The distribution and value of early warning signals in food webs under stress

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Abstract

Stress caused by human activity has many impacts on ecosystems, which may result in extinctions and tipping points to detrimental alternate stable states. Early warning signals (EWS) are a tool developed in simple theoretical systems, to predict when extinctions or tipping points are approaching. Current understanding of EWS in complex systems, which better represent natural ecosystems, is limited. Through a series of simulation experiments, this thesis provides insight into the expected strength and distribution of EWS in complex food webs, providing greater applicability for EWS empirically. Chapter 2 assesses the ability of EWS, biomass-based metrics and species' topological properties to predict where and when extinctions will occur in a food web under stress. EWS were found to be the best predictors, indicating distinctively low resilience in species approaching extinction. This provides value for EWS in complex food webs. Chapter 3 uses a network's topological properties to predict EWS distribution, finding that specialists of low trophic levels have the greatest capacity for EWS. This makes such species ideal candidates for monitoring, particularly under widespread stress. This is important where monitoring the entire network is impractical. Chapter 4 explores how the location of localised stress impacts EWS distribution, and how EWS propagate from species directly under stress. Here, changes in biomass flux were found to have a crucial role. Change in biomass flux is mediated by a species' trophic relationship with directly stressed species. This provides crucial context for how a species may be being impacted by stress, based upon the observed EWS. In Chapter 5 I discuss how the key findings of my work, such EWS capacity and the role of biomass flux, can be utilised to improve our understanding of EWS in complex systems. Valuable future research directions include understanding EWS cascades and the impact of more complex stress regimes.

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Ironically, for someone who has just written a thesis I feel like I've never been good with words.

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Statement of intellectual contribution

The work in this thesis would not have been possible without the intellectual contributions listed below. All data chapters (Chapters 2-4) have been presented as manuscripts for publication.

Chapter 1: T.M. wrote the manuscript. D.C., L.M., & C.R. contributed critically to the manuscript.

Chapter 2: T.M. and D.C. conceived and designed the study. T.M. produced the data, carried out the analysis and wrote the manuscript. D.C. & C.R. contributed critically to the manuscript.

Chapter 3: T.M. and D.C. conceived and designed the study. T.M. produced the data, carried out the analysis and wrote the manuscript. D.C. A.B., & C.R. contributed critically to the manuscript.

Chapter 4: T.M. and D.C. conceived and designed the study. T.M. produced the data, carried out the analysis and wrote the manuscript. D.C. & C.R. contributed critically to the manuscript.

Chapter 5: T.M. wrote the manuscript. D.C. & C.R. contributed critically to the manuscript.

Additional contributions

Banville, F. *et al.,* [**8th author**] (2025) Deciphering Probabilistic Species Interaction Networks

Lajaaiti, I. *et al.,* [**7th author**] (2025) EcologicalNetworksDynamics.jl: A Julia package to simulate the temporal dynamics of complex ecological networks

Jones *et al.,* [**7th author**] (in revision) Reevaluating New and Existing Challenges Early Career Researchers face across Regulatory Ecotoxicology

Blyth *et al.,* [**3rd author**] (in review) The Critical Role of Coefficients: Updating Allometric Normalisation Constants for Modern Ecology and Modelling

Declaration

I, the author, confirm that the Thesis is my own work. I am aware of the University's Guidance on the Use of Unfair Means (https://www.sheffield.ac.uk/study-skills/assessment/academic-integrity/academic-integrity). This work has not previously been presented for an award at this, or any other, university.

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Chapter 1 - General Introduction

“The literature on this subject is so vast and so well known to ecologists that it cannot and need not be referenced here” - Lewontin, 1969

The origins: critical transitions and alternate stable states

In the 1970s, accepted wisdom shifted from ecosystems possessing either a single point equilibrium or stable limit cycles (May, 1972; Holling, 1973) to recognition that ecosystems may exist in multiple stable states (Sutherland, 1974; May, 1977). Since then, there have been many different cases of alternate stable states documented, such as lakes (Schröder, Persson and De Roos, 2005), arid environments (Rietkerk and Van De Koppel, 1997; Guttal and Jayaprakash, 2008), and marine systems (Sutherland, 1981; Génin *et al.*, 2024). The transition between alternate stable states is known as a regime shift (Scheffer *et al.*, 2001). Regime shifts occur when the system moves from the basin of attraction of one stable state to another; the boundary between is known as a tipping point (Wissel, 1984). Once the tipping point has been reached, the system typically undergoes positive feedback to reach the new stable state (Scheffer and Carpenter, 2003). Transitions to alternate stable states in ecosystems are often caused by undesirable human activity, such as desertification caused by overgrazing (Guttal and Jayaprakash, 2008) or climate change collapsing fish stocks (Vert-pre *et al.*, 2013).

A challenge with systems that have alternate stable states is tipping points may be reached by gradual perturbation (Scheffer *et al.*, 2001; Guttal and Jayaprakash, 2008). Gradual perturbations can cause only small changes in system state, such as slight population decline, before the tipping point, and radical changes, such as the population collapsing, afterwards. This type of transition to an alternate stable state is known as a critical transition, and due to its nature is difficult to predict from the system state alone. Moreover, critical transitions can display a phenomenon known as hysteresis (Scheffer and Carpenter, 2003; Staal *et al.*, 2020), where reversing the transition requires the system's state to be returned to a point before the tipping point (Figure 1). The nature of hysteresis means that it is often thought more desirable to prevent critical transitions than it is to reverse them – if they could reliably be predicted.

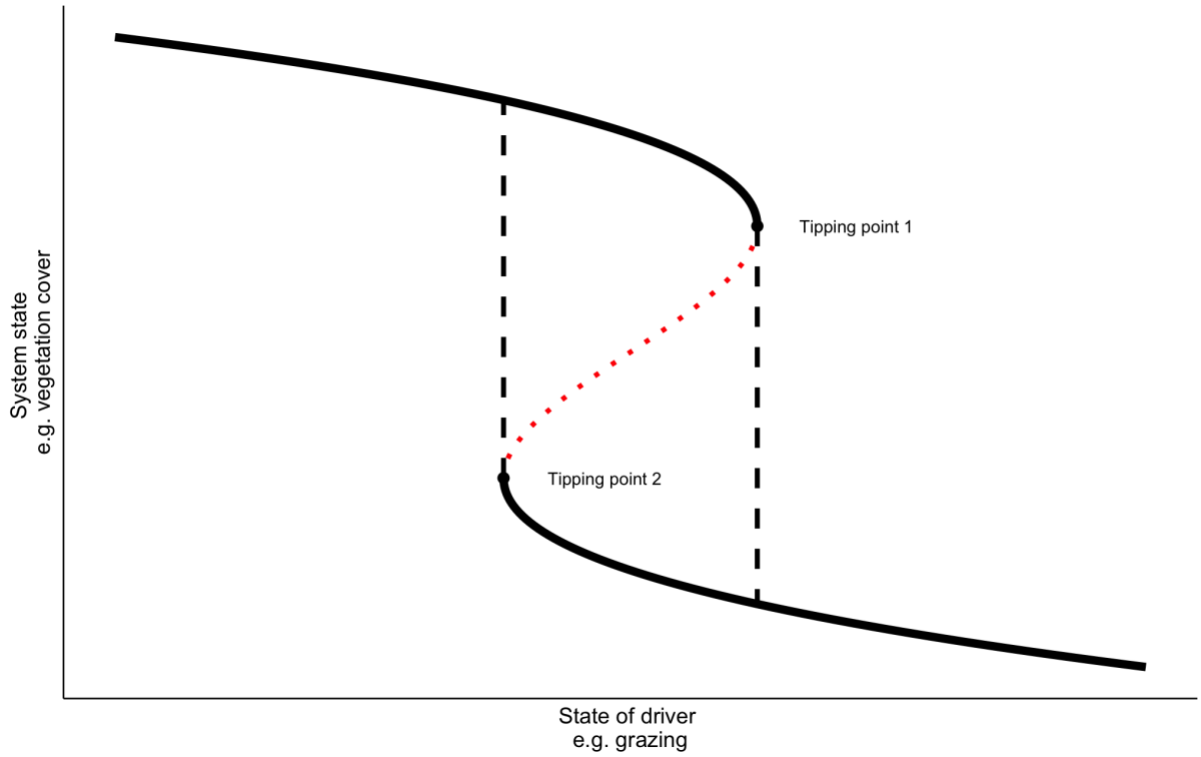

Figure 1: Schematic of hysteresis. A gradual increase in an environmental driver leads to a gradual change in the system state, until a tipping point (tipping point 1) is reached, at which point the system transitions rapidly into an alternate stable state (lower solid line). To revert back to the original state (upper solid line), the driver needs to be reduced sufficiently to reach a tipping point (tipping point 2), which is beyond the original tipping point

Predicting critical transitions: the need for early warning signals

Regime shifts in natural systems can be difficult to study because they can occur on large spatial and temporal scales (Scheffer and Carpenter, 2003). In addition, a system might be experiencing stress simultaneously from multiple sources, all possessing the potential to cause regime shifts (Carpenter and Brock, 2006; Crain, Kroeker and Halpern, 2008). For example, a lake may experience the introduction of an invasive species, overfishing, and increased pollution levels, with each scenario potentially resulting in a different regime shift to a different community. Because complex ecosystems cannot be modelled with sufficient accuracy to predict the timing of such transitions (Scheffer *et al.*, 2009), identifying general indicators which provide an early warning is critical for the anticipation and management of critical transitions.

Systems approaching a critical transition display a phenomenon called critical slowing down (CSD). This phenomenon is generated by the underlying dynamical properties of a system approaching a tipping point (Wissel, 1984). Mathematically, CSD is a result of the dominant eigenvalue of the Jacobian matrix (characterising rates of change in the system) tending to zero (Strogatz, 2001). Practically, this manifests as a loss of resilience: following a perturbation, the return rate to equilibrium of a system exhibiting CSD will decrease. It is possible to take advantage of the universal occurrence of CSD in systems approaching tipping points, as this means a wide range of systems will display the same general properties. These properties, relating to a loss of resilience, can then be used to predict the upcoming critical transition. These generic indicators are known as early warning signals (EWS). A major benefit of EWS is that they are general enough to be applied to many different ecosystems, without specific knowledge of the underlying dynamics and regardless of how well-studied the ecosystem in question is.

It is simpler to understand, and more practical to measure, resilience loss than it is to estimate changes in eigenvalues. Loss of resilience is measurable in several ways which can thus be used as EWS (Scheffer *et al.*, 2009). Over time, if a system has begun CSD, each observation of the system state will become more similar to the previous one, and the return rate following stochastic perturbation will decrease. This causes an increase in summary statistics such as autocorrelation and variance, which are easy to calculate from observations of the system state. These two simple summary statistics are still the most widely used (Carpenter and Brock, 2006; Dakos *et al.*, 2010; MacLaren, Aihara and Masuda, 2025), but are not the only potential EWS that have been proposed in the literature – there are now over 30 (Scheffer *et al.*, 2015), though most have not been tested empirically. As simple summary statistics such as autocorrelation and standard deviation are still widely used, with successful application in empirical systems, I have focused on these metrics.

Applications of EWS

EWS were originally designed to provide an estimate of a system's proximity to a tipping point, and therefore predict precisely when a critical transition would occur under the current levels of perturbation (Wissel, 1984). Such information is of great importance to the organisation of any intervention, as it provides a timescale for action. However, it is now recognised that calculating the exact time to tipping is impossible. While systems are driven towards a tipping point by external stressors, it is stochastic noise which causes the tipping point to be reached, which adds a level of uncertainty (Scheffer *et al.*, 2012; Gsell *et al.*, 2016). However, while

EWS do not predict exactly when a transition will happen, they do still provide an indication that a system is approaching a tipping point. Understanding when a population is at risk of collapse is crucial for a number of scenarios which seek to intervene and prevent the transition, such as conservation and environmental risk assessment (ERA). EWS can provide this information, and indeed are one of the only tools if the population is at risk of a critical transition.

For conservation efforts, understanding which populations are most at risk of collapse is more important than understanding those which are most impacted by stressors (Cerini, Childs and Clements, 2023), particularly because resources are often limited (Brook, Traill and Bradshaw, 2006). Traditional methods for understanding extinction risk include population viability analysis, which calculates probability of extinction (Shaffer, 1981; Ludwig, 1999), and estimations of minimum viable populations (Flather *et al.*, 2011). However, the accuracy of such tools has been questioned (Brook, Traill and Bradshaw, 2006). EWS have been suggested as a tool to improve predictions of extinctions in systems with critical transitions (Drake and Griffen, 2010), and in systems where management of ecosystems is important for ecosystem services (Bernardino *et al.*, 2025). This is because EWS can be calculated from little understanding of the underlying system's dynamics (Scheffer *et al.*, 2009), which is important for their application in complex systems such as natural ecosystems (Clements and Ozgul, 2018). Therefore, EWS should be considered a powerful tool for the protection of ecosystems.

Another area where understanding impacts of stress at an ecosystem level has become increasingly important is ERA. ERA aims to describe the risk to the environment of chemical contamination (De Luca Peña *et al.*, 2022). ERAs are transitioning from being focused on single species to becoming more ecosystem-level, for instance focusing on the preservation of ecosystem services (Maltby *et al.*, 2021), and systems impacted by multiple simultaneous chemicals in the form of chemical mixtures (Sumpter, Johnson and Runnalls, 2022). However, with this transition there is a need to develop new tools for informing ERA, and there is recognition of a need for "early warning" signals which provide an indication of ecosystem health (Borja *et al.*, 2008). Suggested improvements include the use of changes in behaviour, which are more sensitive than changes in mortality and thus provide earlier indication of stress (Hellou, 2011). An alternative method of providing early warning could be the use of EWS. Studying EWS in large food web models as a response to stress should improve EWS theory, creating a tool which has the potential to increase the efficacy of ERA.

Limitations of EWS

There is a school of thought that suggests that EWS were developed to predict critical transitions, and therefore need to be able to discriminate between a system approaching a traditional, bifurcation-based critical transition (B-tipping) from other types of transition, such as non-critical transitions, and noise-induced or rate-induced tipping (Jäger and Füllsack, 2019). Non-critical transitions are gradual changes in system state which do not produce tipping points. They do not display hysteresis, making them easier to reverse, or the unpredictability of critical transitions, rendering EWS unnecessary. However, non-critical transitions do still display CSD, and therefore will produce EWS (Kéfi *et al.*, 2013). Alternatively, noise-induced tipping is driven by an underlying shift in the noise regime of the system, rather than an external driver. While noise-induced tipping does not involve CSD, the system may display increased autocorrelation (Boettiger and Hastings, 2013), although there is debate as to whether this constitutes an EWS (Boettiger and Hastings, 2013; Drake, 2013), and there is also evidence of noise-induced transitions without EWS (Sharma *et al.*, 2015).

Rate-induced tipping (R-tipping) is a relatively new field (Ashwin *et al.*, 2012), with the transition caused by the rate of change of the external driver, rather than the magnitude of the effect (see Abbott *et al.*, 2024 for an excellent description). R-tipping has been recorded in models of complex ecological systems (Kaur and Sharathi Dutta, 2022; Panahi *et al.*, 2023) and can also produce EWS prior to critical transitions (Siteur *et al.*, 2016). Although distinguishing between R-tipping and B-tipping for observations of system state is difficult, it is essential for understanding how to prevent the approaching critical transition. While there is merit to the idea that EWS should be able to indicate which type of transition is occurring to best inform intervention efforts, this thesis has focused on exploring the use of traditional EWS in multispecies trophic networks with B-tipping and non-critical transitions. It is important to acknowledge the caveat that EWS cannot inform the type of transition which is approaching, but this issue is out of the scope of this work.

A more pertinent issue of EWS is how well they perform in multidimensional systems. The studies that developed the use of autocorrelation and variance as EWS in ecology (Carpenter and Brock, 2006; Van Nes and Scheffer, 2007) were based on simple systems with one or two species. However, natural systems are much more complex than this, and it has long been known that they are better represented by large networks of interacting species (Elton, 1927; Lindeman, 1942), which has retained value for inferring ecosystem-level processes to this day (Poisot, Stouffer and Kéfi, 2016). Multi-species systems exhibit a range of behaviours

as they approach tipping points. Of particular concern is the potential for catastrophic transitions to occur silently, when no warning signals are produced, even when critical slowing down occurs (Boerlijst, Oudman and De Roos, 2013). Indeed, there is a widening consensus that in complex networks most species will not display EWS (Dakos, 2018; Weinans *et al.*, 2019; Patterson, Strang and Abbott, 2021; Masuda, Aihara and MacLaren, 2024). Tackling this challenge is one of the most important areas for current EWS research. If the distribution of signals across a network follows predictable patterns, this could provide a way forward in developing more usable EWS. Establishing whether such patterns exist is a key aim of this thesis.

There is limited theory for the mechanisms controlling how EWS manifest in multidimensional systems. This means there are few *a priori* methods for explaining EWS for such systems. However, one study that modelled the distribution of EWS in a multispecies system found that in state space, critical slowing down occurs in one direction, represented by the dominant eigenvector (Patterson, Strang and Abbott, 2021). Species whose dynamics align with this direction will show clear EWS, while species whose dynamics are perpendicular to the dominant eigenvector will not display EWS and undergo silent transitions. The practical applications of this finding is limited, however. Calculating eigenvectors to directly infer which species will display EWS is only possible using a well-parameterised model in the vicinity of a locally stable equilibrium, which is unlikely to be available for natural systems (Dakos, 2018). However, a number of alternative solutions have been proposed, which aim to identify the characteristics of species which do and do not display EWS.

A challenge for EWS is distinguishing genuine signals from stochastic noise, which is a ubiquitous feature of ecosystems (Vasseur and Yodzis, 2004). Most EWS have been developed using long-term high-resolution time-series data, where the signal is more likely to stand out from the noise (Perretti and Munch, 2012; Boers, 2018). Indeed, it is possible for noise to mask EWS entirely in systems with low-resolution time-series (Perretti and Munch, 2012; Clements *et al.*, 2015; O'Regan and Burton, 2018). While high resolution data are becoming available for a range of ecosystems (Jeong, Sanders and Grant, 2006), this demand is an important consideration when using EWS, particularly in light of the potential for some species to not display EWS. The length of time series is another factor in determining the strength of EWS. It was found that increasing the length of the time series allows more modest signals to stand out, with most EWS expected to be modest until after the tipping point is reached, (Biggs, Carpenter and Brock, 2009) - at which point the signal strength increases as the system begins positive feedback. A more recent study corroborated this finding (Arkilanian *et al.*, 2020), although they found no relationship between time series resolution and the

performance of EWS. There is a clear demand for EWS which can provide reliable signals from shorter timeseries, with a possible solution discussed in the next section.

Solutions to EWS limitations

It remains a challenge to identify species which will best display warning signals. As a rule of thumb, species that either invade or go extinct following a transition are the best to monitor for EWS (Dakos, 2018). However, this information is challenging to ascertain prior to a transition, rendering this method impractical - though it provides a useful expectation which can easily be corroborated. A number of studies using mutualistic networks, which contain the type of interactions which lend themselves to critical transition research, find that specialist species are associated with strong EWS (Dakos and Bascompte, 2014; Aparicio et al., 2021). This was considered to be a consequence of not interacting with multiple species, each with asynchronous dynamics, which has a dampening effect on any signal. A more recent pragmatic method is to monitor the entire network, then take two cross-sections from all species time series, and identify the set of species which show the largest change in an EWS metric (e.g. standard deviation). These species can then be monitored more intensively going forward to optimise the chance of observing EWS (Masuda, Aihara and MacLaren, 2024). Expanding on methods to identify species with strong EWS is a major motivation for this thesis.

An alternate method to identifying the best candidate species for displaying traditional EWS is to develop new EWS. The simplest way to do this is to combine multiple EWS into an integrated metric (Drake and Griffen, 2010). However, experiments comparing the effectiveness of various composite EWS found that different composite EWS performed best in different treatments, and it was impossible to distinguish between true and false positives (Clements and Ozgul, 2016). EWS discussed thus far have been focused on trends in population size and therefore can be considered abundance-based early warning signals. However, changes in population are likely to be one of the final impacts of stress in a “timeline to collapse”, following changes in behaviour and physiological traits (Cerini, Childs and Clements, 2023). Trait-based EWS examine the dynamics of species’ traits, such as body size, with the expectation that changes in traits occur earlier to collapse in the timeline, which allows for approaching tipping points to be detected earlier, thus enabling a quicker response and a greater likelihood of averting the tipping point (Clements, McCarthy and Blanchard, 2019; Cerini *et al.*, 2025). Additionally, including both abundance and trait-based EWS has

been found to reduce false positive and false negative signals (Clements and Ozgul, 2016; Baruah *et al.*, 2019), making them a powerful resource if the data is available.

Two areas which have become increasingly popular in EWS research are the development of novel EWS which use either deep learning or information from multiple time series. Collectively, these are known as second generation EWS (O'Brien et al., 2023). Multivariate EWS synthesise information from the time series of all species within a network, aiming to maximise the signal-to-noise ratio. Multivariate EWS are typically developed around an *a priori* hypothesis, e.g. in a complex network the region with the highest autocorrelation is most likely to be experiencing CSD, and therefore the best monitoring candidate for observing EWS. Dimension reduction techniques, such as maximum autocorrelation factor (MAF) analysis (Haugen, Rajaratnam and Switzer, 2015), can transform the multispecies timeseries into a unidimensional timeseries which maximises the signal-to-noise ratio. Traditional univariate EWS can then be calculated based upon summary statistics (Weinans *et al.*, 2019). An alternative method of dimension reduction is using principal component analysis, projecting the data on the first principal component, which maximises variance over time (Weinans *et al.*, 2021). There have also been a number of more novel EWS developed using data from multiple timeseries; these take the maximum value and dominant eigenvalue of the variance-covariance matrix of the time series (Dakos, 2018; Chen *et al.*, 2019), and cross-correlation of multiple time series to identify regions within the network at risk of tipping (Chen *et al.*, 2012). An acknowledged shortcoming of multivariate EWS is that they are even more data-hungry than univariate EWS, requiring high resolution time series data from multiple time series, and they do not always outperform the best univariate EWS in the same network (Weinans *et al.*, 2021).

Alternatively, there has been a boom in the use of deep learning models, which incorporate changes in higher-order approximations of the dynamics into its predictions of regime shifts (Deb *et al.*, 2022; Dylewsky *et al.*, 2023; O'Brien *et al.*, 2023; Dylewsky, Anand and Bauch, 2024). In a deep learning context, the dominant eigenvalue is derived from a first-order approximation and is known to dominate dynamics near an equilibrium. However, as a system approaches a bifurcation, higher-order terms were shown to also be significant (Bury *et al.*, 2021). The deep learning algorithm used by Bury was found to predict ecosystem collapse with better sensitivity (more true positives found) and specificity (fewer false positives). In addition, the algorithm could also use qualitative information about the new state to predict the type of bifurcation being approached. Most research in the deep learning EWS space is in predictions of climate change, where there are vast quantities of data available to train

machine learning tools, and missing a tipping point is considered too risky (Lenton *et al.*, 2019).

Table 1: A summary of the current state of EWS research. Column 1 summarises the known limitations of EWS introduced in the section "Limitations of EWS". Column 2 summarises the proposed solutions to these limitations which have been introduced in "Solutions to EWS limitations". Any outstanding issues, which are either shortcomings of current solutions or necessary developments required to resolve a proposed solution, are included in column 3. Finally, whether my work attempts to address the highlighted limitation is summarised in column 4, which also indicates the relevant chapter.

Limitations of EWS	**Proposed solution to limitation**	**Issues with the solution**	**Will it be addressed in my work?**
EWs are not specific to critical transitions	Create EWS which either only appear before the correct type of transition (critical bifurcations)	No candidate EWS have been proposed	No
	Development of EWS which can identity upcoming transition type		No
	Accept this as a feature of EWS	Show EWS have value in noncritical situations and this is not a problem	Chapter 2 - compare EWS metrics to other predictors of extinction
In multidimensional systems some components won't show EWS	Identification of best candidate species for EWS	Development of methods which don't require impractical monitoring	Chapter 3 - focus on network properties based on network structure only
	Understand mechanisms which influence EWS strength	Current methods have limited practical application	Chapter 4 - assess role of biomass flux in EWS strength in food webs
	Development of second generation EWS	Second generation EWS are data hungry	Chapter 3 & 4 - improve the utility of classic EWS
EWS may be weak relative to background noise	Development of trait-based EWS	Trait data may not have been collected	No
	Development of second generation EWS	Second generation EWS are data hungry	Chapter 3 & 4 - improve the utility of classic EWS

Improving EWS performance

An ongoing conundrum for EWS is perhaps the most fundamental: in the real world, away from the carefully parametrised theoretical space where they were designed, do they actually work? A recent study, which uses both classic and second-generation (multivariate and machine learning) EWS, suggests that EWS only perform slightly better than chance (O'Brien *et al.*, 2023). Furthermore, the authors consider the inability of EWS to reliably identify critical transitions a major flaw, and recommend future work shifts to concentrate on measures of resilience, which focus on stability rather than transitions. Other research finds EWS in marine systems with nonlinear dynamics and hysteresis, a hallmark of critical transitions, but not in systems with linear dynamics (Litzow and Hunsicker, 2016). This also leads to the recommendation of testing systems for nonlinearity prior to employing EWS techniques – although they note that many real world datasets may be too short for this to be possible. These criticisms suggest that, in ecology, EWS as tools to predict critical transitions may have limited applicability. Even if this is the case, EWS do still detect changes in resilience, which may be valuable information for conservation and risk assessment.

Even when long-term data is available, most systems do not display nonlinearity, and false positive EWS are more common than true positive (Burthe *et al.*, 2016). Common findings from applying EWS to real world data are that agreement between the various tested EWS indicators is low, EWS in general are unreliable, and EWS developed for simple systems can be inappropriate for use in complex systems (Gsell *et al.*, 2016; O'Brien *et al.*, 2023; MacLaren, Aihara and Masuda, 2025), although there have been successes (Clements, McCarthy and Blanchard, 2019; Hennekam *et al.*, 2020). Recent literature reviews of the empirical use of EWS find that EWS successfully precede tipping points in 60-70% of cases (Stelzer *et al.*, 2021; Dakos *et al.*, 2024), although they note that these numbers are likely inflated by positive publication bias. Overall, it is apparent that while EWS can usually be extracted from empirical systems, their unreliability may undermine their utility. There are cases of silent transitions, frequent false positive signals, and disagreement between metrics. Understanding how best to monitor a complex network for reliable EWS is an area of much-needed research.

There is clearly debate as to whether classic EWS should be abandoned in favour of more complex, second generation EWS, or even whether true critical transitions are too rare and difficult to prove for EWS to be necessary. Despite this, classical EWS do have several factors

in their favour. A significant issue for many of the modern approaches to EWS in multispecies systems, such as multivariate EWS and cross-sectional sampling, is that they need long term, high resolution monitoring of all species within an ecosystem. This is recognised as a large, potentially impractical, data demand (Weinans *et al.*, 2021). Therefore, there is a need to develop methods to understand the distribution of EWS within complex networks, without requiring an unrealistic quantity of data. This is one of the central themes of my work.

Another benefit of EWS based upon summary statistics is that the data required is often available; population trends are a widely used indicator of ecosystem health (IUCN, 2022). EWS were designed for use in systems with critical transitions and alternate stable states, where their ability to predict the seemingly unpredictable is clearly valuable. However, EWS in all systems have the ability to quickly and easily highlight changes in resilience. While an awareness of the potential for false positives and negatives is important, calculating EWS is a quick and easy way to get additional insight into the state of the system. If EWS do not appear then minimal effort has been spent, whereas a strong signal can provide additional evidence for mitigating action. Exploring roles for EWS outside of strict critical transition detection may provide a future direction for EWS use and research.

There are clear gaps in the current understanding of EWS in multispecies systems. The performance of EWS can be improved by a better understanding of the mechanisms underlying their distribution, which would allow for targeted monitoring to be better placed to detect strong EWS. Although the ultimate aim for EWS is to support conservation efforts and ERA in empirical systems, this thesis focuses on simulation-based analysis using models of food webs. The benefits of using a model system are that EWS for all species can easily be calculated and compared, using long time high resolution time series data. Stress regimes can also be tightly controlled, and target any combination of species, as can levels of stochastic noise. This means that reliability of any observed EWS is high. In these controlled conditions, an understanding of where and why strong and weak EWS are produced in complex systems can be developed, which then has applicability to the limited data of empirical scenarios.

A modelling approach

Current EWS research in modelled multispecies systems tends to use mutualistic systems, represented by bivariate networks containing two trophic levels e.g. plants and pollinators (Dakos and Bascompte, 2014; Aparicio *et al.*, 2021). Additionally, there has been occasional use of very small trophic networks, such as two species or tri-trophic systems (Baruah *et al.*,

2019; Patterson, Strang and Abbott, 2021). However, this means there is limited understanding of how EWS manifest in larger, more complex food web networks. Such networks allow for a wide range of interaction types which are not possible in smaller networks or mutualistic networks, such as competition, and far-reaching indirect effects. It is known that increasing species richness and connectivity increases stability in food webs (Williams and Martinez, 2000), and also reduces the propagation of disturbance (Iles and Novak, 2016), both of which are likely to have an impact on the strength and distribution of EWS. This means that any findings regarding the strength and distribution of EWS in ecosystems from current models may not be applicable to natural systems, which are far larger and more complex than the simple systems used previously. Therefore, for EWS to be a useful tool in ecology, understanding how EWS manifest as a response to stress in complex food webs is an important area of research.

The tool which I have chosen to study EWS in food webs is the bioenergetic food web model (BEFW). The BEFW is a method for simulating population dynamics. It is a widely-used adaptation of the classic Lotka-Volterra Predator-Prey equations that has been standardised using allometric relationships (Brown *et al.*, 2004), and calculates changes in biomass rather than abundance (Yodzis and Innes, 1992). The use of allometry to calculate biological parameters such as metabolic and consumption rates is a key part of the BEFW, which allows for complexity from a small number of parameters and assumptions. This scales these rates by body mass, allowing for trophic level - which determines body mass - to impact population dynamics in a realistic fashion. It is important for trophic levels to have a clear and realistic impact on species dynamics, as they are one of the major distinctions between the food webs used in this study and mutualistic networks. Since its inception, the BEFW has been expanded to incorporate any number of species (Brose, Williams and Martinez, 2006), and implemented into the programming language Julia (Delmas *et al.*, 2017; Lajaaiti *et al.*, 2025). Using the BEFW as a model means that stress can be implemented through alterations in the parameters representing biological rates, with a wide range of stress regimes being easy to implement.

A crucial first step for this thesis was adapting the BEFW modelling infrastructure used throughout, as part of the team developing the EcosystemsNetworksDynamics (END) package (Lajaaiti *et al.*, 2025). I added two major components essential for my thesis; (i) introducing a stochastic element into species dynamics, and (ii) introducing an Allee effect.
Stochasticity was implemented via an Ornstein-Uhlenbeck process with a drift term (Uhlenbeck and Ornstein, 1930), which allows a parameter (growth rate for producers, metabolic rate for consumers) to vary around a mean value. Too much stochastic noise can

cause extinction without an external stressor, as the stochastic biological parameter will quickly reach a level which is incompatible with species persistence. Therefore, a decay rate was added to the noise term (detailed in chapters 2-4), which prevents the parameter from deviating too much from the mean value. Stochasticity is necessary for producing EWS because EWS are calculated from trends in the ability of a population to return to the mean following perturbation, and stochasticity provides that perturbation. In the classic deterministic BEFW, species either reach a stable equilibrium or stable oscillations, and neither dynamic is sufficient.

An Allee effect is a simple way to introduce tipping points in an otherwise stable model, and is known to produce critical transitions (Dijoux and Boukal, 2021). This is because an Allee effect adds density dependence to a biological rate. If the population biomass drops too low then the biological rate either increases (e.g. mortality rate) or decreases (e.g. consumption rate) to the point at which the population becomes unviable and goes extinct. As the rate of change in the biological rate with respect to population is exponential, the population dynamics after the tipping point will resemble that of a critical transition; where a linear change in the external driver causes a nonlinear response in the population, facilitated through the density dependence from the Allee effect impacting the underlying biological rates.

Additionally, a mechanism for varying biological parameters dynamically across the course of a simulation was implemented. While not essential for EWS or tipping points, much of the analysis in this thesis occurred on timeseries subjected to stress. Allowing rates to vary, which enables stress to drive species extinct and to tipping points within a single simulation, leads to a simpler analysis pipeline. The END package has been designed to be modular, with each of these alterations of the package optional modules which can be activated on top of the traditional BEFW model structure. All these modules are dynamic, and so required an extensive rewrite of the internal architecture of the package (as opposed to other possible modules such as temperature dependence, which is a modifier of parameters only). The building of this coding infrastructure required for the simulation experiments detailed in later chapters took months to correctly implement and test, and was a considerable amount of the work involved in producing this thesis.

Another key part of the BEFW is that the species which it models can interact in any configuration. There are a number of ways a network which represents a food web can be constructed, using two parameters: species richness (**S**), and connectance (**C**), where connectance is the proportion of potential trophic links (**L**) in the network which are realised ($\mathbf{C} = \mathbf{L}/\mathbf{S}^2$). The simplest is the random model, in which any species can eat any other, with a

probability equal to the food web's connectance (Solow and Beet, 1998). A step towards a realistic structure is the cascade model, which sees species assigned a random value between 0 & 1, and then consume species with a lower value, thus adding a hierarchical structure, with a probability 2**CS**/(**S**-1). This structure allows for a realistic arrangement in terms of richness at each trophic level, but overestimates food chain length (Goldwasser and Roughgarden, 1993). The niche model, which is widely used today and I use for constructing networks throughout, improves on this slightly by providing each species with a niche. Species are again assigned a random number, or niche value, between 0 and 1, but can only eat species whose niche value falls within a niche, which is a range of values, whose randomly chosen centre is less than that consumer's niche value. This allows species with similar niche values to be consumed by the same consumers, and slightly relaxes the strict hierarchy of the cascade model by allowing up to half of a consumer's niche to contain values larger than the consumer's niche value (Williams and Martinez, 2000). Additional models for network structure, notably the adaptive diet breath model (Beckerman, Petchey and Warren, 2006), have since been developed, but were not available in Julia when I began.

Outline of my research

This thesis aims to contribute to the understanding of how EWS manifest in complex food webs as a response to external stressors: whether EWS occur; which EWS perform best; whether there is value in calculating EWS; how the distribution of EWS can be predicted; and how EWS propagate through networks. In a series of simulation experiments, I show that EWS have value in complex food webs. EWS strength appears to be highly variable between species but this variability is, to an extent, predictable. The thesis is composed of three research chapters, each written as distinct work in independent manuscripts, but with shared and cascading themes, particularly within Chapters 3 and 4. Research focuses on both identifying species which are expected to show strong EWS, and understanding which aspects of population dynamics are driving the underlying changes in autocorrelation that produces EWS.

In Chapter 2, *A comparative approach to predicting extinction in complex food webs,* I compare the ability of EWS metrics, food web structural properties, and trends in biomass to predict where and when an upcoming extinction event will occur in a complex food web. The purpose of this is to assess the value of EWS relative to other prediction methods, because EWS indicate species resilience, which may be related to extinction risk. I explore the role of a prediction horizon, assessing the performance of the predictors when the most up-to-date

time series data becomes increasingly outdated. I find that generally using a combination of all metrics provides the best prediction for extinction, with the ability of models to predict extinction events correctly decreasing as forecast horizon increases. Additionally, I find that the most influential group of predictors are EWS metrics, especially at shorter forecast horizons. This implies that extinctions can occur following gradual trends in biomass, but not without distinctive levels of EWS metrics, and suggests value for EWS in ecosystem monitoring, even without upcoming critical transitions.

In Chapter 3, *Linking topological properties to early warning signal strength in complex food webs approaching a tipping point*, as EWS have been identified as informative of species' extinction risk, I compare the strength of four classic univariate EWS produced by species in food webs which are approaching a tipping point. This is with the intention of identifying network properties associated with species which produce the strongest signals, which is critical as (i) most species in complex food webs won't display EWS, and (ii) monitoring all species in a complex food web is impractical. I find that the strongest signals from the strongest two EWS metrics, autocorrelation and standard deviation, are associated with species with high interaction strength, which in this model indicates specialist species of low trophic levels. I find that preferentially sampling species with high interaction strength leads to a subset of species with stronger EWS than random, particularly with small sample sizes, highlighting a monitoring strategy for scenarios with limited resources. I suggest that the mechanism for these species displaying strong EWS is that they possess low levels of autocorrelation and standard deviation prior to stress, which provides them with the greatest capacity for EWS in a scenario when all species are approaching a tipping point.

In Chapter 4, *Exploring the role of species interactions in the propagation of early warning signals through complex food webs,* I simulate multiple scenarios where stress induces a tipping point within the same network, to explore whether the distribution of EWS within a food web is determined by stress regime or network topology. Finding that stress regime determines EWS distribution and the EWS a species produces is highly variable, I investigate how the relationship between a species and the source of stress determines the strength, direction and honesty of that species' EWS. I find that EWS strength is determined by changes in biomass flux, and that predators of stressed species tend to display EWS if stressed species form a large part of their diet. Prey of stressed species tend to display EWS if stressed species form a large proportion of their predators, while competitors of stressed species display negative EWS if they have a high overlap in their prey with stressed species. These findings indicate that the nature of EWS observed in a species may provide an indication as to the resilience and tipping risk in unobserved neighbouring species.

In Chapter 5, the general discussion, I review the key findings from the three research chapters, and how it fits into the overall understanding of EWS in multispecies systems and its potential role for ecosystem management and risk assessment. I discuss the future for EWS and any changes which may be beneficial to facilitate their practical applications, with an emphasis on understanding how to distinguish between signal and noise. Finally, I outline future directions of research using ideas of the relationship between species, network properties and EWS strength developed during this research.

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Chapter 2 - A comparative approach to predicting extinction in complex food webs

Abstract

Ecosystems are often subjected to external stress which pushes populations to the point of extinction. Conservation efforts try to prevent local and global extinctions. However, conservation is often resource limited, which therefore makes it important to understand which species are most vulnerable to extinction. There are several methods which have been previously used to assess a species' extinction risk, the most common being analysing trends in population. Here, three of these methods were simultaneously applied; biomass metrics, early warning signal (EWS) metrics, and network properties, to simulations of complex food webs approaching extinction, with the aim of determining the best group of predictors under a range of assumptions of the nature of the stress and the system. Time was also varied between final observation of the system and point of extinction to assess how far in advance extinction can be predicted. EWS were typically found to be the best metrics for determining where and when extinctions occur, but that a combination of predictors is always best. This suggests that species approaching extinction may not have greater population decline than other species, but display a distinctively high reduction in resilience. These findings suggest that a greater understanding of ecosystem health and species extinction risk could be achieved by incorporating EWS metrics into traditional risk assessments.

Introduction

Ecosystems are currently under heavy pressure from human activity, with threats including climate change, habitat destruction, pollution and invasive species (Intergovernmental Panel On Climate Change (IPCC), 2023; IPBES, 2019)). There is a growing consensus that this accumulation of stressors has raised extinction levels to the point where the Earth is going through the 6th mass extinction event in the history of life (Cowie *et al.,* 2022), with one million species currently threatened with extinction (Tollefson, 2019). There are significant efforts currently being undertaken to conserve many species and prevent local and global extinctions (Balmford *et al.,* 2005). To that end, it is important to understand which species are most at risk, with as much warning as is possible (Ricketts *et al.,* 2005).

Several methods exist for predicting a population's risk of future extinction. The most direct approach is to monitor trends in species' population abundance or biomass through time to inform extinction risk at local scales (IUCN, 2022). Information about such trends can be used to inform conservation of individual populations, and in aggregate, provide estimates of global biodiversity trends - e.g. the living planet index, (Loh *et al.,* 2005). In addition to trends, species time-series contain additional information that may help predict impending extinctions. In recent years a suite of tools called Early Warning Signals (EWS) have been proposed to predict impending shifts in system state from time series data (Scheffer *et al.,* 2001). As a system approaches a tipping point to a state shift such as an extinction event, the system's resilience, or ability to recover from perturbation, decreases (Holling, 1973). This leads to changes in various statistical metrics – such as temporal autocorrelation (Van Nes and Scheffer, 2007) and variance (Carpenter and Brock, 2006; Patterson *et al.,* 2021). Increases in these metrics can serve as early warning signs of an impending ecological shift, whereby higher values indicate lower resilience and, consequently, a greater risk of extinction. While EWS are typically based on single time series, more recent work into higher level EWS has examined system-level metrics, such as the dominant eigenvalue of the variance-covariance matrix (DEVCM) of a food-web's biomass dynamics (Dakos, 2018), or multivariate EWS which aggregate time series data from multiple species (Weinans *et al.,* 2019).

Species exist within a network of trophic interactions with other species, i.e. a food web (Carpentier *et al.,* 2021; Elton, 1927; Han *et al.,* 2023; Manlick *et al.,* 2023). Therefore, biomass dynamics in one species can be tightly linked to others (Eschenbrenner and Thébault, 2023; Vasseur and Fox, 2009; Volterra, 1928). Interspecific interactions mean that species can be at risk of extinction even when experiencing no direct pressure. This extinction can be

as part of an extinction cascade, or as a response to the perturbation elsewhere in the web without other extinctions (Huang *et al.,* 2023; Wignall, 2023).

The network properties of food webs are known to influence a species' extinction risk. For example, food webs with a lower species richness (Dunne and Williams, 2009) or connectance (Pękalski *et al.,* 2008) are at greater risk of extinction following a given perturbation than larger, better connected food webs. Additionally, network properties related to a species' position within a food web can also be important. For instance, species at higher trophic levels (Eschenbrenner and Thébault, 2023; Pimm and Lawton, 1978; Shanafelt and Loreau, 2018) or specialists with fewer resources (Dumoulin and Armsworth, 2022; Reed and Tosh, 2019) are known to be at greater risk of extinction.

Theoretical work into extinction risk in food webs has predominantly focused on a topological approach, where species are removed in a predetermined sequence, and secondary extinctions occur when a species loses all its prey (Berg *et al.,* 2015). One key insight from such topological approaches is that losing highly connected "keystone" species results in the most secondary extinctions (Dunne and Williams, 2009). Another method for studying extinction risk is to remove a species and then dynamically simulate the response of the community, which allows for indirect secondary extinctions caused by top-down effects, where both a higher connectedness and lower trophic level of the removed species increases the number of secondary extinctions (Curtsdotter *et al.,* 2011).

The various methods for understanding extinction risk described above have seldom been applied simultaneously to the same system. Doing so may have an improved performance in predicting extinction over any individual metric. This is because EWS, changes in biomass and network properties work in different ways which have great potential for synergy. Network properties are time-independent, which means that they have the same capacity for predicting extinction regardless of monitoring effort, at any time before the extinction event occurs. The predictions made by network properties should be sensitive to the way stress impacts the system, as this alters which properties predispose species to extinction. However, whilst network properties will be able to pick up which species have a greater intrinsic vulnerability to extinction, they are unable to predict when such an extinction will take place. In contrast, biomass metrics and EWS are time-dependent. This means that collecting more data should better inform extinction risk using these metrics. Knowledge of the state and dynamics of the system should be greater predictors of extinction closer to the event itself. This means that these metrics should be sensitive to the length of time between extinction and last observation of the system, or the prediction horizon. In systems approaching extinction, maximising the

prediction horizon at which reliable predictions can be made is advantageous as this gives the most time for mitigating actions to occur.

The aim of this study was to identify which indicators most effectively predict species extinctions in complex food webs under environmental stress. Specifically, it was investigated (i) how the predictive performance of biomass metrics, EWS, and food web network properties depends on the size and resolution of observation windows, (ii) how the system's inherent stability influences the effectiveness of these predictors, and (iii) how different stress regimes, in which stress is unevenly distributed among producers, affect their relative performance. To address these questions, a dynamic bioenergetic model was used to simulate biomass time series for algorithmically generated food webs, with species richness, connectance, and consumer–resource body mass ratios systematically varied. After establishing equilibrium dynamics, extinctions were induced by gradually reducing producer growth rates. Time series properties and food web network characteristics were then calculated and used to predict future extinction events in consumer species, comparing the predictive power of five groups of metrics across varying prediction horizons. Several simulation experiments were performed to assess the robustness of the findings across different model assumptions and parameter settings.

Methods

Bioenergetic Food Web Model

Simulation of food web biomass dynamics was performed using a stochastic version of a classic multispecies biomass dynamics model, the bioenergetic food web model, or BEFW (Lajaaiti *et al.,* 2025; Yodzis and Innes, 1992). The BEFW was chosen because it can support biomass dynamics of *n* species trophically interacting, using allometric scaling to handle differences in biological rates between species. Biomass dynamics for the primary producers and consumers are modelled as follows:

Producers:

$$B_i' = p_{it}B_i - r_iB_i^2 - \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (1)$$

Consumers:

$$B_i' = -x_iB_i + \sum_{j \in resources} x_i y_i B_i F_{ij} - \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (2)$$

Here, B_i represents the biomass of species i. The parameters r_i and p_i are components of producers' mass-specific intrinsic growth rate, where p_i sets density-independent growth, and r_i the density-dependent decline. x_i is the mass-specific metabolic rate of species i, and y_i is species i's maximum consumption rate relative to its metabolic rate. e_{ji} is j's assimilation efficiency (proportion of consumed biomass that is converted to own biomass) when consuming i. $e_{ji} = 0.45$ if i is a producer, and 0.85 otherwise (Yodzis and Innes, 1992).

Crucial to the parameterisation of an allometric model such as this are species body masses, M, which are determined via $M_i = Z^{T_i - 1}$, where T_i is the prey-averaged trophic level of species i, and Z is that food web's consumer-resource body mass ratio. Body masses and metabolic types are used to scale metabolic and consumption rates using the principle of allometry (Brown *et al.,* 2004). In the BEFW, all biological rates are scaled to the mass of the smallest producer. Here, all body masses were calculated based on trophic level, and as all producers have a trophic level of 1 by definition (Levine, 1980; Williams and Martinez, 2004), all producers have the same body mass of 1, resulting in $r_i = 1$ & $p_i = 1$ for all species. All consumers were considered to be invertebrates with respect to their metabolic type, resulting in $y_i = 8$ for all consumers, and $x_i = 0.314M_i^{-0.25}$.

F_{ij} is the density-dependent multi-resource functional response of i consuming j. It takes the form:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c_i B_i B_0^h + \sum_{k \in resources} \omega_{ik} B_k^h} \quad (3)$$

ω_{ij} is the relative prey preference of consumer i for resource j. Here, $\omega_{ij} = \frac{1}{n_i}$ where n_i is the number of resources of consumer i, B_0 is the half saturation density (set to 0.5) and c_i intraspecific predator interference (set to 0). h is the Hill exponent and determines the shape of the functional response, with a Holling type II functional response when $h = 1$ and type III when $h = 2$ (Holling, 1959a, 1959b).

Stochasticity and Stress

The bioenergetic food web model as originally described is deterministic. EWS metrics rely on detecting critical slowing down – a reduced ability to recover from perturbations – which by definition requires the presence of perturbations. Thus, environmental stochasticity was introduced as stochastic noise process acting through the density-independent growth rate of producers, p_{it} (eq. 1) as follows:

$$dp_{it} = \theta_i(\mu_{it} - p_{it})\, dt + \sigma_i\, dW_{it} \quad (4)$$

$$\mu_{it} = \mu_i + s_i t \quad (5)$$

Here, the noise process is an Orstein-Uhlenbeck process (Uhlenbeck and Ornstein, 1930) with a drift term, μ_{it}, with the expected value given by p_{it} (determined allometrically). θ_i is the noise decay rate controlling rate of return to the mean μ_{it} following stochastic perturbation, and σ_i the standard deviation of the Wiener process W_{it}, which provides the stochastic variation. Stress was simulated via gradual environmental degradation, manifesting in a decrease in growth rate, which has been implemented through μ_i in the noise process (eq. 5), where s_i is the gradient of the change in growth rate, t is time, thus making the decrease in growth rate linear. The strength of the stochastic noise in each simulation is determined by a combination of the decay rate, θ_i, which was set to 0.1 unless otherwise stated, and the noise covariance, $\sigma_i^2 / 2\theta_i$, also set to 0.1 unless otherwise stated.

Simulations of biomass dynamics were carried out in Julia (Bezanson *et al.,* 2017) using an adapted version of the *EcosystemsNetworksDynamics* package (Lajaaiti *et al.,* 2025).

Generating and Initialising Food Webs

Food webs were probabilistically generated using the niche model (Williams and Martinez, 2000). The niche model determines the position of trophic links (L) within a food web according to the number of species (S) and connectance ($C = L/S^2$). Combinations of S (ranging from 10 – 50) and C (0.1 – 0.3) were determined using a Sobol sequence, along with the consumer-resource body mass ratio (Z), the average ratio between predator body mass and prey body mass. This is used to determine biological rates, and was varied between 10 and 100, reflecting the range observed in empirical food webs (Brose *et al.,* 2006). As food webs generated by the niche model do not always stabilise with all species present, biomass dynamics were firstly simulated using the deterministic bioenergetic food web model (Delmas *et al.,* 2017; Lajaaiti *et al.,* 2025; Yodzis and Innes, 1992) to ensure each web reached a stable equilibrium. All species were initialised with a biomass of 0.5 (half the carrying capacity for producers) and simulated until the rate of biomass change fell below 0.0001 per time step. Once deterministic equilibrium was reached, stochastic noise was applied and simulated for a further 15,000 time steps. The food webs were then pruned to remove producers with no consumers, and consumers disconnected from any producer-based trophic chains.

Structuring Time Series for Forecasts

Following the initialisation phase, a 16,000-time step stochastic simulation was run, with environmental stress introduced at time step 6,000 as a slow decline in producer growth rates (see *Simulation Design* for details). Biomass was recorded at each time step to six decimal places until each species went extinct, providing a high resolution time series of biomass for all species in a food web, alongside the time of any extinction events. To construct forecasting analyses, time series were broken down into segments (referred to as observation windows) using a rolling window approach with windows constructed every 150 times steps (Figure 1). Within every observation window, relevant time series properties such as EWS metrics and biomass changes were calculated. To assess how the data influences future prediction accuracy, the prediction horizon – the number of time steps between the end of the final observation window and the extinction event – was also varied in each simulation. For example, a prediction horizon of 1000 means that predictions were based on species biomass and EWS metrics recorded 1000 time steps prior to extinction.

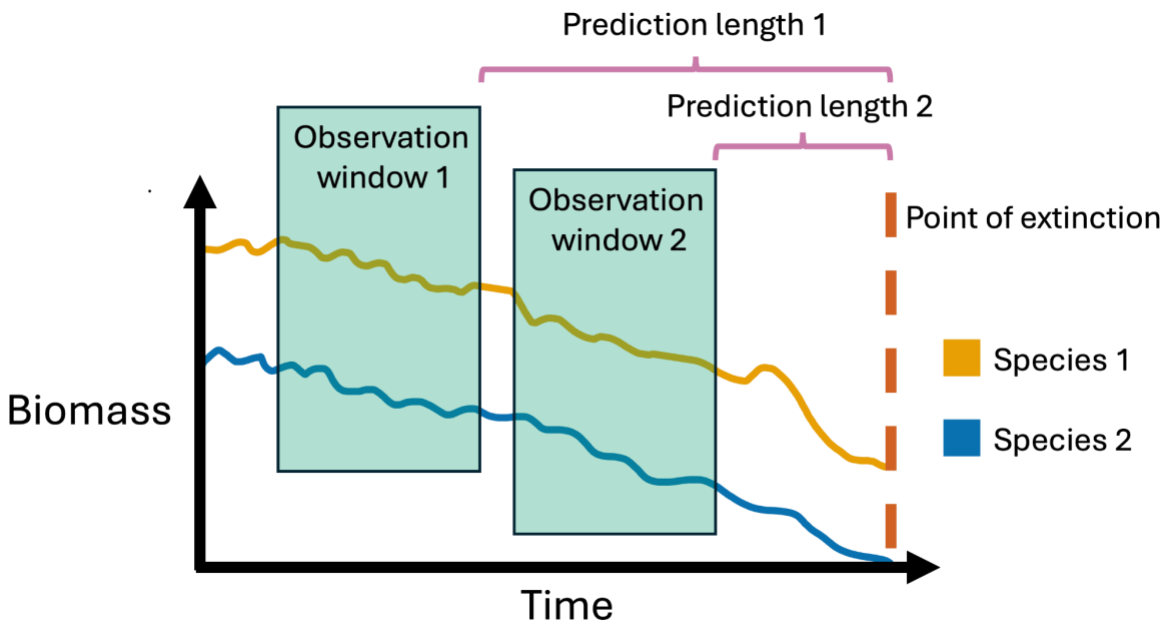

Figure 1. Schematic of the conversion of simulated biomass dynamics to time series metrics for predicting extinction. The time series is broken up into multiple regularly-spaced observation windows, within which time series metrics are calculated. The prediction horizon is the time between the end of the final observation window and the point of extinction.

Simulation Design

Using this general framework, three simulation experiments were designed based on the set of food webs described above. The first experiment assessed the overall performance of the five predictor groups (biomass metrics, node level EWS, food web EWS, node level network properties, and food web level network properties) and the sensitivity of the performance of the time series predictors – biomass and EWS metrics – to the structure of the observation window used to calculate these properties.

The second experiment varied the Hill exponent, which governs the type of functional response, and the level of stochastic noise, both of which are known to influence the amount of variation in biomass dynamics, with the expectation that more variable systems will show less predictable time series based signals prior to extinction.

Biomass based metrics and EWS indicate the species most vulnerable to perturbation (either through their high rate of loss of biomass or low stability), and thus should work best as predictors when species are equally prone to experiencing perturbation. However, this may not be the case, so for the final experiment the degree of stress experienced by the different producers in the food web was varied, which then cascaded through the food webs. The

different groups of predictors used in this study should pick up upon different facets of a species' vulnerability to extinction. Biomass metrics should indicate that a species does or does not have the population to withstand perturbation (i.e. lower loss of biomass means lower extinction risk). Statistical metrics based upon EWS indicate species stability. However, a species with high biomass and stability may still be at greater risk of extinction if it experiences high levels of stress.

Performance of Predictor Groups and Effect of Observation Window Size

To explore the sensitivity of extinction predictions to observation window properties, both the size of the observation window and the sampling resolution within it were systematically varied. During the stress phase, growth rates (μ_i) started at 1 and declined linearly at a rate of 0.0001 per time step, reaching 0 by the end of the simulation. For each simulation, time series properties were calculated within observation windows of 100, 200, and 400 time steps, and applied three different sampling resolutions: every 1, 2, or 4 time steps. This resulted in nine combinations of window size and resolution. The predictive performance of each combination was then compared to assess how observation window structure influenced the ability of different metrics to predict future extinction.

Impact of Functional Response and Environmental Noise

To test the impact of functional response and stochastic noise parameters on the predictability of extinction, their values were varied in a fully factorial design. The growth rate of producers was fixed at declining equally, and the observation window fixed at 200 time steps wide, with a sampling resolution of every 2 timesteps. The Hill exponent was varied between 1 (a type II functional response) and 2 (type III). Whilst both type II and III functional responses saturate at high prey densities, type III functional response features exponentially increase of predator consumption at low prey densities, providing more of a refuge from consumption when prey is at low densities, which causes more stable dynamics.

In addition, two parameters controlling the strength of the noise process (e.q. 4) were varied; the noise decay rate, θ_i, was varied between 0.02, 0.1, & 0.5, and the covariance of the noise process, ${\sigma^2}/{2\theta}$, through 0.05, 0.1 & 0.2. A maximum noise covariance of 0.2 was chosen as it was considered sufficiently large to be a high noise regime, yet small enough for food webs to be able to reach a stable composition. During the stress phase, growth rates (μ_i) started at 1 and again declined linearly at a rate of 0.0001 per time step, reaching 0 by the end of the simulation.

Impact of Stress Distribution Over Producers

For the final simulation experiment analysis, the assumption that all producer growth rates decline at the same rate was relaxed. The equation describing how stress operates through producer growth rate (eq. 5) was updated to include a weighting term:

$$\mu_{it} = \mu_i + W_i s_i t \tag{6}$$

Where s_i is the mean gradient of the change in growth rate, fixed to -0.0001, t is time from the point stress began, and W_i is a weighting on individual producer growth rates, which takes the form:

$$W_i = \frac{p_i^S}{\frac{1}{N}\sum_{k \in producers} p_k^S} \tag{7}$$

Where p_i is a network property of each producer, S is the exponent used to scale the weight, and N is the total number of producers in the food web.

Two different network properties of producers were tested as the basis of p_i. The first was the number of predators of species i (weighting by producer vulnerability). Here, a positive value of S results in producers with many predators experiencing a faster decline in growth rate, and a negative value of S resulting in producers with few predators experiencing a faster decline. The other network property used to define p_i was the mean number of producers consumed by the predators of i (weighting by mean predator generality). In this scenario, a positive value of S means that producers with generalist predators experience the greatest declines in growth rate, and a negative value disproportionately stresses producers with specialist predators. In both cases, the Hill exponent (2), noise covariance (0.1) and decay rate (0.1), and window size (200), were all fixed, whilst S was varied through -2, -1, 0, 1, & 2; with $S = 0$ the conditions where producers all experienced an equal decline in growth rate.

The weighting has been designed such that, whilst varying S changes the distribution of stress within each food web, the mean growth rate at any time point remains constant between stress regimes (values of S) and between food webs.

Analysis of Extinction Forecasting

To investigate the ability to predict extinction, a discrete time survival analysis was performed. This uses the observation windows to transform the continuous time series into discrete

observations. Within each observation window each species contributes a row, with an associated variable indicating system state; does that species go extinct within that observation window (1) or not (0). A discrete time survival analysis calculates the probability of each species going extinct in each observation window, given that it has survived until that point, using a logistic regression model - specifically, a generalised linear model, with a logit distribution used as the link function.

Within each observation window all predictors for each species used to fit the model were calculated, which could then be associated with whether the species had gone extinct or not in that window. Three groups of predictors were calculated from the biomass time series: biomass metrics, node-level EWS metrics, and food web-level EWS metrics, while two groups of predictors were based upon the food web network properties: node-level properties and food web-level properties.

To determine the success of each model the area under the receiver operating characteristic curve (AUC) was used. AUC measures how well a model can discriminate between two outcomes. This is a commonly used metric for classification models that has previously been used when predicting extinctions (Smits and Finnegan, 2019) or comparing EWS performance (Dakos, 2018). AUC varies between 1, which is perfect discrimination (where all extinction events were modelled to have a higher probability of extinction than all non-extinct events classification), to 0, an inverse prediction (i.e. all trues as false). An AUC of 0.5 cannot discriminate at all and the extinction events are no better predicted than random chance.

Time series properties (summarised in Table 1) are as follows. The biomass metrics were log change in biomass across each observation window, and log biomass change relative to the log of mean biomass within each window. Four widely used node-level EWS – autocorrelation, skewness, kurtosis, and standard deviation – were calculated using log-transformed biomass. A multivariate food web level EWS was also included: the dominant eigenvalue of the variance-covariance matrix (Dakos, 2018). While this measure does not identify which species is at greatest risk, it provides an overall indicator of the approach of an extinction event. The food web network properties have been taken from previous studies of food web structure and stability, (Vermaat *et al.,* 2009; Williams and Martinez, 2004, 2000) and adapted where possible for use at the node level. These properties were recalculated after each extinction event. For each observation window, the network properties of all species were aligned with the corresponding food web structure at that point in time. A summary of these network properties is provided in Table 2.

In all experiments, the first observation window ends at the 6,000th time point of the simulation, when stress begins. Additional observation windows are taken through the timeseries by shifting the window's endpoint 150 time steps, until an extinction occurs. Therefore, an extinction which occurs after 1500 time points of stress will be preceded by 10 observations. Fixing the position of the endpoints of each observation window in time allows control of the number of windows while varying the window length, which occurred during the first sensitivity analysis of this study.

To understand which groups of predictors were best able to assess extinction risk, the AUC of a model using all five predictor groups was initially calculated. Then, each of the predictor groups (biomass metrics, node-level EWS metrics, food web level EWS metrics, node-level network properties, or food web-level network properties) were dropped in turn, and the model refitted without that group. The difference in AUC compared to the complete model gives the predictive power for that group.

This analytical pipeline was performed with varying prediction horizons of 150, 1500, 3000, 4500 & 6000 time steps, effectively shifting the extinction forward up from 150 – 6000 time steps and assessing the ability of the time series up until that point to predict the extinction. As all simulations contained 6000 unstressed timesteps, even extinction events which occur immediately after stress is applied to the food web were able to be predicted using the maximum 6000-time step prediction horizon.

Table 1: Time series properties, which are calculated within each observation window, and the corresponding predictor groups within which they have been categorised.

Time-series Property (within window)	**Predictor group**
Log biomass change	Biomass metric
Log biomass change / mean biomass	Biomass metric
Lag-1 Autocorrelation	Node-level EWS
Standard deviation of log biomass	Node-level EWS
Skewness of log biomass	Node-level EWS
Kurtosis of log biomass	Node-level EWS
Dominant eigenvalue of variance-covariance matrix	Food Web-level EWS

Table 2: Food web properties from Vermaat (2009) & Williams and Martinez (2000, 2004), and the corresponding node level properties. n/a in the table refers to properties that have no translation available.

Food-web-level network property	Node-level network property
Percentage of basal taxa	Is this a basal species?
Connectance	n/a
Percentage of cannibals	Is a cannibal?
Mean clustering coefficient	Individual clustering coefficient
Normalised standard deviation of generality	Number of resources
Percentage of herbivores + detritivores	Is this a primary consumer?
Percentage of intermediate taxa	Is this an intermediate species?
Normalised standard deviation of links	n/a
Trophic links per species	Number of trophic links
Mean of the maximum trophic similarity of each taxon to other taxa	Maximum trophic similarity & Mean trophic similarity
Percentage of omnivores	Is an omnivore?
Characteristic path length	Closeness centrality
Number of trophic species	n/a
Mean trophic level	Trophic level
Percentage of top taxa	Is this a top species?
Normalised standard deviation of vulnerability	Number of consumers

Calculation of the time series metrics was carried out in Julia, and R was used to analyse extinctions forecasts (R Core Team, 2023).

Results

Performance of Predictor Groups and Effect of Observation Window Size

Across all scenarios, the full predictive model containing all five predictor groups consistently achieved the highest AUC scores at every prediction horizon, while the performance of all models declined as prediction horizon increased (Fig. 1, inset figures). The contribution of each predictor group to model performance varied depending on prediction horizon (Fig. 1, main panels). At shorter prediction horizons, removing node-level EWS metrics led to the largest drop in AUC, indicating that these metrics are the most influential for near-term extinction prediction. However, as the prediction horizon increased, the predictive value of node-level EWS metrics declined, and food web level EWS became more important. The large loss in AUC when node level EWS were dropped occurred when the observation window spanned 400 time steps (Fig. 1, right panel), demonstrating the importance of sample size for the performance of this time series based predictor group. This is likely driven by the longer observation window allowing time series metrics to be calculated with greater accuracy. Varying the sampling resolution within the observation window had no impact on the results (Supplementary figure 1).

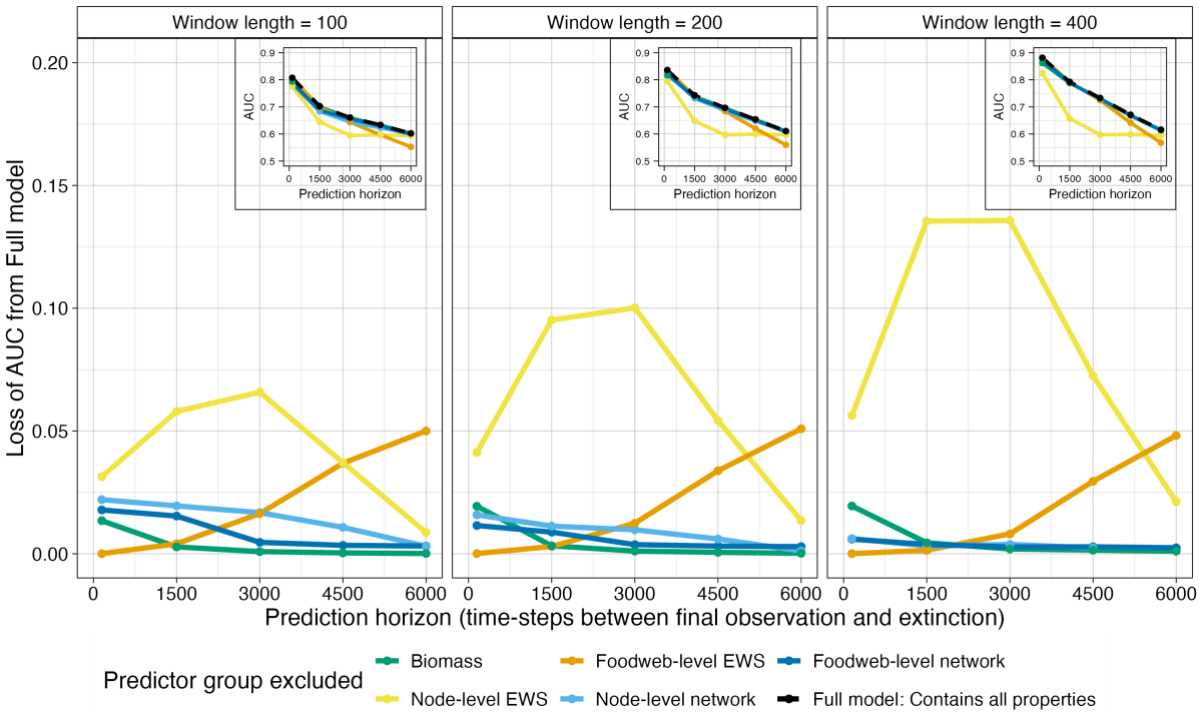

Figure 1: Comparisons of the relationship between prediction horizon (the number of time steps between the final observation window and the extinction event) and AUC across combinations of predictors, as observation window length varies from 100 to 400 time steps (panels left to right). The coloured lines represent the loss of AUC (and therefore loss of ability to distinguish extinction events) of the model with a predictor group taken out compared to that of the full model with all predictor groups. In the inset, the dashed black line in the inset plots the AUC of the full model, while the other colours represent the AUC from dropping one group of predictors in turn.

Analysis of the regression coefficients from the full model indicates that these results are largely driven by a small number of predictors: with a high coefficient of variation or autocorrelation (node level EWS), low DEVCM (food web level EWS), and high trophic links per species (food web level network property) all associated with greater probability of extinction (Fig. 2). The food web level network property trophic links per species has a high regression estimate, and thus appears to be a useful predictor for explaining variation within the model. However, as dropping food web network properties has minimal influence on AUC (Fig. 1), this suggests that this predictive ability is redundant, and covered by other correlating predictors when trophic links per species is missing. There is an increase in the predictive power of both coefficient of variation and autocorrelation as the size of the observation window increases. Since sampling resolution within the window has no effect, this suggests that the improvement is due to larger windows capturing the underlying dynamics of the time series more effectively.

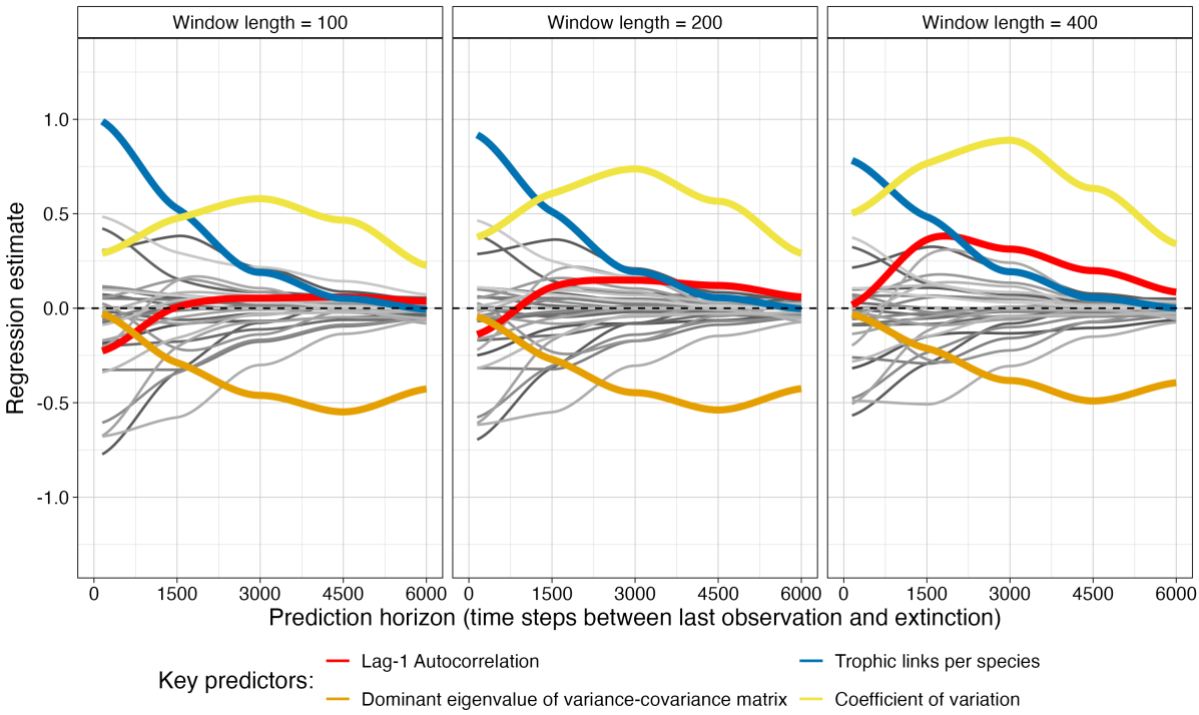

Figure 2: Effect of prediction horizon on the regression estimate (y axis) of individual predictors across varying observation window length (x axis). The model fitted includes all predictor groups. Four key predictors are coloured, with all others a shade of grey.

Impact of Functional Response and Environmental Noise

The previous experiment found that EWS at node and food web level are the most influential predictors. These are both calculated using properties of the timeseries. Here, the variation of the Hill exponent, noise decay rate, and noise covariance was found to alter both the overall AUC of a given model and the relative predictive power of EWS at node level compared to food web level. Decreasing the noise covariance, increasing the decay rate and introducing a type III functional response (Hill exponent = 2), all of which reduce the variance of the timeseries, all increase the AUC of both models (Figure 3).

Dropping node level EWS resulted in a model with a lower AUC than dropping food web level EWS when using a type II functional response, except at a very long prediction length, where both models converge at a low AUC. This result is most pronounced with a higher noise decay rate and a lower noise covariance. However, when using a type II functional response, after a forecast length of ~1500 the AUC of the model containing food web level EWS (where node level EWS are dropped) stabilises, whereas dropping food web level EWS results in an AUC decreasing as prediction horizon increases. This results in food web level EWS significantly outperforming node level EWS, unless the system's noise level is very high (covariance of 0.2, decay rate of 0.02 or 0.1).

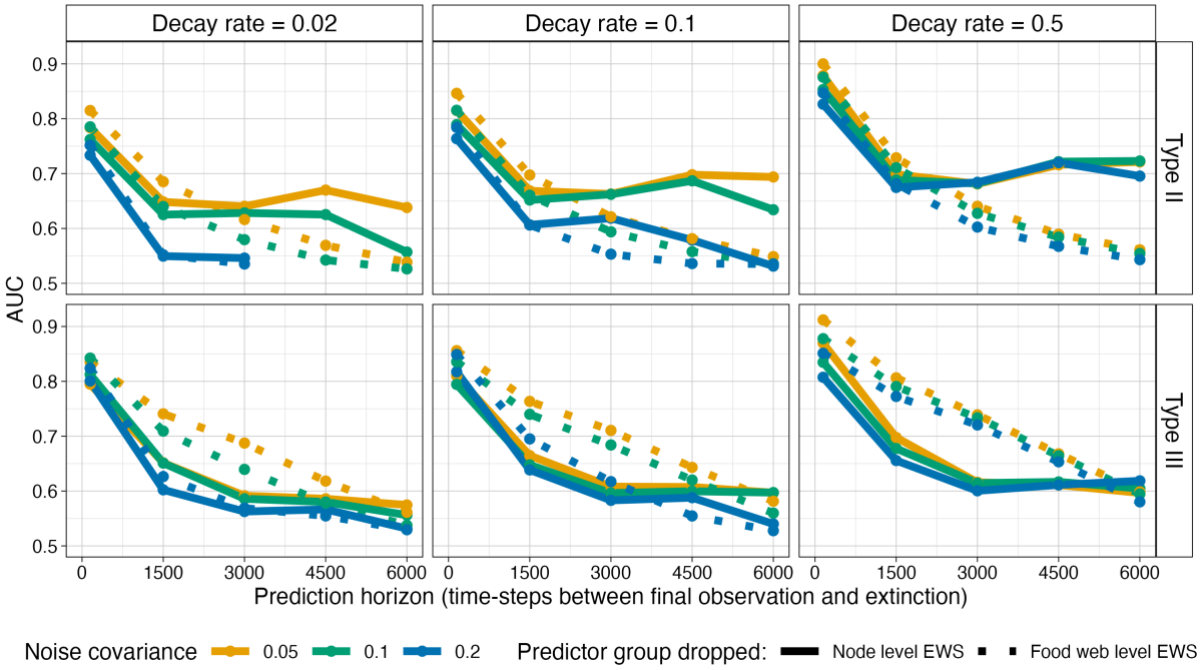

Figure 3: The influence of functional response (top row for type II, bottom row for type III), level of noise decay rate (panel, increasing left to right) and noise covariance (line colour) on AUC on the 2 most influential predictor groups. Solid line represents the model that has dropped node level EWS, but kept food web EWS, dashed line is the model which has dropped food web level EWS, and kept node level EWS. Both models contain biomass metrics, node level and food web level network properties.

Impact of Stress Distribution Over Producers

The impact of prediction horizon and predictor class was broadly consistent across scenarios where the weighting of stress on producers varied (Fig 4). In particular, node level EWS remain the most influential predictor group at short forecast horizons. However, changing the distribution of stress did have some impact at longer prediction horizons. Food web level EWS, which are the most influential predictor group at long prediction horizons when all producers experience equal stress, lost all of their impact in 3 of the 4 tested scenarios where stress is weighted. There was also a reduction in predictive power in the remaining scenario - where producers with generalist predators experience greater stress.

Instead, under weighted stress scenarios, both food web level and node level network properties were observed to increase in their relative performance as the prediction horizon increases. This is likely because under weighted stress certain species are predisposed to extinction based upon their position within the network, thereby increasing the value in understanding network properties and reducing the information provided by the time series at

longer forecast horizons. When examining individual predictors, the direction of effects was observed to be consistent with the AUC results in Figure 4 (Supp. figure 2).

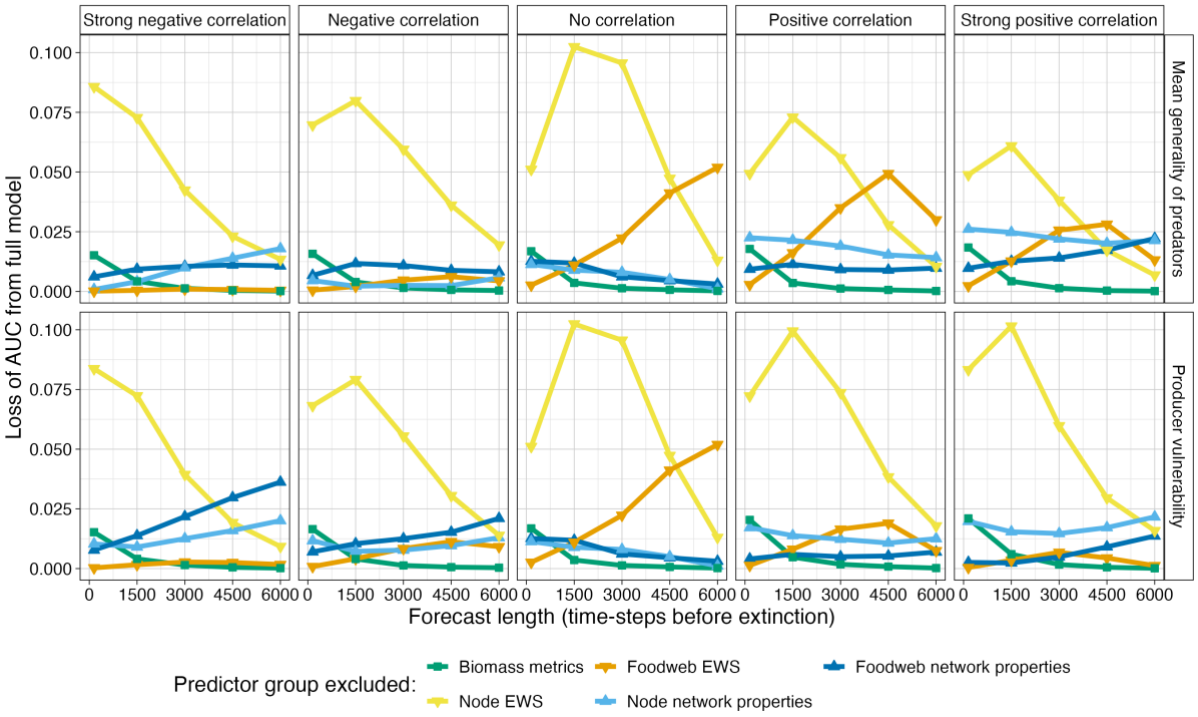

Figure 4: The effect of weighting producer stress by number of predators (top row) or mean generality of predators (bottom row) on the loss of AUC caused by dropping a group of predictors (indicated by colour) from the model, as prediction horizon varies. Producer stress has been weighted such that having a greater vulnerability or more generalist predators is associated with a greater degree of stress (right column), where there is no weighting applied and all producers experience equal stress (middle row), or where a lower vulnerability or predator generality is associated with greater stress (left column).

Discussion

This study demonstrates the relative importance of a number of commonly used metrics for understanding ecosystem state and extinction risk. Understanding the circumstances under which each group of predictors performs best is essential for optimising the available tools for preserving natural ecosystems under stress. Here, a combination of biomass metrics, EWS, and network properties was found to offer the best ability to identify where and when extinction will occur in complex food webs. The best predictions were made when observing the time series right up to the point of extinction, and predictive ability deteriorated as the prediction horizon increased. However, the contribution of each of the tested predictor groups to the overall model was varied. Typically, at short prediction horizons, node level EWS dominated - especially in systems with lower intrinsic variability and therefore a higher signal to noise ratio.

When stress assigned to each producer was varied, EWS typically did worse than when all producers were equally stressed. While at most tested forecast horizons still were the most influential group, network properties became more influential at long prediction horizons.

A distinctively high coefficient of variation, one of the classic EWS metrics (Carpenter and Brock, 2006), was recorded in observation windows of species shortly before they went extinct. This resulted in predictive models with a high AUC, and thus it was concluded that coefficient of variation was acting as a distinctive indicator of impending extinction. This is expected from theory; EWS were designed to be positive trends in metrics, such as the coefficient of variation, as tipping points, such as an extinction event, approach (Scheffer *et al.,* 2009). This suggests that here EWS metrics may be capturing underlying system properties such as reduced resilience or growing instability, which predispose certain species to collapse under the applied stress regime.

When the prediction horizon was increased by using outdated time series data, the overall model AUC decreased, but node level EWS remained the most important predictor group. A species' coefficient of variation should be a good predictor of extinction as long as it is distinct from that of species which don't go extinct, and its own historic state. Increasing the forecast horizon makes the latter less likely, as the observations associated with extinction become less distinct from that species' baseline coefficient of variation. In most of the experiments there became a point at which the food web level EWS metric became more important than any node level EWS metric. As this metric, the dominant eigenvalue of the variance-covariance matrix (DEVCM) for the biomass time series within an observation window, uses all species' time series within the food web, the same value is applied to all species for that observation window. Therefore, this metric provides an understanding that the food web as a whole is approaching a tipping point, but cannot discriminate as to which species are most vulnerable (Dakos, 2018). This suggests that when the DEVCM becomes the most influential metric it is possible to conclude that extinction risk is increasing, but the prediction horizon is too long to identify which species are most at risk, providing a kind of ecological forecast horizon (Petchey *et al.,* 2015) for species-level extinction risk assessment. The food web level EWS tested here is one of several which have been developed in recent years (O'Brien *et al.,* 2023b; Weinans *et al.,* 2019). Multivariate EWS may have a future role as the earliest indicators that ecosystems are under stress, if their high data requirements can be met (Weinans *et al.,* 2021).

The power of EWS metrics to resolve extinctions was found to be increased by introducing a type III functional response, increasing the high noise decay rate or reducing the noise

covariance. EWS metrics depend on the presence of stochastic variation, as detecting system responses to perturbations requires such disturbances. Results indicate that elevated noise levels can suppress the performance of EWS metrics, consistent with previous findings (Ma *et al.,* 2018; Perretti and Munch, 2012). In addition, the predictive power of EWS metrics was found to increase with longer observation windows, but not with higher sampling resolution within those windows–a result previously reported (Arkilanian *et al.,* 2020). This suggests that the duration over which observations are collected is more critical than the number of observations, potentially offering practical guidance for resource-constrained real-world monitoring efforts. The food web–level EWS, DEVCM, also performed best under conditions of low stochastic noise but with a type II functional response, which typically produces greater oscillatory dynamics than a type III response. This highlights the importance for this metric of distinguishing between random noise, which can obscure signals, and intrinsically-driven variation in biomass. Furthermore, the effectiveness of this higher-level EWS underscores the value of considering community-level dynamics rather than analysing species biomass in isolation. Obtaining biomass data for all species within a real-world food web remains an extremely challenging, if not infeasible, task (Besson *et al.,* 2022; Weinans *et al.,* 2021), but there are a growing number of tools which have been developed to take advantage of it (Bury *et al.,* 2021; Dylewsky *et al.,* 2024; O'Brien *et al.,* 2023a).

Current conservation practices often use trends in population to prioritise interventions, which has a history of being successful, reducing extinction rates in birds and mammals (Bolam *et al.,* 2021). However, biomass trends were found to be always outperformed by EWS based upon the same data. This could be because a species displaying a consistent population decline, however rapid, would score relatively poorly in terms of AUC – the rate of decline may indicate which species is likely to go extinct, but a consistent decline gives no indication as to when – whereas a particularly high EWS metric (e.g. coefficient of variation) indicates both. While short-term predictions based on biomass can prevent immediate extinctions, they do not account for the functional role of species within the ecosystem.

Increasing the prediction horizon universally decreases the model's ability to discriminate where and when extinctions will occur within a food web. Making reliable predictions some distance ahead of extinction is important as this allows for anticipatory action (Bradford *et al.,* 2018); which has been applied to conservation activities such as sustainable management of harvested species (Henden *et al.,* 2020) and coral reefs (Liu *et al.,* 2018). A last minute prediction may be of higher certainty, but leaves little time for mitigating action. In addition, species maintained at very low abundances by last-minute conservation efforts may persist demographically but can become functionally extinct, contributing little to ecosystem

processes. This functional loss may, in turn, increase the risk of cascading secondary extinctions, further destabilising the food web (Säterberg *et al.,* 2013). In all scenarios tested, there was a prediction horizon beyond which node level EWS ceased to be the most effective predictor group, although the group that became most predictive varied depending on the context. This highlights the challenge of forecasting extinctions well in advance and underscores the need to consider multiple predictor types when aiming to support early conservation interventions.

Network properties were only good predictors of extinction risk at very long forecast horizons, when stress was weighted. Network properties are independent of the prediction horizon, changing only when extinctions alter the network structure. However, network properties cannot indicate when extinction will occur, and so they cannot compete with time series based predictors at shorter prediction horizons, when the time series is providing valuable information. EWS metrics have been designed to pick up on how close a species is to a tipping point using resilience. When all producers are equally stressed, the species displaying the lowest resilience is at greatest risk of extinction, and EWS metrics are good predictors. However, when stress is weighted such that it correlates with either producer vulnerability or mean predator generality, species with higher resilience but experiencing greater stress may be at higher extinction risk, which is why EWS metrics perform worse and network properties better, particularly as prediction horizon increases.

In all scenarios the best model contained all predictor groups, with weighted stress scenarios in particular highlighting the potential importance of synergy between groups of predictors. Here, a combination of network properties and EWS metrics helps better predict extinction by discriminating between species with similar properties in one predictor group (e.g. assuming specialists are vulnerable, the specialist with the highest coefficient of variation is most at risk). Complex and multivariate predictors of system state have been used with some success in the EWS space (Clements and Ozgul, 2016; Drake and Griffen, 2010), and clearly have value in identification of extinction risk too.

In this study, stress was applied to a single trophic level (producers) and considered only one type of stress mechanism, reducing growth rate. However, in real ecosystems, stress is rarely so simple. Natural systems are typically exposed to multiple, co-occurring stressors (Brook *et al.,* 2008; Simmons *et al.,* 2021), the combined effects of which are poorly understood. These stressors may interact in ways that mask or amplify EWS, complicating efforts to predict extinction events. Understanding how different types of stress interact, and how this affects the performance of various predictor types, remains an important area for future research.

Furthermore, the poor performance of biomass metrics in the simulations may be partly due to the linear relationship assumed between stress and population decline. Introducing density dependence – such as Allee effects – could increase the reliability of biomass as an early indicator. In such cases, extinction may occur after sudden, distinct, increases of biomass loss. Investigating how different population dynamics influence predictor performance would help extend the applicability of these findings to more complex and realistic ecological systems.

Conclusion

Recent work into ecological predictions has introduced the concept of an ecological forecast horizon; how far into the future reliable predictions can be made (Lewis *et al.,* 2023; Petchey *et al.,* 2015). Making reliable predictions with distance ahead of extinction is important to allow for anticipatory action (Bradford *et al.,* 2018). A short term prediction may be of higher certainty, but leaves little time for mitigating action. The results presented here demonstrate that combining network properties, biomass metrics, and EWS (EWS) could improve the ability to predict the identity of species at risk of extinction in a food webs. While classic node level EWS metrics are strong short-term predictors they offer limited utility for forecasting events far in advance. From a conservation perspective, the value of prediction lies not merely in identifying collapse, but in enabling timely intervention. The findings show that as forecast horizons lengthen, food web level EWS outperform the node level, suggesting that there is clear signal that an extinction is approaching, but the ability to identify the species most at risk has been lost. Understanding how environmental stress is distributed across the system is critical, as this strongly influences which species are most vulnerable. In real-world ecosystems, where multiple interacting stressors are the norm, identifying the dominant drivers of extinction risk is essential. Results indicate that the nature of these stressors can substantially alter the relative performance of different predictor types. This highlights the importance of tailoring extinction forecasting approaches to both the structure of the system and the characteristics of the stress it experiences, in order to maximise the potential for effective early intervention.

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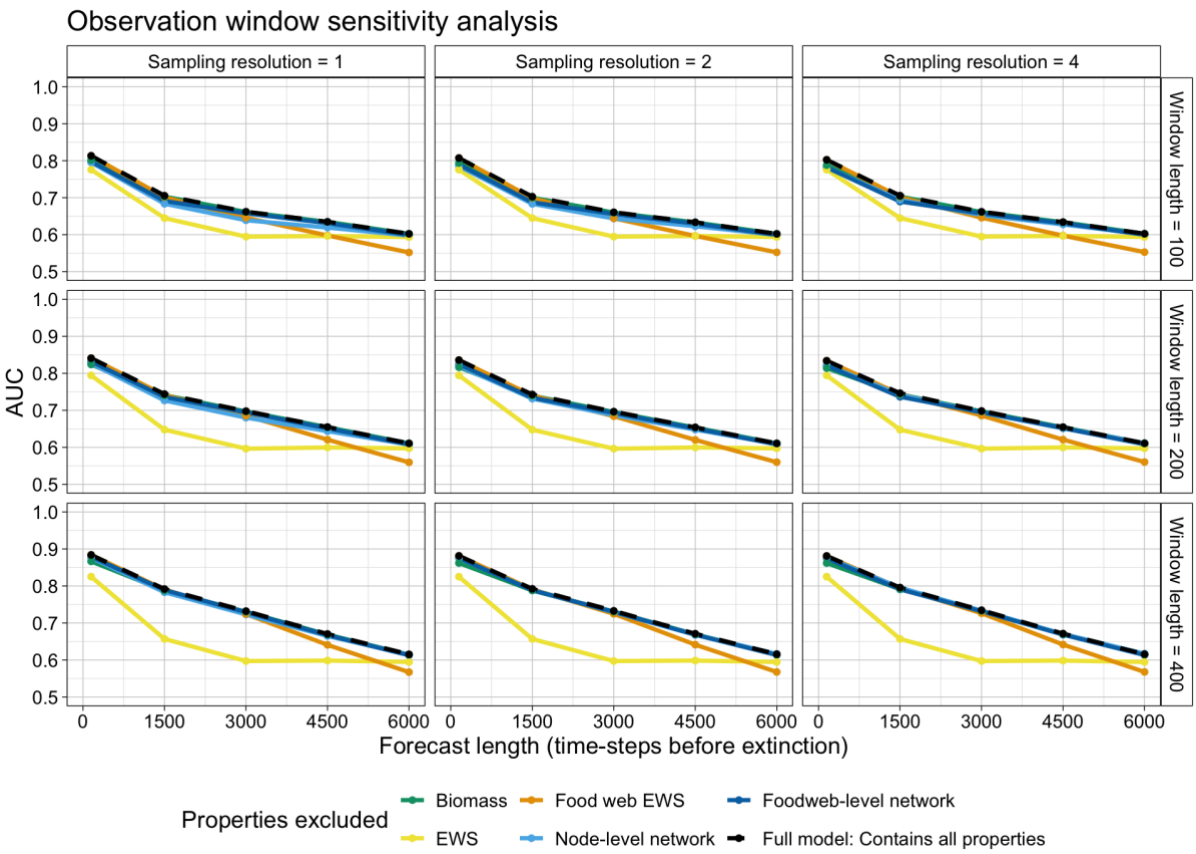
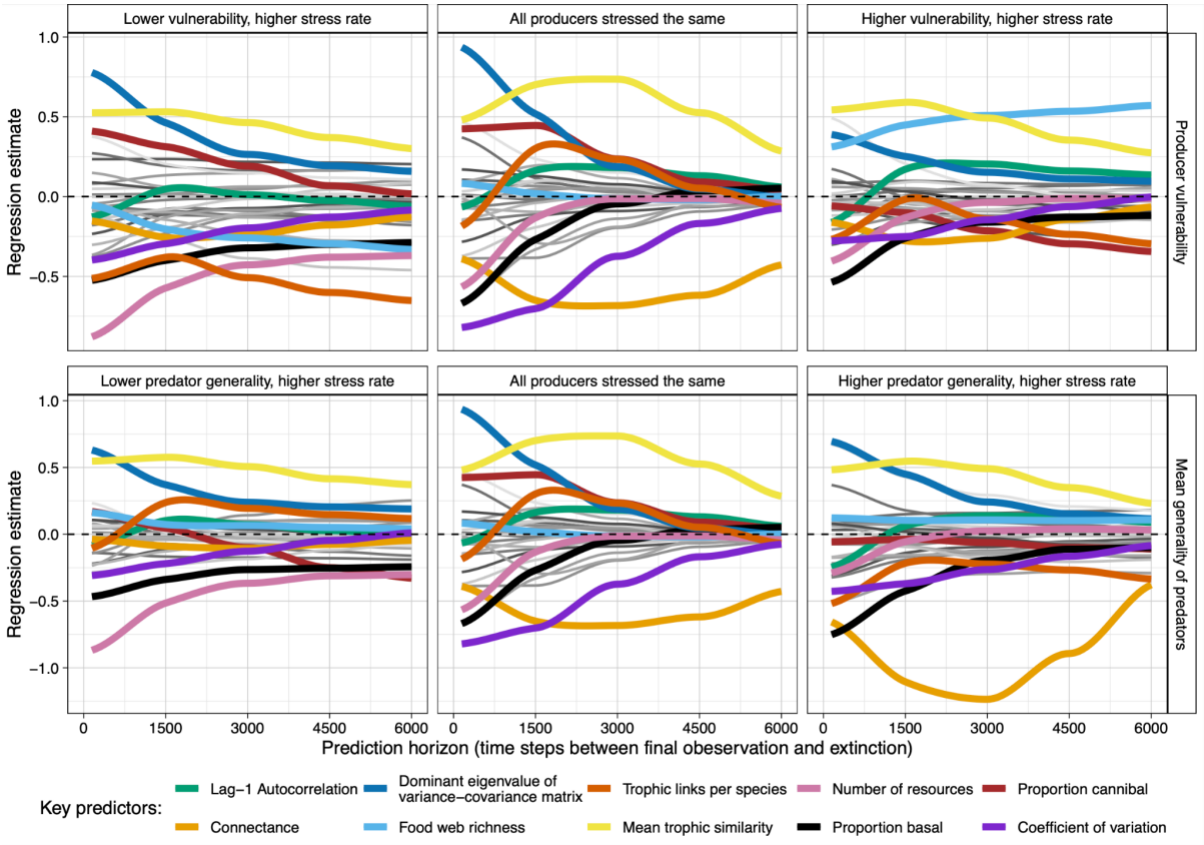
Supplementary material



Supplementary figure 1: Comparisons of the relationship between prediction horizon and AUC across combinations of predictors, as window length varies from 100 to 400 time steps, and within-window sampling resolution varies from every time point to every 4. Different colours represent dropping each group of predictor in turn, with the dashed black line representing the model containing all predictors.



Supplementary figure 2: Effect of prediction horizon (x axis) on the regression estimate (y axis) of individual predictors across varying stress regimes (panels). The model fitted includes all predictor groups. Ten key predictors are coloured, with all others a shade of grey.

Chapter 3: Linking topological properties to early warning signal strength in complex food webs approaching tipping points

Abstract

When subjected to external stress, ecosystems may reach a tipping point before undergoing a critical transition to an alternate stable state. Critical transitions are sudden and involve rapid change in the system state, making prevention preferable to reversal. Early warning signals (EWS) are a tool developed to predict when a system is approaching a tipping point using trends in statistical metrics. However, most species in complex networks such as a food web are not expected to display EWS. Conservation is often resource limited, meaning that monitoring all species in a complex food web is considered impractical. Therefore, an understanding of which species are likely to display strong EWS that does not require knowledge of population dynamics is desirable. Here, the ability of a series of network properties, calculable from the structure of the food web, were assessed for their ability to explain variation in EWS strength in simulations of complex food webs approaching tipping points. Species with high theoretical maximum interaction strength, which is found in specialist species of low trophic levels, were found to be associated with strong EWS. It is known that lower trophic levels have faster dynamics, and more specialist species have less muffled dynamics, which appear to both contribute to these species having lower baseline levels of the metrics used to calculate EWS. This is important as it provides a greater potential for EWS to develop against environmental noise, and suggests that preferentially monitoring such species will provide a greater probability of observing strong EWS prior to a tipping point.

Introduction

Natural systems can experience sudden shifts, or tipping points, to alternate stable states (Scheffer *et al.*, 2001, 2015), known as critical transitions. The alternate stable states that follow tipping points are often detrimental for biodiversity and ecosystem functioning, such as algae overgrowth of coral reefs (Mumby, Hastings and Edwards, 2007) and desertification of arid ecosystems (Kéfi *et al.*, 2007). Such critical transitions are marked by difficult to reverse processes such as positive feedback and hysteresis. Consequently, preventing such transitions is typically considered far more effective (Scheffer *et al.*, 2001). However, predicting when a system is approaching a critical transition is challenging (Scheffer *et al.*, 2009).

As systems approach tipping points, the capacity of system components to mediate/resist perturbations is compromised, a phenomenon known as critical slowing down. This occurs because the dominant eigenvalue of the system's Jacobian matrix, which dictates how fast a system can respond to changes, tends to zero as the system reaches a tipping point (Strogatz, 2001). Statistical indicators of critical slowing down, called early warning signals (EWS), have been developed to predict upcoming critical transitions (Scheffer *et al.*, 2009). These specifically signal a system's loss of resilience which is associated with critical slowing down. EWS are typically an increase in a statistical metric calculated from a time series of monitoring the system, such as standard deviation (Carpenter and Brock, 2006) or autocorrelation (Dakos *et al.*, 2010) in the abundance or biomass dynamics. The idea behind EWS is that a population may appear stable until the tipping point is reached, followed by a sudden collapse, but will show an underlying increase in one or more EWS metrics, such as autocorrelation. The strength of these EWS is typically assessed using Kendall's τ correlation coefficient between the metric of interest and time (Chen, Ghadami and Epureanu, 2022; MacLaren, Aihara and Masuda, 2025), with a strong correlation reflecting critical slowing down.

EWS were originally developed for low-dimensional systems (Brock and Carpenter, 2010; Weinans *et al.*, 2021), and their application to ecology initially focused on dynamics of individual populations (Carpenter and Brock, 2006; Guttal and Jayaprakash, 2008). Focusing on individual populations overlooks the important role of species interactions and indirect effects among species in shaping the ecological dynamics that would influence the emergence of tipping points and EWS metrics. To better capture these complexities, researchers have increasingly turned to studying EWS in networks of interacting species, which provide a more realistic view of ecological systems (Van Nes and Scheffer, 2007; Dakos, 2018; Patterson, Strang and Abbott, 2021).

Although critical slowing down is almost universally found in systems approaching tipping points, there is recognition that not all species within a network will exhibit EWS of the same strength, and most species timeseries will produce only weak warning signals (Boerlijst, Oudman and De Roos, 2013; Dakos and Bascompte, 2014; Ghadami, Chen and Epureanu, 2020). This poses a problem when monitoring ecological communities for biodiversity change, as not all species will respond equally. Consequently, there is growing interest in identifying network-level indicators that consistently produce strong and reliable warning signals (Dakos and Bascompte, 2014; Aparicio *et al.*, 2021).

One approach to improve EWS in multispecies systems is the development of multivariate EWS, which combine information from multiple time series to summarise community-level dynamics. Multivariate EWS have their origins in univariate approaches, where it was recognised that combining multiple metrics from a single population, such as trait and abundance data, can enhance signal strength (Clements and Ozgul, 2016). Building on this, most multivariate EWS rely upon an *a priori* hypothesis e.g. that species exhibiting higher autocorrelation will yield stronger warning signals, and then employ dimension reduction techniques to either synthesise multiple species time series and estimate EWS signals, or synthesise multiple EWS estimates from among time series into a univariate signal (Weinans *et al.*, 2019).

For example, maximum autocorrelation factor analysis constructs a single time series that maximises the signal-to-noise ratio, thereby improving the detectability of EWS (Weinans *et al.*, 2019, 2021). Alternatively, researchers have also averaged univariate EWS estimates among an optimised set of species to reduce noise and uncertainty (Masuda, Aihara and MacLaren, 2024). Additional methods include more novel indicators, such as the dominant eigenvalue of the covariance matrix of species time series (Dakos, 2018), which cannot identify species at risk of tipping, but does give an overall indication of whether the system is slowing down or not.

A key limitation of these multivariate EWS is their high data demand; they typically require high-resolution time series data for all components within a network – an impractical requirement in many real-world systems (Weinans *et al.*, 2019). Nevertheless, evaluations in mutualistic networks have shown that multivariate EWS can, in some cases, outperform even the best-performing univariate indicators (Weinans *et al.*, 2021), although calculating all univariate indicators to find the best has the same data demand as multivariate EWS.

This challenge has motivated efforts to identify which species in a food web/community/network are most likely to yield strong warning signals, enabling more targeted and efficient monitoring strategies. Approaches include identifying species at high risk of extinction (Dakos, 2018), selecting those that best align with the dominant eigenvector of the system's Jacobian matrix (Patterson, Strang and Abbott, 2021), or using pairs of cross-sectional samples to identify candidate species for more intensive monitoring (Masuda, Aihara and MacLaren, 2024). However, these methods still require at least some sampling of all species within the community.

An alternative approach that requires no sampling is to use node-level species' metrics derived from the community's network structure *per se* to inform species' EWS potential. Examples of node level metrics include generalism and specialism, and other characteristics related to a network's degree and centrality. Here, each species has properties derived from its position within a network, which, in contrast to directly estimating EWS from their time series, may be correlated with EWS strength as the system approaches a tipping point. For example, a previous study found that specialists tend to display stronger EWS (Dakos and Bascompte, 2014; Aparicio *et al.*, 2021). This result has been attributed to the relative isolation of specialist species allowing them to distil perturbations from other species into a clear signal. A recent study, using a coupled double well model, found a similar result (MacLaren, Kundu and Masuda, 2023), where more highly coupled species displayed stronger EWS.

Despite these insights, trophic networks representing highly diverse communities with a large array of indirect effects, differ from mutualistic networks both in the type of interactions between species and their topology - e.g. more than two trophic levels. This is likely to influence how EWS are distributed in trophic networks and what node-level metrics might be correlated with EWS. In this study this knowledge gap was addressed by using a trophic food web model to address three research questions:

(1) Which of the classic univariate EWS, known to work in simple systems and mutualistic networks, produce the strongest signals in complex food webs?
(2) Assuming knowledge of food web structure but not the species' biomass time series, how well can the distribution of EWS be predicted from node-level network metrics?
(3) Does the best node-level metric provide a better sample of EWS than choosing species

Methods

In the following sections, the model used to evaluate the questions above is introduced, followed by details on the specific sequence of data collection from the model: estimating key EWS metrics, estimating correlations between node-level metrics and EWS metrics and finally testing the efficacy of using these node-level metrics as indicators of a critical transition.

Model parameterisation

The strength of EWS in complex food webs was assessed using simulated biomass dynamics from a set of 10,000 artificial food webs. These food webs were built using the niche model (Williams and Martinez, 2000), with variation in initial food web richness (20 - 50), connectance (0.1 - 0.3), consumer-resource body mass ratio (10 - 100; Brose *et al.*, 2006), and Hill exponent (1 - 2). Simulations of biomass dynamics were then run using a stochastic version of the bioenergetic food web model (BEFW) (Yodzis and Innes, 1992; Lajaaiti *et al.*, 2025) with an embedded Allee effect. The Allee effect was included to produce critical transitions in the simulated dynamics (Dijoux and Boukal, 2021).

Biomass dynamics for the primary producers and consumers were modelled as follows:

Producers:

$$B_i^{'} = p_{it}B_i - r_iB_i^2 - \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \qquad (1)$$

Consumers:

$$B_i^{'} = -(x_i + \frac{\alpha_i \beta}{\beta + B_i})B_i + \sum_{j \in resources} x_i y_i B_i F_{ij} - \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \qquad (2)$$

B_i represents the biomass of species i, r_i & p_i are both components of species i's mass-specific intrinsic growth rate, with p_{it} controlling density-independent growth and r_i the density-dependent loss. x_i is the mass-specific metabolic rate of species i, and y_i is species i's maximum consumption rate relative to its metabolic rate. e_{ji} is j's assimilation efficiency (proportion of consumed biomass that is converted to own biomass) when consuming i.
$e_{ji} = 0.45$ if i is a producer, and 0.85 otherwise (Yodzis and Innes, 1992).

An Allee effect was included by introducing density dependence into the metabolic loss term for all consumers, generating increased mortality at low population densities. Here, $\alpha_i = 0.1$ for all consumers, and is the maximum additional metabolic losses (when $B_i = 0$), and $\beta = 0.0001$, influencing the slope of the Allee effect. The additional metabolic loss term is included only in the biomass dynamics of consumers. As a result, only consumer species are capable of undergoing critical transitions, and therefore all analyses have been restricted to consumers.

Environmental stochasticity is implemented via a stochastic noise process which acts through the growth rate, p_{it} , of all producers:

$$dp_{it} = \theta_i(\mu_i - p_{it})\, dt + \sigma_i\, dW_{it} \tag{3}$$

Here, the noise process is an Orstein-Uhlenbeck process (Uhlenbeck and Ornstein, 1930) with a drift term, with μ_i the initial value of p_i (determined allometrically), θ_i a decay rate controlling rate of return to the mean μ_i following stochastic perturbation, and σ_i the standard deviation of the Wiener process W_{it} , which provides the stochastic variation. Stochastic noise has been parameterised with the decay rate, θ_i , set to 0.05, and the covariance, $\sigma_i^2 / 2\theta_i$, set to 0.005, as these parameters are sufficient to produce EWS without producing a level of noise which makes the signals undetectable.

Body masses, M, for all species are determined via $M_i = Z^{T_i - 1}$, where T_i is the prey-averaged trophic level of species i, and Z is that food web's consumer-resource body mass ratio. Body masses and metabolic types are used to scale metabolic and consumption rates using the principle of allometry (Brown *et al.*, 2004). In the BEFW all biological rates are scaled to the mass of the smallest producer. Here, all body masses are calculated based on trophic level, and all producers have a trophic level of 1, meaning all producers have the same body mass of 1, resulting in $r_i = 1$ & $p_{i0} = 1$ for all species. All consumers are considered to be invertebrates with respect to their metabolic type, resulting in $y_i = 8$ for all consumers, and $x_i = 0.314 M_i^{-0.25}$.

F_{ij} is the density-dependent multi-resource functional response of i consuming j. It takes the form:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c_i B_i B_0^h + \sum_{k \in resources} \omega_{ik} B_k^h} \quad (4)$$

ω_{ij} is the relative prey preference of consumer i for resource j. Here, $\omega_{ij} = {}^{1}/_{n_i}$ where n_i is the number of resources of consumer i, B_0 is the half saturation density, set to 0.5, and c_i intraspecific predator interference, set to 0. h is the Hill exponent and determines the shape of the functional response, with a type II functional response when $h = 1$ and type III when $h = 2$ (Holling, 1959b, 1959a).

Model setup

10,000 steady-state communities of appropriate species richness, connectance, body-mass ratio and Hill exponent were obtained by simulating the dynamics of 10,000 food webs, with each species given an initial biomass of 0.5, and allowing biomass dynamics to stabilise. This was necessary to allow networks with transient species destined for extinction to be removed from the set of baseline networks. Furthermore, food webs with a stable species richness of 2 were removed from the analysis.

Following this selection process, external stress was introduced among all networks by altering the intrinsic growth rates of producers to induce tipping behaviour. Three different stress scenarios were performed on each food web; where either all producers, half selected at random, or one selected at random, were stressed, which was expected to have knock-on impacts on the number of consumers influenced by the stress. Stress was applied in a stepwise manner, following an approach similar to that of Dakos (2018). At each step, the intrinsic growth rate of the selected producers was decreased by 0.002, after which the system's biomass dynamics were simulated for a further 600 time steps. The biomass values from the final 200 time steps were recorded to assess system state. This process was repeated iteratively until a tipping point was observed. At a step before a tipping point, the network reaches an equilibrium after the change in growth rate with all species extant. After a tipping point at least one species goes extinct.

Question-specific methods

Question 1: Which warning signals perform best in complex trophic networks?

Standard deviation, autocorrelation, skewness, and kurtosis were estimated from the log biomass of all consumers in each 200-timestep window following a decrease in producer growth rate. These are four widely used EWS metrics (Carpenter and Brock, 2006; Van Nes and Scheffer, 2007; Guttal and Jayaprakash, 2008). Kendall's τ correlation coefficient (KT) for each metric and time was calculated for each consumer's time series, with a higher KT indicating a stronger signal.

Question 2: Predicting EWS strength from node level metrics

In order to identify which node level metrics predict EWS, it was first assessed whether there was a need to normalise/standardise the EWS signals between networks. Therefore, the impact of network size and time to tipping point for each network on KT was modelled using a general additive model (GAM). Following this, statistical models were constructed to estimate the ability of each of 17 node level metrics to explain variation in KT. Finally, it was assessed whether the performance of the models was improved by including multiple predictors.

The need to normalise EWS strength (KT) estimates among food webs was first assessed by fitting a GAM where KT was predicted by food web species richness and the distance a food web is from tipping point before stress was added, quantified by the reduction in growth rate necessary to reach the tipping point. Food webs which begin close to a tipping point are less likely to display strong EWS as a response to stress. Therefore, species in these networks approaching tipping points will be less likely to display distinct EWS from those unaffected by stress, which is expected to reduce EWS predictability.

Next correlation between EWS strength and 17 node-level properties of the networks (Table 1) was assessed. The network properties used in this study have been adapted from studies into the role of food web structure in stability (Williams and Martinez, 2000, 2004; Vermaat, Dunne and Gilbert, 2009), as species with low stability were expected to produce strong EWS. Additionally, several metrics have been included which are derived from a species' theoretical maximum interaction strength, $\omega_{ij}x_iy_i / B_0^h$, when consuming a resource (McCann, Hastings and Huxel, 1998). Theoretical maximum interaction strength is realised when resource biomass is 0, and only requires food web structure to calculate. In this model, x_i declines

exponentially as body mass increases, while $\omega_{ij} = {}^{1}/_{number\ of\ prey}$, and therefore maximum theoretical interaction strength is highest in specialist species of low trophic levels.

Although the main focus of this study is finding network properties which are associated with strong EWS, three non-structural properties which require a complete biomass time series for each species have been included in the analysis. These are the identity of any extinct species, found to be related to EWS strength previously (Dakos, 2018), and thought here to be impacted by the stress regime, along with loss of growth rate required to reach the tipping point from the initial conditions, and the initial value of the EWS metric. These metrics have been included because they were expected or found to be important in understanding variation in KT, and as such provide important context and comparison points for node-level network properties.

Table 1: The properties which have been used to explain distribution in EWS strength using statistical modelling. Properties are categorised as structural if they can be calculated from the food web topology alone, and non-structural if not.

Predictor	**Description**	**Predictor type**
Tipping window	How many iterations of growth rate reduction occurred before an extinction	Non-structural
Is extinct	Whether the species in question went extinct as part of the first extinction event (yes/no)	Non-structural
Pre-stress EWS metric	What was the value of the EWS metric before stress was introduced	Non-structural
Body mass	Body mass of species (determined by Z-ratio and trophic level)	Structural
Is primary consumer	Does the species only consume producers (yes/no)	Structural
Is top	Is the species a top predator - with no predators (yes/no)	Structural
Is an omnivore	Does the species feed from	Structural

	multiple trophic levels (yes/no)	
Is a cannibal	Is a species a cannibal (yes/no)	Structural
Trophic level	Prey-averaged trophic level of species	Structural
Number of consumers	How many predators does a species have (vulnerability)	Structural
Number of resources	How many prey species does a species consume (generality)	Structural
Number of trophic links	How many predators + prey does a species have	Structural
Maximum trophic similarity	What is the greatest proportion of trophic links shared with another species (Jaccard's similarity)	Structural
Closeness centrality	Mean trophic distance to all other species in the food web	Structural
Individual clustering coefficient	Probability that two species trophically linked to another species are also linked	Structural
Maximum interaction strength with resource	Maximum theoretical interaction strength between a species and any of its resources	Structural
Maximum interaction strength with consumer	Maximum theoretical interaction strength between a species and any of its consumers	Structural

To identify the relative strength of these properties, a series of GAM models were fitted, where each network property was used as the single predictor for Kendall's τ across all consumers in all food webs. The proportion of variance explained by that network property (R^2) was recorded. The property which returned the highest value of R^2 was then identified.

Once the top predictors had been identified, each model was refitted with these predictors included, and then one of each of the remaining predictors. This provides an estimate of the reduction in residual variance gained from including an additional predictor, on top of the best predictors. This allows for the assessment of whether any predictive ability observed in other variables is accounted for by the best performing predictor.

This analysis was repeated for each of the three stress scenarios (all producers stressed, half of producers stressed, one producer stressed). Additionally, as distance to tipping point was found to influence the strength of EWS produced in a food web, this was controlled for by taking five subsets of the food webs determined by how far the web is from the tipping point, with these subsets only including food webs which had tipping points occurred after growth rate had been reduced by 0.1, 0.2, 0.3, 0.4, and 0.5. This increases the signal to noise ratio within the dataset, and allows for the establishment of whether the distance a food web begins from the tipping point impacts how EWS are distributed across the network, or just their strength.

Question 3: Using network properties to inform monitoring

Once the structural property that was most important for explaining variation in EWS strength was identified (Question 2), the capabilities of this metric in identifying species with the strongest EWS in each food web was further assessed by calculating the scaled EWS in samples of species based upon maximising this metric, and then compared this with selecting species at random, using the following design: Species were selected, starting with a sample size of 1 and then increasing by 1 until all species were included, either (i) at random or (ii) in order of highest to lowest in the network property which best explains variation in KT. The maximum and mean of KT of each sample was calculated, scaled to control for variation between food webs, as the strongest EWS in a food web may not be particularly strong overall. This allowed for the assessment of whether this sampling method selects for species with stronger warning signals than average, and how large a sample is necessary to be monitoring the strongest EWS in a food web.

Results

Question 1: Which warning signals perform best in complex trophic networks?

The rank order strength of EWS metrics among the simulated data scenarios was SD, autocorrelation, skewness and kurtosis (Figure 1). Standard deviation is the strongest EWS metric in approximately 75% of the food webs irrespective of scenario, followed by lag-1 autocorrelation (Figure 1). Therefore, further analysis into which species within a web possess strong EWS focused on these two metrics, as they are most likely to produce strong signals. Values for mean and maximum Kendall's τ within each food web averaged across all food webs are provided in supplementary table 1.

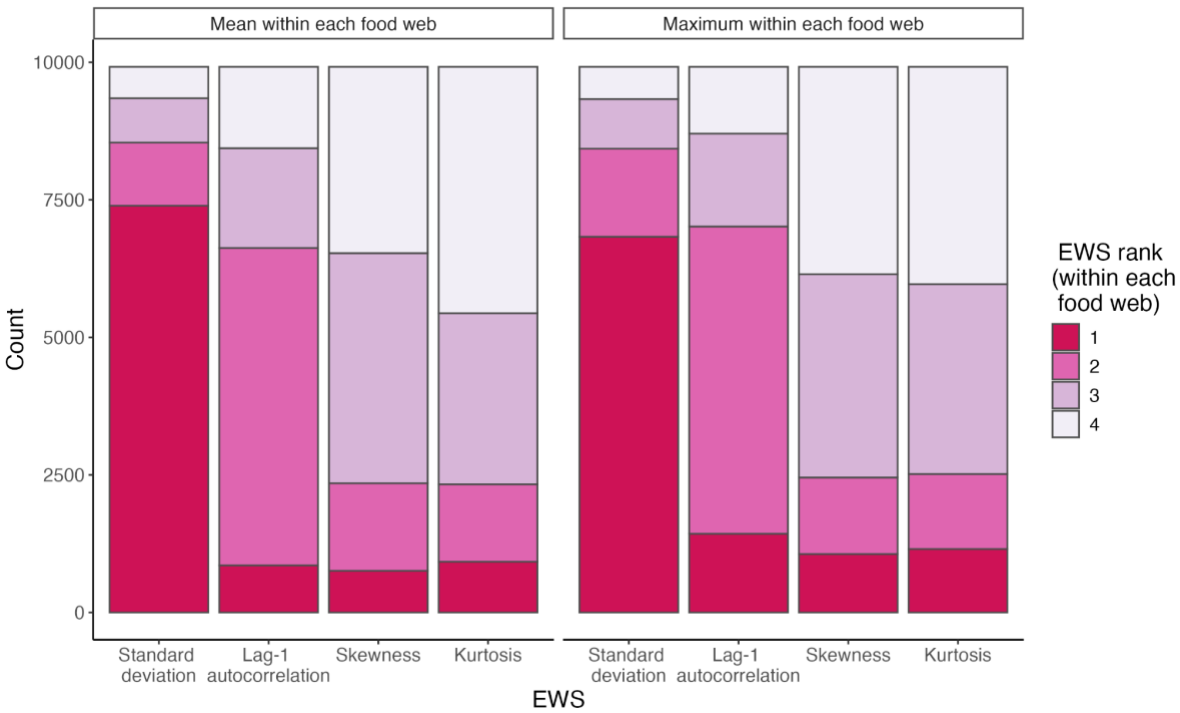


Figure 1: The comparative strength of the four classic warning signals used in this study. The mean (left) and maximum (right) strength of each of the four calculated EWS (x axis) in each food web have been ranked, with the count of each rank for each EWS across the set of 10,000 food webs visualised here. The stress regime targets all producers.

Question 2: Understanding distribution of EWS within a food web

Q2 - Part 1 - EWS normalisation

The standard deviation and autocorrelation based EWS were stronger in food webs which were further from the tipping point prior to the stress, (Figure 2). Additionally, species in very small food webs (species richness < 5) display stronger EWS than species in larger webs. This effect of species richness is largely absent once species richness is greater than five. The effect of species richness was much more pronounced when <100% of the producers are stressed (Supplementary Figures 1 & 2).

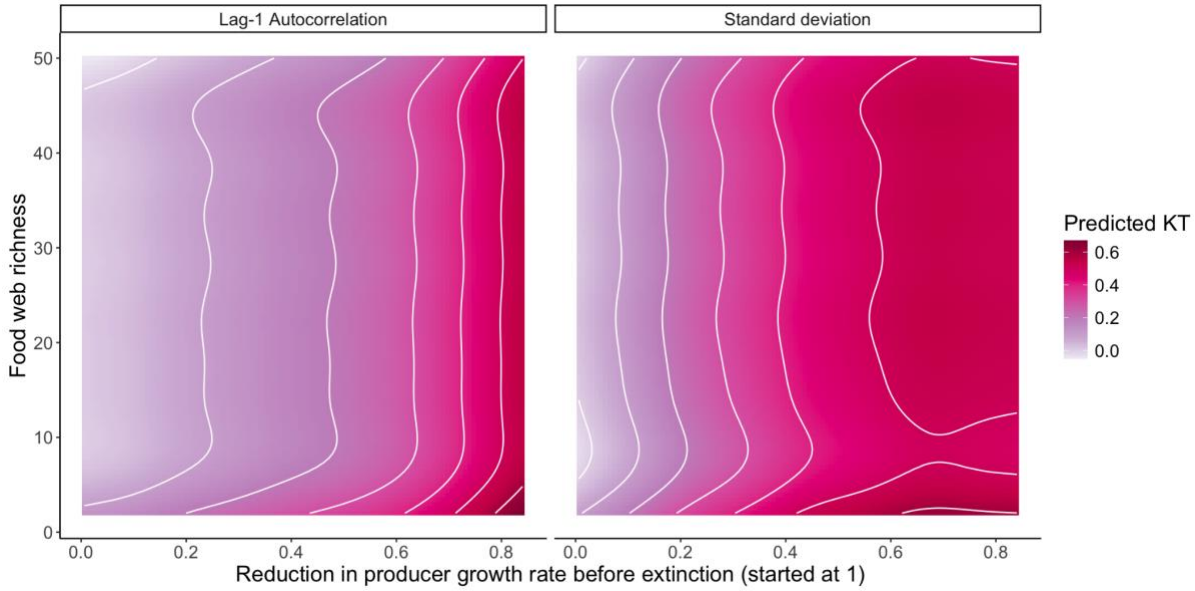


Figure 2: Relationship between amount of stress imposed before tipping occurs (x axis) and food web richness (y axis) on the predicted strength of the warning signal that is produced (colour) using a GAM. The result when predicting KT calculated using Lag-1 autocorrelation is presented on the left, and standard deviation on the right. The stress scenario presented here is where all producers are stressed.

Q2 - Part 2 - Rank importance of node-level properties

17 metrics explain a degree of the observed variance in EWS strength (Figure 3). The best two predictors of strength of EWS signal were whether a species goes extinct following the tipping point being reached, and the value of the EWS metric at equilibrium, prior to stress being applied. Species that go extinct have stronger EWS than those which don't, as did species with lower values of the EWS metric (i.e. autocorrelation or standard deviation) before stress was applied (Figure 3). Both of these metrics are non-structural, and therefore cannot be calculated from network topology alone. The best performing structural network property is maximum interaction strength between a species and its resource (Figure 3). This is likely

because it is strongly associated with pre-stress autocorrelation, explaining ~40% of its variance (Supplementary Figure 3).

Having identified the strong individual predictors, GAMs were refitted with both of these metrics included. When either of these two predictors were in the model, there was no significant reduction in residual variance associated with any other predictor (Figure 3 inset), suggesting that these two metrics account for all the variation explained by other metrics.

For most metrics, predictive power increases as the data is subset by starting distance from the tipping point, but the relative power of individual predictors to each other remains unchanged. This suggests that EWS in food webs that begin far from the tipping point are not only stronger (Figure 2), but more distinct. However, the mechanisms determining the distribution of EWS within a food web, such as pre-stress autocorrelation, are unchanged.

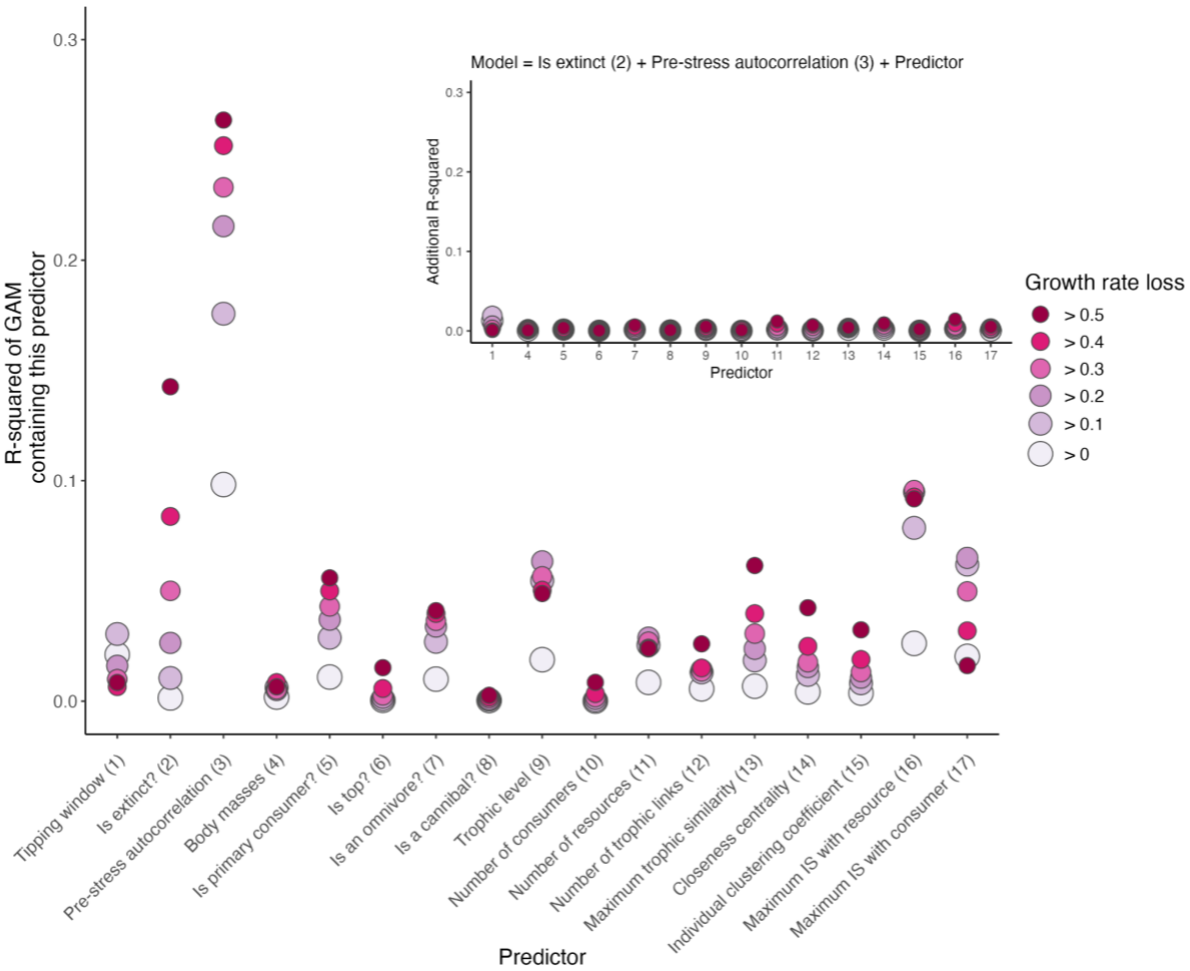


Figure 3. EWS strength is driven primarily by pre-stress autocorrelation and whether a species goes extinct or not. Variance explained (y axis) by node-level network properties (x axis) predicting EWS strength. Colour indicates subset of data, based upon distance to tipping point, quantified by loss of growth rate before tipping. Inset shows that adding more predictors to a

model containing the top two, "pre-stress autocorrelation" and "is extinct?", explains very little additional variance (numbers on x axis correspond to main plot). The stress scenario here is where half of all producers are stressed.

Q2 - Part 3 - Impact of the stress regime

The performance of the top 2 predictors varies greatly with the stress regime applied to each food web. Across both standard deviation and autocorrelation, pre-stress metric level performs very well when all producers are stressed, very poorly when one at random is, and in-between when half of producers are stressed at random. Whether a species goes extinct or not displays the opposite trend. Furthermore, it is the only metric with any predictive power when a single producer is stressed. That "goes extinct" does so poorly when all producers are stressed suggest that in this scenario extinct species do not possess distinctively high EWS, as all species are heading towards a tipping point.

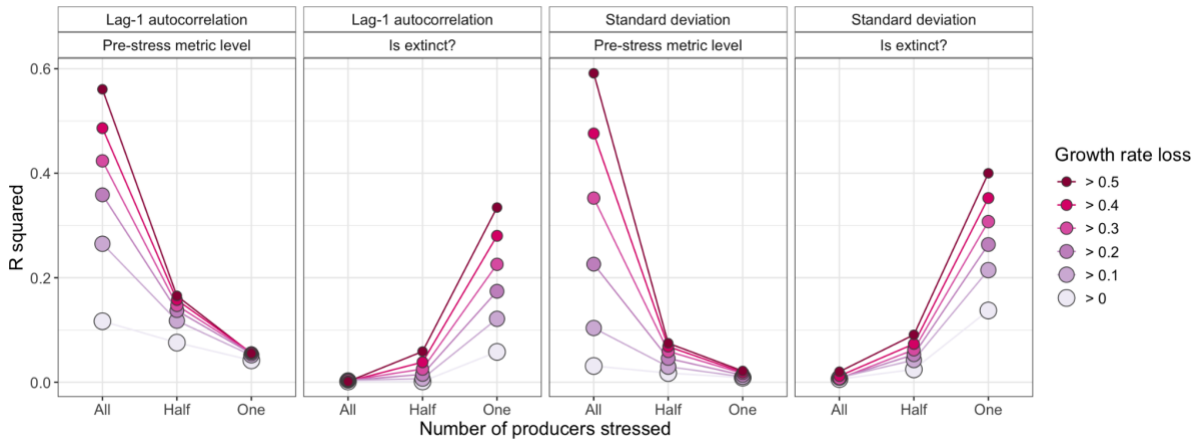


Figure 4: The relationship between the number of producers stressed (x axis) and the predictive power (measured in R squared) of the top 2 network properties from figure 3 - "pre-stress metric level" (panels 1 & 3) or "is extinct" (panels 2 & 4) for explaining the distribution of warning signal strength for autocorrelation (panels 1 & 2) and standard deviation (panels 3 & 4).

Question 3: Using network properties to inform monitoring

Analysis of efficacy was restricted to metrics which were purely structural (see Table 1). As a species' maximum theoretical interaction strength with its resources (IS) was identified as the best structural node-level network property for explaining variation in KT, this metric was chosen as the property of choice for optimising monitoring efforts.

Compared to random selection of species, sampling species for monitoring using IS produced, on average, higher predictive power measured by the scaled warning signal strength (see Methods). This result remains whether using the maximum or mean scaled EWS strength of the sample (Figure 5). The effect is particularly noticeable at small sample sizes, with the difference in EWS strength between sampling by interaction strength and at random decreasing as sample size increases. Increasing the sample size increases the probability of sampling the species with the strongest EWS by chance, resulting in an increase in the maximum EWS when sampling at random. Additionally, a larger sample size increases the proportion of the food web sampled, resulting in the mean scaled EWS when sampling by interaction strength tending to 0. Sampling by IS performs better when more producers are stressed, likely because IS correlates with pre-stress metric, which also was found to do better under these conditions (Figure 4). However, even when a single producer is stressed, sampling by interaction strength outperforms sampling at random.

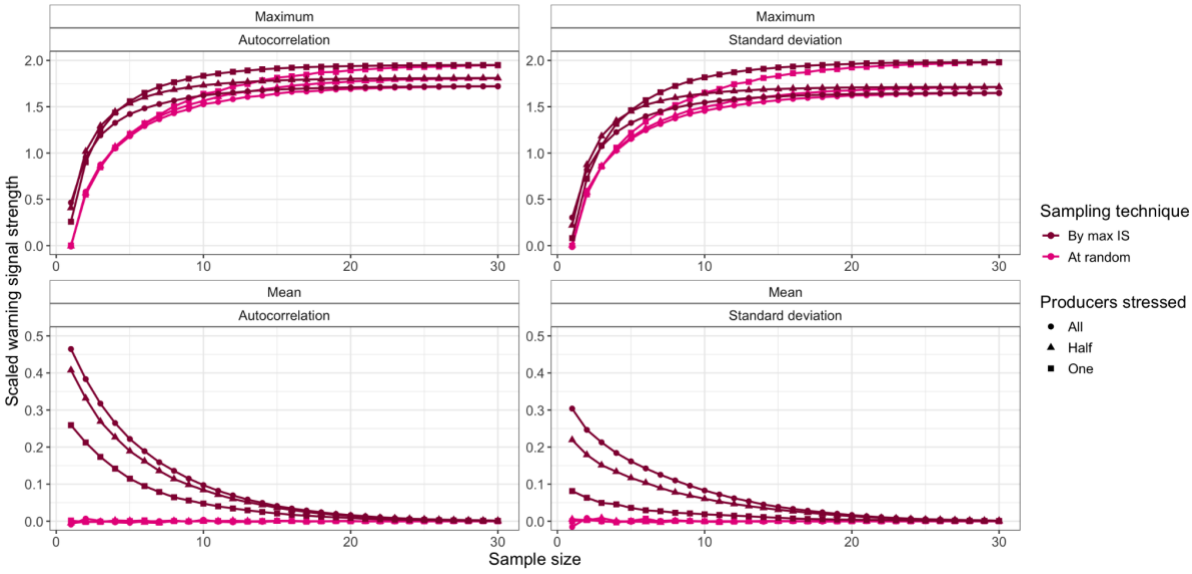


Figure 5: Sampling by interaction strength outperforms sampling at random until almost the entire food web has been sampled. The mean of the maximum (top row) or mean (bottom row) of the scaled warning signal strength of sample from each food web, increasing in size from 1-30. Samples have either been selected either by: highest maximum theoretical interaction strength (purple) or at random (pink). If multiple species in a food web tied for interaction strength the species sampled first is whichever appeared first in the dataset.

Discussion

Here it was evaluated whether structural network properties might be used as indicators of EWS metrics signalling critical transitions/tipping points in complex, trophic food web networks. Motivated by challenges associated with using time series data among multiple species impacted by direct and indirect effects, how EWS metrics varied with species richness, network complexity and the ratio of body masses in ecological communities was first estimated. Then a ranking of network properties that are associated with EWS metrics was developed, and finally evaluated the efficacy of using the best structural network property, the theoretical maximum interaction strength between a species and its prey (IS).

This investigation clearly assumes full knowledge of the trophic food web containing all species. Therefore, inference was based upon network properties of species that stem from this food web topology. This enables a move away from a dependence on monitoring all species to identify promising candidates (Patterson, Strang and Abbott, 2021), which even in the short term (Masuda, Aihara and MacLaren, 2024) may be practically almost impossible (Weinans *et al.*, 2021).

Results first show that node-level properties derived from time series information would perform best, if they were easily accessible. Results further show that, in the absence of such data, IS is likely the best metric. As it is calculated in this model, IS is a compound metric, with higher values indicating both a low tropic level and a low number of resources. The value of IS corroborates insight from mutualistic networks where tight coupling and specialisation, often synonymous with strong interaction strengths, are associated with EWS metrics (Aparicio *et al.*, 2021). Although Aparicio *et al.,*'s (2021) objective was to find a minimal set of species which could be monitored to ensure that tipping points that occurred anywhere in the network could be detected, and found specialist species condensed information from others, they also found that specialist species produced stronger warning signals that provided earlier warning. Here, a high IS was found to be the structural property which explains EWS strength best, with high IS associated with specialists of low trophic levels. IS is also closely related to the best overall predictor, pre-stress autocorrelation/standard deviation (Supplementary Figure 3). Therefore, this suggests a potential mechanism for specialists displaying strong EWS. Consuming fewer resources possibly leads to less highly autocorrelated dynamics, and has been found previously to reduce buffering from the asynchronous dynamics of multiple resources (Dakos and Bascompte, 2014).

The study system used here differs from mutualistic networks in its dimensionality - consumer resource networks typically contain more than two trophic levels. This allows an assessment of the impact of trophic level on warning signal strength. A small effect where lower trophic levels have stronger EWS was found. This effect appears to be entirely associated with the relationship between lower trophic levels (higher IS), and lower pre-stress metrics (Supplementary Figure 3). A likely mechanism for this is how the bioenergetic food web model, used in this study, calculates biological rates for all species. Using the principles of allometry (Brown *et al.*, 2004), trophic level (which dictates body size) is inversely proportional to *per capita* rates of metabolism, which in this model determines a species' gain of biomass through consumption, and loss of biomass through respiration. Therefore, species at higher trophic levels are slower to respond to changes in their resources, leading to greater autocorrelation - and a lower capacity for EWS. This is not expected to be a model-specific result, however; it is known that growth and mortality rates scale with body mass in eukaryotes (Hatton *et al.*, 2019, 2024). Focusing sampling on species with faster population dynamics, such as lower trophic levels, would be expected to be a worthwhile strategy for finding strong signals. This goes against the spirit of recent attempts to scale recovery rates between species (Zhang *et al.*, 2022), however, but feels more in line with real world monitoring practicalities and limitations.

When all producers in a network were stressed, all species in the network approached a tipping point. This suggests that in the scenario where all species display EWS, the strongest EWS were found in species with the lowest levels of autocorrelation or standard deviation before stress occurred, which was found to be specialist species of low trophic levels, possessing a high IS. Pre-stress metric levels indicate a species' capacity for displaying EWS; a lower initial value allows for a greater change in the EWS metric as the species approaches tipping, producing a signal that is clearer relative to background noise. Using a correlation coefficient like Kendall's τ to quantify strength of warning signals means that stochastic noise can mask the signal, potentially at ecologically realistic levels (Perretti and Munch, 2012). Therefore, this result suggests focusing monitoring on species with lowest pre-stress metrics, as this provides them with the greatest potential for producing strong EWS.

However, the stress regime has a clear impact on the predictability of EWS. When the number of producers being stressed was decreased, the relationship between strength of EWS and pre-stress metric (and by association interaction strength, trophic level and number of resources) decreased. The way a network is stressed has no impact on the pre-stress EWS metric values; meaning that a species' capacity to show strong EWS if it approaches a tipping point is unchanged. It does, however, affect the proportion of the web directly and indirectly

affected stress, and therefore approaching a tipping point. This highlights that for a species to be expected to show strong EWS, it needs to both have a low initial value of the EWS metric (to have high potential for EWS), and be impacted by stress and approaching a tipping point (for that potential to be realised).

In the scenario where a single producer chosen at random was stressed, no network properties were generally associated with strong EWS. The best indicator of EWS strength was whether species went extinct following tipping, which is consistent with previous research (Dakos and Bascompte, 2014; Dakos, 2018). Going extinct is likely the best predictor in this scenario as these are the only species reliably associated with tipping, irrespective of their capacity for EWS. However, on the other side of the spectrum when all producers were stressed, knowledge of where extinctions occurred was a poor predictor of EWS strength. Here, the entire network was approaching tipping, and so there was a strong link between signal strength and pre-stress level. An interesting area for further research would be applying stress to the network through species which aren't producers, as when producers are stressed then species with the highest capacity for EWS are also those most closely impacted by the effects of stress.

Overall, this work builds upon the concept that species in food webs approaching tipping points have variable strengths of EWS by suggesting species have varying potentials for warning signal strength, with greater potential in species possessing a lower baseline of the warning signal metric as monitoring begins. Species possessing lower levels of autocorrelation in a pre-stressed state are typically those with lower interaction strengths, a compound network property indicating low trophic levels and specialist feeding behaviour. This builds upon previous understanding that specialists display strong EWS by suggesting that the less dampened dynamics intrinsic to specialists directly relates to lower levels of autocorrelation, granting them increased capacity for EWS to manifest. Furthermore, species at lower trophic levels, which display faster population dynamics, also have been found to possess lower autocorrelation.

However, the location of stress within a food web plays a critical role in the realisation of a species' EWS potential. Properties which give species high potential for EWS may also reduce their capacity to realise this potential. Further exploration would be valuable in identifying whether this is the case.

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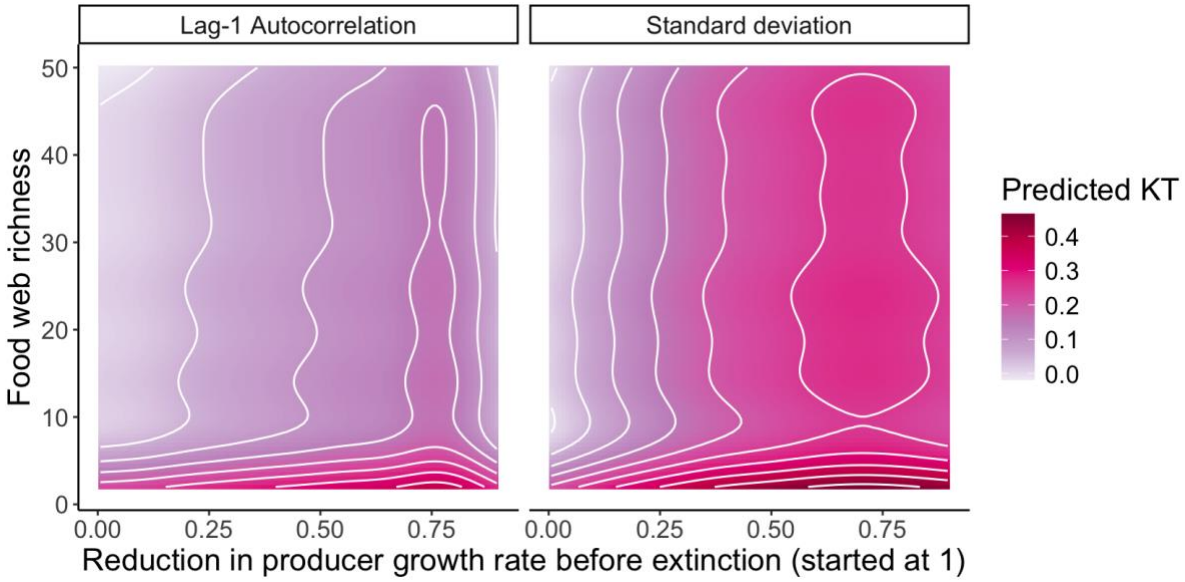
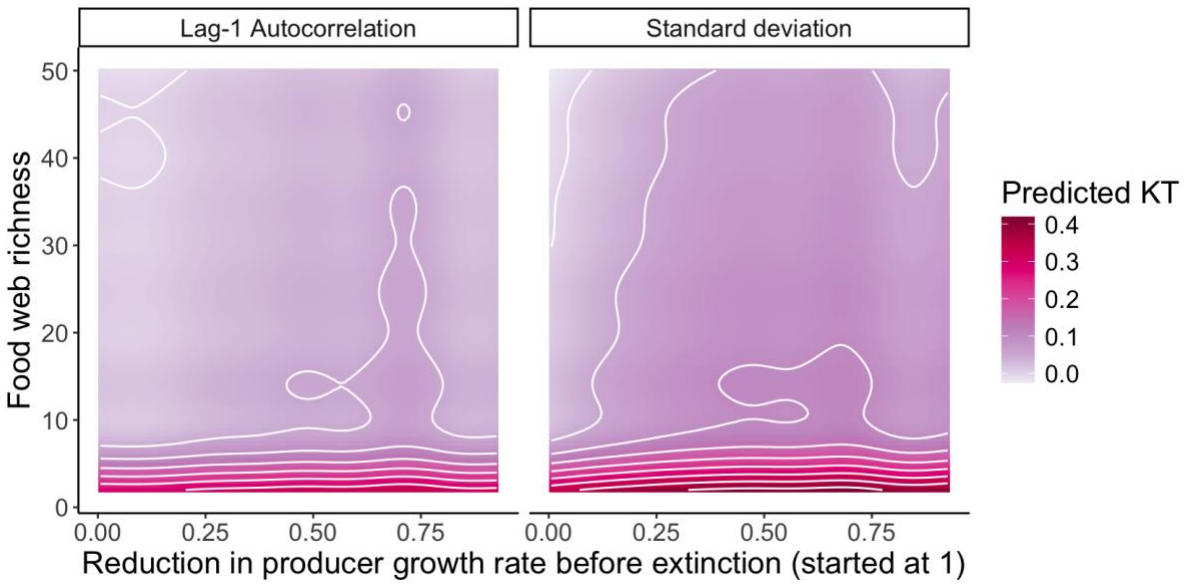
Supplementary material

Supplementary table 1: The maximum and mean Kendall's τ (KT) correlation coefficient for each early warning signal with each food web, averaged across all food webs.

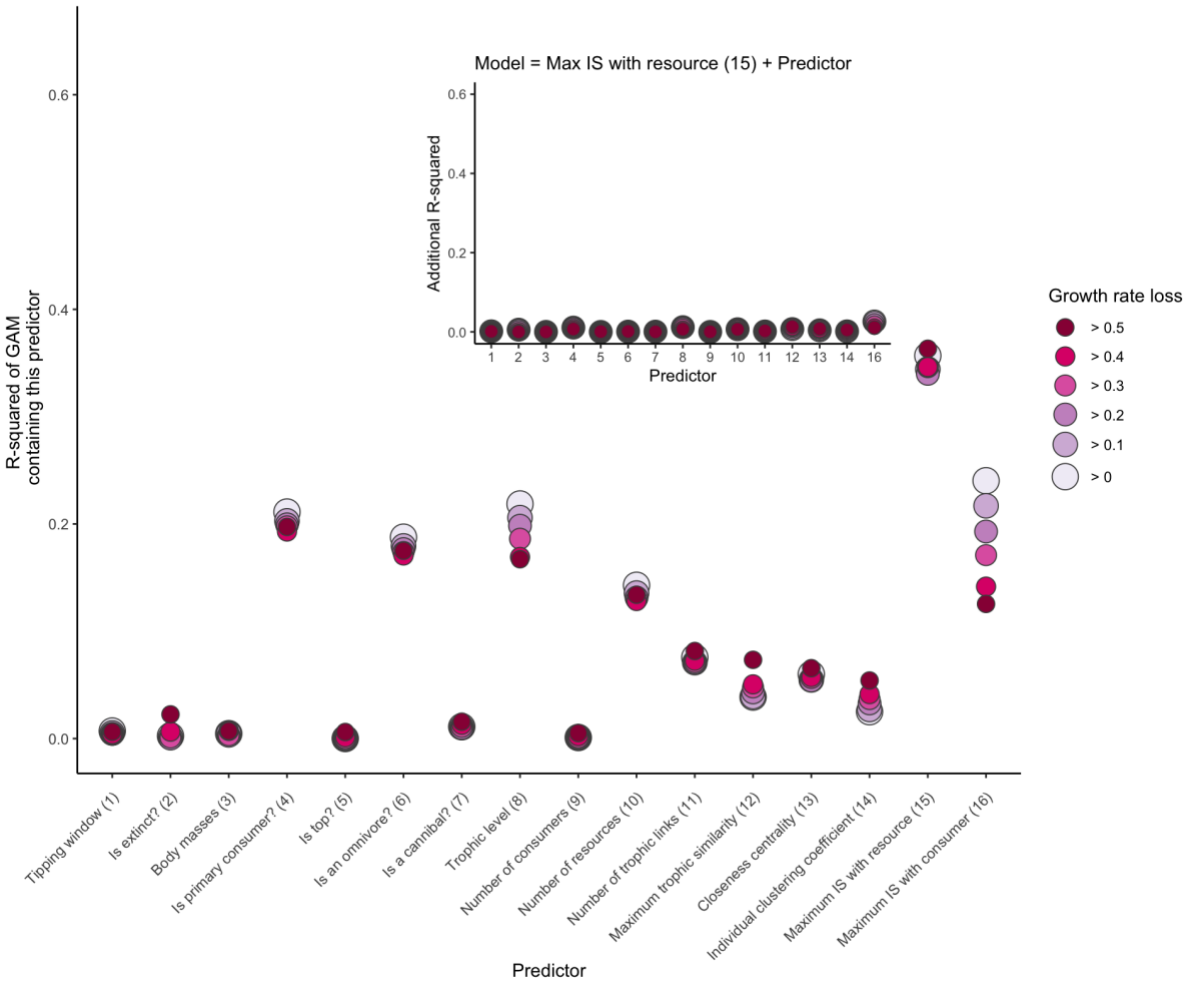
Early Warning Signal	Metric	Mean KT across all food webs
Lag-1 autocorrelation	Mean	0.06
Standard deviation	Mean	0.17
Skewness	Mean	-0.01
Kurtosis	Mean	-0.01
Lag-1 autocorrelation	Maximum	0.29
Standard deviation	Maximum	0.39
Skewness	Maximum	0.17
Kurtosis	Maximum	0.18



Supplementary figure 1: Relationship between amount of stress imposed before tipping occurs (x axis) and food web richness (y axis) on the predicted strength of the warning signal that is produced (colour) using a GAM. The result when predicting KT calculated using Lag-1 autocorrelation is presented on the left, and standard deviation on the right. The stress scenario presented here is where half of producers are stressed.



Supplementary figure 2: Relationship between amount of stress imposed before tipping occurs (x axis) and food web richness (y axis) on the predicted strength of the warning signal that is produced (colour) using a GAM. The result when predicting KT calculated using Lag-1 autocorrelation is presented on the left, and standard deviation on the right. The stress scenario presented here is where a single producers is stressed.



Supplementary plot 3: Pre-stress autocorrelation is best explained by maximum theoretical interaction strength with resource. Variance explained (y axis) by node-level network properties (x axis) predicting pre-stress autocorrelation. Colour indicates subset of data, based upon distance to tipping point, quantified by loss of growth rate before tipping. Inset shows that adding more predictors to a model containing the top predictor, "maximum theoretical interaction strength with resource", explains very little additional variance (numbers on x axis correspond to main plot). Stress scenario here is where half of all producers are stressed.

Chapter 4 - Exploring the role of species interactions in the propagation of early warning signals through complex food webs

Abstract

The prevention of critical transitions, where species reach a tipping point before rapidly progressing to a detrimental alternative stable state, is an important challenge for conservation and environmental risk assessment. Early warning signals (EWS) are a tool which has been developed to facilitate this by indicating when a tipping point approaches, using trends in statistical metrics such as autocorrelation. While it is known that in a complex food web nearing a tipping point most species will not show EWS, the variation in EWS strength in a species as a response to variation in the stress regime is less well understood. Here, the link between the relationship of a species and the source of stress was explored in simulations of complex food webs. It was found that almost all species showed high variation in signal strength, displaying both positive and negative signals depending on their relationship to species being directly stressed. When clear EWS were observed, it was found that predators, prey, and competitors of the stressed species often produced a distinctive combination of signal strength and population trend. This result suggests that it may be possible to use EWS strength in an observed species to predict EWS strength, and likelihood of being stressed, in neighbouring unmonitored species. Such a development would be valuable in conservation or risk assessment, where monitoring all species is impractical.

Introduction

When ecosystems are under persistent pressures they may reach a tipping point, before going through a critical transition to an alternate stable state (Scheffer *et al.*, 2001). Transitions to alternate stable states are often considered detrimental to biodiversity and ecosystem functioning, such as the desertification of arid areas (Guttal and Jayaprakash, 2008), or eutrophication of lakes or coral reef systems (Schröder, Persson and De Roos, 2005; Guarini and Coston-Guarini, 2024). A common characteristic of critical transitions is a phenomenon known as hysteresis, where reverting an alternate stable state requires returning to a system state past the original tipping point (Scheffer and Carpenter, 2003). Because reversal is so difficult, preventing a tipping point is generally more desirable than attempting to restore the original state. However, critical transitions often occur abruptly, with little advance warning from the system's state, making them inherently difficult to predict.

To address this unpredictability, researchers have developed early warning signals (EWS) that exploit a universal property of systems approaching a tipping point: critical slowing down – a loss of resilience, or reduced ability to recover from perturbations (Scheffer *et al.*, 2009). Critical slowing down occurs because the dominant eigenvalue, which controls how fast the system can change, tends to zero (Strogatz, 2001). EWS detect this phenomenon by tracking statistical metrics such as standard deviation and autocorrelation, that are theoretically and empirically linked to declining resilience (Carpenter and Brock, 2006; Van Nes and Scheffer, 2007; Burthe *et al.*, 2016). Both metrics are expected to increase as resilience decreases, rising because the system takes progressively longer to return to equilibrium after perturbation. Thus, an increasing trend in standard deviation or autocorrelation over time can serve as an EWS; an indicator of an approaching tipping point.

EWS were originally developed and applied ecologically in unidimensional systems, and as such have been used with some success in predictions of tipping points (Scheffer *et al.*, 2009; Dakos *et al.*, 2010). Building on these foundations, modern research has focused on developing more sophisticated approaches such as deep learning to optimise the signal-to-noise ratio and improve the ability to identify potential tipping points early (Bury *et al.*, 2021; Dylewsky, Anand and Bauch, 2024). EWS have also been applied to more complex systems, such as models of ecosystems and disease spread (Chen *et al.*, 2012; Dakos, 2018), where individual components interact, e.g. through trophic relationships in a food web. In such systems, a key challenge is that most species may not exhibit detectable EWS, making it

difficult to identify an impending tipping point from limited observations (Boerlijst, Oudman and De Roos, 2013; Weinans *et al.*, 2019).

Previous research into the mechanisms behind EWS production found that species whose dynamics aligned with the eigenvector associated with critical slowing down in state space were more likely to display EWS (Patterson, Strang and Abbott, 2021). Calculating eigenvectors requires a well parameterised model of the system in proximity of the equilibrium, which makes it difficult to calculate for natural systems (Dakos, 2018). However, this finding does suggest that the properties of the system, including the stress regime, may impact a species' EWS strength. Therefore, an understanding of how species relate to a system's properties, such as the dominant eigenvector or the stress regime, should make it possible to rank species' expected EWS.

There have been other attempts to identify candidate species which consistently display EWS. It has been shown that species which go extinct following the tipping point will show EWS (Dakos, 2018). This implies that species which are highly impacted by stress, ultimately driving them to extinction, will show strong EWS - as has been suggested previously (Carpenter *et al.*, 2014). Such species would be ideal targets for monitoring efforts if they could be identified in advance of tipping. An alternate strategy, designed to optimise the signal to noise ratio in multispecies systems, is the development of multivariate EWS. This approach combines multiple species time series using dimension reduction techniques such as PCA or MAF (Weinans *et al.*, 2019, 2021), and then applies classic EWS metrics to the resulting timeseries. Multivariate EWS attempt to move away from the prescience or providence required for monitoring the soon-to-be-extinct species by instead providing a single metric for the entire ecosystem. However, while this means that multivariate EWS can indicate that a tipping point is approaching, they cannot reveal which species are going to be impacted. Moreover, evidence on whether multivariate EWS outperform the best single-species EWS remains inconclusive and appears to be context dependent (Weinans *et al.*, 2021).

Another challenge with predicting tipping points in complex systems is the virtual impossibility of monitoring all species at a high enough temporal resolution to produce reliable EWS. This limitation makes the calculation of multivariate EWS, and other metrics based upon the time series of all species, impractical (Weinans *et al.*, 2021). Recent advances have reduced the data requirement to monitoring all species twice, with the intention of identifying candidate species for strong EWS which can then be monitored more intensely (Masuda, Aihara and MacLaren, 2024). A benefit of this technique is that it will recognise the species most likely to

display EWS irrespective of how the system is stressed, making it applicable to any system, but it does still require some monitoring of all species.

This chapter also builds upon ideas developed in chapter 3, which identified low trophic level specialists as most reliably showing strong EWS under the scenario where all producers experienced stress. This finding was attributed to these species possessing the lowest levels of the statistical metrics which EWS are based upon prior to stress, and therefore having the greatest potential for clear EWS. However, when stress was localised to a random producer, EWS were weaker and could not be predicted from network properties. Although species retained the same baseline potential for strong EWS, this potential was not realised. Therefore, there is a need to understand how the distribution of stress in a food web affects the distribution of EWS.

If species display highly variable EWS depending on the nature of stress impacting the food web, then the role of a species' position in the network, its structural network properties, must be limited, as these are unchanged by the location of stress. Stress drives a system towards a tipping point by altering the flows of biomass through a network, impacting population dynamics. Therefore, 2 key areas for understanding the distribution of EWS are (i) understanding which changes in population dynamics are responsible for producing EWS, and (ii) whether a species' relationship to the source of stress leads to consistent change in population dynamics, and therefore has a role in explaining variation in EWS. Understanding these processes has great potential for increasing the information gained from limited monitoring. Trends in population are expected to be closely related to EWS; EWS are designed to indicate the approach to a tipping point. If this tipping point is a population collapse to extinction, population change will clearly indicate whether a species is approaching or moving away from a tipping point. A relatively unexplored area, however, is the role of biomass flux on determining EWS strength.

Biomass flux is the amount of biomass moving between two species via predation. It has been shown, using a very simple system with a single consumer and resource, that increasing biomass flux between the two species, relative to the consumer's mortality rate, decreases stability (Rip and McCann, 2011). Interestingly, the chosen metrics for stability were both the system's dominant eigenvalue, which tended to zero, and the coefficient of variation, which increased. Therefore, although the paper does not mention EWS, it does display clear evidence of a relationship between flux and EWS, and is supported by other studies in similar systems (Gilbert *et al.*, 2014; Nilsson and McCann, 2016). However, further exploration into the role between biomass flux and EWS, particularly in larger networks, is clearly needed.

Current EWS research typically focuses on developing EWS metrics which are most likely to produce a strong signal against background noise (Dakos *et al.*, 2023; Dylewsky, Anand and Bauch, 2024), or to understand which species, if monitored, will produce the strongest signal (Patterson, Strang and Abbott, 2021; Masuda, Aihara and MacLaren, 2024). However, in the context of limited monitoring capacity, maximising the information obtained from available data is also a critical objective. The ideal scenario for generating EWS is not just monitoring the optimal species, but producing long term high resolution time series (Arkilanian *et al.*, 2020). These two demands are often at odds. Monitoring efforts which have already begun may not be targeting the best species for producing EWS. It has been found previously that species directly impacted by stress, such as overfishing, display strong EWS, but species some distance from stress but easier to monitor, such as phytoplankton, display weaker EWS (Carpenter *et al.*, 2014). Therefore, there is a need to maximise the information gained from monitoring any given species. This information comes from understanding the variability in EWS a species can provide, alongside the circumstances which influence this behaviour. While a strong EWS is often interpreted as evidence of direct exposure to external stress, alternative explanations may exist. Conversely, observing no EWS in species may also provide information regarding potential signals in neighbouring, unmonitored species.

Another challenge with EWS in complex systems is that the perfect candidate species can be producing strong EWS, indicating that the system is approaching a tipping point, but unless it is clear how the system is being stressed, then preventing that tipping point is still impossible (O'Brien *et al.*, 2023). Systems can be at risk of multiple tipping points, depending on the nature of the stress (Carpenter and Brock, 2006). The practical use of EWS should therefore be twofold. Firstly, they need to clearly indicate that the system is approaching a tipping point, which can be achieved by monitoring species which produce strong EWS. Secondly, they need to identify how the system is being stressed, so that mitigating action can occur. Here, an understanding of how stress impacts the distribution of EWS can be utilised.

Here, the aim is to identify consistent patterns in the occurrence and strength of EWS by examining the role of a species' relationship to the source of stress, along with relevant network properties, and the underlying mechanisms which control EWS propagation through a food web. To explore this idea, the applied stress is localised to a single species, so that any observed signals can be unambiguously attributed to the correct source. The objectives of this research are to: (i) quantify the typical variation in EWS strength for a species as the location of a localised press perturbation is altered; (ii) determine how the distribution of EWS can be explained in relation to a species' interactions with those directly impacted, e.g. as

competitor or prey, and the underlying mechanisms driving this variation, e.g. changes in biomass; and (iii) assess whether all EWS reliably indicate proximity to a tipping point, and identify potential causes of misleading or “unreliable” signals. To address these objectives, a dynamic bioenergetic food web model was used to simulate biomass time series, under localised stress targeting each consumer in turn, from an unstressed equilibrium to a tipping point in a number of artificial food webs. EWS were then calculated for all species, along with their relationship with the stressed species and other network properties, to assess under which scenarios species display which strength EWS.

Methods

In the following sections, the model used to evaluate the research questions is introduced, followed by details on the data collection from the model: estimating intraspecific variation in EWS strength, calculating the relationship with the source of stress under which these occurred, understanding the mechanism behind EWS strength, exploring the role of relationship to stress in influencing EWS strength via changes in biomass flux, and finally understanding where reliable and unreliable signalling is expected.

Bioenergetic Food Web Model

Simulation of food web biomass dynamics was performed using a stochastic version of a classic multispecies biomass dynamics model, the bioenergetic food web model, or BEFW (Yodzis and Innes, 1992). The biomass dynamics for primary producers and consumers are as follows:

Producers:

$$B_i' = B_i - B_i^2 - \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (1)$$

Consumers:

$$B_i' = -(x_i + \frac{\alpha_i \beta}{\beta + B_i})B_i + \sum_{j \in resources} x_i y_i B_i F_{ij} - \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \quad (2)$$

Here, B_i represents the biomass of species i. x_i is the mass-specific metabolic rate of species i, and y_i is species i's maximum consumption rate relative to its metabolic rate. e_{ji} is j's assimilation efficiency (proportion of consumed biomass that is converted to own biomass) when consuming i. $e_{ji} = 0.45$ if i is a producer, and 0.85 otherwise (Yodzis and Innes, 1992). Producers can only increase in biomass if $B_i > B_i^2$ (i.e if $B_i < 1$), thus each producer has a carrying capacity of 1.

An Allee effect was included by introducing density dependence into the metabolic loss term for all consumers, generating increased mortality at low population densities. Here, $\alpha_i = 0.3$ for all consumers, and is the maximum additional metabolic losses (when $B_i = 0$), and $\beta = 0.001$, influencing the slope of the Allee effect. The additional metabolic loss term is included only in the biomass dynamics of consumers. As a result, only consumer species are capable of undergoing critical transitions, and therefore all analyses have been restricted to consumers.

Species body masses, M, are determined allometrically via $M_i = Z^{T_i - 1}$, where T_i is the prey-averaged trophic level of species i, and Z is the consumer-resource body mass ratio, here set to 100. Body masses and metabolic types are used to scale metabolic and consumption rates using the principle of allometry (Brown *et al.*, 2004). In the BEFW, all biological rates are scaled to the mass of the smallest producer. Here, with all producers having a trophic level of 1 by definition (Levine, 1980; Williams and Martinez, 2004), this is 1 for all producers. All consumers are considered to be invertebrates and therefore $y_i = 8$ for all consumers, and $x_i = 0.314 M_i^{-0.25}$.

F_{ij} is the density-dependent multi-resource functional response of i consuming j. It takes the form:

$$F_{ij} = \frac{\omega_{ij} B_j^h}{B_0^h + c_i B_i B_0^h + \sum_{k \in resources} \omega_{ik} B_k^h} \qquad (3)$$

ω_{ij} is the relative prey preference of consumer i for resource j. Here, $\omega_{ij} = \frac{1}{n_i}$ where n_i is the number of resources of consumer i, B_0 is the half saturation density (set to 0.5) and c_i intraspecific predator interference (set to 0). h is the Hill exponent and determines the shape of the functional response, with a Holling type II functional response when $h = 1$ and type III when $h = 2$ (Holling, 1959b, 1959a). Here, the Hill exponent is set to 2, for a type III functional response.

Stochasticity and stress

Environmental stochasticity is essential to provide the perturbations necessary for EWS to develop. In this model, this was facilitated by applying a stochastic noise process to the metabolic rate of all consumers, x_i (eq. 2) as follows:

$$dx_{it} = \theta_i(\mu_{it} - p_{it})dt + \sigma_i \, dW_{it} \quad (4)$$

A single consumer was then stressed by reducing its maximum consumption rate, y_i in a stepwise fashion:

$$y_{it} = y_0 - \left(\frac{y_0 - y_{tipping}}{100}\right) t \quad (5)$$

Here, $y_{tipping}$ is the maximum consumption rate of species i before the tipping point, to 2 decimal places. This is calculated by simulating biomass dynamics of the food web to equilibrium, reducing y_i for from its initial value, y_0 (set to 8 for all species), by 0.01 until an extinction occurs. The tipping point therefore lies somewhere between that value and the previous, with $y_{tipping}$ the value of y_i which is 0.01 greater than that which causes extinction (and is therefore past the tipping point) is used as $y_{tipping}$. t is the current step within the simulation, taking the values 0-100.

Generating food webs and reaching equilibrium

Food webs were probabilistically generated using the niche model (Williams and Martinez, 2000). The niche model determines the position of trophic links (L) within a food web according to the number of species (S) and connectance ($C = L/S^2$). Here, 100,000 networks with species richness of 20 and connectance of 0.15 were generated. Biomass dynamics were simulated using the bioenergetic food web model without stochastic noise (Yodzis and Innes, 1992; Delmas *et al.*, 2017; Lajaaiti *et al.*, 2025) to equilibrium, here defined as the state where rate of change in biomass fell below 0.00001/time step, from a starting biomass of 0.5 for all species. Extinct species and disconnected species, which are either producers with no predators or consumers in a food chain with no extant producers at the base, were subsequently removed. From these stable food webs, a set of 100 food webs, each with 5 producers and 10-15 consumers, were selected for this study.

Stepwise stress experiment

To calculate EWS for each species as the food web approached a tipping point, stress was applied gradually in a stepwise fashion (Figure 1), similar to Dakos (2018), where stress is increased in set increments (steps). A stepwise approach to stress is useful in systems with a tipping point, as at each step it can be determined whether a tipping point has been reached. If a tipping point has not been reached, after each step the system is at a new equilibrium dictated by the change in underlying parameters as a result of the stress. At this new equilibrium, species biomass and EWS metrics can be calculated with a high degree of accuracy, indicating whether the system is approaching a tipping point, is biomass decreasing, and the effects of that on EWS metrics for each species.

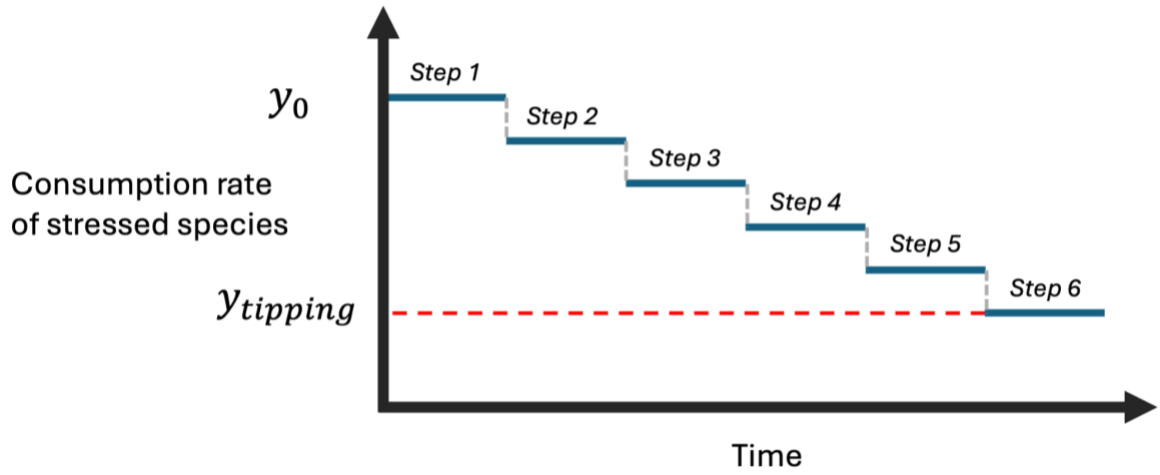


Figure 1: A visual representation of the stepwise stress process. Each step is an 8000 time step simulation of food web dynamics, over which time series metrics (autocorrelation and final biomass) for the food web are calculated (here 6 are shown, in the experiment there are 101). After each step the maximum consumption rate is reduced by an increment equal to 1/100th of the distance between y_0 and $y_{tipping}$.

Within each food web, multiple stress scenarios were generated by sequentially designating each consumer as the target of stress. Stress was implemented as a reduction in the maximum consumption rate of the focal consumer (eq. 5). For each target consumer, stress was applied in 100 evenly spaced increments between the unstressed state and the point immediately prior to the tipping point, which was determined in advance. This produced 101 stress levels per scenario, providing a consistent basis for comparison across consumers and across food webs. At each stress level, biomass dynamics were simulated for 8000 time steps, with data recorded at a resolution of 5 time steps. From these simulations, the biomass at the end of each step and the within-step lag-10 autocorrelation were calculated. EWS were then

estimated for each species in the web as the Kendall's τ correlation coefficient between stress level (0–100) and lag-10 autocorrelation. Kendall's τ is widely used as a measure of EWS strength (Chen, Ghadami and Epureanu, 2022). A step length of 8000 time steps was chosen as it minimised sampling variation in autocorrelation estimates. This procedure was repeated for every consumer in each of the 100 food webs, yielding a total of 1,273 stress scenarios.

Impact of relationship on EWS strength

Several metrics were calculated to try to explain distribution of EWS across scenarios. Each species was defined by its relationship to the stressed species; whether it was a predator of stressed species or not, prey of stressed species or not, or competitor of stressed species (sharing prey) or not. Primary producers were excluded from the analysis as they do not have an Allee effect, which is necessary in the current model for tipping points.

For each food web, the EWS each species produced were ranked across stress scenarios, resulting in 10-15 ranks, depending on food web species richness. The relationship of each species to the stressed species was calculated, and then the relationship between rank and relationship assessed using a linear model.

Mechanisms underlying EWS strength

To explore the relationship between changes in population dynamics and EWS, several metrics related to changes in biomass or biomass flux were calculated for each species. Biomass at pre-stress equilibrium and immediately prior to the tipping point were recorded, with these values used to calculate biomass flux into a consumer from its resources, out of a consumer to its predators, and the sum of both combined.

Biomass flux in (from equation 2):

$$Flux\ in_i = \sum_{j \in resources} x_i y_i B_i F_{ij} \tag{6}$$

Biomass flux out (from equation 2):

$$Flux\ out_i = \sum_{j \in consumers} \frac{x_j y_j B_j F_{ji}}{e_{ji}} \tag{7}$$

Full descriptions of metrics are available in Table 1. Additionally, the ability of trophic level to explain variation in KT was assessed to provide a comparison point, with trophic level chosen as it is a key topological property of food webs. For all tested metrics, ability to explain variation in EWs strength was carried out by fitting a generalised additive model (GAM) containing each property to explain Kendall's τ, with the R^2 of each GAM, which quantifies proportion of overall variance explained by that metric, used as a comparison point. This analysis was performed on 4 subsets of the data: all consumers, predators of stressed species only (cannibals not included), competitors of stressed species only, and prey of stressed species only (cannibals not included).

Table 1: A list and description of all metrics used to explain variation in Kendall's τ.

Metric	Description
Relative change in biomass	Change in biomass between pre-stress (B_0) and at tipping point (B_T) relative to initial biomass: $\frac{B_T - B_0}{B_0}$
Relative change in biomass flux	Change in biomass flux between pre-stress (F_0) and at tipping point (F_T) relative to initial biomass flux: $\frac{F_T - F_0}{F_0}$
Per capita change in biomass flux	Change in biomass flux per unit biomass between pre-stress ($\frac{F_0}{B_0}$) and at tipping point ($\frac{F_T}{B_T}$) relative to initial biomass flux: $\frac{\frac{F_T}{B_T} - \frac{F_0}{B_0}}{\frac{F_0}{B_0}}$
Per capita change in biomass flux in	Change in biomass flux per unit biomass in between pre-stress ($\frac{F_{in.0}}{B_0}$) and at tipping point ($\frac{F_{in.T}}{B_T}$) relative to initial biomass flux: $\frac{\frac{F_{in.T}}{B_T} - \frac{F_{in.0}}{B_0}}{\frac{F_{in.0}}{B_0}}$
Per capita change in biomass flux out	Change in *per capita* biomass flux out between pre-stress ($\frac{F_{out.0}}{B_0}$) and at tipping point ($\frac{F_{out.T}}{B_T}$) relative to initial biomass flux: $\frac{\frac{F_{out.T}}{B_T} - \frac{F_{out.0}}{B_0}}{\frac{F_{out.0}}{B_0}}$

Necessary conditions for strong EWS in each relationship

To investigate the conditions under which strong EWS arise, the dataset was partitioned by species' ecological relationship to the stressed species; predators, prey, and competitors. This approach allowed for an exploration into how changes in biomass dynamics linked to each relationship shape the propagation of EWS to species not directly experiencing stress. Conceptually, as a stressed species declines in biomass while approaching a tipping point, its predators lose prey, its prey lose predators, and its competitors experience competitive release. These impacts can be quantified as changes in biomass and biomass flux through the interaction pathways: from stressed species to their predators, from prey to the stressed species, and from shared prey to competitors.

Variation in EWS strength among species within the same relationship type can also be interpreted in terms of network properties, which reflect the extent to which a species depends on the stressed species. To capture this, the following metrics were calculated: (i) the number of alternative resources available to each predator of the stressed species, (ii) the number of alternative predators for each prey of the stressed species, and (iii) Jaccard's index (Jaccard, 1912), the intersection of the prey of the focal species and the stressed species as a proportion of their total prey, for competitors of the stressed species. To assess how these topological and flux-based metrics influence EWS propagation, generalised additive models (GAMs) were fitted, incorporating the relevant metrics for each relationship category.

Reliability of EWS

The reliability of EWS can be assessed by categorising a signal based upon its strength and direction, measured by KT, and the direction of biomass change. Signals were classified as *reliable* when a positive KT coincided with biomass decline, or a negative KT with biomass increase (true positives and true negatives). Conversely, signals were classified as *unreliable* when a positive KT was associated with biomass increase, or a negative KT with biomass decline (false positives and false negatives). Species were grouped by their ecological relationship to the stressed species, and the reliability of signals within each group was quantified. To further distinguish between genuine signals and those likely arising from sampling variation, signals were also categorised as weak ($-0.2 < KT < 0.2$) or strong ($KT > 0.2$ or $KT < -0.2$). The threshold of 0.2 is arbitrary, reflecting that KT is a correlation coefficient and values of this magnitude still indicate weak associations; however, in the absence of a precedent this cut-off provides a pragmatic means of separating signals of potential ecological relevance from those more likely attributable to noise.

Results

Intraspecific variation in EWS strength

Species showed substantial intraspecific variation in EWS across stress scenarios. Although species typically display no EWS (median Kendall's *τ* of 0.01), almost all species can display strongly positive EWS, with on average a maximum KT of 0.86 including when stressed, and a maximum of 0.53 when not directly stressed. Species also often showed strongly negative signals under certain scenarios (mean minimum kendall τ = –0.45), resulting in an average within-species range of 1.28 between the strongest positive and strongest negative signals (Figure 2). Together, these results demonstrate that the strength and even the direction of EWS for a given species can vary widely depending on where stress is applied in the food web, highlighting that EWS reliability cannot be assumed to be an intrinsic property of species but is strongly context-dependent.

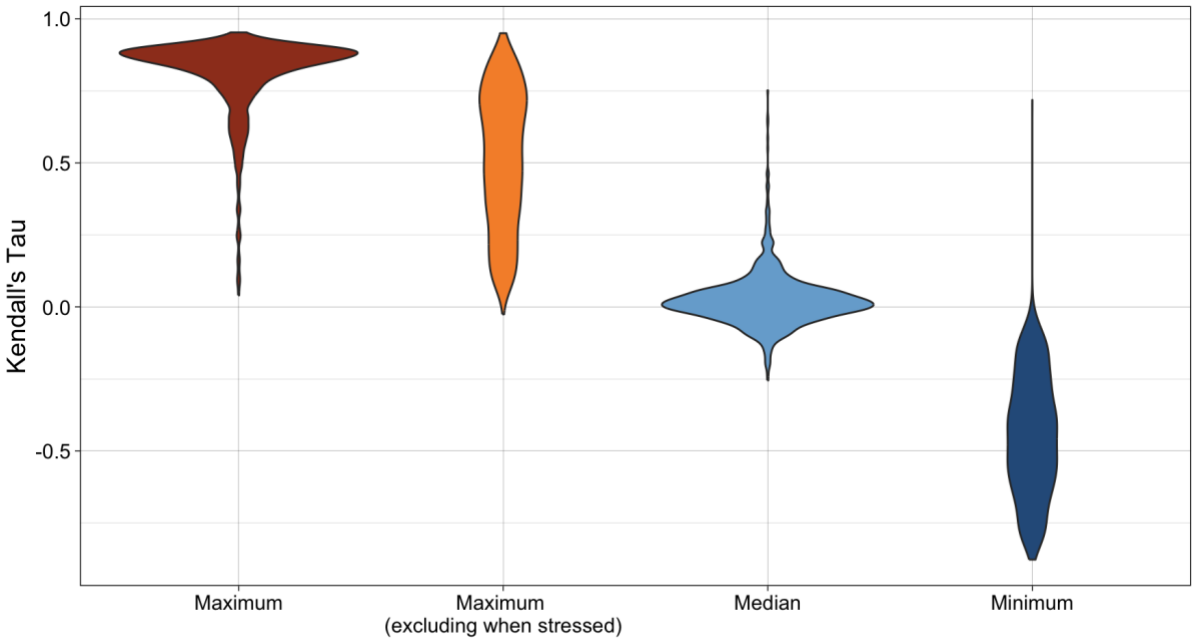


Figure 2: Distribution of summary statistics of variation in Kendall's τ (EWS strength) for each species as the consumer being stressed within each food food web changes. Calculated summary statistics are maximum, median, and minimum. The maximum KT a species displays is split into the maximum KT of all scenarios, and excluding the KT when that species is stressed.

Impact of relationship on EWS strength

EWS strength varied systematically with the ecological relationship between a focal species and the stressed species, as revealed by the ranking of signals across stress scenarios. Most species (85%) produced their strongest signal when they were the species subjected to stress. Strong signals were also common when species were directly linked as predators or prey of the stressed species, with these relationships disproportionately represented among the top five strongest signals (Figure 3). By contrast, species with no direct relationship to the stressed species tended to occupy intermediate ranks, being overrepresented in the 4th–9th highest and lowest positions (Supplementary Figure 1).

Competitive relationships were most often associated with weak or negative signals: although only 35% of all relationships were competitive, competitors accounted for 48% of cases among the five weakest signals, and 67% of cases where species produced their single weakest signal. A linear model confirmed these patterns. Relative to a baseline rank of 6.9, being the stressed species reduced rank by 5.13, being a prey reduced rank by 0.77, and being a predator reduced rank by 0.87, whereas competing with the stressed species increased rank by 2.02. Together, these results show that direct trophic connections to a stressed species amplify the strength of EWS, while competitors are more likely to generate weaker or misleading signals. This suggests that the predictive value of EWS depends not only on species identity, but also on their functional relationship to the source of stress.

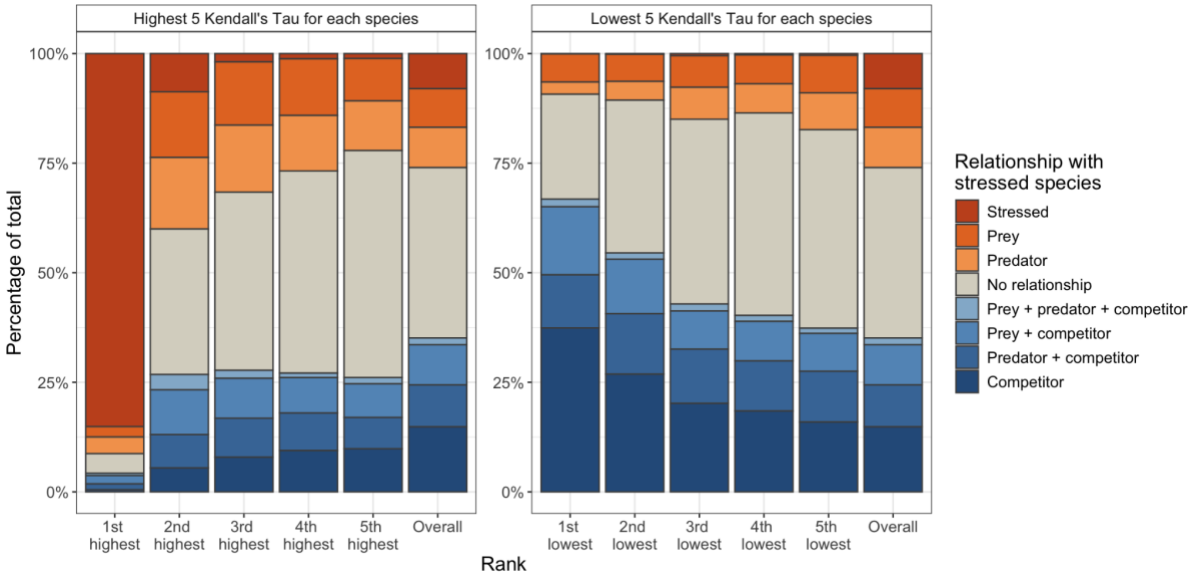


Figure 3: The relationship between each species and the stressed species when it produces its top 5 (left panel) and bottom 5 (right panel) strongest EWS, measured by Kendall's τ. Each species produced between 10 & 15 EWS, one for each stress scenario (as each of the 10-15

consumers in its food web were stressed in turn). The column labelled "Overall" is the distribution of relationships over all stress scenarios.

Mechanisms underlying EWS strength

EWS strength was best explained by changes in biomass flux rather than by changes in biomass. Across species and stress scenarios, flux-based metrics consistently showed stronger associations with Kendall's τ than biomass change, with the relative change in per capita biomass flux from a species to its predators emerging as the single best predictor (Figure 4A). Explanatory power was highest when models were fitted across all consumers, followed by predators of stressed species, then competitors, and lowest for prey of stressed species. The direction of flux change was also important: greater losses of biomass flux were associated with stronger positive signals (Figure 4B), particularly in stressed species themselves. Increases in biomass flux were generally linked to negative signals, most often among competitors of stressed species experiencing competitive release. Overall, these results show that the mechanisms driving EWS strength are rooted in changes to biomass flux. Declining flux tends to amplify positive signals, while increasing flux produces negative or misleading signals.

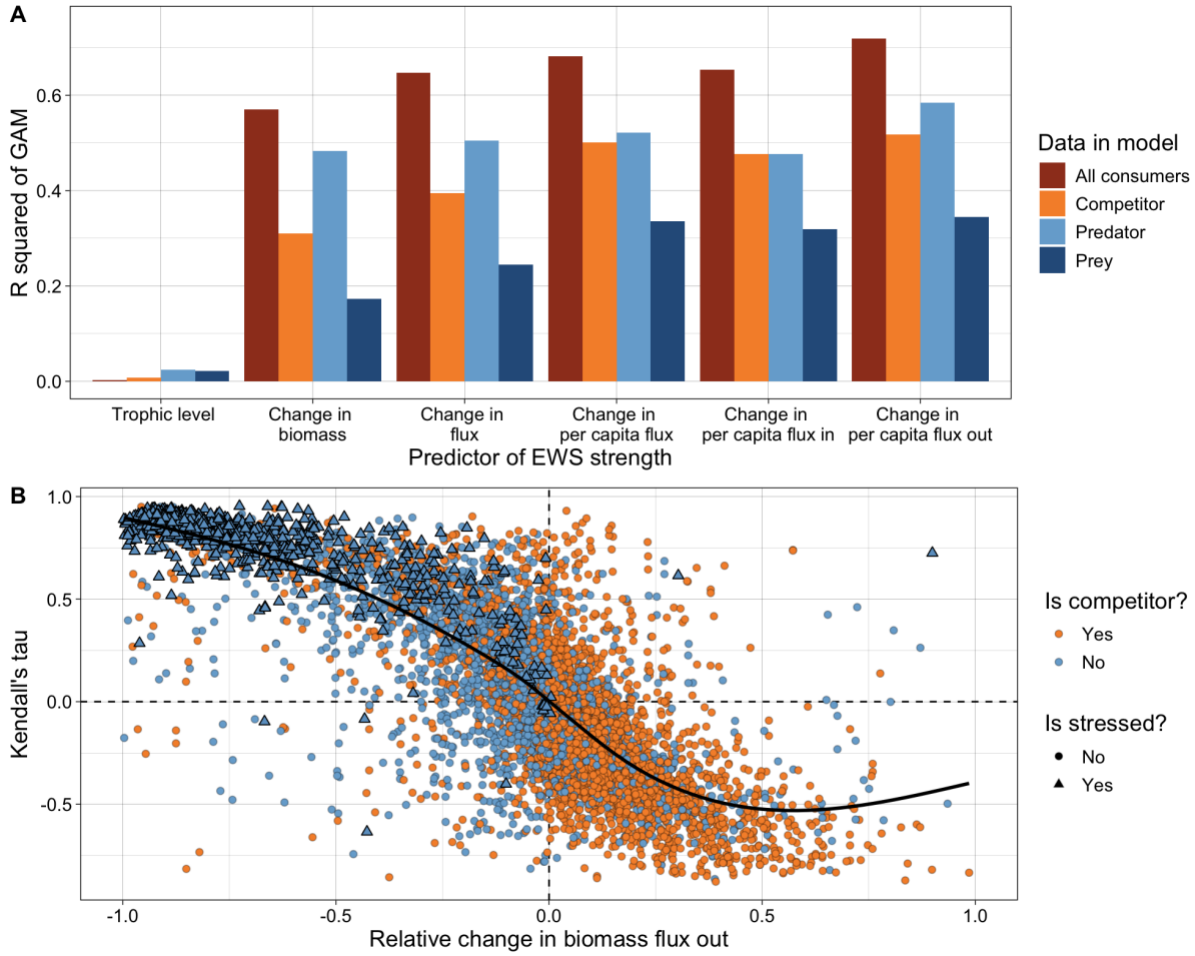


Figure 4: EWS strength, measured by Kendall's τ, correlates most strongly with relative change in biomass flow out of a consumer. Panel A compares the amount of variation explained using a GAM, quantified by R^2, (y axis) of five measures of biomass dynamics and a network property, trophic level, (x axis). 4 different subsets of data are included, distinguished by fill; all consumers, competitors of stressed species only, predators of stressed species only, and prey of stressed species only. Panel B displays the fit of the best model, relative change in biomass flux out (x axis) to the Kendall's τ of all species (y axis). Points are coloured by whether they represent a species which competes with the stressed species (orange) or not (blue). Species which are directly stressed, are represented by triangles, which are all blue as by definition they cannot be competitors with the stressed species (themselves).

Necessary conditions for strong EWS in each relationship

When do competitors show EWS?

Competitors tended to show EWS with a negative KT. Competitors of stressed species were overrepresented in species displaying negative KT, and underrepresented in species displaying positive EWS, resulting in competitors of stressed species displaying an average KT of -0.1, which was 0.15 lower than the average KT of non-competitors (Figure 5A). Change in biomass flux out explained the majority of variation in KT in competitors, with an R^2 of 0.51 when fitting a GAM (Figure 5B). The overlap in resources between stressed species and the competitor, measured using Jaccard's index, explained only a small amount of variation (5.9%) in KT, with a weakly negative relationship between KT and Jaccard's index (Figure 5C). The relationship between Jaccard's index and biomass flux is slightly stronger, with Jaccard's index explaining 9.7% of the variation in biomass flux (Figure 5D). Including both biomass flux and Jaccard's index in a GAM explaining KT does not improve on a GAM containing just biomass flux, suggesting that Jaccard's index explains KT through its relationship with biomass flux.

While species displaying strongly negative signals tend to have greater Jaccard's index (e.g. only 11% of competitors have a KT < -0.5, but they make up 72% of competitors with a Jaccard's index of 1), Jaccard's index has weak explanatory power because many species with weak EWS also have a high Jaccard's index. Overall, these results suggest that competitors of stressed species display negative EWS, which is a result of stress increasing the biomass flux out of these species. However, while having a high prey overlap, captured using Jaccard's index, is important for displaying strongly negative EWS, it is clear that it is not sufficient.

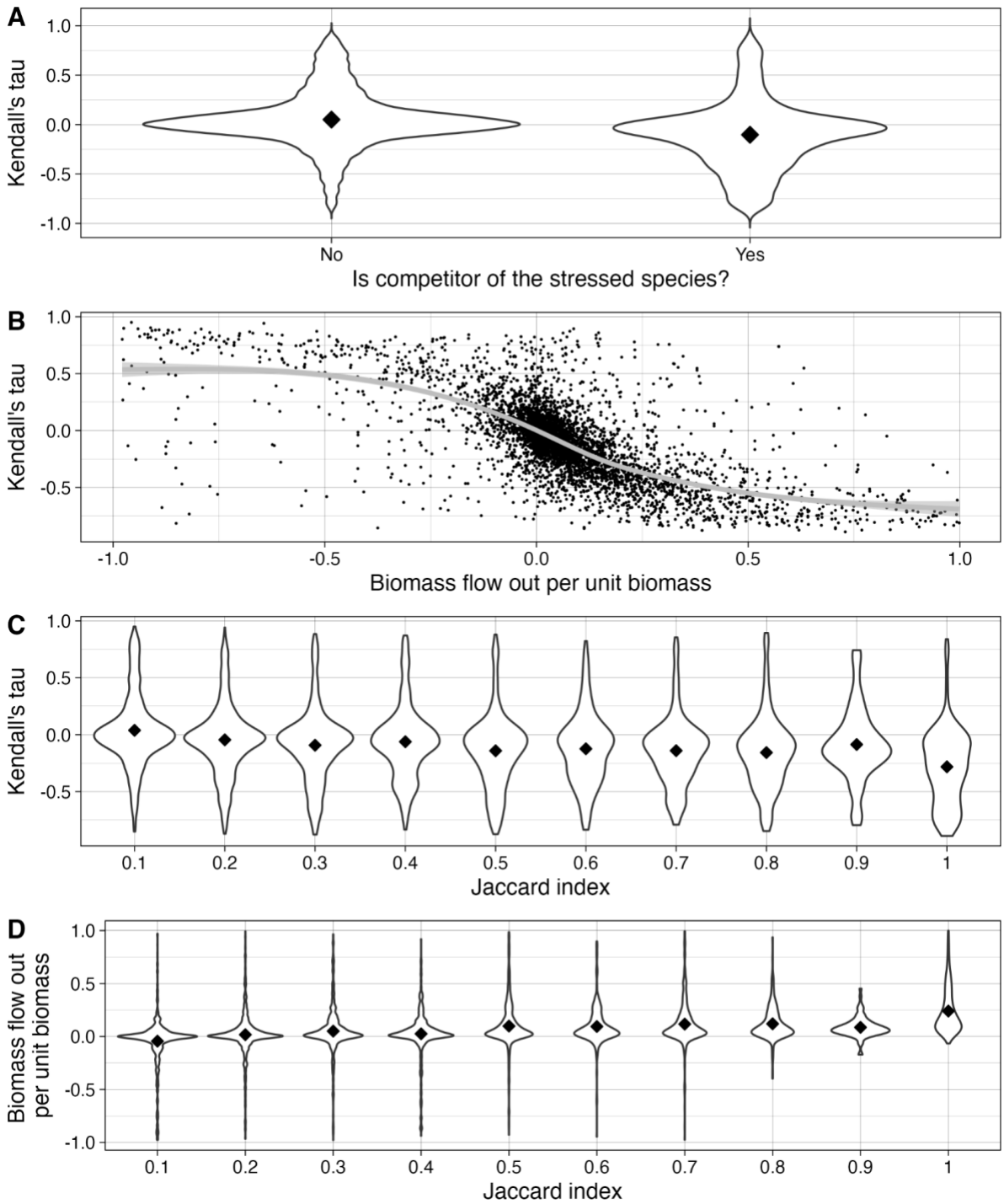


Figure 5: A breakdown of the relationship between EWS strength and various traits among species which compete with stressed species by having shared prey. Panel A shows the distribution of KT among competitors, compared to other unstressed consumers. Panel B shows the relationship between KT and biomass flux out of the competitor. Panel C shows the relationship between Jaccard index, a measure of dependency on shared resources, rounded to the nearest 0.1, and KT. Panel D shows the relationship between Jaccard index, rounded to the nearest 0.1, and biomass flux out of the competitor.

When do predators show EWS?

Predators which displayed strong EWS tended to be specialists, predominantly with a single resource. On average, 30% of unstressed consumers were predators of the stressed species. Predators of stressed species showed a similar distribution of EWS to non-predators, but with a slightly higher proportion of species with strong (KT > 0.5) EWS, and slightly fewer species displaying EWS with a negative KT (Figure 6A). Biomass flux out of a species again explained a majority of the variation in KT, with an R^2 of 0.59 when fitting a GAM (Figure 6B). The number of resources the predator has explained only a small amount of variation (7.8%), with a weakly negative relationship between a species' KT and number of resources (Figure 6C). Including both biomass flux and number of resources in a GAM explaining KT does not improve on a GAM containing just biomass flux, suggesting that the number of resources explains KT through its relationship with biomass flux.

Predators which only consumed the stressed species were very rare, accounting for 2% of all predators, but they produced much stronger EWS than their more generalist counterparts, with a mean KT of 0.6; other predators had a mean KT of 0.02, and predators with 2 resources produced a mean KT of 0.12. The relationship between number of resources and biomass flux was slightly stronger than with KT, with number of resources explaining 15.7% of the variation in biomass flux, and mirrors the relationship between KT and the number of resources - with predators with a single resource experiencing a much greater loss of biomass flux than others (Figure 6D). Overall, these results suggest that most predators of stressed species display no EWS. However, those which only predated upon the stressed species saw a large decline in biomass flux, which resulted in strong EWS, although having additional prey quickly reduced the strength of EWS observed.

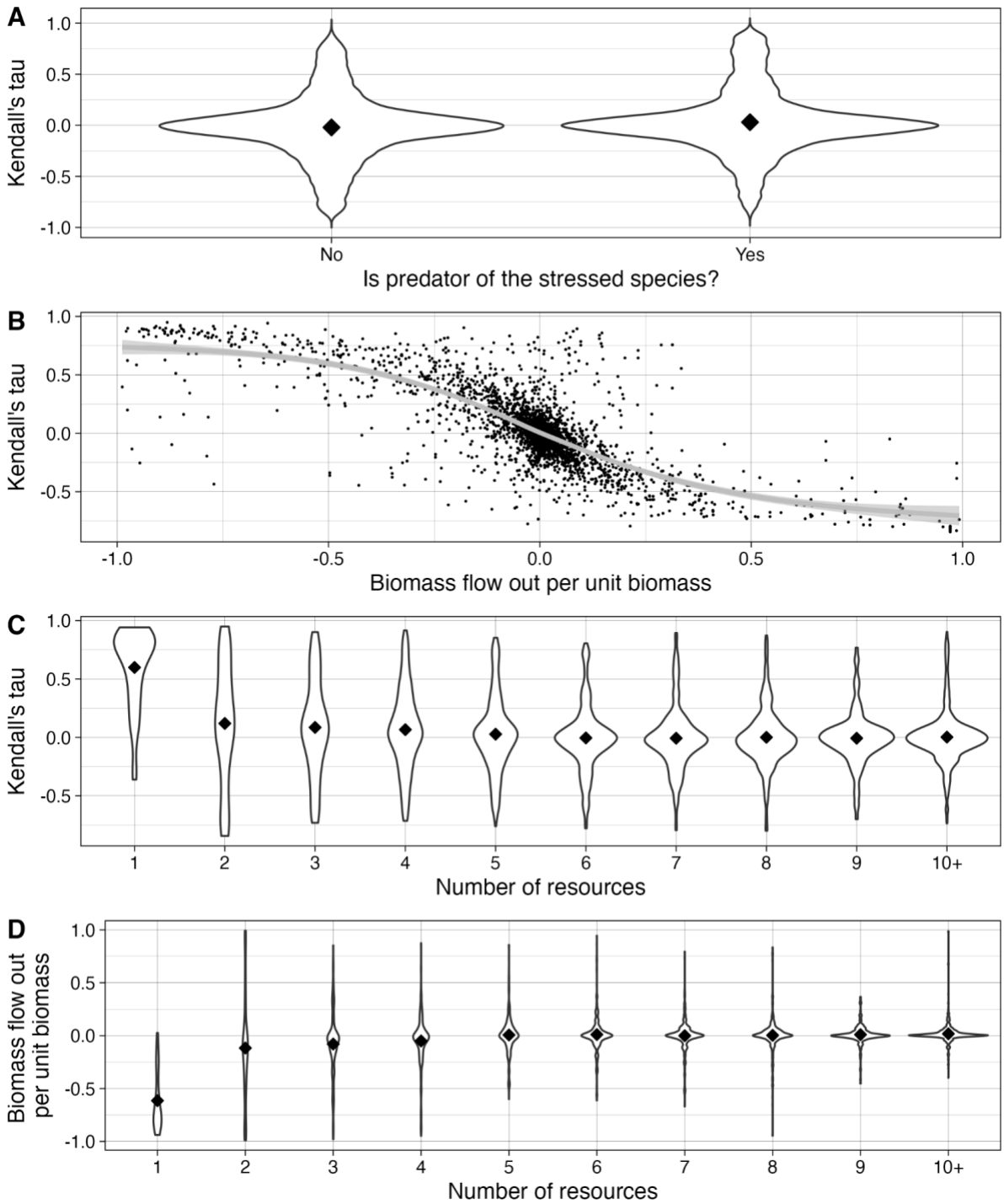


Figure 6: A breakdown of the relationship between EWS strength and various traits among species which predate upon the stressed species. Panel A shows the distribution of KT among predators, compared to other unstressed consumers. Panel B shows the relationship between KT and biomass flux out of the predator. Panel C shows the relationship between number of resources, a measure of dependency on the stressed species, and KT. Panel D shows the relationship between number of resources and biomass flux out of the predator.

When do prey show EWS?

Prey of stressed species follow the same overall trend as competitors and predators, indicating a relationship between EWS strength and changes in biomass flux. Prey of stressed species were overrepresented in species showing strong EWS, especially when positive, and underrepresented in species showing weak EWS (Figure 7A). As found in competitors and predators, KT in prey of stressed species was associated with trends in biomass flux, though it is weaker, with a GAM explaining 31% of variation (Figure 7B). There is a weak relationship between KT and number of consumers for prey species of stressed, explaining 4.8% of the observed variation (Figure 7C), but a stronger relationship between number of consumers and biomass flux, with number of consumers explaining 22% of the variation in biomass flux (Figure 7D). A lower number of consumers is associated with stronger EWS and a greater loss of biomass flux out of a prey species. Including both biomass flux and number of consumers in a GAM explaining KT does not improve on a GAM containing just biomass flux, suggesting that the number of consumers explains KT through its relationship with biomass flux. Overall, these results suggest that prey of stressed species are associated with positive EWS when stress reduces their predation, leading to a loss of the ability of biomass to flow from them to their predators.

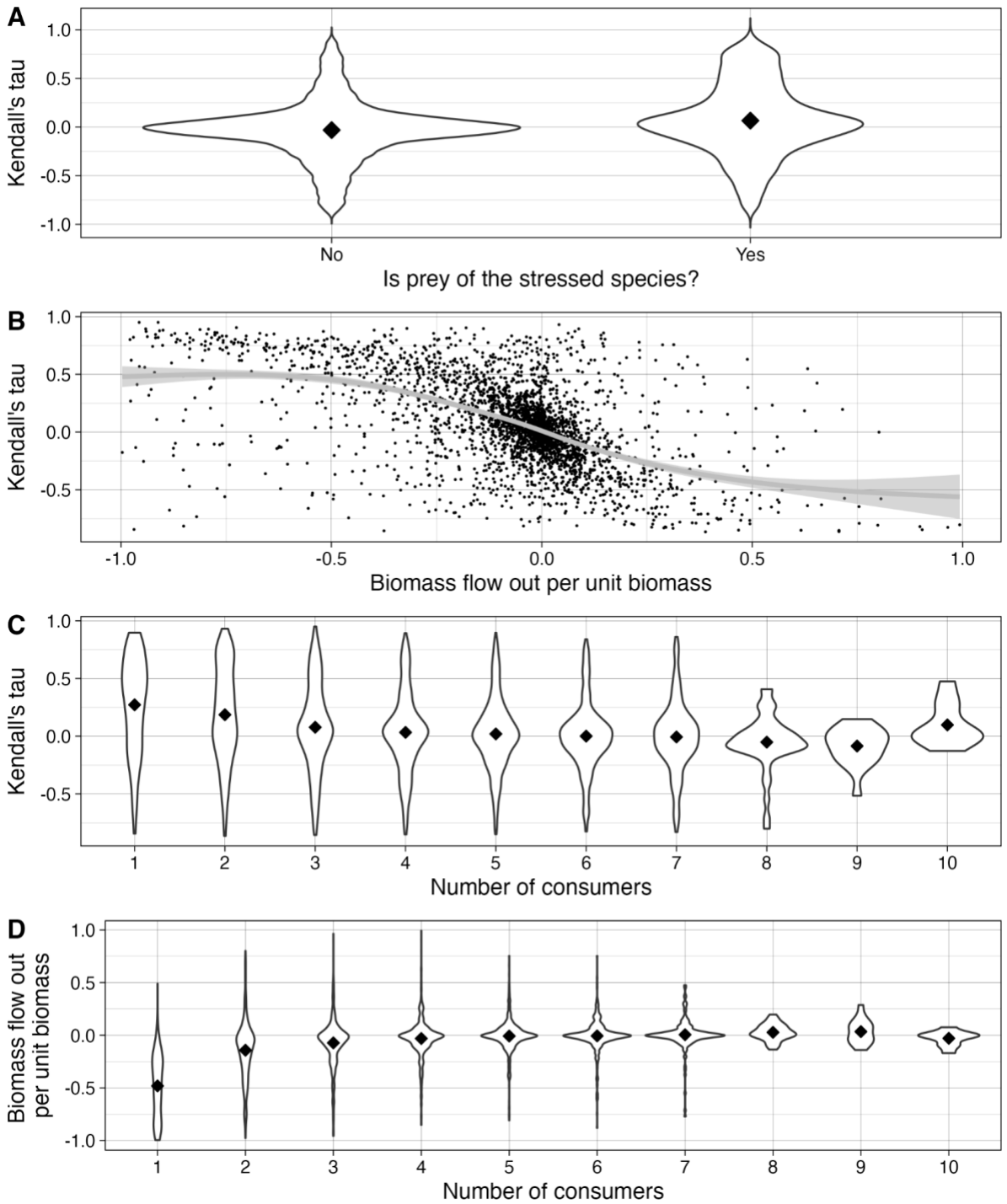


Figure 7: A breakdown of the relationship between EWS strength and various traits among species which are prey of the stressed species. Panel A shows the distribution of KT among prey, compared to other unstressed consumers. Panel B shows the relationship between KT and biomass flux out of the prey. Panel C shows the relationship between number of consumers, a measure of dependency on the stressed species for biomass flux out, and KT. Panel D shows the relationship between number of consumers and biomass flux out of the prey.

Reliability of EWS

When predators, prey, and competitors of stressed species displayed strong EWS, the combination of trends in biomass and KT presented by each group were generally distinctive. Species which display a positive KT and a loss of biomass were considered true positive EWS, while a positive KT and a gain in biomass were false positive, negative KT and a gain in biomass true negative, and negative KT and a loss of biomass were considered false negative signals.

The predators of stressed species were typically reliable, with 69% of signals either true positive or true negative (Figure 8A). When predators of stressed species showed false positive signals, they were usually weak (80% of false positive signals have a KT < 0.2). Stronger false positive EWS (KT > 0.2) were mostly found in species which were both predators and prey of stressed species (67% of species with strong false positive signals). False negative signals were also usually weak (80% have a KT > -0.2).

Competitors of stressed species were also usually reliable (71% of signals), and tended to be negative, with 57% of signals considered to be true negative (Figure 8B). As with predators, most false positive signals in competitors were weak (73% of false positive signals < 0.2), with the majority of the strongly false positive signals species which were both competitors and the prey of stressed species (80% of false positive signals with a KT > 0.2). False negative signals were rare (7% of all signals) and typically weak (69% of false negative signals have a KT > -0.2).

While prey of stressed species displayed reliable signals in 54% of observed cases, their most common signal type was false positive, which accounted for 42% of produced signals (Figure 8C). Additionally, prey of stressed species made up the majority (74%) of false positive signals with a KT > 0.2. In prey of stressed species which displayed false positive signals, it was observed that even though biomass was increasing, *per capita* biomass flux out of these species was decreasing, which caused autocorrelation to increase and lead to a positive KT.

Overall, these results suggest that predators and competitors of stressed species were typically reliable, whereas most unreliable false positive signals came from the prey of stressed species. This result holds when analysis is repeated while dropping species with multiple relationships to the stressed species, i.e. both prey and competitor (Supplementary Figure 2).

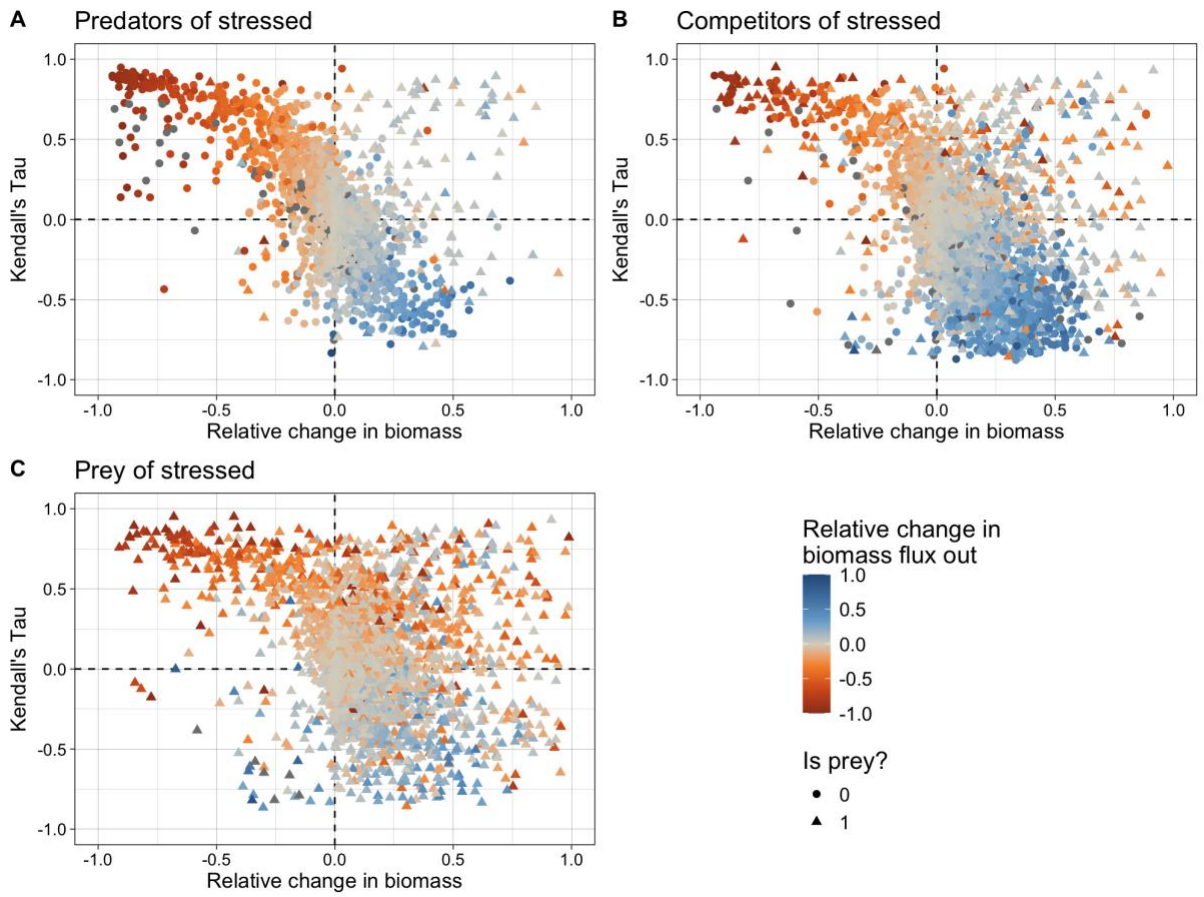


Figure 8: The reliability of EWS of predators of stressed species (panel A), competitors of stressed species (panel B) and prey of stressed species (panel C). True positive signals are a positive KT and negative change in biomass (the top left quadrant of each graph), false positive have a positive KT but positive change in biomass (top right quadrant), true negative signals have a negative KT and positive change in biomass (bottom right quadrant), while false negative have a negative KT and negative change in biomass (bottom left quadrant). The prey of stressed species are designated as triangles, including in the top two panels, when they are also predators or competitors.

Discussion

This study demonstrates that EWS in complex food webs are highly variable within species and across stress scenarios. The same species can produce strong positive, strong negative, or no signals at all - depending on where stress is applied. This shows that the reliability of EWS is not an intrinsic property of species but is strongly context dependent. By linking this variation to trophic relationships and to underlying changes in biomass flux, the mechanisms that determine when signals are strong or weak were identified, and when they conform to the expectations of classic EWS theory. This moves beyond species-level generalisations to show how EWS emerge from network interactions, and why they may be absent or misleading in some contexts. Understanding these dynamics is essential if EWS are to be interpreted reliably under the limited and noisy monitoring conditions typical of real ecosystems, and it highlights the importance of considering not just whether signals occur, but why they arise in particular species and relationships.

The strength and direction of a species' EWS shows a strong relationship with changes in biomass flux from that species to its predators, with a loss of flux related to strongly positive EWS. The trophic relationship between a focal species and the species being stressed is highly influential in determining its EWS strength, likely due to the effect this has on biomass flux. Species generally show positive warning signals when they are either directly stressed, predators of stressed species, or the prey of stressed species. The strength and direction of these signals are strongly linked to changes in biomass flux to predators, with losses in flux – particularly in more specialised interactions – producing the strongest positive signals. Species display negative EWS, where autocorrelation decreases and biomass increases as the species moves away from a tipping point, when they compete with stressed species. The strength of negative EWS of competitors increased as the proportion of their prey which is shared with the stressed species increased.

A relationship between changes in resilience and changes in biomass flux has been observed before, in a simple system consisting of a single consumer and resource (Rip and McCann, 2011). They seemingly find the opposite relationship between biomass flux and EWS strength than in this study, with increased biomass flux into the consumer resulting in increased coefficient of variation. This result was attributed to increases in biomass flux changing the ratio between the consumer's metabolic losses and biomass flux into the consumer. Here, in a larger network, consumers also experience biomass flux out to their predators, meaning that an increase in biomass flux into a species may lead to increase in biomass flux out. The

exception to this is prey of stressed species, which do see a similar result to Rip & McCann (2011); an increase in biomass flow in, alongside an increase in biomass and positive EWS. This suggests that the relationship between flux and resilience reported by Rip & McCann (2011) is an artefact of their system.

It appears that biomass flux out of a species is the component of a species dynamics which correlates most strongly with EWS strength. This implies that autocorrelation is therefore not directly driven by biomass change itself, but by whether a species is tightly regulated by predation or whether this control is relaxed or absent. The underlying mechanism of EWS production therefore lies in the shifting balance between top-down control by predators and intrinsic metabolic losses. When a species is strongly regulated by predation, biomass flux to predators is relatively high compared to metabolic losses, and autocorrelation is generally low. When released from predation due to predator stress, metabolic losses become an increasingly dominant part of a species' dynamics.

Most EWS are faithful indicators of a species approaching or moving away from a tipping point, as determined by a gain or loss of biomass. However, with EWS strength seemingly being determined by change in flux rather than change of biomass, unreliable signals, where positive trends in EWS metrics are associated with species moving away from a tipping point and vice versa, can also arise. These occurred most often among the prey of stressed species, particularly when they had few predators. In such cases, species experience a biomass flow to their predators without any corresponding loss of biomass flux from their prey, leading to simultaneous increases in biomass and autocorrelation. Not all species display EWS, and indeed strong EWS are rare, but there is great practical value in understanding the circumstances that consistently produce strong signals. It has been suggested previously that distance to stress is influential in EWS strength (Carpenter *et al.*, 2014; Dakos *et al.*, 2024), but it is clear that the type of relationship a species has with stressed species is also important.

Strong signals tended to occur in species whose dynamics were tightly coupled to those of the stressed species, with competitors being a key example. Competitors which showed strongly negative EWS were rare but shared certain characteristics. Species which produced strongly negative EWS typically had a high Jaccard's index with stressed species, representing a high degree of overlap in prey. This appears to be necessary for the large increases in biomass flux required for strongly negative EWS. However, the relationship between KT and Jaccard's index was weak; many species with high Jaccard's index did not produce strong EWS. This is likely because Jaccard's index only partially determines strength of competitive release - species which already dominate in their competition (Fox, 2002) with

the stressed species will see little release as a result of the stress, and therefore should not be expected to produce EWS. Critical transitions are known to alter species' competitive dominance (Doncaster *et al.*, 2016), and a more careful characterisation of competition strength between species is needed to fully understand when competitive release generates strong EWS.

One of the key findings of this study is that specialist links facilitate the transfer of EWS from species directly impacted by stress to species connected through local interactions. Specialist species have previously been identified as good candidates for strong EWS in mutualistic systems (Dakos and Bascompte, 2014; Patterson, Strang and Abbott, 2021); generalists tend to show weaker signals because regulation by multiple partners dampens their dynamics. Here, it seems that specialism creates a dependency on stressed species, meaning that stress generates the large changes in biomass flux needed for EWS production. Although increasing the distance to the source of stress is expected to reduce EWS strength (Carpenter *et al.*, 2014), there is no reason to assume that EWS cannot cascade through a food web, so long as species are connected through specialist links. This may provide an explanation as to why a quarter of species showed their second strongest EWS when neither directly stressed, predators, prey, nor competitors of stressed species.

The relationship observed between specialist interactions and propagation of EWS could be a result of the localised stress regime used in this study. Localised stress is a traditional mechanism for simulating collapse in communities (Baruah, Ozgul and Clements, 2022), and can represent scenarios such as overfishing a specific species (Link and Watson, 2019). However, it is important to consider whether any results observed are artefacts of the choice in stress regime. Under localised stress, only species with specialist interactions have a high proportion of their predators, prey or consumers directly affected by stress, and see large changes in biomass flux. However, ecosystems may also face multiple stressors simultaneously (Crain, Kroeker and Halpern, 2008; Simmons *et al.*, 2021), making understanding the distribution of EWS under a more complex stress regime an important expansion of this study. Implementing a wider impacting stress regime would disentangle whether species which propagate EWS are always specialists, or any species with a high proportion of their neighbours impacted by stress. This is important for the applicability of EWS to empirical food webs, which are more complex than the food webs tested here, and have long been known to be highly connected, made up from many weak trophic interactions (McCann, Hastings and Huxel, 1998; Vallina and Le Quéré, 2011). However, increasing connectance between species reduces the number of specialists (Dunne, Williams and Martinez, 2002; Petchey *et al.*, 2008). Therefore, a crucial area of further research is

understanding how food web richness and the extent of the stress regime impacts EWS propagation.

When a species produces EWS, the combination of the direction of change in biomass and the sign of the KT can indicate a species' relationship with the stressed species. Understanding how a system is stressed is essential for effective mitigating action (O'Brien *et al.*, 2023). Here, competitors of stressed species produced negative values of KT and increased in biomass if they experienced competitive release and moved away from a tipping point. Predators of stressed species produced positive values of KT and decreased in biomass if they saw a significant reduction in prey, which resulted in them approaching a tipping point. Prey of stressed species produced positive values of KT but increased in biomass if they saw a significant reduction in predation, which resulted in them moving away from a tipping point. While the positive EWS found in prey are unreliable as a signal of an impending tipping point, there is no risk of misidentifying these species as approaching a tipping point from their EWS. This is because EWS are calculated from biomass trends, which makes it impossible to produce the positive EWS without being aware of trends in biomass. There is great potential in being able to predict a species' relationship to stress from its combination of trends in biomass and autocorrelation. Monitoring of ecosystems is likely to be incomplete (Weinans *et al.*, 2021; Dakos *et al.*, 2024), and understanding how an ecosystem is being stressed is almost as important as understanding that a tipping point is approaching.

Another application of an improved understanding of the drivers of EWS production in food webs is increasing the information gained when a species produces no EWS. Although species may not produce EWS because the monitoring regime is insufficient to separate signal from noise. If it is possible to ascertain that monitoring efforts are enough to observe EWS when species are approaching tipping points, then understanding that EWS in food webs is related to biomass flux suggests that any species not showing EWS is not experiencing a large change in biomass flux. An extension of this is that this species is not seeing a significant reduction in predation or prey availability, nor is it experiencing competitive release. Therefore, the observed non-signal can be used to predict the state of unmonitored neighbouring species, particularly if the relationship is via specialist links.

A difficulty with interpreting the distribution of EWS across a network is that there is no consensus on what constitutes an EWS. EWS strength is strongly influenced by both levels of environmental noise (Perretti and Munch, 2012) and time-series length (Arkilanian *et al.*, 2020). Additionally, with a metric such as KT, the threshold for which an EWS becomes significantly distinct from the distribution of KT values expected from no signal is inversely

proportional to the number of observations (Chen, Ghadami and Epureanu, 2022). This study uses long periods of observation for each estimation of autocorrelation to ensure accuracy, and many (~100) observations of the timeseries. This provides favourable conditions for EWS production, and indeed almost all species do produce strong EWS under at least one stress regime.

However, even under these conditions, most species displayed weak EWS, consistent with previous research (Patterson, Strang and Abbott, 2021; Weinans *et al.*, 2021; Masuda, Aihara and MacLaren, 2024). Real world application of EWS requires a threshold for triggering action, with past examples including a significant increase in EWS metric (Burthe *et al.*, 2016; Clements, McCarthy and Blanchard, 2019), or a value of KT significantly different from that expected from species with no underlying changes (Chen, Ghadami and Epureanu, 2022). Moreover, the distribution of EWS strength within a complex food web is a continuum from strong to weak signals, suggesting that setting a threshold to separate signal from noise would be arbitrary. EWS cannot be used to quantify proximity to a tipping point, and instead should be considered an indication that the tipping point is approaching (Scheffer *et al.*, 2012; Gsell *et al.*, 2016). Stronger EWS, represented by higher values of KT, therefore do not suggest that a tipping point is closer - although within a system they do have a role in indicating a species' proximity to stress (Carpenter *et al.*, 2014; Dakos *et al.*, 2024). In this context, the key takeaway from observing an EWS is to understand the range of scenarios which could potentially produce that type of signal, rather than focusing on specific KT values, as this approach likely maximises the information gained from real-world signals.

Overall, this study shows that species produce EWS in complex food webs when stress significantly alters biomass flux to their predators. These signals can be positive or negative, depending on trophic relationships and changes in biomass flux. Strong signals are most likely when species are tightly linked to stressed neighbours, particularly through specialist interactions that amplify shifts in biomass flow. Negative signals often arise in competitors experiencing major release from competition, but only when they are not already dominant. Importantly, mismatches between changes in standing biomass and biomass flux can generate unreliable signals, especially among prey of stressed species. Metrics such as autocorrelation are therefore best understood as reflecting how stress propagates through trophic interactions. They are driven by impending tipping but often manifest in non-stressed species, with the strength and direction of shifts mediated by the trophic relationship between the focal and stressed nodes. Thus, EWS-like metrics provide insight not only into whether a system is nearing a tipping point, but also into how signals of stress propagate via trophic

interactions. Recognising this broader role increases the practical value of EWS metrics: strong, traditional EWS signals, though rare, are more reliable and informative, while weak or negative signals can help narrow down the conditions under which change is occurring. Extending this framework to larger networks and multiple simultaneous stressors will be an important next step for conservation and risk assessment in real-world ecosystems.

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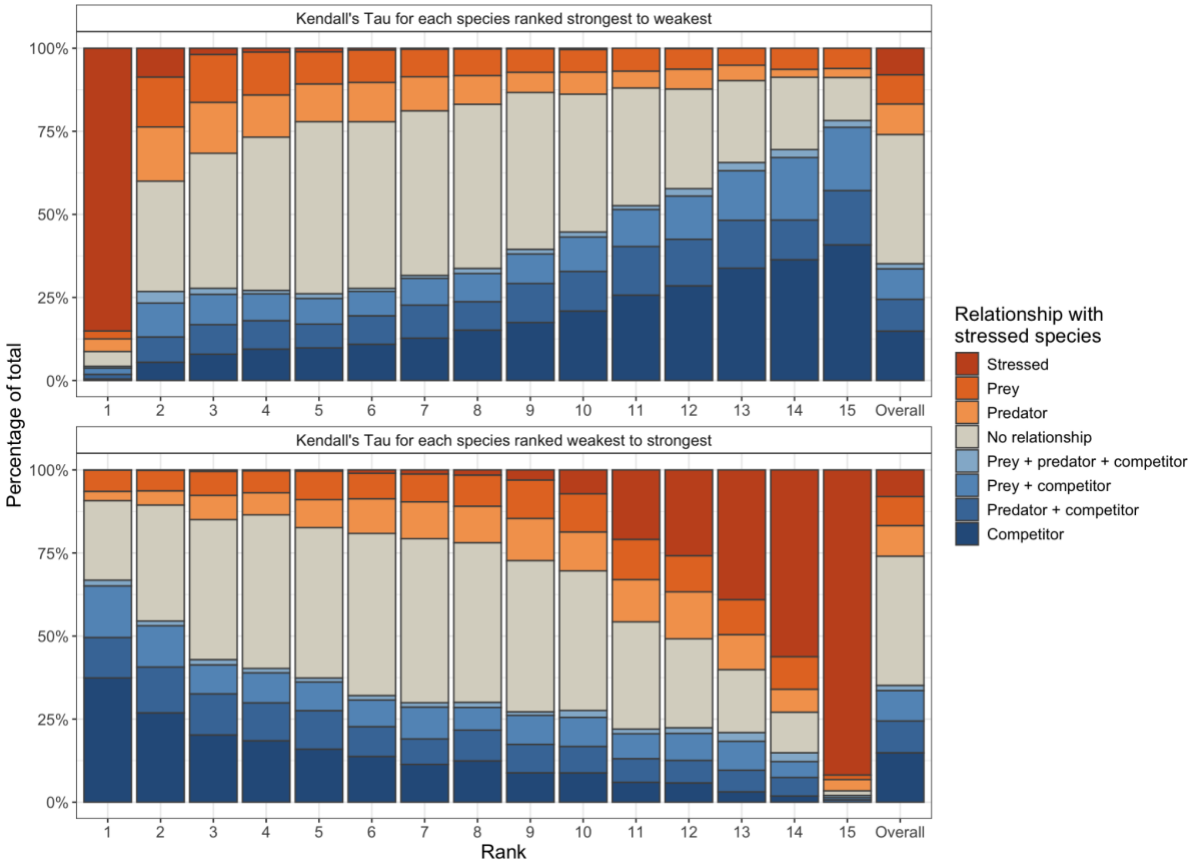
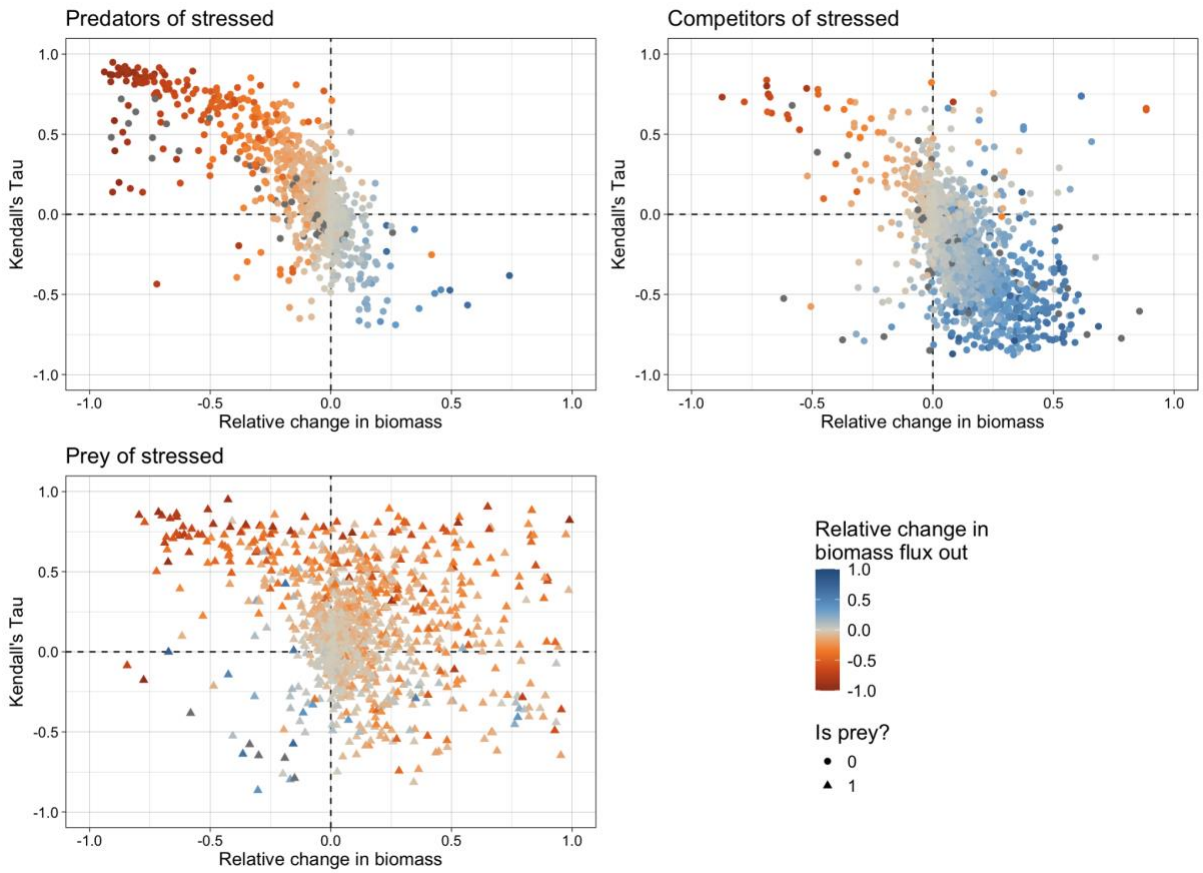
Supplementary material



Supplementary figure 1: The relationship between each species and the stressed species when it produces its full range of EWS, ranked from strongest to weakest (top panel) and weakest to strongest (bottom panel), measured by Kendall's τ. Each species produced between 10 & 15 EWS, one for each stress scenario (as each of the 10-15 consumers in its food web were stressed in turn). The column labelled "Overall" is the distribution of relationships over all stress scenarios.



Supplementary figure 2: The reliability of EWS of predators of stressed species (panel A), competitors of stressed species (panel B) and prey of stressed species (panel C). True positive signals are a positive KT and negative change in biomass (the top left quadrant of each graph), false positive have a positive KT but positive change in biomass (top right quadrant), true negative signals have a negative KT and positive change in biomass (bottom right quadrant), while false negative have a negative KT and negative change in biomass (bottom left quadrant). Species which have multiple relationships (i.e. both competitor and prey of stressed species) have been removed.

Chapter 5: General Discussion

Summary of thesis achievements

The purpose of this thesis was to explore the capabilities of classic EWS within complex food webs using simulation-based analyses. Specifically, it examined their potential roles, limitations, and patterns of expression in such systems through three strands of work. First, it was assessed whether EWS have value for conservation and environmental risk assessment by aiding prediction of extinction risk or loss of resilience, thereby extending their application beyond their original use in systems approaching critical transitions, which in the natural world are rare and difficult to identify conclusively. Second, recognising that most species in complex food webs do not display EWS and that monitoring all species is impractical, general properties of species associated with strong EWS were investigated, to provide guidance for more efficient monitoring. Third, properties and mechanisms underlying the propagation of EWS through ecological networks, from directly stressed species to their neighbours, was analysed. This final strand is especially important when monitoring has already begun and the choice of focal species is constrained, as it helps clarify how stress is distributed across a system through observed EWS.

In Chapter 2, *A comparative approach to predicting extinction in complex food webs*, I investigated how EWS metrics compared to trends in biomass and topological properties of the food web in their ability to predict where and when upcoming extinctions occurred. The underlying motivation for this work was to assess whether EWS provide added value in predicting extinctions, or whether focusing on other, more commonly used predictors, such as trends in biomass, would be sufficient. This work was carried out in a system without critical transitions, meaning that species went extinct following gradual declines. Additionally, in this Chapter I did not calculate formal EWS, but instead assessed whether summary statistics used in EWS, such as autocorrelation and standard deviation, were elevated in species approaching extinction. I found that EWS metrics were the most influential group of predictors, and that the ability to predict extinctions worsened as the time between the final observation used for the prediction and the extinction event increased. This suggests that species near extinction have low resilience represented by distinct levels of EWS metrics. Additionally, trends in biomass were found to be a far less influential measure. Together, this work suggests that in systems under pressure, where many or all species are declining in population, those at the highest risk of extinction produce the highest levels of EWS metrics, even though they may not be declining at a faster rate than other species. Therefore, EWS may have a role in ecosystem management and risk assessment, even if critical transitions are not anticipated.

In Chapter 3, *Linking topological properties to early warning signal strength in complex food webs approaching a tipping point*, I extended the model to include Allee effects, allowing the system to undergo critical transitions. Using this framework, I simulated food webs approaching collapse, calculated several classic EWS, and assessed which network properties best predicted strong signals. The central aim was to address two challenges: that most species in a food web are unlikely to display EWS, and that monitoring all species is impractical, with there being limited guidance on which species should be prioritised to maximise detection of strong signals. I found that the way stress is distributed throughout the food web had a major impact on the strength and predictive value of EWS. When all producers were stressed, population loss cascaded up the food web and all consumers approached tipping points. Under this scenario, the species with the strongest EWS were found to be those with the lowest levels of autocorrelation and standard deviation before stress was applied, which was associated with species with high interaction strength, which were specialists of low trophic levels. I suggested that having a lower starting level of autocorrelation or standard deviation gives these species the greatest capacity for EWS, which is especially relevant when all species are approaching a tipping point. By contrast, when only a single producer was stressed, only a subset of species were pushed close to their extinction threshold, while the rest of the system remained relatively stable. Under these conditions, EWS were weaker and less predictable, with strong signals observed mainly in species that ultimately went extinct. Nonetheless, selecting a sample of species with high interaction strengths to monitor returns stronger EWS than average. This sampling method works best when all producers are stressed but has a noticeable effect even under single-producer stress. This suggests that this result may have general applicability, providing guidance for monitoring efforts.

Chapter 4, *Exploring the role of species interactions in the propagation of early warning signals through complex food webs*, built upon ideas developed in Chapter 3. It has been implied in the literature but never explicitly stated that the distribution of EWS strength in a complex network such as a food web is dependent on the source of stress. Here, I tested this hypothesis by stressing each consumer in a network in turn, and calculating EWS. I found that the EWS strength of a given species varied greatly depending on which consumer was stressed. This suggests that network properties, which are invariant to the stress location, play only a limited general role in explaining species-level EWS strength when the target of stress is unknown. I then assessed which dynamic properties of a species were most related to EWS strength, and explored how the relationship between a species and the target of stress influenced EWS strength. EWS strength was most closely related to the changes in biomass flux from a species to its predators, with this leading to the potential for unreliable signals, where changes in biomass flux and overall biomass do not align. Analysis of trophic

relationships showed that species whose dynamics depended most heavily on the stressed species exhibited the strongest EWS. Species which compete with stressed species often displayed negative EWS, particularly if they had a high prey overlap, which was related to increases in biomass flux from shared prey. Predators of stressed species which specialised on the stress species showed stronger EWS than those which did not, as they saw greater losses of biomass flux following the collapse of this feeding link. Species for which the stressed species was one of their major predators showed positive EWS, relating to the loss in biomass flux leaving these species. However, these signals were often unreliable: as biomass flux out decreased, any increases in biomass flux into the species were balanced by increased metabolic losses, causing biomass accumulation and positive EWS. Overall, this work indicates the ways in which a species' relationship to species which are being stressed, and approaching tipping points, influences traditional EWS. The manifestation of these signals is mediated by trophic interactions, and without accounting for these relationships it is difficult to interpret traditional EWS reliably. Considering these relationships increases the information gained from any observed EWS, which is beneficial in a world where incomplete monitoring of a food web is likely, providing inference on potential stress impacting local unobserved species. This would in turn allow for a better understanding of the overall system's health, which could lead to a more effective intervention, with a greater probability of avoiding tipping points.

The concept of EWS capacity

A central theme of this thesis is how different stress regimes shape the distribution of EWS across food webs. Chapters 3 and 4 both used a very similar setup, analysing the timeseries of complex food webs approaching a tipping point. However, the stress regimes were very different, which allowed different research questions to be addressed. This led to different findings, which merit further discussion.

In Chapter 3, stress was applied to the producers of each network, either targeting one at random, half at random, or all. The two ends of this spectrum of stress impacts have very different consequences for the degree to which stress impacts the overall web. When all producers are stressed, all primary consumers lose their food, which cascades to the next trophic level until the entire network is impacted. This means that all species are approaching extinction, and because all consumers are subject to positive density dependence through an Allee effect, all consumers are approaching a tipping point. This is important because all species are expected to show EWS under these conditions. Most previous multispecies studies of EWS have been in systems where this is not considered to be the case (Patterson,

Strang and Abbott, 2021; Weinans *et al.*, 2021). Therefore, the expected generality of the findings of Chapter 3, that the strongest EWS are found in species with the lowest baseline autocorrelation and standard deviation, needs to be further explored.

A useful starting point for this exploration is the scenario in which only a single producer was stressed. This stress regime was implemented on the same networks, but generated a much more localised impact, with a much less predictable distribution of EWS. When a single producer is selected at random and stressed, no network property was found to be consistently associated with EWS. Instead, about the only conclusion that could be made was that the species which went extinct as the tipping point was reached displayed strong EWS. Whilst this was consistent with the literature (Dakos, 2018), it is a finding with limited practical applicability. The middle stress regime used in Chapter 3, where half the producers at random were stressed, provides a way to synthesise the ideas from stressing all producers versus stressing only one. Here, low baseline EWS metrics had more explanatory power than when one producer was stressed, and less than when all producers were. The opposite held true for the predictive power of whether a species went extinct, which decreased in predictive power as more resources were stressed.

Taken together, these results suggest that a species' baseline level of EWS metrics helps determine its capacity to generate strong signals under stress. Species with lower baseline levels experience larger changes in the EWS metric as they approach tipping points, resulting in stronger EWS. This aligns with recent findings (Masuda, Aihara and MacLaren, 2024), which showed that species with the largest changes in EWS metrics across a time series were the best candidates for producing strong signals. In my system, high EWS capacity was associated with specialists at lower trophic levels with high theoretical maximum interaction strength. While Masuda *et al.,*'s (2024) findings provide clear practical guidance, and are advantageous because their method will work under any stress regime, they do require monitoring all species, albeit just twice. Using network properties to predict species likely to produce large changes in EWS metrics provides an alternate method, reducing accuracy but requiring far less data.

Identifying species with the highest capacity for EWS is only part of the challenge for observing these signals in practice. Species with the lowest baseline levels of EWS metrics will display the strongest EWS possible in the system, but only if they are approaching a tipping point. This is the clear advantage of Masuda *et al.,*'s (2024) study, as it indicates species which are producing the greatest change in EWS metrics, not those with the greatest potential. This is because species with the highest capacity for EWS are not guaranteed to be approaching a

tipping point, which is highly dependent on how stress is impacting the system. Evidence for this is that baseline EWS metric levels, which are associated with EWS capacity, were a poor predictor of EWS strength when stress was localised to a single producer. Interestingly, the idea that species with low autocorrelation or standard deviation being the best candidates for EWS is at odds with the theory behind multivariate EWS, which assumes that the areas with the highest autocorrelation and standard deviation have the lowest resilience, and therefore should be targeted to isolate strong signals (Weinans *et al.*, 2019, 2021).

What information can be gathered from EWS strength?

Traditional EWS research focuses on developing methods to improve the ability to detect strong EWS, either by creating new EWS metrics which produce strongly positive signals (Dakos, 2018; Nijp *et al.*, 2019; Bury *et al.*, 2021), or by identifying properties of species associated with strong EWS (Dakos and Bascompte, 2014; Patterson, Strang and Abbott, 2021). However, in a complex network signals do not need to be strong or positive to contain information about the wider system state. In Chapter 4, stress is highly localised. The initial direction for this Chapter was to build off the findings of Chapter 3. Specialist species of low trophic levels were expected to have the greatest potential for EWS would be specialists of low trophic levels. However, as specialists, these species appear to only respond to stress when it occurs in a small part of the network, even though the opposite has been reported in mutualistic systems (Aparicio *et al.*, 2021). This raised the possibility of a trade-off: while specialists may have a high capacity for EWS, generalists might be more likely to produce signals as a response to a broader range of stress scenarios. Therefore, my working hypothesis was that species which most consistently showed strong EWS would be somewhere between the two extremes. However, one of the major findings of Chapter 4 is that, under variation in the target of stress, most species show large variation in the strength of EWS produced. Therefore, it is probably sensible to conclude that a species' capacity for EWS, measured by their baseline EWS metric levels, has the most applicability if the stress regime causes a large proportion of the food web to approach a tipping point. Because EWS produced by a species were variable but not random, the EWS displayed by a species can provide insight into the stress regime, even when they are not strongly positive.

Not only did species show highly variable EWS as the location of stress varied, but many consistently produced negative EWS (KT < 0), indicating decreasing autocorrelation. By definition, EWS are characterised by increases in these metrics, reflecting a system's approach to a tipping point. For this reason, previous studies have ignored negative trends in

EWS metrics (Burthe *et al.*, 2016). It is known, however, that increases in biomass or population can also be associated with EWS (Clements, McCarthy and Blanchard, 2019), because such dynamics may precede critical transitions associated with recovery. By contrast, in my study species often increased in biomass while moving *away* from a tipping point, which was reflected in declining EWS metrics and negative KT values. This suggests that negative EWS should not simply be dismissed: they do not occur in isolation and may instead provide information about nearby species or parts of the network approaching a tipping point.

However, perturbations do not always drive systems towards a tipping point. Species may show negative EWS because external pressures are relaxing, e.g. reducing harvesting from an overfished population. Therefore, an important consideration when observing a negative EWS is whether there is an expectation that the system is being driven towards a tipping point. This is often the case - with environmental risk assessment a good example; the system is only being monitored to detect the negative impacts of chemicals. Under these conditions, observing a population displaying negative EWS because it is doing well is indicative of declines elsewhere, while potentially indicating which species are negatively impacted.

The role of biomass flux

The finding that autocorrelation of biomass dynamics in food webs is more closely linked to biomass flux than standing biomass is a significant result. A link between biomass flux and EWS has been observed theoretically before (Rip and McCann, 2011). The authors stated that an increase in the biomass flux into the consumer caused an increase in the coefficient of variation (CV), with the dominant eigenvalue of the system tending to zero, which is the textbook definition of EWS. Rip and McCann (2011) interpret this as a sign of resilience loss and categorise their findings as a more general case of the paradox of enrichment (Rosenzweig, 1971), which is how they explain observing a loss of resilience and a gain in population. Their result appears to be the opposite of that found in Chapter 4: Rip and McCann (2011) find that increasing biomass flux causes an increase in CV and positive EWS, whereas I found that increasing biomass flux causes a decrease in autocorrelation and a negative EWS. However, a deeper consideration reveals both parallels and important differences between the two pieces of work. The system used in Rip and McCann (2011), is a two-species, consumer resource system. Therefore, any differences between these results can be considered due to the complexity of the network within which my focal species were embedded, which allowed for more sophisticated dynamics - crucially, that in a larger network

consumers also lose biomass through predation. This is a significant difference, because change in biomass flux through this mechanism was the strongest predictor of EWS strength.

Rip and McCann (2011) found that increasing biomass flux caused an increase in the consumer population, and produced EWS. This finding is very similar to the case in Chapter 4 where prey of stressed species produced false positive EWS. As with Rip and McCann (2011) these were species which gained biomass and showed positive EWS, and gained biomass because the ratio between biomass flowing in and out was increasing. The mechanisms are slightly different, however, with Rip and McCann (2011) increasing flux in or decreasing mortality, and prey species in Chapter 4 reducing in flow out. In the food webs used in Chapter 4, if a species saw an increase in biomass flux in, for instance from competitive release, this was typically matched by an increase in biomass flux out, and negative EWS. This opposite result is observed for species approaching a tipping point, which showed both a loss of biomass & biomass flux, and positive EWS. The exception to this pattern is in some prey of stressed species, when stress effectively causes the loss of predation. This suggests that the result of Rip and McCann (2011) may be a product of their system, and complex food webs, with more complex interactions between species, should in general be expected to show the opposite trend.

Overall, it can be concluded that EWS appear to be related to changes in biomass flux rather than changes in biomass. This has significant implications for the use of EWS in complex food webs, as the combination of biomass change and EWS strength observed in a species can together provide crucial information on exactly how stress in an ecosystem is impacting that species. If a species is increasing in population size and showing negative EWS, it is likely experiencing competitive release, i.e. something is stressing its predators. If a species is increasing in population size but displaying positive EWS it is likely experiencing a loss of predation. If a species is declining in population size and exhibiting positive EWS it is clearly approaching a tipping point, but this may be because it is being directly stressed or because its prey is being impacted. Understanding the ways in which EWS propagate to species clearly has the potential to advance the understanding of the risks to an ecosystem under limited monitoring.

Advancing applicability of EWS

One of the motivations for this thesis was to assess whether increasing the understanding of EWS in complex systems could improve ecosystem monitoring efforts. EWS have been applied to empirical systems previously, but often to long-term datasets for the purpose of

testing whether they appear (Burthe *et al.*, 2016; Gsell *et al.*, 2016; O'Brien *et al.*, 2023). Results of such studies are mixed (Stelzer *et al.*, 2021; Dakos *et al.*, 2024), with EWS appearing in most studies, but with an understanding of publication bias potentially skewing the data. The next step for EWS would be a wider uptake in management, such as conservation or environmental risk assessment (ERA). ERA in particular is a field moving towards a multispecies approach, with a focus on preserving ecosystem services under chemical stress (Maltby *et al.*, 2021; Van Den Brink *et al.*, 2021). Therefore, a wider understanding of a system's state could be beneficial. EWS are a potential tool here; as evidenced in Chapter 2, they can identify species which are at risk of extinction before traditional metrics such as population trends. The value in providing earlier warning is evident in both fields, with discussion of behavioural changes predating demographic changes in ERA (Borja *et al.*, 2008) and EWS (Cerini, Childs and Clements, 2023; Cerini *et al.*, 2025). If the only available data is observations of population, however, then it is clear that EWS can provide additional information compared to changes in biomass. Ultimately, one of the barriers to the uptake of EWS in fields such as ERA is awareness, although EWS are now becoming more widely known,

A need for a better metric?

The strength of EWS is typically measured using Kendall's τ (KT) correlation coefficient (Chen, Ghadami and Epureanu, 2022). As with any metric, there are advantages and disadvantages with KT. Other metrics have on occasion been used, particularly in empirical applications of EWS (Burthe *et al.*, 2016; Clements, McCarthy and Blanchard, 2019). The breadth of analysis of EWS in complex food webs within this thesis provides a basis for evaluating both the strengths and limitations of KT as a measure of EWS, which has been critiqued as a measure of EWS for almost as long as the use of EWS in ecology (Boettiger and Hastings, 2012).

In Chapter 2, I used the summary statistics underlying EWS, and used AUC as a metric to quantify their ability to discriminate between species at risk of extinction. This approach does not directly quantify trends in EWS metrics using KT. Chapters 3 & 4 both use KT in a number of different ways, such as exploring variation in EWS, ranking EWS, and exploring reliability of signals. As a metric, KT is a correlation coefficient, which means it is quantitative and bounded by -1 & 1. This makes comparison between KT values straightforward, and interpretation of a given value is intuitive and tangible. In addition, a positive or negative value gives some insight into the nature of the underlying relationship between the two metrics being correlated, namely a summary statistic, such as autocorrelation, and time. These properties mean it is easy to rank EWS among species, as has been done in Chapter 3 when using

interaction strength to sample species, and in Chapter 4 when comparing EWS strength within a species across stress regimes.

However, when considering the application of EWS measured by KT, a question as simple as "What is an EWS?" becomes surprisingly difficult. From the literature, most species in a network are expected to not show EWS (Aparicio *et al.*, 2021; Patterson, Strang and Abbott, 2021; Masuda, Aihara and MacLaren, 2024), but it is not clear what this means either, as there is no standard threshold between signal and noise. This leads to a number of challenges. Research questions throughout this thesis have been addressed by explaining variation in KT, without knowing how much of the observed variation is explainable, and how much is sampling variation. When discussing reliability in EWS in Chapter 4, the lack of a clear definition for no signal was prohibitive; is a species with a 1% increase in biomass and a KT of 0.01 really a false positive EWS? If not, then what is sufficient? Providing a generalisable solution to these questions is hindered by sampling variation; any threshold between signal and no signal is specific to the monitoring being undertaken.

The likelihood that an observed KT is produced by a time series with no underlying trend can be calculated. The distribution of KT from 100 random observations, the sample size used in Chapter 4, is a normal distribution with a mean of 0 and a standard deviation of 0.07 (Figure 1). Therefore, any KT > ±0.13 has a 95% chance to be not sampling variation of no signal, and is likely to be a true signal of an underlying change in autocorrelation and resilience. This exercise can be performed for any number of samples, with the range of values associated with no signal shrinking as sample size increases, has been generalised (Chen, Ghadami and Epureanu, 2022). Chen *et al.,* (2022) recommended the use of a non-parametric Mann-Kendall test to assess significance in KT. Other methods of significance testing using KT have been proposed, which compare the observed KT to a distribution of KT values generated from surrogate time series (Dakos *et al.*, 2012; O'Brien *et al.*, 2023).

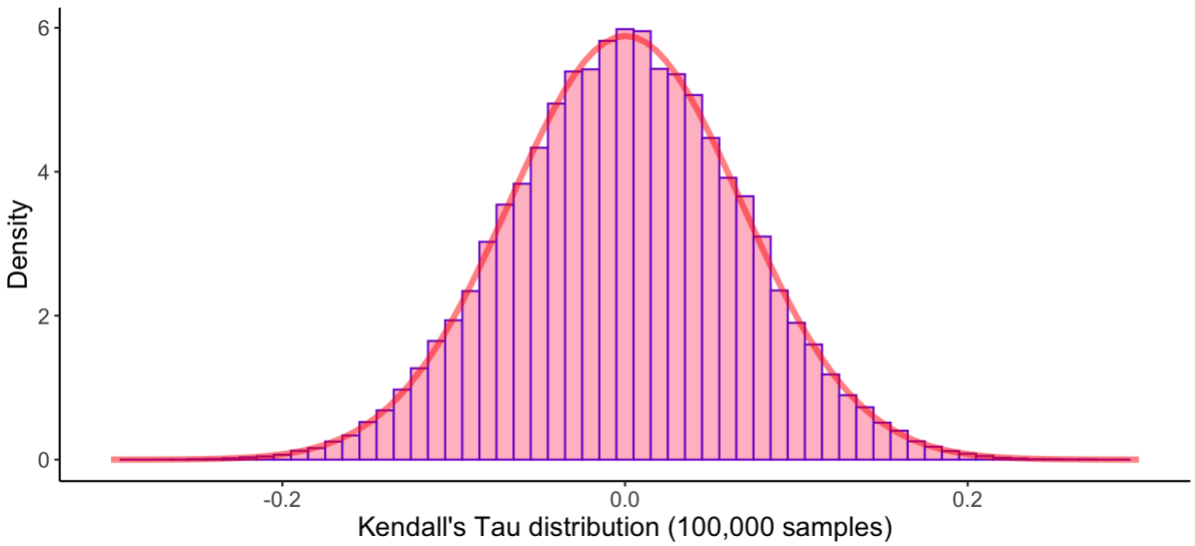


Figure 1: Kendal's τ from time series with no underlying signal is normally distributed. Data shown here is Kendall's τ calculated from 100 samples of a uniform distribution, representing 100 observations from a system with no signal, against the integers 1-100 in order, representing time. This process was repeated 100,000 times to create a distribution of expected KT from no signal, with the raw data plotted in a histogram. A normal distribution (red line) has been fitted to the data.

An alternative approach, seen a number of times in studies using empirical data, is not to use KT at all. If a baseline level of the EWS metric, such as autocorrelation or standard deviation, can be ascertained, then an EWS can be considered a significant deviation from this baseline level. This has been measured as either 2 standard deviations (Drake and Griffen, 2010; Clements, McCarthy and Blanchard, 2019), or whether the slope of the trend in autocorrelation or standard deviation was significantly non-zero, using a GAM (Burthe *et al.*, 2016). These approaches are effective for estimating whether a single time series is producing EWS, but less useful in comparing between EWS in a single multispecies system.

A recent study using EWS developed an alternate metric, which may be better equipped to indicate proximity to tipping point, utilising the tendency for the rate of change of EWS metrics to increase if a tipping point is nearby (MacLaren, Aihara and Masuda, 2025). Indicating distance to tipping point was one of the original purposes of EWS (Wissel, 1984), but has been widely recognised as impossible from current EWS (Scheffer *et al.*, 2012; Kéfi *et al.*, 2013; Gsell *et al.*, 2016). Even being able to distinguish between near and far from a tipping point could have wide-reaching implications for EWS research. As it stands, however, it is clear the successful practical application of EWS in multispecies systems needs to consider several factors. Firstly, there needs to be a threshold for when a signal is likely a signal and not noise. The above approaches provide various ways to do this. Secondly, there needs to be a threshold regarding when a signal is considered sufficiently strong to trigger intervention.

There is an argument that these two thresholds should be the same; EWS cannot currently indicate distance to tipping, and so therefore any EWS which clearly indicates that a system is approaching a tipping point should be acted upon. This is especially relevant in multispecies systems - as seen in Chapter 4, species display EWS for many reasons, and the strongest observed signal may be indirectly impacted by stress, and an unobserved species may have been producing stronger signals for some time. If the first step of mitigating action is to take time to ascertain where stress is impacting the network, then responding to the earliest observed signals is likely the safest option.

Directions for further research

Chapter 4 only considers the EWS of species closely linked to species under stress, focusing on their predators, prey and competitors. However, there is no reason to believe that the observable impacts of stress on species resilience would be confined to these immediate interactions. Trophic cascades are known to have wide-reaching impacts on populations linked through networks, with the reintroduction of wolves in Yellowstone National Park a classic example (Ripple *et al.*, 2025). In this system, the arrival of the wolves has been implicated in a 1500% increase in willow tree crown cover. This impact is several trophic levels away and will likely have caused further knock-on effects within the ecosystem. Similarly, EWS can propagate from species approaching a tipping point to their neighbours when strong interactions connect them. For example, Chapter 4 showed that predators dependent on a single resource exhibited much stronger EWS when that resource was stressed than predators with multiple resources. Therefore, understanding the extent and limiting factors of EWS propagation in complex networks is a key area for further research. Another related question would be whether distance from the original sources of stress causes a dampening effect on produced EWS, which would eventually lead to signals indistinguishable from sampling variation.

I would hypothesise that EWS would spread through networks with no limit in distance. Evidence for this would be in Chapter 3, where all producers were stressed, as most species produced EWS. However, as propagation of EWS requires species to experience significant changes in biomass flux, where stress is more limited then EWS propagation would be expected to end as species experience insufficient perturbation. Furthermore, distance from the origin of stress could be expected to introduce a lag. Consider the example of a food chain, with a producer with one consumer, who in turn has a single consumer, and so on. The loss of each trophic level would cause the collapse of the one above, but likely not simultaneously.

Therefore, while each species may be expected to produce EWS before it's own extinction, they may not produce EWS before the first tipping point. The lag in response to the stress should cause a corresponding lag in EWS.

While understanding how EWS are distributed through an ecosystem under relatively simple stress regimes is an essential first step, it is not overly realistic. Ecosystems are typically subjected to multiple simultaneous stressors, which may interact synergistically or antagonistically (Simmons *et al.*, 2021). An understanding of how this impacts the distribution of EWS is critical; ideally, knowledge of how EWS can propagate through a system can be used to inform likely locations of stress, which would allow for mitigating action. However, multiple stress has the potential to confuse the picture; if species are responding to stress from multiple directions, would their EWS be clear enough to isolate potential relationships to stress, or could the impact of any or all of the stressors be masked within a species' population dynamics?

Another interesting avenue for multistress research would be to understand whether having multiple sources of stress in a network could facilitate EWS propagation. Currently, Chapter 4 suggests that EWS as a result of localised stress spreads to neighbouring species only if they have a strong relationship with the stressed species. This appears to be analogous to the concept of trophic redundancy in extinction cascades (Sanders *et al.*, 2018); species which have a stressed species as either their predator, prey or competitor see a smaller impact to their biomass flux, and weaker EWS, if they also have unstressed predators, prey, or competitors. In Chapter 3, when all producers were stressed, essentially all primary consumers saw all of their prey approaching a tipping point, whether they were specialist or generalist, which then cascaded up the food chain to produce EWS in most species. This provides some evidence that food webs subjected to stress impacting more species should be expected to see stronger EWS cascades, but it would be useful to explore further.

A key area for further research is the use of more complex statistical models, particularly looking at interactions between predictors. This would be especially interesting in Chapters 3 & 4, which look at individual network properties to explain variation in KT. That the network property found in Chapter 3 to best explain variation in EWS strength was interaction strength, which as a metric is a combination of trophic level and number of resources, is telling. In Chapter 4, network properties were found to be associated with changes in biomass flux, but their identity varied depending on the relationship between stress and focal species. For predators of stressed species, the number of resources was related to changes in biomass flux, whilst for the prey of stressed species, the number of consumers had an impact.

Additionally, species could have more complex relationships with stressed species, such as being both a predator and a competitor. In such instances, a species' network properties likely influence whether they behave more like a competitor, and produce negative EWS following competitive release, or a predator, and display positive EWS as their prey declines. Using alternate models such as random forests may be an effective way to pick up on this additional information, as they are well suited for picking up on interactions between predictors.

The full distribution of EWS within a network is useful for a number of reasons. If there are the resources available for monitoring all species, this provides the best chance of detecting strong EWS. Additionally, species with the strongest signals are most likely to be directly affected by stress (Carpenter *et al.*, 2014; Patterson, Strang and Abbott, 2021), which is critical information for successful mitigating action. Using information from the EWS of observed species to predict unobserved EWS would therefore be a useful tool, if it were possible. A food web for which EWS are known for some species and not others, but with the complete network structure, is known in graph theory as a missing attribute problem. There are a number of tools available to solve missing attribute problems (Tu *et al.*, 2023), which may have potential to be applied to predicting EWS in food webs. As these tools involve machine learning, they are best used in large networks. In these situations, information about EWS in certain sections of the network can be learned i.e. that negative EWS share prey with positive EWS, and can then be applied to the wider network. Such a strategy is impossible in the relatively small networks with localised stress such as have been used in Chapter 4, but there is no limit to network size when using the bioenergetic food web model, as this work has done. If an approach to recover the complete distribution of EWS in a food web from limited monitoring is successful, then key research questions would centre around understanding (i) the degree of missingness which is permitted, and (ii) whether some species are better suited for preserving information than others. A similar question has been asked in mutualistic networks (Aparicio *et al.*, 2021), who identified specialist species as the key to a minimum set of sensor species, capable of picking up disturbances anywhere within the network. In terms of reconstructing the distribution of EWS across a network for the purpose of informing likely sources of stress, I would expect that species which show stronger signals give more reliable information regarding their neighbour's signals, and therefore are more important to measure for a faithful reproduction of the overall distribution of EWS.

Conclusions

Ultimately, EWS metrics provide a simple way to measure the resilience of a system. They were designed to be used when a system is approaching a tipping point before a critical transition. Here, I have shown they have multiple other uses, such as aiding in assessments of species extinction risk and indicating changes in the resilience of species that interact with those under stress. It is clear that the nature of the stress driving the system to a tipping point has a big impact on the strength and distribution of EWS within a network. It seems that all species have different capacity for displaying EWS, with strong EWS associated with higher baseline levels of the statistical metrics used to calculate EWS. However, in a complex food web, many species won't be impacted by stress, and therefore won't show EWS. Whilst understanding species' EWS capacity is a useful starting point, it is perhaps more practically useful to understand how a species' EWS are influenced by their relationship to the source of stress in the network. In the trophic systems I have studied, EWS strength appears to be dictated by changes in biomass flux, which means that observing an EWS can provide insight into how stress is affecting a species' dynamics. If this information can be used to identify likely species being directly impacted by external pressures, then mitigating action can be more targeted and more effective. Overall, this means that EWS may have a future in conservation and risk assessment in complex food webs, but only if their interpretation accounts for species' trophic relationships, stress regimes, and the potential information contained in both strong and weak signals.

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