediella* Riedl (Saner, 1991, Saner and Müller-Schärer, 1994).

In the UK, *L. vulgaris* leaves and non-woody parts of the stem were observed to be grazed by rabbits during periods of drought, but usually surrounding species were more heavily grazed (personal observation). Cattle, sheep, goats, deer and rodents are known to graze on *L. vulgaris* in North America (Sing and Peterson, 2011). There is uncertainty about the toxicity of *L. vulgaris* to grazing animals and the extent to which grazing animals avoid it (Saner et al., 1995, Sing and Peterson, 2011).

5.10.2 Plant parasites

None reported.

5.10.3 Plant diseases

Alternatia sp and *Cladosporium* sp. fungi occurred on seeds from Ontario (Clements and Cavers, 1990). In Europe the fungi *Melanotaenium cingens* has been found on the entire plant, *Peronospora corolla* on flowers, *P. flava* and *Entyloma linaicae* on leaves and *Synchytrium aureum* on leaves and stem (Hartl 1974 in Saner et al., 1995). In New York it has been observed as an alternate host for broad bean wilt virus and cumber mosaic virus (Rist and Lorbeer, 1989). *Agrobacterium rhizogenes* induces root tumours through the Ri (root-inducing) plasmid and *L. vulgaris* was the only species out of 127 screened that contained sequences homologous to these transfer-DNA sequences (Matveeva et al., 2012). This is the first species outside of *Nicotiana* where horizontal gene transfer and subsequent vertical transfer through sexual reproduction has been found, and might confer ecological advantages such as maintaining beneficial bacterial around the roots (Matveeva et al., 2012).

5.11 HISTORY

L. vulgaris is native to the British Isles and has been identified in late glacial and early post-glacial deposits (Matthews, 1955). Seed have tentatively been identified from substage III of the Hoxnian interglacial (mid-Pleistocene) at Clacton-on-sea (Godwin, 1975). Later unqualified records are from the early, mid and late Weichselian (Earith, Elstead, Hartford, Nant Ffrancon and Nazeing) (Godwin, 1975). *L. vulgaris* was introduced to North America as an ornamental garden plant by 17th century colonists and was considered invasive there by the mid-18th century (Mack, 2003).

Chapter 6. Conclusion

6.1 INTRODUCTION

This thesis has examined the density of *L. vulgaris* and density effects at multiple spatial scales (Chapters 2 and 3), aspects of *L. vulgaris* biology (Chapters 4 and 5) and has compared density and reproduction in native UK and invasive Alaskan populations (Chapters 2 and 3). Work in chapter 3 shows that the effect that conspecific density can have on an individual's growth and reproduction can vary with the spatial scale at which density is recorded. Dispersal and recruitment is also influenced by the density of both con- and heterospecifics (Chapter 4). These are just some of the factors that contribute to the typical emergent density pattern of a species across spatial scales (Chapter 2). Experimental and modelling approaches might help to understand when and why this density pattern differs or remains the same in different environments. Work here has also contributed to greater knowledge about the biology of *L. vulgaris* in the UK, which is covered in the review in chapter 5. However, the focus for this discussion will be on the comparison between the UK and Alaskan populations (Chapters 2 & 3), because this is of interest for both understanding invasions and for developing control options. Here I examine how the comparison of *L. vulgaris* density at different scales relates to the stage of invasion, the possible reasons for the higher broad scale density in Alaska and the implications for impact and control.

6.2 DENSITY COMPARISON AND INVASION STAGES

The lack of difference in fine spatial scale density of *L. vulgaris* between the UK and Alaskan populations is consistent with Firn and colleagues' (2011) findings that the abundance of herbaceous species where native predicts the abundance where introduced. This suggests that processes affecting fine spatial scale *L. vulgaris* density are similar between ranges. *L. vulgaris* may be occupying a similar niche and be surrounded by species with similar traits in both ranges (Firn et al., 2011). With concurrent species introductions in human disturbed areas, the same communities may develop as in the native range (La Sorte et al., 2007, HilleRisLambers et al., 2010). In a 2007 survey, the Haines area had 61 non-native species and roadsides had little native vegetation cover (Arhangelsky, 2007). Five species present in UK *L. vulgaris* populations were also present in Alaskan populations, because of a circumpolar distribution or introduction (Table B1). Of the 13 species present in Haines that are highly invasive or likely to become highly invasive in Alaska, ten are native to the UK (Arhangelsky, 2007, Lamb and Shephard, 2007, Biological Records Centre, 2013).

With a similar biotic and abiotic environment, morphological and physiological characteristics affecting local density, such as distance between shoot initiation within a clone (section 4.4.4), may not have changed (Leifso et al., 2012, Benot et al., 2013). The maximum density in both ranges may be defined by the same processes of relatively restricted seed and vegetative dispersal, inter and intra-specific competition for resources and facilitation of processes such as pollination (Antonovics and Levin, 1980, Bullock et al., 2002, Seabloom et al., 2005). The assumption of increased density in the invasive range may have arisen because comparisons between ranges may have focused on the most invasive species (Simons, 2003, Firn et al., 2011, Parker et al., 2013). There is also the possibility of bias towards the larger and denser invasive range populations, as these are more likely to be noticed and recorded. As with most comparisons of density or cover between ranges (Table 1), Firn and colleagues' (2011) study was at the 1 m^2 scale only. However, this study shows that density difference between ranges may exist for a species at one spatial scale, but not at other scales. Species where no difference has been found at fine spatial scales (Cripps et al., 2010, Firn et al., 2011, Maurel et al., 2013), may be denser in the invasive range at broader spatial scales, as found here. Confidence in density difference or similarity for a species between ranges can only occur when density has been compared at a range of scales within one study (Lamarque et al., 2012), or between several studies, as for *Hypericum perforatum* and *Lythrum salicaria* (Edwards et al., 1998, Bastlová-Hanzélyová, 2001, Vilà et al., 2005, Beckmann et al., 2009).

This study focused on fine to medium spatial scale density, so had low replication at a broader spatial scale. The finding of more populations within the Haines study area compared with the native study areas was based on existing records and limited surveys. Follow up work could check for recording biases of *L. vulgaris* populations between the ranges, with larger scale surveys of population presence (Pauchard et al., 2003, Lamarque et al., 2012), from several areas of the native and invasive range (Jakobs et al., 2004, Vilà et al., 2005, Beckmann et al., 2009). This would help with contrasting the density patterns across scales in the native and invasive range and could show if the invasion is at different stages in different areas of the introduced range (Colautti and MacIsaac, 2004). It would also be useful to understand and contrast density patterns and demography in areas where *L. vulgaris* may be at an earlier stage of invasion, such as in New Zealand (Webb et al., 1988).

At the scale of Haines town, *L. vulgaris* is both widespread and dominant and so has reached Colautti and MacIsaac's (2004) stage V (Figure 1). However, as the spatial extent of analysis is broadened, the pattern becomes more similar to the localized dominance of stage IVb because there are unoccupied habitats (Colautti and MacIsaac, 2004). If the pattern in the UK is compared with these invasion stages, then this localized dominant pattern holds at both a broad spatial extent and down to finer spatial extents than in Alaska, because there are fewer populations in the UK study area and these populations are smaller (section 2.4.2). Of course in reality invasives will have a more complex density pattern than Colautti and MacIsaac's framework. An invasive species can be widespread and dominant at some spatial scales and within some areas of the introduced range, while only locally dominant or rare at other scales and areas.

L. vulgaris in the Haines region could be described as still being in Dietz and Edward's (2006) primary phase of invasion. This is because *L. vulgaris* is largely restricted to disturbed habitats (Dietz and Edwards, 2006). This is also supported by the finding of a lack of post-invasion change in traits associated with competitiveness, with no increased height or fine scale density (sections 3.4.1 and 2.4.2.1). Colautti and MacIsaac (2004) assume that to move from stage IVb to stage Va species only has to overcome dispersal restrictions. However, this is assuming environmental homogeneity across the whole spatial extent being considered. For *L. vulgaris* to move towards being both widespread and locally dominant at broader scales within Alaska, it also needs to pass through environment and community suitability filters. This is because it would need to occupy areas at higher elevations and/or with less human mediated disturbance. Climatic matching work suggests that the Arctic-Alpine ecogeographic region of Alaska currently not occupied by *L. vulgaris* could be invaded (Carlson et al., 2008, Nawrocki et al., 2011). There is also evidence of *L. vulgaris* invading at higher elevations and in less disturbed environments elsewhere in North America (Pauchard et al., 2003, Pauchard et al., 2009, Wilke and Irwin, 2010). This expansion at a broad spatial scale is similar to Dietz and Edward's (2006) secondary phase of invasion. Invasion into more closed competitive communities might be expected to be accompanied by trait changes associated with increased competitive ability, while invasion into abiotically limiting areas might favour trait changes associated with stress tolerance (Dietz and Edwards, 2006).

6.3 POSSIBLE REASOSNS FOR GREATER INVASIVE BROAD SCALE DENSITY

The higher *L. vulgaris* density in the invasive range at broader spatial scales can be explained by altered processes due to abiotic and biotic differences between the ranges. These differences might include increased seed production and historical factors that have affected propagule pressure, and changes in dispersal and disturbance that have affected site availability.

Release from seed herbivory in the Haines area is the major, although not the only, reason for the higher seed production compared with ramets in the native populations. There was no difference between UK and Alaska in the proportion of flowers that became mature fruit, suggesting that there may not be a difference in pollen limitation. Arnold (1982) stated that one *Bombus* pollination visit transfers sufficient pollen to fertilise all *L. vulgaris* ovules. Evidence from other species suggests that pollen limitation is relatively common in self-incompatible plants, due to both the quantity and quality of pollen receipt, and that complete fertilisation from a single pollinator visit is unusual (Burd, 1994, Larson and Barrett, 2000, Sahli and Conner, 2007, Dauber et al., 2010). Arnold's (1982) study did find a correlation between a lack of pollinators and a low seed set a few weeks later. The density of surrounding conspecific flowering ramets had no effect on seed per fruit, although there may have been insufficient numbers of UK fruit to detect this (section 3.4.4). The density of conspecific flowering ramets did have a positive effect on mature fruit number (section 3.4.3). However, at most spatial scales, there was no difference in this density effect between the UK and Alaska. Any greater availability of outcrossing pollen in is confounded with other effects of populations with higher flowering density. Further work would be needed to investigate the relative importance of pollen limitation as a cause of lower seed set in the UK.

The lower seed set in UK fruit not predated by *R. antirrhini* compared with Alaskan fruit could also be caused by fewer ovules or by greater early seed abortion. The fewer black seed in the UK were not replaced with greater numbers of grey seed, showing that the difference is not in the late inadequate seed resourcing. A difference in ovule number could be the result of selection for larger flowers in the garden plants that subsequently invaded (Kitajima et al., 2006, Ross and Auge, 2008). Both a difference in ovule number and in seed abortion could also be caused by a different availability of resources between the UK and Alaskan populations. Sampling over more years and more intensive sampling at different times in the autumn in both ranges would be needed to understand the influence of varying weather conditions. A common garden experiment in which some of the plants are hand pollinated, resource limited, exposed to *B. pulicarius* and/or *R. antirrhini* would help to unpick the different influences on *L. vulgaris* seed production.

Work here in the UK (Chapter 4), and by Repath (2005), Egan and Irwin (2008) and Lehnhoff (2008) in North America suggests that seedling recruitment plays little role in maintaining established populations. This is supported by the finding here of no difference in fine scale density between ranges, despite greater seed production of Haines ramets. Competition might be limiting seedling recruitment within populations to the same extent in both ranges. However, the higher seed production of Haines ramets might be contributing to the larger population extents and the greater number of populations in the Haines area. This is because long distance dispersal events and establishment in suitable sites is more likely, both at the edges and distant from populations.

In addition to higher seed production from individual ramets, Haines may have a history of repeated introductions of large numbers of progagules (Lockwood et al., 2005). This increases the chance of establishment over a large area (Lockwood et al., 2005). *L. vulgaris* may have arrived as an ornamental garden plant, through the movement of soil and aggregate and/or in hay, straw and seed imports (Conn et al., 2010, Nawrocki et al., 2011). The greater seed production of individuals largely due to enemy release, combined with a likely history of multiple introductions to the Haines region, might be sufficient to explain invasion without other species trait changes compared with the native range (Lockwood et al., 2005, Leifso et al., 2012).

The relative contribution of greater seed production in explaining the higher density of *L. vulgaris* at broad spatial scales is unknown compared with other factors, such as the availability of sites for seedling establishment or the role of vegetative reproduction. Both changes in demographic and dispersal vital rates are important in explaining invasion and various parameters can contribute to different extents to population growth rate and spread (Jongejans et al., 2008a). For example, Jongejans and colleagues found that invasive populations of *Carduus nutans* had higher seed production than a native population, but that the contribution of this to spread was partly buffered by lower seedling survival and establishment in New Zealand and Australian populations. However, for an invasive population in Kansas the taller plant heights contributed most to increased spread. This shows that the same species can invade for different reasons in different locations of the introduced range (Jongejans et al., 2008a). Such changes in vital rates between native and invasive areas are driven by different underlying changes between the native and introduced environment.

Therefore, in addition to release from seed herbivory in the Haines region, there could be other environmental differences that affect the disturbance regime and/or dispersal and impact on life stage transitions in *L. vulgaris.* More disturbed locations tend to decrease the propagule pressure necessary for a population to establish (Lockwood et al., 2005), with disturbance creating a temporary increase in available resources (Davis et al., 2000, Mata et al., 2013). Disturbance appears to be important for the establishment of new *L. vulgaris* populations or spread of existing populations. Seedlings did not establish within existing populations (Chapter 4), both UK and Alaskan populations show evidence of historical disturbance and disturbance resulted in a large new population in the UK (IG3). Of course, disturbance can also result in the death of established plants and extinction of populations (Buckley et al., 2007). However, if at least some roots are left intact then these can rapidly shoot (section 4.3.3) and may benefit from reduced competition with other species, meaning that *L. vulgaris* can benefit from disturbance events and resist control efforts (Buckley et al., 2007, Carlson et al., 2008, Wilke and Irwin, 2010). There may be greater availability of appropriate habitat in Alaska because of gravel roads. The types of disturbance common in the Haines region may also cover a larger area than typical disturbance events in the UK, resulting in larger *L. vulgaris* population sizes.

In addition to physical disturbance events resulting in fluctuating resources (Davis et al., 2000), it is interesting that the nitrogen-fixing clovers *Trifolium pratense* and *T. repens* were present in every studied Alaskan population, but in none of the UK populations (Table B1). Both symbiotic nitrogen fixing and non-nitrogen fixing invasive species can result in changes to nutrient cycling (Stock et al., 1995, Ehrenfeld, 2003, Von Holle et al., 2013). This raises the possibility that some invasives in the Haines area could be facilitating the establishment and spread of other species – ‘invasional meltdown’ (Simberloff and Von Holle, 1999, Simberloff, 2006, Molina-Montenegro et al., 2008, Von Holle et al., 2013). Nitrogen addition is known to strongly increase *L. dalmatica* seed production and biomass (Jamieson et al., 2012).

The possibly greater disturbance of sites in Alaska might also be correlated with greater dispersal opportunities. Fill importation during building and repair work accounts for over 70 % of all recorded new invasive populations in Alaska (Nawrocki et al., 2011) and this could be particularly important for the movement of *L. vulgaris* root fragments to newly disturbed well drained sites. Experimental work is needed to investigate the extent to which the establishment of new populations is seed limited, and the importance of types of disturbance in establishing new *L. vulgaris* populations from seed and roots. Quantifying demographic and dispersal rates in both ranges would allow the development of demographic and dispersal models. These could be used to analyse which changes between ranges contribute most to invasiveness (Jongejans et al., 2008a, 2008b).

6.4 IMPLICATIONS FOR IMPACT AND CONTROL IN ALASKA

The best management option for controlling an invasive can vary depending on whether the priority is to reduce spread to new areas or to reduce local density (Shea et al., 2010). In Alaska, limiting the spread of existing invaders and preventing the establishment of new invaders are prioritised over reducing the density of invaders that are well established (Nawrocki et al., 2011). If the establishment of new populations is reasonably sensitive to seed number, then using a seed feeder such as *R. antirrhini* as biological control for *L. vulgaris* may be a means to limit spread to new areas, but not to reduce local density. Biological control agents that target other plant structures might also reduce seed numbers through restricting flowering and seed resourcing (McClay, 1992, Saner and Müller-Schärer, 1994, Barnewall, 2011). Any effects on local density would depend upon whether the herbivore impacts on adult and seedling survival, growth and vegetative reproduction (Saner and Müller-Schärer, 1994, Egan and Irwin, 2008, Barnewall, 2011) and how this interacts with inter and intra-specific competition (Volenberg et al., 1999). The effectiveness of biological control would depend on whether the agent can establish in sufficiently high densities and whether it has a high enough impact compared with other factors affecting seed output, plant density and recruitment (Jamieson et al., 2012). Chemical control and grass competition can reduce the local density of *L. vulgaris* (Carder, 1963, Baig et al., 1999, Jenks, 2010). Wilke and Irwin (2010) found that up to three years of hand pulling in late August had no significant effect on the number of stems in the following year. If cover is not rapidly established by native species following control there is the potential for re-invasion by the same or another species (Buckley et al., 2007). Actions to reduce disturbance and dispersal and the monitoring of sites where there has been disturbance would help to prevent the establishment of new outlying populations (Moody and Mack, 1988).

Although *L. vulgaris* in the Haines area is at the same fine-scale density as in the UK, this does not necessarily mean that there are no negative impacts in the introduced range (Ricciardi and Cohen, 2007). There is potential for disruption of native plant – pollinator interactions (Ghazoul, 2004, Dietzsch et al., 2011). For example, native yellow *Castilleja* species are pollinated by *Bombus* species, while native red *Castilleja* species are pollinated by the Rufous hummingbird *Selasphorus rufus* Gmelin (Trochilidae), both of which visit *L. vulgaris* flowers (Duffield, 1972, Burkle et al., 2007, personal observation.). In Colorado, *Bombus* sp. preferentially visited *L. vulgaris* over native plants, resulting in a lower seed of native plants (Rebecca Irwin, unpublished data). However, it is also possible for invasion to result in little change in native plant- pollinator interactions (Nielsen et al., 2008, Vilà et al., 2009, Bartomeus et al., 2010) and in some circumstances an invasive may facilitate native species pollination by acting as a ‘magnet’ species or by supporting larger populations of pollinators (Thomson, 1978, Nielsen et al., 2008). Invasive plants can also have both positive and negative direct and indirect impacts on native pollinator populations (Stout and Morales, 2009). *Bombus* colonies were larger in areas with *L. vulgaris* (Rebecca Irwin, unpublished data). This suggests that *L. vulgaris* in Alaska may be important in supporting *Bombus* populations, such as the declining populations of *B. occidentalis* that nectar rob from *L. vulgaris* (Koch, 2011).

At a fine spatial scale, the relatively high density of *L. vulgaris* in Haines may be excluding native vegetation following disturbance. This might have a stronger impact than pollinator competition (Palladini and Maron, 2013). In Colorado subalpine meadows, *L. vulgaris* invaded plots had lower native flower production and shorter native flowering duration than uninvaded plots (Wilke and Irwin, 2010). However, Lehnhoff (2008) found no difference in plant diversity between invaded and uninvaded sites in Montana. Arhangelsky (2007) noted that roadsides and adjacent areas around Haines contained very little native vegetation. However, it is unclear to what extent *L. vulgaris* in Haines can be considered to be a driver of the reduction in native species or a passenger of underlying ecosystem changes (MacDougall and Turkington, 2005, HilleRisLambers et al., 2010). The invasion could be considered as a consequence of human mediated disturbance creating fluctuations in resources that *L. vulgaris* and other invasive species with high propagule pressure can more rapidly exploit than native species (Davis et al., 2000, MacDougall and Turkington, 2005, HilleRisLambers et al., 2010).

6.5 CONCLUSION

There was no difference in the fine scale or mean field density between native UK and invasive Alaskan *L. vulgaris* populations, but the invasive populations covered a larger area. The greater seed production of the invasive compared with the native ramets is consistent with enemy release from seed predators. However, the effectiveness of biological control using seed predators to limit spread would depend on whether the establishment of new populations is seed limited. This research has shown how important it is to consider both the spatial scale at which the density of an invasive plant is measured, and the spatial scale of conspecific density effects on individual fitness. It has also demonstrated the value of understanding invasive species in their native range.

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Appendix A: Matching the climate of *L. vulgaris* native and invasive range study squares.

The aim was to find a 0.5 degree grid square within the *L. vulgaris* North American invasive range that had a similar climate to the two UK 0.5 degree study squares with centres 51.75° N, 0.25° E and 53.75° N, 1.25° W. The 1961-1990 monthly means of the Climatic Research Unit's (CRU) Global Climate dataset is a 0.5° lat x 0.5° long resolution mean monthly time series for global land areas, excluding Antarctica (New et al., 1999, Intergovernmental Panel on Climate Change, 2008). The variables used for climate matching were diurnal temperature range (°C), mean temperature (°C), maximum temperature (°C), Minimum temperature (°C), precipitation (mm/day), wet day frequency (days), vapour pressure (hPa), cloud cover (%), radiation (W/m^2) and wind speed (m/s). Ground frost frequency was not available at monthly means. Each datum is one variable in one month in one year for a single 0.5 degree grid cell. The areas of interest were temperate regions, so months were combined into seasons to reduce the dataset before ordination. For example, in the Northern hemisphere spring was the mean of March, April & May and in the Southern hemisphere the mean of September, October and November. A Principle Component Analysis was carried out on the resulting dataset using SPSS version 15.0 (SPSS Inc., 2006).

The first five components of the analysis explained 90 % of worldwide climatic variability (Table A1). These components were used to calculate the climatic distance in five dimensional space between the West Essex and East Yorkshire grid cells and the rest of the world as Distance = $\sqrt{(\sum (\text{Component I to } V_a - \text{Component I to } V_b)^2)}$. The first five components were chosen because the eigenvalues of the following components are less than one, meaning that the component contributes less to explaining variability than one of the original variables (Kaiser, 1960). Temperature, radiation and vapour pressure load strongly positively and cloud cover and wet day frequency negatively onto component one, cloud cover, precipitation and wet day frequency load positively and diurnal temperature range negatively onto component two, while wind speed loads positively onto component three (Table A2).

Table A1. Components of a worldwide 0.5 degree grid cell climate dataset with ten climate variables in four seasons.

Component	Total	% variance explained	Cumulative % variance explained
1	19.014	47.535	47.535
2	9.575	23.937	71.472
3	3.217	8.043	79.515
4	2.265	5.662	85.177
5	1.930	4.824	90.001
6	.986	2.465	92.466
7	.601	1.502	93.968
8	.444	1.111	95.079
9	.427	1.069	96.148
10	.275	.689	96.836

Table A2. Continued on next page. Loadings of climatic variables from a worldwide 0.5 degree grid cell climate dataset onto the first five principle components.

Climatic variable	Component				
	1	2	3	4	5
Winter cloud cover	-0.507	0.571	0.196	-0.303	0.366
Winter diurnal temperature range	0.364	-0.392	-0.420	0.644	0.256
Winter precipitation	0.064	0.560	0.272	-0.100	0.474
Winter radiation	0.949	-0.015	-0.072	0.193	-0.083
Winter minimum temperature	0.931	0.237	0.185	0.026	-0.003
Winter mean temperature	0.944	0.195	0.141	0.087	0.022
Winter maximum temperature	0.949	0.152	0.098	0.144	0.045
Winter vapour pressure	0.737	0.547	0.075	0.152	-0.009
Winter wet day frequency	-0.552	0.538	0.198	-0.310	0.362
Winter wind speed	-0.402	-0.096	0.758	0.427	0.061
Spring cloud cover	-0.430	0.744	-0.051	-0.052	0.253
Spring diurnal temperature range	0.296	-0.592	-0.371	0.390	0.428
Spring precipitation	0.315	0.759	0.010	0.044	0.306
Spring radiation	0.848	-0.445	0.055	0.010	-0.075
Spring minimum temperature	0.964	0.171	0.131	-0.076	-0.012
Spring mean temperature	0.978	0.110	0.092	-0.036	0.031
Spring maximum temperature	0.983	0.050	0.054	0.002	0.071
Spring vapour pressure	0.780	0.536	0.063	0.132	-0.044
Spring wet day frequency	-0.354	0.782	0.031	-0.134	0.341

Table A2 continued.

Climatic variable	Component				
	1	2	3	4	5
Spring wind speed	-0.432	-0.238	0.747	0.370	0.078
Summer cloud cover	-0.362	0.717	-0.279	0.389	-0.214
Summer diurnal temperature range	0.217	-0.620	-0.144	-0.050	0.670
Summer precipitation	0.367	0.633	-0.197	0.303	-0.087
Summer radiation	0.355	-0.737	0.266	-0.378	0.210
Summer minimum temperature	0.910	0.072	0.168	-0.234	-0.097
Summer mean temperature	0.918	-0.031	0.140	-0.235	0.015
Summer max temperature	0.904	-0.125	0.110	-0.230	0.118
Summer vapour pressure	0.780	0.473	0.068	0.074	-0.127
Summer wet day frequency	-0.124	0.791	-0.272	0.275	-0.019
Summer wind speed	-0.432	-0.281	0.727	0.290	-0.042
Autumn cloud cover	-0.565	0.739	-0.011	0.044	0.018
Autumn diurnal temperature range	0.421	-0.582	-0.271	0.342	0.500
Autumn precipitation	0.321	0.814	0.035	0.182	0.135
Autumn radiation	0.942	-0.236	0.017	0.020	0.020
Autumn minimum temperature	0.944	0.197	0.200	-0.091	-0.058
Autumn mean temperature	0.970	0.123	0.162	-0.048	0.003
Autumn maximum temperature	0.982	0.052	0.125	-0.007	0.061
Autumn vapour pressure	0.814	0.500	0.078	0.142	-0.082
Autumn wet day frequency	-0.423	0.812	-0.013	0.018	0.112
Autumn wind speed	-0.567	-0.169	0.684	0.380	0.027

Regions within the invasive range of *L. vulgaris* which are most similar to the Essex grid square are coastal East Canada, the Great Lakes region of North America, Kodiak Island Alaska, areas of New Zealand, Humboldt Bay California and South East Alaska. I decided to focus on Western North America, as *L. vulgaris* has been reported as currently more invasive in this region than in other parts of the range (Saner et al., 1995, Allan Herbarium, 2000, Mack, 2003, Pauchard et al., 2003, Randall, 2007, USDA, 2010). The closest matching grid square to Essex in Western North America with a climatic distance of 0.69, which also had records of *L. vulgaris* (Blythe Brown, personal communication), was on Kodiak Island, Alaska (57.75° N, W 152.75° W). However, as travel to Kodiak was too expensive, Haines, Alaska, (59.25° N, 135.25° W), was chosen as the next closest climatically matching square with *L. vulgaris* records (Melinda Lamb & Pam Randles, personal communication). Haines had a climatic distance of 1.29 from Essex and 1.35 from East Yorkshire. The worldwide range of climatic distance from the Essex grid square was to 18.78, while the climatic range North of 23.5° and between 110° and 180° West was 0.41 to 4.51 from the Essex grid square.

After the field study, maximum and minimum temperatures for the Essex grid square in 2008 and 2009 were obtained from Writtle weather station (51.73° N, 0.43° E). Daily rainfall data are from South Ockendon weather station (51.51° N, 0.28° E) and Writtle weather station, due to missing data (UK Met Office, 2006). The East Yorkshire grid square 2008 and 2009 daily maximum and minimum temperatures are from Cawood weather station (53.83° N, 1.15° W), with daily rainfall data from Gale

Common weather station (53.69° N, 1.19° W) and Leeds Knostrop weather station (53.78° N, 1.51° W) due to missing data (UK Met Office, 2006). Maximum and minimum temperatures and daily rainfall for Haines for 2009 and 2010 are from Haines airport weather station (59.23° N, 135.50° W) (National Climatic Data Centre, 2010).

Actual maximum and minimum temperatures in the study years were lower in Haines compared with Essex and East Yorkshire (Figures A1 & A2). However, Haines maximum and minimum temperatures in 2010 were higher than the Haines 30 year means (Table A3), making the two grid squares more similar in temperature for the study years than in the principal components analysis. Haines has far more severe winters and has a shorter growing season, with a later increase in spring temperatures and an earlier decrease in autumn temperatures in 2010 compared with the UK. Haines rainfall in 2010 was higher than in Essex, Yorkshire and the Haines 30 year mean (Table A3, Figures A3 & A4).

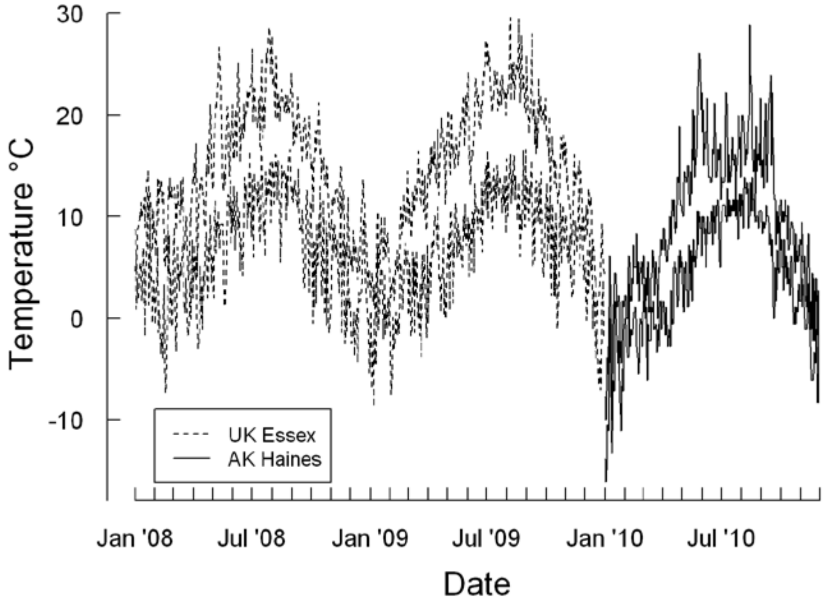

Figure A1. Maximum and minimum daily temperatures for Essex (UK) in 2008 and 2009, and Haines (AK) in 2010.

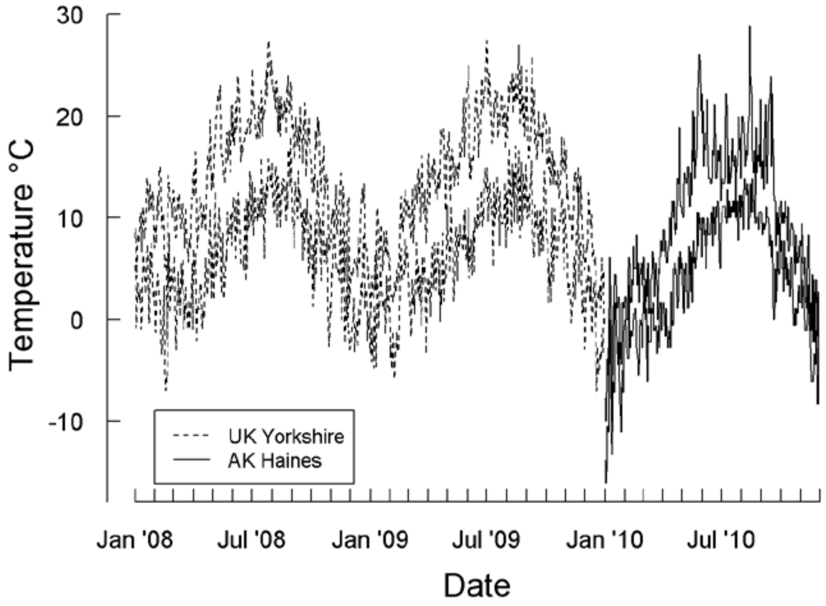

Figure A2. Maximum and minimum daily temperatures for East Yorkshire (UK) in 2008 and 2009, and Haines (AK) in 2010.

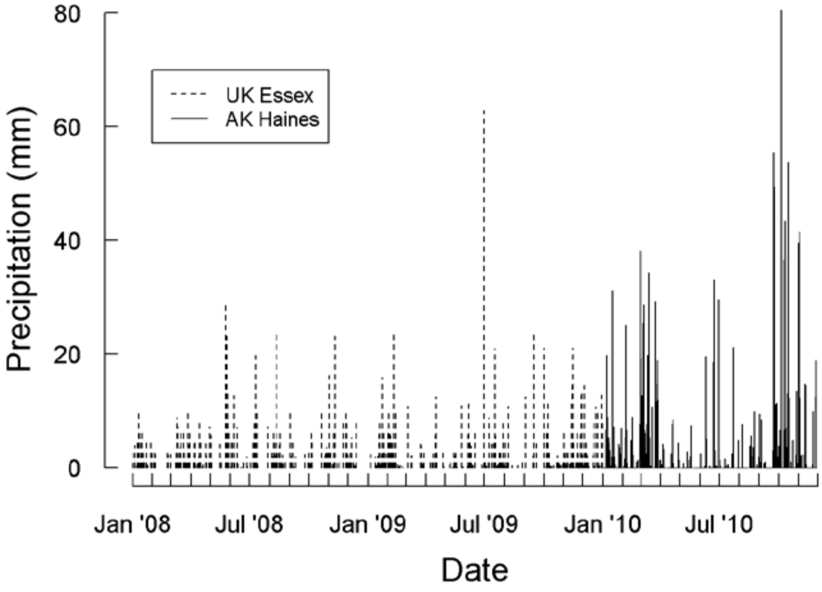

Figure A3. Daily rainfall for Essex (UK) in 2008 and 2009, and Haines in 2010.

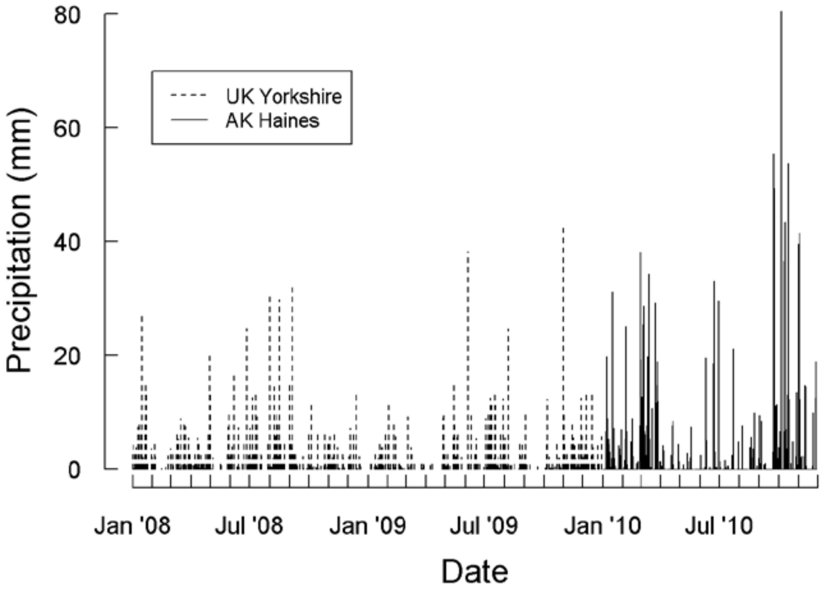

Figure A4. Daily rainfall for East Yorkshire (UK) in 2008 and 2009, and Haines (AK) in 2010.

Table A3. Continued on the next page. 30 year means of climatic variables for Haines and Essex, compared with precipitation, maximum and minimum temperatures in Haines during 2010 and Essex and East Yorkshire during 2009.

	Haines 30 year mean	Haines Dec 2009 - Nov 2010	Essex 30 year mean	Essex Dec 2008 – Nov 2009	East Yorks. 30 year mean	East Yorks. Dec 2008 – Nov 2009
Winter cloud cover %	68.67		81.33		84.67	
Winter diurnal temperature range °C	7.67		5.73		5.27	
Winter precipitation mm	2.87	4.2	1.60	1.70	1.93	1.26
Winter radiation W/m^2	22.00		32.00		25.33	
Winter minimum temperature °C	-13.73	-4.86	1.00	0.61	0.70	0.67
Winter mean temperature °C	-9.87		3.87		3.33	
Winter maximum temperature °C	-6.07	0.56	6.73	6.51	5.97	6.49
Winter vapour pressure hPa	2.80		7.43		6.97	
Winter wet day frequency	14.03		15.17		16.27	
Winter wind speed m/s	3.93		5.20		5.33	
Spring cloud cover %	70.67		73.67		77.67	
Spring diurnal temperature range °C	10.03		8.63		7.80	
Spring precipitation mm	1.67	3.7	1.50	0.87	1.77	1.12
Spring radiation W/m^2	119.67		128.67		116.00	
Spring minimum temperature °C	-4.80	2.29	4.10	4.98	3.63	4.85
Spring mean temperature °C	0.23		8.40		7.50	
Spring maximum temperature °C	5.27	10.16	12.73	15.04	11.43	14.17
Spring vapour pressure hPa	5.17		9.13		8.57	
Spring wet day frequency	10.33		14.23		14.53	

Table A3 continued.

	Haines 30 year mean	Haines Dec 2009 - Nov 2010	Essex 30 year mean	Essex Dec 2008 – Nov 2009	East Yorks. 30 year mean	East Yorks. Dec 2008 – Nov 2009
Spring wind speed m/s	3.77		5.00		5.00	
Summer cloud cover %	74.00		69.67		75.67	
Summer diurnal temperature range °C	11.17		9.97		8.93	
Summer precipitation mm	1.80	2.0	1.67	2.02	1.97	2.48
Summer radiation W/m^2	158.00		173.33		157.33	
Summer minimum temperature °C	5.03	10.28	10.87	11.62	10.20	10.92
Summer mean temperature °C	10.57		15.83		14.63	
Summer max temperature °C	16.20	16.61	20.83	22.41	19.13	20.80
Summer vapour pressure hPa	9.90		14.23		13.37	
Summer wet day frequency	12.93		11.30		12.67	
Summer wind speed m/s	3.23		4.23		4.27	
Autumn cloud cover %	75.33		75.33		79.33	
Autumn diurnal temperature range °C	7.43		7.67		6.83	
Autumn precipitation mm	3.87	7.2	1.77	2.36	1.97	1.69
Autumn radiation W/m^2	49.67		68.67		58.00	
Autumn minimum temperature °C	-2.67	2.91	6.67	8.40	6.13	7.45
Autumn mean temperature °C	1.07		10.47		9.53	
Autumn maximum temperature °C	4.80	9.00	14.33	16.24	12.97	15.25
Autumn vapour pressure hPa	6.30		11.33		10.47	
Autumn wet day frequency	16.00		13.57		14.93	
Autumn wind speed m/s	4.03		4.60		4.77	

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Appendix B. *L. vulgaris* study populations.

Cirsium arvense, Leucanthemum vulgare, *Plantago major, Polygonum aviculare* and *Taraxacum officinale* agg. were present in both the UK and Alaskan (AK) *L. vulgaris* study populations (Table B1). Figures B1 - B28 are maps of ramets in all the populations.

Table B1. Location, site details and size of *L. vulgaris* study populations in the UK and Alaska. The length and width are when the smallest possible rectangle is placed that encompasses all the ramets within the population. Plant taxa that occurred in most quadrats, were dominant in a few quadrats or that were shading the site, were identified at least to genus. Species in bold are post-1492 introductions to the UK or Alaska: some infra-taxa of *Taraxacum* are introduced in Alaska and others are considered native (USDA, 2013). * only part of the FS population was surveyed. Continued on the following pages.

Population	Latitude & Longitude	Description	Dominant species	Length x width (m) and year surveyed.
UK - AW	N 51.5149° E 0.0811°	Open disturbed brown field site.	***Buddleja davidii***, ***Euphorbia* sp**.	1.23 x 0.93, 2008
UK - BP1	N 51.5222° E 0.2674°	Shaded sandy disturbed bank at path edge by lake.	*Holcus lanatus, Plantago lanceolata, Hypochaeris* sp.	10.71 x 1.07, 2008 44.36 x 4.65, 2009
UK - BP2	N 51.5222° E 0.2660°	Partially shaded ditch edge by path.	*Arrhenatherum elatius*, *Dactylis glomerata, Holcus lanatus, Rubus fruiticosus* agg., *Urtica dioica.*	2.55 x 1.84, 2009

Table B1 continued.

Population	Latitude & Longitude	Description	Dominant species	Length x width (m) and year surveyed.
UK - BP3	N 51.5222° E 0.2660°	Open grassland. Grazed by rabbits.	*Arrhenatherum elatius*, *Holcus lanatus, Plantago lanceolata.*	2.61 x 2.99, 2009
UK - CM	N 51.5475° E 0.2600°	South facing protected alcove in hedgerow next to meadow. Partly shaded. Grazed by rabbits.	*Agrostis stolonifera, Arrhenatherum elatius, Holcus lanatus, Lamium purpureum, Phleum pratense, Rubus fruiticosus* agg., *Urtica dioica.*	3.83 x 2.62, 2008 2.77 x 2.80, 2009
UK - HC	N 51.5324° E 0.2045°	Growing up through South facing hedgerow next to meadow. Partly shaded.	*Agrostis stolonifera, Crataegus monogyna, Prunus spinosa, Rosa canina.*	3.19 x 1.95, 2008 3.67 x 2.21, 2009
UK - IG1	N 51.6630° E 0.3785°	Beneath young oak tree in field margin next to railway line. Shaded.	*Arrhenatherum elatius, Quercus robur, Urtica dioica.*	0.80 x 0.41, 2008
UK - IG2	N 51.6630° E 0.3785°	Beneath oak tree on a bank next to railway line. Partly shaded.	*Arrhenatherum elatius.*	0.60 x 0.50, 2009
UK - IG3	N 51.6621° E 0.3770°	Field margin next to railway line. Open. Spoil from railway side works tipped over fence after which Linaria population appeared.	*Agrostis stolonifera, Arrhenatherum elatius, Artemisia vulgaris, Bromus sterilis, Bromus squarrosus, Cirsium arvense, Elymus repens, Helictotrichon pubescens, Holcus lanatus, Urtica dioica, Rumex obtusifolius.*	48.00 x 5.08, 2009

Table B1 continued.

Population	Latitude & Longitude	Description	Dominant species	Length x width (m) and year surveyed.
UK - LP1	N 51.5122° E 0.2698°	Open grassland next to path and near motorway. Burned in 2009.	*Agrostis stolonifera, Arrhenatherum elatius, Dactylis glomerata, Elymus repens, Phleum pratense, Sonchus* sp*., Senecio* sp*., Torilis japonica.*	4.65 x 3.32, 2008 4.89 x 3.42, 2009
UK - LP2	N 51.5123° E 0.2683°	Shaded path edge leading to motorway bridge.	*Arrhenatherum elatius, Festuca arundinaceae, Lolium perenne, Rosa canina, Torilis japonica.*	2.64 x 0.65, 2008
UK - MF	N 53.7650° W 1.2392°	Open steep bank of rubble near railway and also flat grass area partially shaded by ash.	*Arrhenatherum elatius, Centaurea nigra, Cirsium arvense, Convolvulus arvensis, Epilobium angustifolium, Galium aparine, Holcus lanatus, Hypericum perforatum, Lamium* spp*, Leucanthemum vulgare, Origanum vulgare, Plantago lanceolata, Potentilla reptans, Rubus fruticosus* agg*, Rumex spp., Senecio* sp., *Taraxacum, Urtica dioica.*	2.91 x 0.21, 2008 14.26 x 6.83, 2009
UK - WL1	N 51.8242° E 0.4959°	Partially shaded base of roadside hedgerow. Occasionally cut.	*Arrhenatherum elatius, Helictotrichon pubescens, Hedera helix, Prunus spinosa.*	16.08 x 0.73, 2008 15.05 x 1.07, 2009
UK - WL2	N 51.8242° E 0.4959°	Shaded roadside slope by hedgerow. Occasionally cut.	*Arrhenatherum elatius, Carex otrubae, Glechoma hederacea, Hedera helix, Prunus spinosa.*	6.48 x 1.26, 2009

Table B1 continued.

Population	Latitude & Longitude	Description	Dominant species	Length x width (m) and year surveyed.
UK - WL3	N 51.8242° E 0.4959°	Open grass between paved path and ditch. Occasionally cut.	*Agrostis stolonifera, Arrhenatheum elatius, Helictotrichon pubescens.*	4.49 x 1.6, 2009
AK - CK	N 59.20407° W 135.43497°	Low grass and herbs on promontory between gravel pull in and estuary. Regularly disturbed by foot. Open.	*Achillea millefolium, Agropyron trachycaulum, Festuca rubra,* ***Taraxacum officinale*** **agg.**, ***Trifolium pratense***, ***Trifolium repens***.	10.35 x 6.62, 2010
AK - FS	N 59.227365° W 135.442681°	Tall grass and herbs with occasional shrubs between road and ruined building. Patches of rubble and gravel. Short mown verge for 1 m next to pavement. Open.	*Achillea millefolium, Agropyron trachycaulum, Agrostis scabra,* ***Cirsium arvense***, *Equisetum arvense,* ***Plantago spp.***, *Populus balsamifera,* ***Ranunculus spp.***, ***Taraxacum officinale*** **agg.**, ***Trifolium repens, Trifolium pratense***.	16.47 x 4.79*, 2010
AK - HR	N 59.23495° W 135.43860°	Track on top of harbour wall. Population on both sides of the track among vegetation and scattered down the rubble slope. Open.	*Achillea millefolium, Agrostis scabra, Arabis lyrata, Cerastium arvense, Senecio* sp., ***Taraxacum officinale*** **agg.**, ***Trifolium pratense***, ***Trifolium repens***.	34.88 x 7.42, 2010
AK - MB	N 59.19327° W 135.41264°	Gravel on edge of small driveway and also running down steep bank of drainage ditch. Partly shaded.	*Equisetum* sp., *Matricaria discoidea,* ***Rumex acetosella***, ***Rumex*** **sp**., ***Trifolium pratense***, ***Trifolium repens***.	4.47 x 1.38, 2010

Table B1 continued.

Population	Latitude & Longitude	Description	Dominant species	Length x width (m) and year surveyed.
AK - NK	N 59.24222° W 135.42848°	Gravel pull in with sparse vegetation. Population spread across the northern and eastern edge with sparse vegetation. Recently disturbed with new gravel and machinery. Open.	*Achillea millefolium, Agropyron trachycaulum, Cerastium arvense, Equisetum* sp., ***Leucanthemum vulgare***, *Matricaria discoidea, Polygonum aviculare, Plantago,* ***Taraxacum officinale* agg.**, ***Trifolium pratense***, ***Trifolium repens***.	32.99 x 28.31, 2010
AK - RV	N 59.21811° W 135.44839°	Grass and herbs among felled trees on slightly higher ground between herbaceous wetland and steep grass bank to road edge. Very high tides reach the edge of population and likely occasionally submerge it. Footpath though patch and disturbance in area from digging by brown bears. Partly shaded.	*Achillea millefolium, Agropyron trachycaulum, Hordeum brachyantheum, Lathyrus japonicas, Rubus arcticus, Rosa nutkana,* ***Rumex spp.,*** *Rubus spectabilis,* ***Taraxacum officinale* agg.**, ***Trifolium pratense***, ***Trifolium repens***, *Tiarella trifoliate, Zigadenus elegans.*	15.03 x 6.36, 2010
AK - TW	N 59.232294° W 135.446390°	Grass and herb verge between concrete pavement and ditch. Periodically cut in Spring and summer. Partly shaded.	*Achillea millefolium, Agrostis* sp., *Alnus viridis,* ***Cirsium arvense***, *Euphrasia arctica, Heracleum lanthanum,* ***Rumex* spp.,** *Phlaris arundinacea,* ***Ranunculus repens***, *Rubus spectabilis, Salix* sp., ***Taraxacum officinale* agg**, ***Trifolium pratense***, ***Trifoliumrepens***.	65.11 x 2.5, 2010

UK - AW 2008

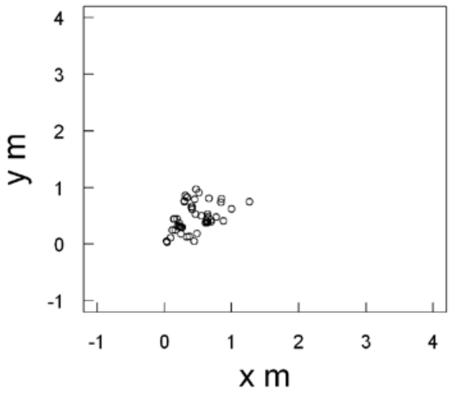

Figure B1. *L. vulgaris* ramets in UK population AW in 2008.

UK - BP1 2008

UK - BP1 2009

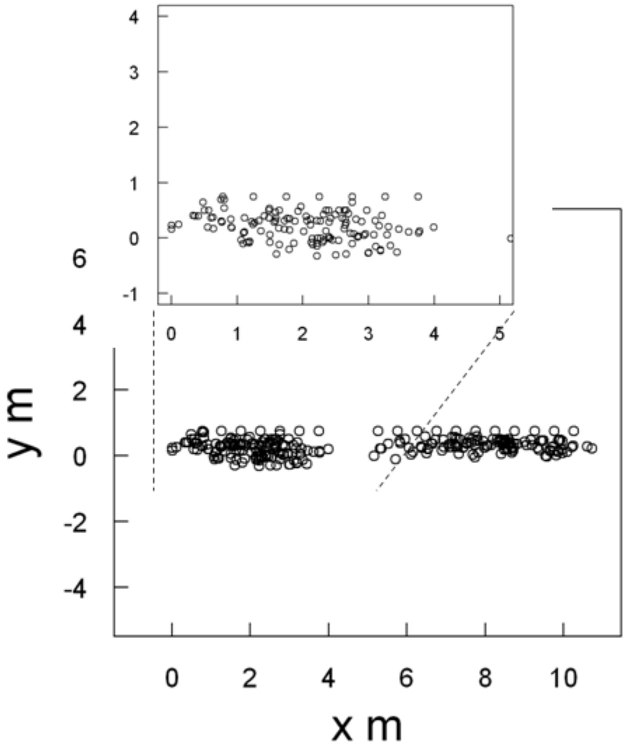

Figure B2. *L. vulgaris* ramets in UK population BP1 in 2008.

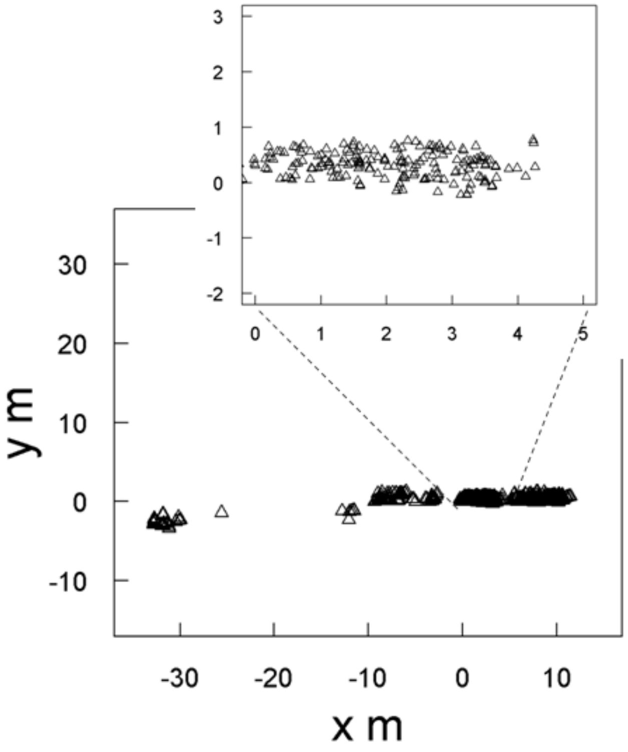

Figure B3. *L. vulgaris* ramets in UK population BP1 in 2009.

UK - BP2 2009

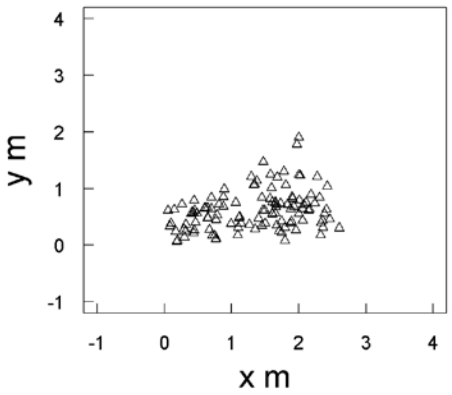

Figure B4. *L. vulgaris* ramets in population BP2 in 2009.

UK - BP3 2009

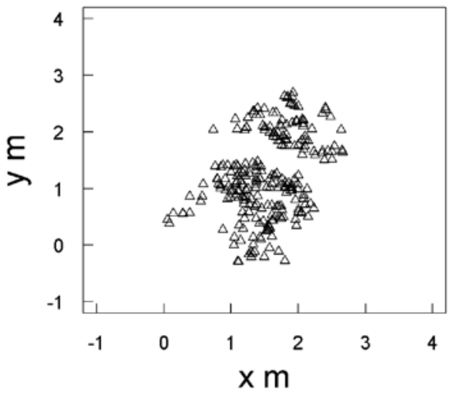

Figure B5. *L. vulgaris* ramets in BP3 population 2009.

UK - CM 2008

UK - CM 2009

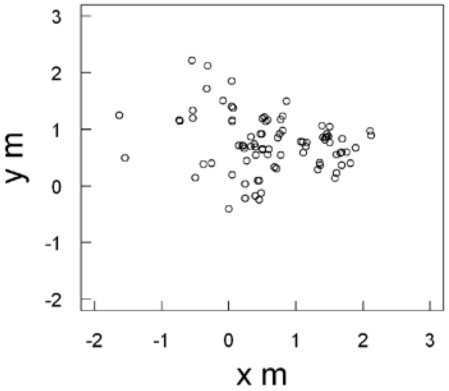

Figure B6. *L. vulgaris* ramets in UK population CM in 2008.

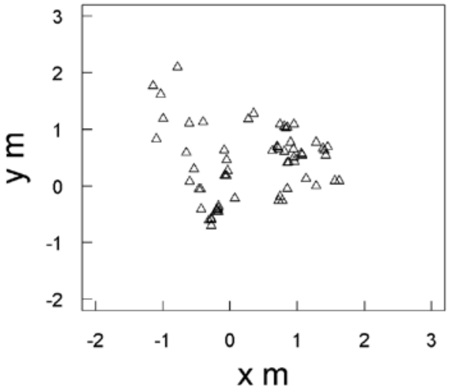

Figure B7. *L. vulgaris* ramets in UK population CM in 2009.

UK - HC 2008

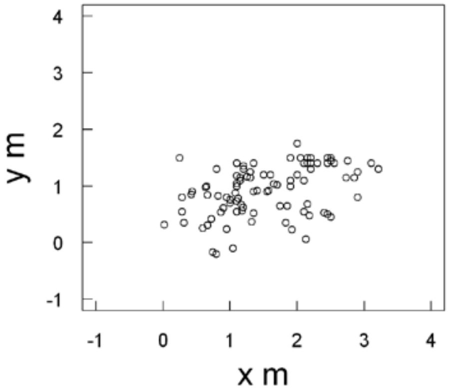

Figure B8. *L. vulgaris* ramets in UK population HC in 2008.

UK - HC 2009

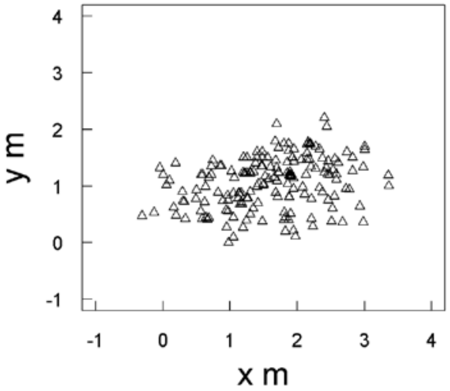

Figure B9. *L. vulgaris* ramets in UK population HC in 2009.

UK - IG1 2008

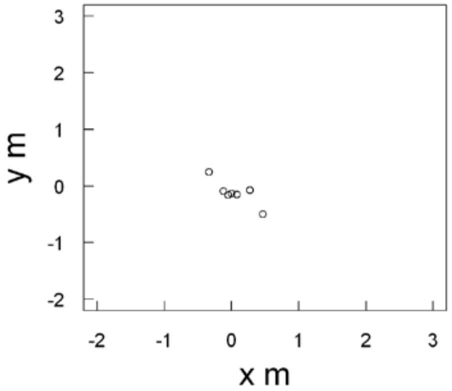

Figure B10. *L. vulgaris* ramets in UK population IG1 in 2008.

UK - IG2 2009

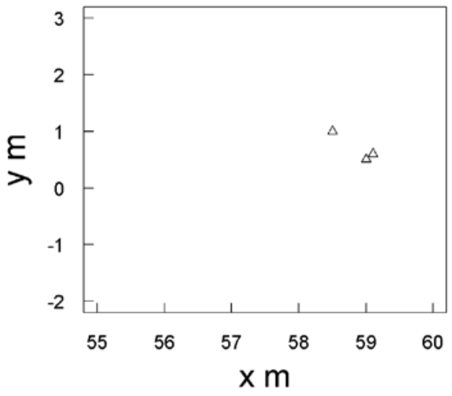

Figure B11. *L. vulgaris* ramets in UK population IG2 in 2009.

UK - IG3 2009

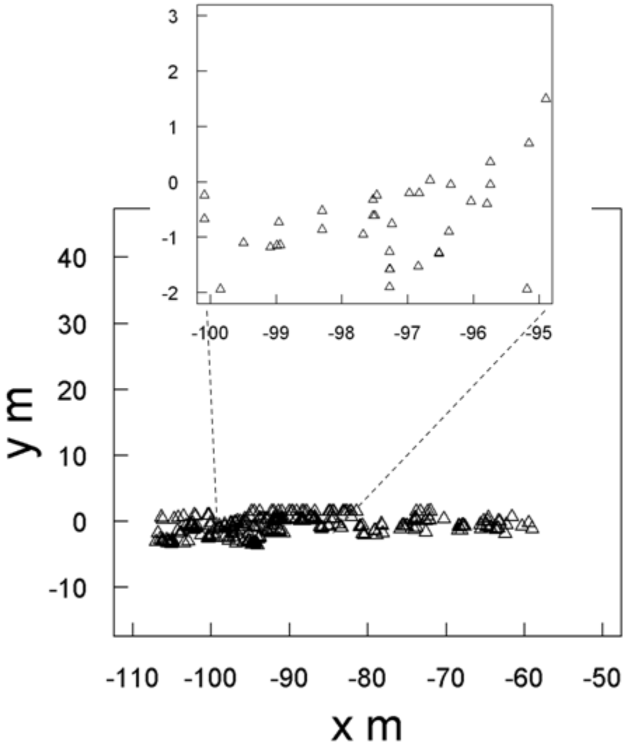

Figure B12. *L. vulgaris* ramets in population IG3 in 2009

UK - LP1 2008

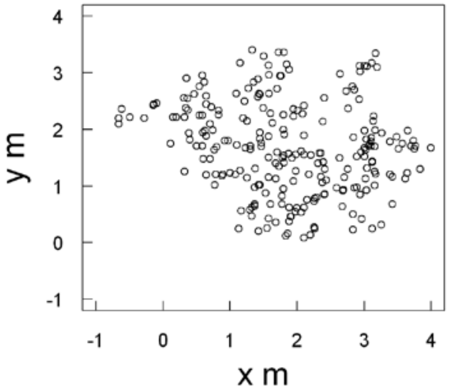

Figure B13. *L. vulgaris* ramets in UK population LP in 2008.

UK - LP1 2009

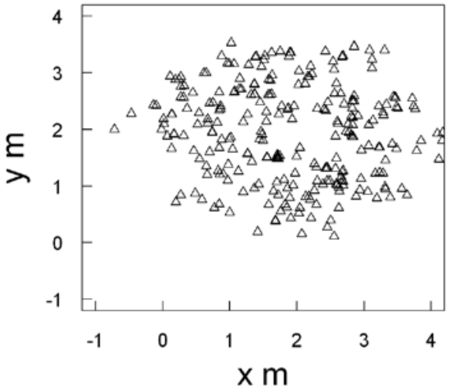

Figure B14. *L. vulgaris* ramets in UK population LP in 2009.

UK - LP2 2008

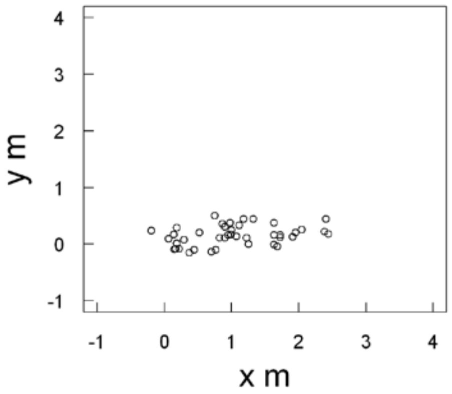

Figure B15. *L. vulgaris* ramets in UK population LP2 in 2008.

UK - MF 2008

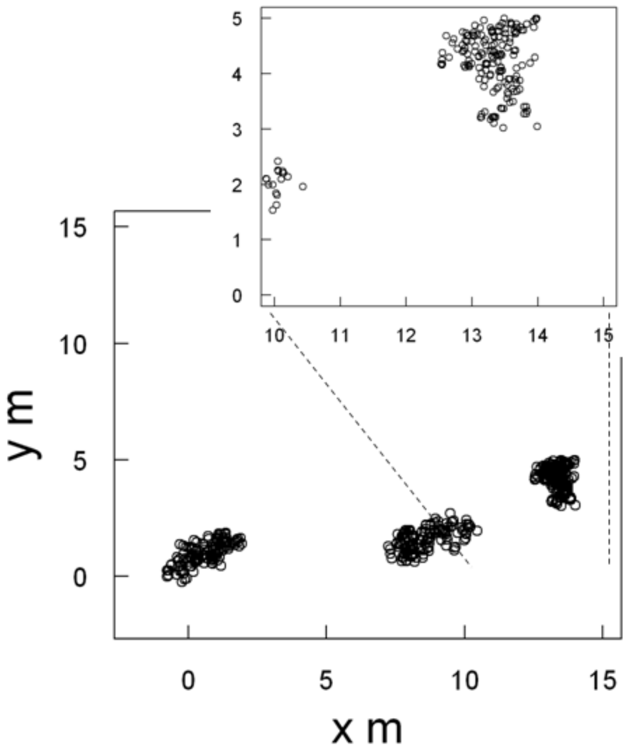

Figure B16. *L. vulgaris* ramets in UK population MF in 2008

UK - MF 2009

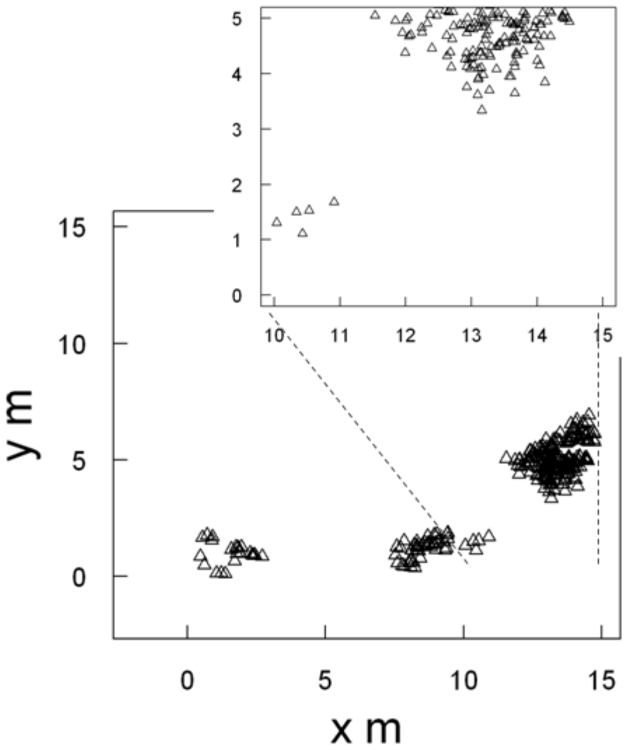

Figure B17. *L. vulgaris* ramets in UK population MF in 2009.

UK - WL1 2008

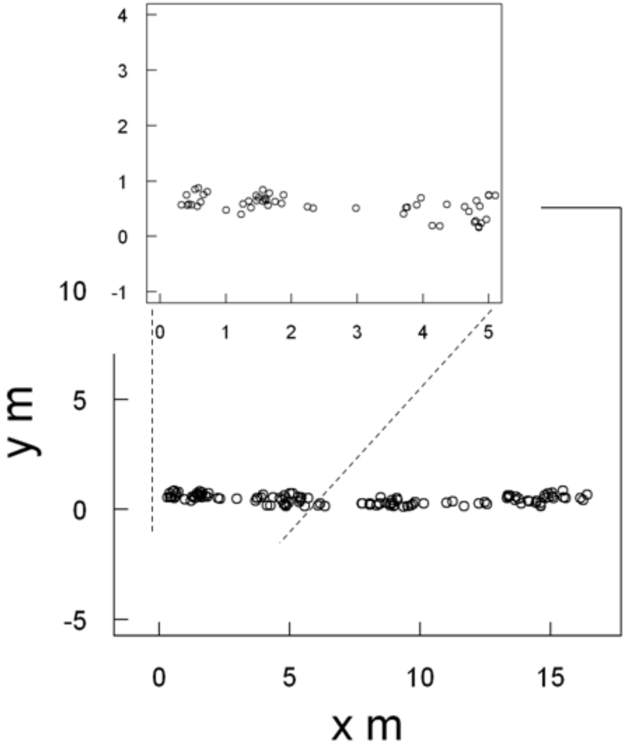

Figure B18. *L. vulgaris* ramets in UK population WL1 in 2008.

UK - WL1 2009

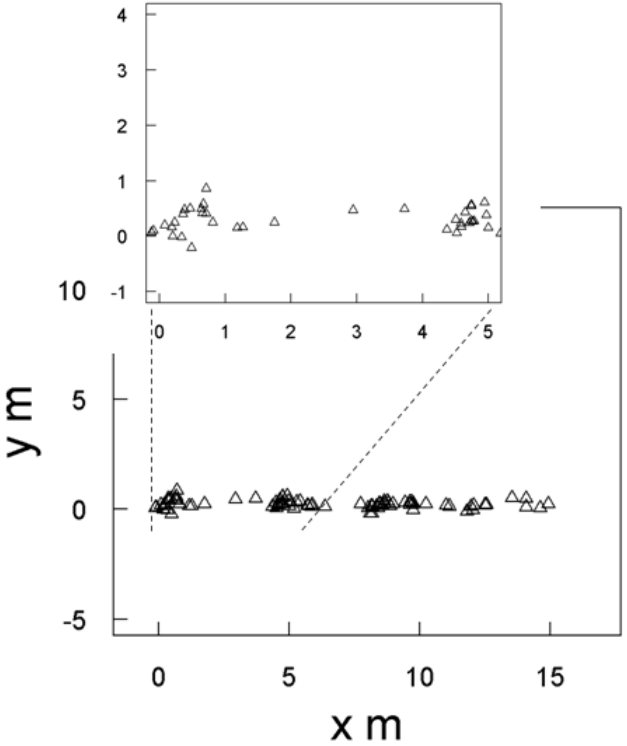

Figure B19. *L. vulgaris* ramets in UK population WL1 in 2009.

UK - WL2 2009

UK - WL3 2009

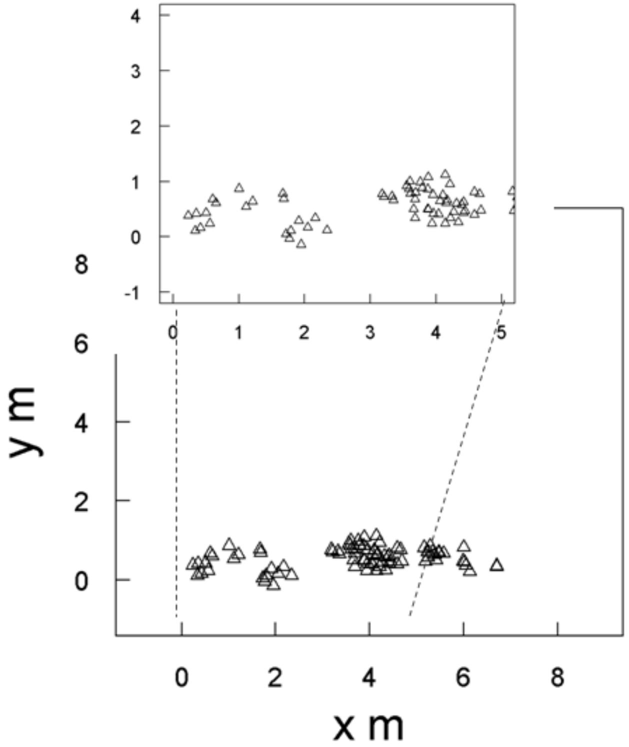

Figure B20. *L. vulgaris* ramets in UK population WL2 in 2009.

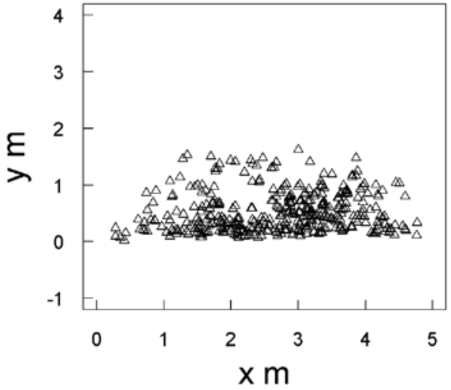

Figure B21. *L. vulgaris* ramets in UK population WL3 in 2009.

AK - CK

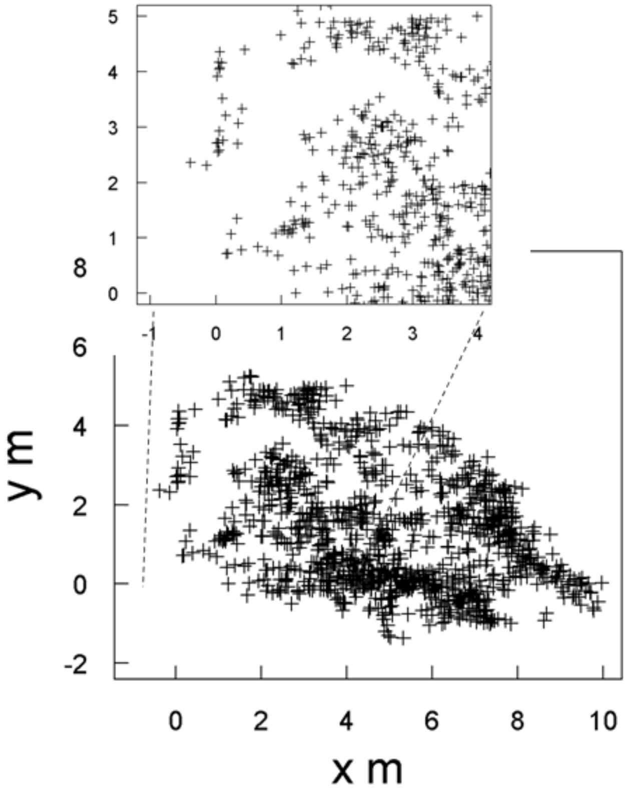

Figure B22. *L. vulgaris* ramets in AK population CK in 2010.

AK - FS

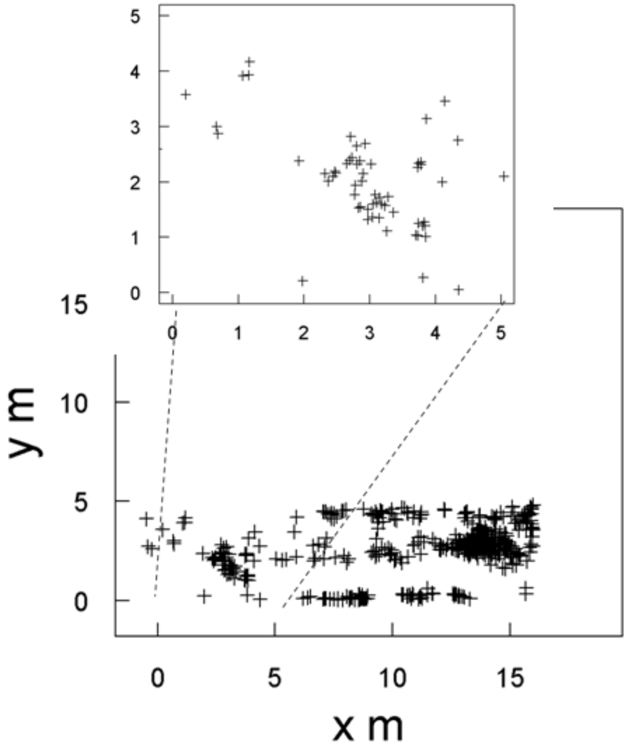

Figure B23. *L. vulgaris* ramets in AK population FS in 2010.

AK - HR

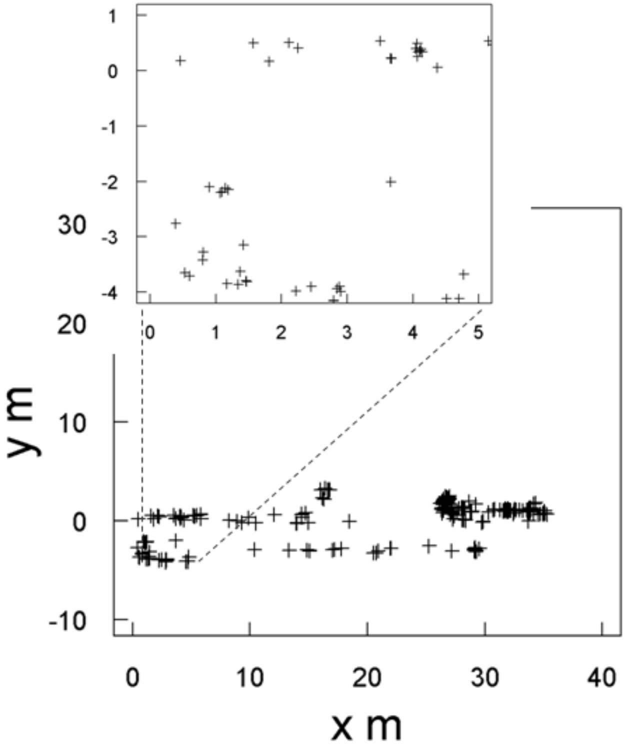

Figure B24. *L. vulgaris* ramets in Alaskan population HR in 2010.

AK - MB

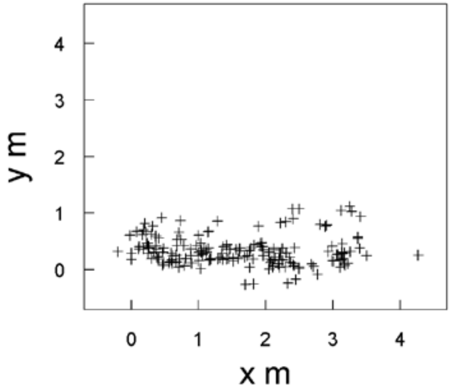

Figure B25. *L. vulgaris* ramets in Alaskan population MB in 2010.

AK - NK

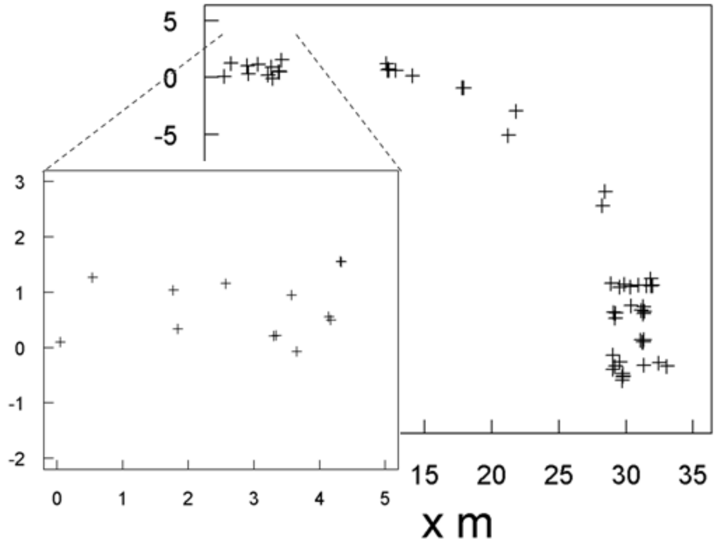

Figure B26. *L. vulgaris* ramets in Alaskan population NK in 2010.

AK - RV

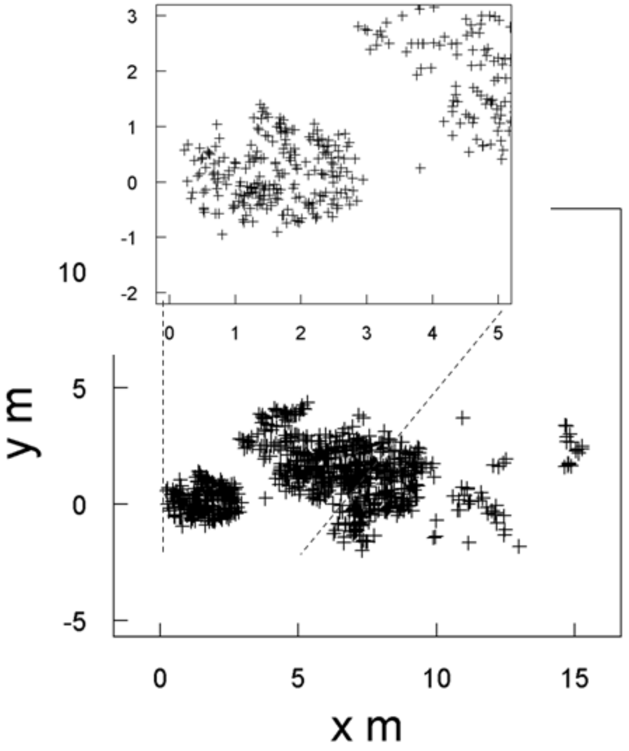

Figure B27. *L. vulgaris* ramets in Alaskan population RV in 2010.

AK - TW

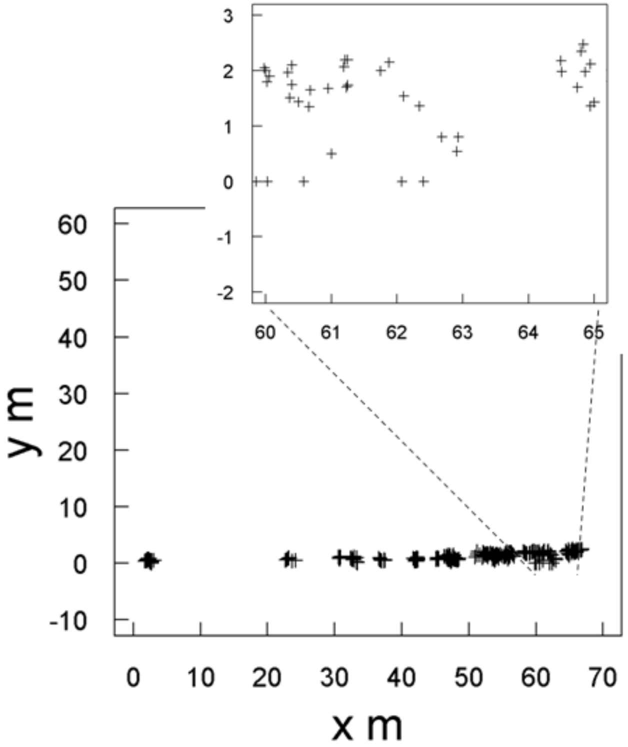

Figure B28. *L. vulgaris* ramets in Alaskan population TW in 2010.

Appendix B references

USDA (2013) PLANTS Database. United States Department of Agriculture. http://plants.usda.gov Accessed 5th August 2013.

Appendix C - Soil analysis.

Soil samples were taken from the eight UK sites, rather than all 12 of the UK 2009 populations within sites, because funding was limited and the soil characteristics were likely to be similar within a few hundred metres. A soil sample was not taken from the Alaskan population MB because all of the substrate was gravel. Three quadrats from the 0.5 x 0.5 m grid across each population were randomly picked and soil samples were taken as near as possible to the centre of the quadrat. Surface vegetation, large roots and stones were removed and then a sample of approximately 5 cm diameter up to a 10 cm depth was taken. The three samples from each population were mixed and double bagged in polythene with a press lock. Soil samples were collected on 14th October 2010 for Alaskan sites and were analysed by Laurie Wilson at the University of Alaska Fairbanks (Palmer Research Center, 1509 S. Trunk Rd., Palmer, AK 99645). Soil samples were collected from Essex sites on 7th and 8th November 2010 and from the MF population in Yorkshire on 11th November. The UK samples were analysed by Francois Bochereau at Forest Research (Alice Holt Lodge, Farnham, Surrey GU10 4LH).

Soil samples were sieved to 2 mm and then the proportions of sand (2 – 0.05 mm), silt (0.05 - 0.002 mm) and clay (0.002 – 0.001 mm) were found using the USDA particle size scales allowing classification into soil families (e.g. sandy loam) using the USDA textural classification guide (Soil Survey Staff, 2011). A laboratory mistake meant that dry moisture content was not recorded for Alaskan soils, so moisture content is only shown as field wet percentage and cannot be compared between the countries. Organic matter content was analysed as loss on ignition. P was analysed using a Mehlich 3 extraction for both UK and Alaskan soils. K, Ca, Na, Mn and Mg were analysed using a1M NH_4NO_3 extraction with a soil:extractant ratio of 1:5 for UK soils, but a Mehlich 3 extraction for Alaskan soils. S was analysed with a 1M NH_4NO_3 extraction for UK soils, but a water extraction for Alaskan soils. Hierarchical cluster analysis of soil results was carried out using the functions dist and hclust in R 2.12.2 using the euclidean distance and complete and single linkage (R Development Core Team, 2011).

Hierarchical cluster analysis of soil chemical elements, pH, loss on ignition and texture, both individually and in combination (Figures 4 & 5), does not group the populations by region. There was no difference between complete and single linkage methods. However, the Alaskan populations had a much lower clay content than all the UK populations and a higher sand content than most of the UK populations (Tables C1 & C2). There is also a smaller pH range for the Alaskan populations (5.68 - 6.25 pH) than the UK populations (4.40 - 8.03 pH).

Appendix C references

R Development Core Team (2011) *R: A language and environment for statistical computing. R Foundation for Statistical Computing. http://www.R-project.org/.* Vienna, Austria.

Soil Survey Staff (2011) Soil survey laboratory information manual. *Soil Survey Investigations Report No. 45* (ed R. Burt). United States Department of Agriculture, Natural Resources Conservation Service & National Soil Survey Center, Lincoln, Nebraska.

Table C1. Soil analysis for Alaskan populations.

Population	USDA texture	%			pH	% field moisture	% loss on ignition	Parts per million						
		San	Silt	Clay				P	K	Ca	Mg	S	Mn	Na
CK	Sand	86.5	13.5	0.0	6.10	30.65	26.06	54	496	3425	521	8.03	56.3	55
FS	Sandy loam	68.2	29.8	2.0	5.89	38.47	14.08	76	124	3558	113	7.45	5.1	13
HR	Loamy sand	73.2	23.8	3.0	6.25	27.16	6.28	112	85	2200	42	6.40	22.2	15
MB	Loamy sand	79.2	18.4	2.4	5.90	11.02	1.74	44	38	488	40	4.95	18.0	13
NK	Loamy sand	79.0	21.0	0.0	5.68	78.32	29.85	24	330	3126	644	9.23	30.8	20
RV	Sand	87.2	11.4	1.4	6.10	15.46	3.50	31	94	674	81	9.06	36.8	12
TW	Sand	86.5	13.5	0.0	6.10	30.65	26.06	54	496	3425	521	8.03	56.3	55

Table C2. Soil analysis for UK 2009 populations.

Population	USDA texture		%		pH	% field moisture	% loss on ignition				Parts per million			
		San	Silt	Clay				P	K	Ca	Mg	S	Mn	Na
BP1	Sand	90.4	3.5	6.1	6.46	12.90	3.01	6.26	251	599	111	3.33	1.26	15.3
BP3	Sandy loam	57.5	29.9	12.6	6.32	24.97	7.60	11.32	256	1560	109	5.76	1.30	9.0
CM	Clay loam	44.9	32.6	22.5	4.4	41.28	25.14	13.37	132	1361	147	39.38	24.79	12.5
HC	Loam	38.4	45.9	15.7	6.66	16.03	7.08	46.23	700	1343	170	5.01	1.77	48.0
IG3	Loam	39.1	34.6	26.3	7.9	26.94	16.91	15.05	844	4195	192	28.91	0.42	16.1
LP2	Sandy loam	57.4	30.5	12.1	7.44	26.10	7.43	16.47	249	2146	116	5.29	0.11	10.0
MF	Loam	48.5	29.8	21.7	8.03	27.45	22.65	23.52	545	3460	292	26.77	0.46	23.8
WL1	Clay loam	37.0	31.8	31.2	7.38	25.44	13.52	12.64	412	3759	347	17.10	0.32	51.8

Appendix D. Supplementary information for Chapter 3: *L. vulgaris* ramet height and reproduction analysis.

Ramet height

Table D1 shows Minimum Adequate Models of *L. vulgaris* ramet height including both the UK 2009 and Alaskan populations, with ramet density measured at varying spatial scales. Ramet height initially increases with vegetation height and then plateaus (Figure D1). The relationship between ramet height and ramet focused conspecific density varies both with the spatial scale and between the UK and Alaskan populations (Figure D2). Tables D2 and D3 show Minimum Adequate Models of *L. vulgaris* height when UK 2009 and Alaskan populations are analysed separately. The AIC values of all the Minimum Adequate Models in tables D1 - D3 are compared in Figure D3 relative to the model with the lowest AIC within each of the combined region and separate region sets of analyses.

Table D1. Continued on the next page. AIC and fixed effects of Minimum Adequate Models of *L. vulgaris* Ln Height with the surrounding ramet density measured at different spatial scales. Models are calculated using Restricted Maximum Likelihood with Population as a random effect.

	Minimum Adequate Models with ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	**1.6 m**	3.2 m	6.4 m	12.8 m
AIC of MAM	16595.33	16641.72	16653.17	16592.30	**16459.26**	16639.06	16603.15	16514.6
Intercept: UK, partly shaded.	2.99	2.86	2.78	2.70	**2.79**	2.67	2.83	2.95
Region AK	-0.551	-0.517	-0.551	-0.626	**-0.703**	-0.587	-0.809	-1.35
Shaded	-0.304	-0.339	-0.311	-0.287	**-0.331**	-0.356	-0.325	-0.329
Unshaded	-0.629	-0.631	-0.542	-0.435	**-0.449**	-0.416	-0.587	-0.651
Vegetation height	0.0272	0.0280	0.0248	0.0221	**0.0204**	0.0220	0.0245	0.0277
Vegetation height^2	-1.72×10^{-4}	-1.87×10^{-4}	-1.80×10^{-4}	-1.72×10^{-4}	**-1.68×10^{-4}**	-1.74×10^{-4}	-1.94×10^{-4}	-2.02×10^{-4}

Table D1 continued.

	Minimum Adequate Models with ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	**1.6 m**	3.2 m	6.4 m	12.8 m
Ramet density	3.84 x 10^{-4}	0.00363	0.00768	0.0167	**0.0229**	0.0691	0.144	0.243
Ramet density^2	NA	-2.80 x 10^{-6}	-2.11 x 10^{-5}	-1.12 x 10^{-4}	**-2.68 x 10^{-4}**	-6.91 x 10^{-4}	-0.00641	-0.117
AK: Veg. height	0.00350	0.00442	0.00566	0.00686	**0.00648**	0.00697	0.00888	0.0101
AK: Ramet density	-6.02 x 10^{-4}	-0.00202	-0.00282	-0.00288	**NA**	-0.0309	NA	0.695
Vegetation height: Ramet density	-4.96 x 10^{-5}	-1.02 x 10^{-4}	-8.91 x 10^{-5}	-6.52 x 10^{-5}	**NA**	-2.10 x 10^{-4}	-9.38 x 10^{-4}	-0.00551

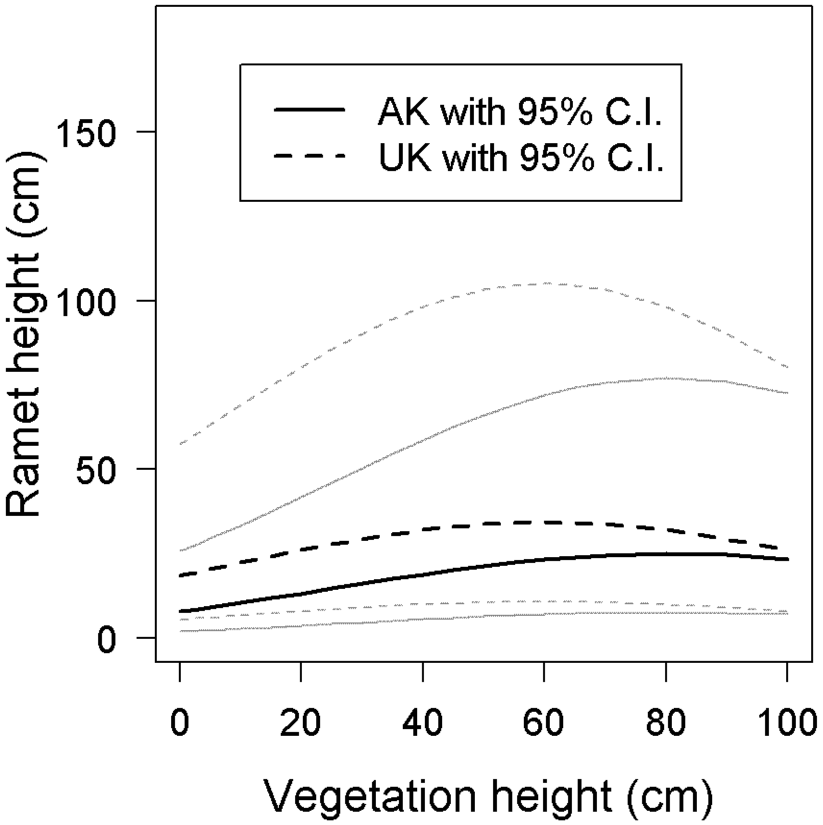

Figure D1. Predictions from a mixed effects model of the height of AK and UK *L. vulgaris* ramets with increasing vegetation height. Surrounding ramet density is held at 173 ramets within 1.6 m (20 ramets / m^2) and surrounding lines are the 95 % Confidence Intervals for the populations.

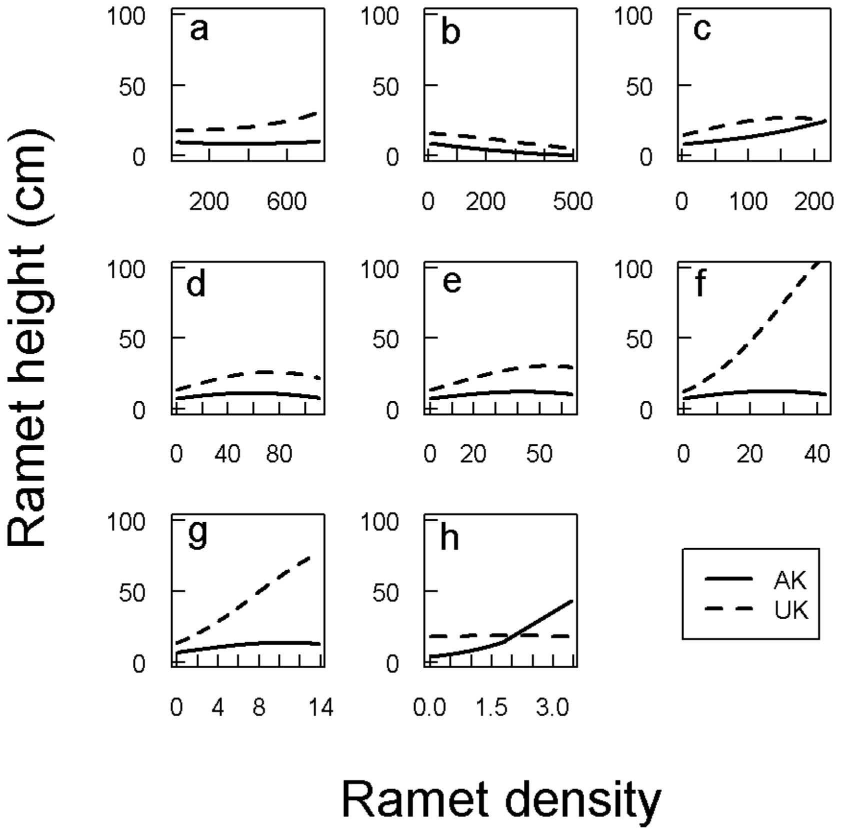

Figure D2. UK and AK *L. vulgaris* mean ramet height predictions for Minimum Adequate Models with surrounding ramet density within a) 0.1 m b) 0.2 m c) 0.4 m d) 0.8 m e) 1.6 m f) 3.2 g) 6.4 m h) 12.8 m. Vegetation height is held at the median of 10 cm.

Table D2. *L. vulgaris* ramet height for UK populations only. AIC and fixed effects of Minimum Adequate Models of *L. vulgaris* Ln height with the surrounding ramet density measured at different spatial scales. Population is included as a random effect.

	Minimum Adequate Models with ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	1.6 m	3.2 m	6.4 m	**12.8 m**
AIC (REML)	7428.19	7439.52	7478.05	7474.91	7465.39	7454.76	7467.93	**7360.17**
Intercept: partly shaded	2.91	2.82	2.84	3.01	2.83	2.63	2.86	**3.19**
Shaded	-0.344	-0.373	-0.343	-0.350	-0.361	-0.366	-0.337	**-0.306**
Unshaded	-0.705	-0.705	-0.642	-0.698	-0.526	-0.408	-0.660	**-0.641**
Vegetation height	0.0344	0.0351	0.0309	0.0296	0.0247	0.0245	0.0330	**0.0430**
Vegetation height^2	-2.48×10^{-4}	-2.58×10^{-4}	-2.60×10^{-4}	-2.62×10^{-4}	-2.50×10^{-4}	-2.50×10^{-4}	-2.60×10^{-4}	$\mathbf{-2.15 \times 10^{-4}}$
Ramet density	7.95×10^{-4}	0.00309	0.00346	NA	0.00877	-0.0758	-0.172	**-1.95**
Ramet density^2	NA	NA	NA	NA	NA	0.0146	0.108	**2.07**
Vegetation height: Ramet density	-4.96×10^{-5}	-1.07×10^{-4}	-4.80×10^{-5}	NA	2.87×10^{-4}	8.86×10^{-4}	-0.00197	**-0.0286**

Table D3. *L. vulgaris* ramet height for Alaskan populations only. AIC and fixed effects of Minimum Adequate Models of *L. vulgaris* Ln height with the surrounding ramet density measured at different spatial scales. Population is included as a random effect.

	Minimum Adequate Models with ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	1.6 m	3.2 m	6.4 m	**12.8 m**
AIC (REML)	9099.53	9227.32	9178.42	9104.69	9115.18	9174.14	9160.92	**9083.33**
Intercept	2.09	2.00	1.88	1.78	1.82	1.85	1.75	**1.34**
Vegetation height	0.0279	0.0287	0.0297	0.0280	0.0270	0.0268	0.0299	**0.0314**
Vegetation height^2	-1.32 x 10^{-4}	-1.43 x 10^{-4}	-1.51 x 10^{-4}	-1.41 x 10^{-4}	-1.41 x 10^{-4}	-1.35 x 10^{-4}	-1.54 x 10^{-4}	**1.54 x 10^{-4}**
Ramet density	-2.52 x 10^{-4}	0.00166	0.00713	0.0175	0.0248	0.0386	0.126	**1.08**
Ramet density^2	1.00 x 10^{-6}	-3.50 x 10^{-6}	-3.46 x 10^{-5}	-1.51 x 10^{-4}	-2.90 x 10^{-4}	-6.95 x 10^{-4}	-0.00575	**-0.216**
Vegetation height: Ramet density	-4.54 x 10^{-5}	-8.06 x 10^{-5}	-1.17 x 10^{-5}	-1.04 x 10^{-4}	-1.09 x 10^{-4}	-2.36 x 10^{-4}	-7.79 x 10^{-4}	**-0.00358**

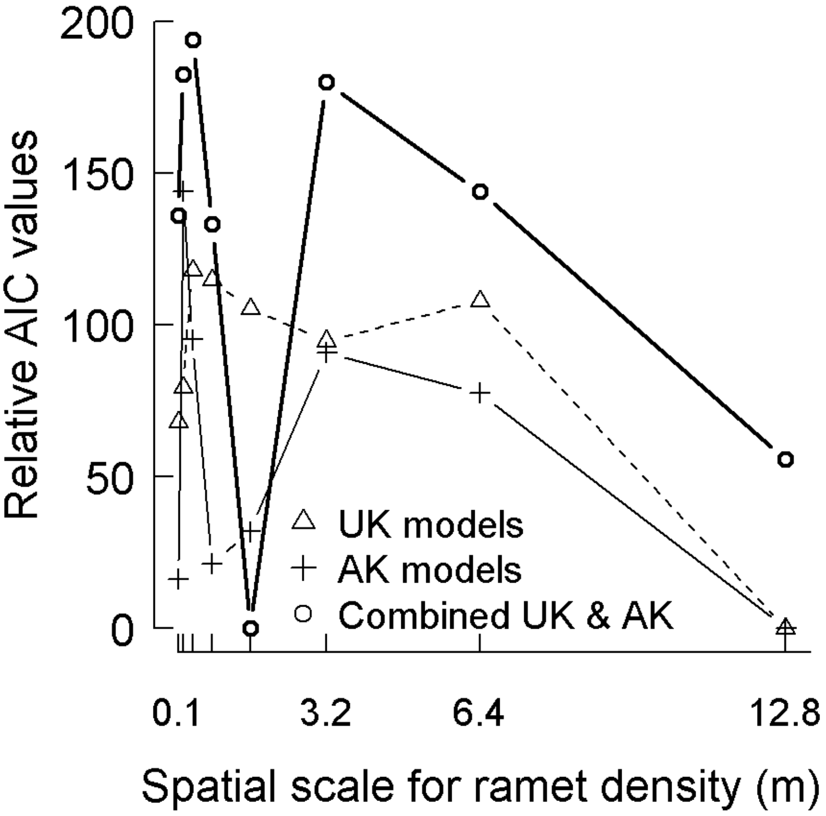

Figure D3. Comparison of the relative Akaike's Information Criterion values across Minimum Adequate Models of *L. vulgaris* Ln ramet height where conspecific ramet density has been measured around ramets within 0.1 m, 0.2 m, 0.4 m, 0.8 m, 1.6 m, 3.2 m , 6.4 m and 12.8 m. Models using these different spatial scales are compared within analyses of UK populations only, Alaskan (AK) populations only and a combined analysis of both UK and Alaskan populations. The values of models within each of the three sets of analysis are shown relative to the model with the smallest AIC. Figure 17 shows a comparison using maximal models so that all models contain the same terms.

Flowering

Tables D4 and D5 show the proportion of ramets in the UK and Alaskan *L. vulgaris* populations that flowered, that produced mature fruit and that were sampled. Table D6 shows the Minimum Adequate Models for flowering probability where density is measured at differing spatial scales. The signs of the fixed effects coefficients in Table D6 do not indicate whether the relationship with flowering probability is positive or negative because this is a binomial model. The model where the density of flowering ramets is measured within 3.2 m has the lowest AIC. When maximal models with the same number of terms were compared, the model with density of flowering ramets at 3.2 m spatial scale remained as the lowest AIC.

Table D4. Number of *L. vulgaris* ramets that flowered, that produced mature fruit and that had fruit collected in UK 2009 populations.

Population	Total ramets:	that flowered.	that produced mature fruit.	with lowest opening fruit collected.
BP1	523	47 (8.99%)	36 (6.88%)	10
BP2	131	21 (16.03%)	14 (10.69%)	6
BP3	320	18 (5.63%)	4 (1.25%)	1
CM	78	12 (15.38%)	4 (5.13%)	3
HC	200	76 (38.00%)	37 (18.5%)	26
IG2	3	3 (100%)	2 (66.67%)	2
IG3	653	65 (9.95%)	24 (3.68%)	2
LP1	356	167 (46.91%)	123 (34.55%)	93
MF	301	4 (1.33%)	3 (1.00%)	0
WL1	93	40 (43.01%)	33 (35.48%)	15
WL2	86	13 (15.12%)	7 (8.14%)	0
WL3	470	93 (19.79%)	84 (17.87%)	9

Table D5. Number of *L. vulgaris* ramets that flowered, that produced mature fruit and that were sampled in Alaskan populations.

Population	Total ramets:	that flowered.	that produced mature fruit.	with lowest opening fruit collected.
CK	1779	370 (20.80%)	309 (17.37%)	108
FS	629	183 (29.09%)	119 (18.92%)	55
HR	651	140 (21.51%)	100 (15.36%)	35
MB	229	4 (1.75%)	0	0
NK	138	40 (28.99%)	28 (20.29%)	13
RV	935	306 (32.73%)	188 (21.28%)	145
TW	324	33 (10.19%)	17 (5.25%)	4

Table D6. Continued on the next page. Minimum Adequate Models of *L. vulgaris* flowering probability, with the density of surrounding flowering ramets at varying spatial scales and random population intercepts. Population standard deviations varied between 1.33 and 1.90.

	Minimum Adequate Models with ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	1.6 m	**3.2 m**	6.4 m	12.8 m
AIC	5076.61	5015.74	5014.10	5009.16	4994.26	**4957.91**	5024.81	5059.74
Intercept (UK, shaded)	-6.89	-6.73	-6.92	-7.12	-7.29	**-7.99**	-9.17	-9.16
Region AK	-1.72	-1.72	-1.86	-1.83	-1.92	**-0.623**	NA	NA
Ln ramet height	1.19	1.09	1.23	1.33	1.42	**1.46**	1.89	1.81
Vegetation height difference	0.0296	0.0282	0.0588	0.0483	0.0138	**0.0171**	0.0169	0.0181
Flowering ramet density	-0.0185	-0.0373	-0.0549	-0.0707	-0.104	**-0.109**	-0.0671	0.818
Unshaded	1.85	1.77	1.77	1.67	1.63	**1.38**	1.36	NA

Table D6 continued.

	Minimum Adequate Models with ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	1.6 m	**3.2 m**	6.4 m	12.8 m
Region AK: Ln ramet height	0.969	0.961	0.879	0.862	0.852	**0.577**	NA	NA
Region AK: Fl. ramet density	0.00323	0.00584	0.0161	0.0257	0.0562	**NA**	NA	NA
Ln ramet height: Veg. height difference	NA	NA	-0.00903	-0.00916	NA	**NA**	NA	NA
Ln ramet height: Fl. ramet density	0.00626	0.0135	0.0182	0.0224	0.0310	**0.0702**	0.144	0.525
Vegetation height difference: Fl ramet density	NA	NA	NA	0.000428	0.000895	**0.00160**	0.00327	0.00982

Mature fruit production

Table D7 shows the models of fruit number on mature ramets with density measured at varying spatial scales. The models with flowering density measured within 1.6 and 3.2 m have a similar AIC. When maximal models with the same number of terms are compared, then the models with density measured at 1.6 and 3.2 m remain the ones with the lowest AIC.

Table D7. Minimum Adequate Models of fruit production of 647 mature *L. vulgaris* ramets, with the density of surrounding flowering *L. vulgaris* ramets measured at varying spatial scales. Models have negative binomial errors, a log link function and 16 populations as random intercepts. Population standard deviations vary between 0.434 and 0.722.

	Minimum Adequate Models with flowering density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	**1.6 m**	**3.2 m**	6.4 m	12.8 m
AIC	3541.50	3539.82	3534.18	3529.04	**3524.08**	**3522.86**	3528.40	3546.26
Intercept	7.27	6.33	6.60	5.91	**7.47**	**7.00**	6.60	4.40
Region AK	0.682	0.450	0.646	NA	**NA**	**NA**	NA	NA
Ln ramet height	-9.04	-7.94	-8.60	-8.17	**-9.59**	**-9.33**	-9.12	-6.75
Ln ramet height^2	3.28	2.92	3.18	3.09	**3.47**	**3.42**	3.38	2.71
Ln ramet height^3	-0.339	-0.303	-0.332	-0.321	**-0.354**	**-0.350**	-0.347	-0.288
Flowering ramet density	-0.00984	-0.0259	-0.0285	0.0298	**0.0758**	**0.176**	0.595	NA
Region AK: Flowering ramet density	NA	0.00635	NA	NA	**NA**	**NA**	NA	NA
Ln height: Fl. r. density	0.00327	0.00313	0.0118	NA	**NA**	**NA**	NA	NA

Seed production

Figure D4 shows the black seed from sampled fruit in UK and Alaskan populations. Table D8 shows the distribution of *Rhinusa antirrhini* across samples from the UK populations. Table D9 is the analysis of black seed presence and number in Alaskan and the UK fruit without *R. antirrhini*, while Table D10 shows analysis for the total (black & grey) seed in Alaskan and UK fruit without *R. antirrhini*. Table D11 shows the full analysis of Alaskan and all UK fruit seed number with flowering ramet density at various spatial scales with two-way interactions.

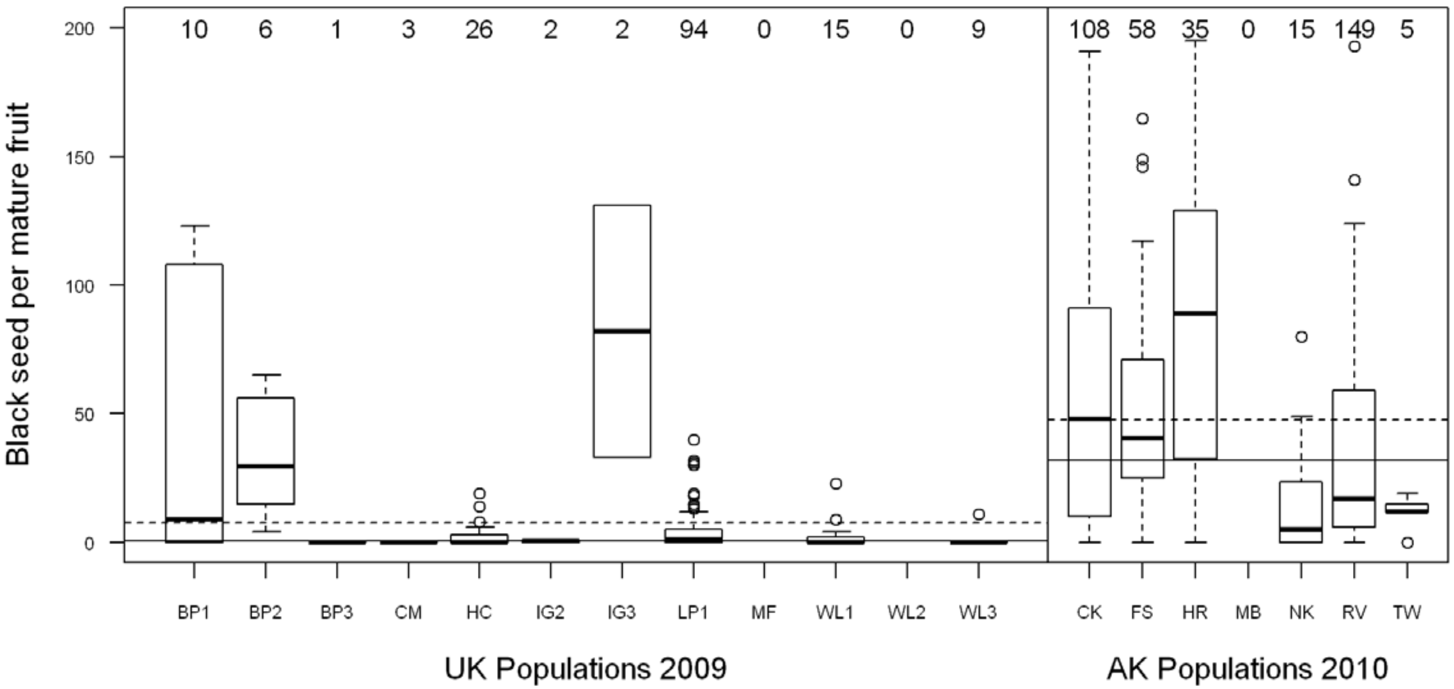

Figure D4. Black seed in mature opening *L. vulgaris* fruit collected from UK and AK populations. The solid line is the median and the dashed line the mean within each region. The number of mature opening fruit collected in each population are above each box. Some populations and fruit with missing values were removed before analysis with generalised linear mixed effects models.

Table D8. *R. antirrhini* and *R. antirrhini* parasitoid presence in opening fruit collected from UK populations in 2009. *R. antirrhini* was absent from Alaskan populations.

Population	Total opening fruit collected:	*R. antirrhini* present	*R. antirrhini* parasitoid exuviae present
BP1	10	3 (30.00 %)	1
BP2	6	1 (16.67 %)	0
BP3	1	0	0
CM	3	3 (100 %)	1
HC	26	10 (38.46 %)	3
IG2	2	2 (100 %)	1
IG3	2	0	0
LP1	94	62 (65.96 %)	1
MF	0		
WL1	15	5 (33.33 %)	4
WL2	0		
WL3	9	4 (44.44 %)	2

Table D9. Models of black seed presence and black seed number for Alaskan fruit and the UK fruit without *R. antirrhini*. The black seed presence model uses binomial errors with a complementary log-log link and has 348 observations with 11 populations as random intercepts. The black seed number model uses truncated negative binomial errors with a log link and has 294 observations with ten populations as random intercepts. For median adult fruit and fruit size the predicted probability of black seed presence is 93.11 % for Alaska and 39.87 % for the UK. The predicted black seed number per fruit is 43.60 for Alaska and 11.94 for the UK.

Model	Variable	Estimate	S.E. estimate	Z-value	p-value
Black seed presence AK & UK *R. antirrhini* absent	Intercept	-3.23	0.664	-4.86	< 0.001
	Region AK	1.66	0.333	4.99	< 0.001
	Adult fruit	0.0417	0.0169	2.47	0.014
	Ln Fruit size	0.469	0.109	4.29	< 0.001
Black seed number AK & UK *R. antirrhini* absent	Intercept	-3.56	0.496	-7.18	< 0.001
	Region AK	1.30	0.443	2.93	0.0034
	Ln Fruit size	1.23	0.0710	17.3	< 0.001

Table D10. Models of total (black and grey) seed presence and total seed number for Alaskan fruit and the UK fruit without *R. antirrhini*. The black seed presence model uses binomial errors with a complementary log-log link and has 348 observations with 11 populations as random intercepts. The black seed number model uses truncated negative binomial errors with a log link and has 313 observations with ten populations as random intercepts. For median adult fruit and fruit size the predicted probability of black and/or grey seed presence is 97.75 % for Alaska and 49.72 % for the UK. The predicted black & grey seed number per fruit is 44.08 for Alaska and 11.24 for the UK.

Model	Variable	Estimate	S.E. estimate	Z-value	p-value
Black & grey seed presence AK & UK *R. antirrhini* absent	Intercept	-3.29	0.709	-4.64	< 0.001
	Region AK	1.71	0.378	4.52	< 0.001
	Adult fruit	0.0401	0.0206	1.94	0.052
	Ln Fruit size	0.545	0.119	4.56	< 0.001
Black & grey seed number AK & UK *R. antirrhini* absent	Intercept	-3.73	0.502	-7.45	< 0.001
	Region AK	1.37	0.487	2.81	0.005
	Ln Fruit size	1.25	0.0676	18.5	< 0.001

Table D11. Continued on the following page. Minimum adequate mixed effects models of the number of black seed from 307 fruit with black seed present in UK and Alaskan *L. vulgaris* populations, with the density of surrounding flowering ramets measured at various spatial scales. Errors are modelled using a truncated negative binomial distribution and models use a log link with the ten populations as random intercepts.

	Minimum Adequate Models with flowering ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	**1.6 m**	3.2 m	6.4 m	12.8 m
AIC	2715.62	2708.72	2718.64	2722.90	**2702.36**	2714.76	2711.10	2711.56
Intercept (UK, *R. antirrhini* absent)	-4.42	-4.48	-4.51	-4.42	**-1.39**	-4.37	-2.65	-3.29
Region AK	1.39	1.37	1.37	1.36	**-0.595**	1.42	0.359	1.15
Ln Ramet height	NA	NA	NA	NA	**-0.368**	NA	-0.280	-0.259
Flowering ramet density	NA	0.00189	0.00318	NA	**-0.255**	NA	-1.07	-0.194
Adult fruit	0.122	0.126	0.137	0.138	**0.151**	0.110	0.158	0.129
Fruit size	1.37	1.38	1.38	1.38	**1.34**	1.36	1.35	1.36
R. antirrhini present	8.96	-7.31	-5.22	-1.71	**-4.37**	1.70	14.5	15.7

Table D11 continued.

	Minimum Adequate Models with flowering ramet density within a radius of:							
	0.1 m	0.2 m	0.4 m	0.8 m	**1.6 m**	3.2 m	6.4 m	12.8 m
Region AK: Flowering ramet density	NA	NA	NA	NA	**0.279**	NA	1.20	NA
Ln Ramet height: *R. antirrhini* present	NA	NA	NA	NA	**NA**	NA	3.07	3.49
Flowering ramet density: *R. antirrhini* present	NA	0.0981	0.0889	NA	**0.418**	NA	-3.80	-19.7
Adult fruit: Fruit size	NA	-0.0236	-0.0256	-0.0235	**-0.0269**	-0.0203	-0.0239	-0.0231
Adult fruit: *R. antirrhini* present	NA	0.145	0.116	NA	**NA**	0.0776	0.148	0.159
Fruit size: *R. antirrhini* present	-1.95	NA	NA	NA	**NA**	-2.11	-5.30	-5.73