The multidimensionality of ecological stability

by

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A thesis submitted in partial fulfillment of
the requirements for the degree of

Doctor of Philosophy

School of Natural Sciences
(Zoology)

Trinity College Dublin

December 2017

DECLARATION

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Summary

Ecological stability is a multifaceted concept, incorporating components such as variability, resistance, resilience, persistence, and robustness. Understanding and predicting the relationships among these many components of stability is fundamental to the optimal management of both biodiversity and ecosystem functioning. In spite of this, the multidimensionality of ecological stability remains remarkably understudied, with most research focussing on one or two components in isolation. We know worryingly little about the mechanisms underpinning relationships among components of stability and whether there are any general features of these that are common across different types of ecosystem or disturbance.

In this thesis, I explore the effect of perturbations on both the relationships between stability components and the predictability of these components. In Chapter 2, I examine the effects of perturbation intensity using theoretical simulations. By analysing the dynamics of food-webs following perturbations of different strengths, I discover that the predictability of stability components and the strength of relationships between them decrease with increasing perturbation strength. Importantly, this decoupling effect of strong perturbations was consistent across a variety of food-web structures. In Chapter 3, I test these predictions in natural communities using data from the Nutrient Network - a globally distributed grassland experimental system - to examine whether perturbations decouple relationships between components of stability at the global scale. Consistent with theory, I found weaker relationships between stability components in perturbed treatments compared to the unperturbed controls.

Natural systems encounter a large variety of perturbations that vary in their spatial extents, durations, frequencies, and intensities. While most models and experiments predicting ecological responses have typically applied static steady-state approaches that focus on a single perturbation event or the mean level of environmental change, few have incorporated environmental stochasticity. Moreover, those that do tend to incorporate it as white noise. In Chapter 4, using food-web modeling I explore how the response and predictability of different stability components are regulated by key characteristics of environmental stochasticity, in-

cluding its temporal autocorrelation (colour), and the strength of correlations in the responses of species to it. I found that different stability components showed distinct responding patterns to changing temporal autocorrelation of environmental noise. Increasing environmental autocorrelation stabilize communities in some dimensions yet simultaneously destabilize them in others. In contrast, the predictability of stability decreases consistently as the temporal autocorrelation of environmental noise becomes increasingly positive. This finding demonstrates the fundamental role played by environmental stochasticity in determining the dynamics and stability of ecosystems and challenges the credibility of models that overlook it or simply incorporate it as white noise.

Taken together, results of the research described in this thesis highlight important difference between different components of ecological stability in their response to external perturbations and environmental stochasticity, and emphasize the necessity of exploring further the multifaceted nature of ecological stability.

ACKNOWLEDGEMENTS

This thesis would not have been possible without the help and encouragement of the people mentioned below.

I would like to express my deep gratitude to my supervisor, Ian Donohue, whose expertise, patience, and inspiration, has always been there supporting me. Thank you for offering illuminating and significant insights into this project and the countless time and energy devoted to the design, discussion, and revision of this thesis.

I also wish to give my special gratitude to my co-supervisor, Andrew Jackson, who helped me a lot in science. He added a lot of invaluable suggestions and insights to my research. And many thanks to Yvonne Buckley and Paula Murphy for serving as my Ph.D. Steering Committee.

During my postgraduate study, I have totally enjoyed the collaboration with Jose Montoya and Mike Fowler. They both made a significant contribution to my research. Jose improved my understanding of ecological networks, while Mike put forward many useful comments on how to improve my study of the effect of environmental stochasticity on ecological stabilities. I give my special thanks to both of them.

A lot of thanks to my lovely former and current colleagues in Zoology department - especially Thomas Guillerme, Deirdre McClean and Luca Coscieme, who have kindly helped me a lot to adapt to the new life in Ireland, and always been there for giving a hand. Many thanks to Sam Ross, who checked and improved the English writing of *Chapter 3*. I also thank Natalie Cooper for introducing a lot of valuable training in computer skills during her stay in Zoology, which benefited my work.

最后感谢我的家人对我一直以来的关心并谅解我不能经常回国团聚，感谢代妞的理解与支持。感谢我的小侄女总是在周末给我带来欢笑。

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GENERAL INTRODUCTION

1.1 THE MULTIDIMENSIONALITY OF ECOLOGICAL STABILITY

Ecosystems underpin most of the resources and services upon which human beings depend (Costanza et al., 1997). The stability of ecosystems thus determines the sustainability of the resources that nature offers us. In an era of increased human activity (Western, 2001; Halpern et al., 2008), significant climate change (Nemani et al., 2003; Zhao and Running, 2010) and accelerated biodiversity loss (Stuart et al., 2004), an understanding of the mechanisms and drivers of ecological stability has crucial implications for both the sustainability and the management of natural resources. For decades, both theoretical and empirical studies have been providing key insights into the factors that regulate ecological stability. Considerable effort has, for example, been devoted to exploring the underlying effects of inherent properties of an ecosystem, such as its species richness (Yodzis 1976; Ives et al. 2000), network connectance (De Angelis, 1975; Rejmanek and Starỳ, 1979), the extent of omnivory (Fagan, 1997), and the distribution of interaction strengths among species (Paine, 1992; McCann et al., 1998; Brose et al., 2006). However, the vast majority of these studies fail to consider two key properties of ecological stability - its multidimensionality and its response to multiple types of perturbations.

The biggest challenge in the study of ecological stability is its multidimensionality. Stability comprises multiple interrelated components such as resistance, resilience, persistence, and invariability, all of which can be measured at a variety of temporal, spatial and ecological scales (Pimm, 1984; Grimm and Wissel, 1997; Ives and Carpenter, 2007). Resistance is a dimensionless ratio of some system variable measured after, compared to before, some perturbation. Resilience is the rate at which a system returns to its equilibrium, often measured as its reciprocal, the return time for the disturbance to decay to some specific fraction of its initial value. Persistence is the length of time a system maintains the same state before it changes in some defined way. It is often used as a measure of the susceptibility of systems to invasion

by new species or the loss of native species. One measures variability, the inverse of stability, as the coefficient of variation of a variable over time or across space.

Another challenge in studying ecological stability is the inconsistencies in terminology among different studies and different types of ecosystems. While stability was recognized as a multidimensional concept even in the early years of stability study, each component of ecological stability may have different definitions. For example, resistance in this thesis refers to the maximum (Euclidean) distance between the "perturbed" food-web and "unperturbed" food-web. However, in other literature, resistance is sometimes defined as the maximum strength of external perturbations the ecosystem can withstand. For example, one might measure the level of disease exposure required to cause infection as resistance (House et al., 2013). Note that the difference between the "resistance" in this example and the one quantified in this thesis is that the latter does not necessarily reflect the maximum perturbation that the ecosystem can bear. Moreover, some properties of ecological stability are themselves multidimensional concept. The best-known one is probably Holling's "resilience" (1973), which is often considered as an alternative concept of stability. In his classic exposition, Holling (1973) defined resilience to be the ability of a system to resist change in the face of disturbance, and stability to be the ability of a system to return to a stable state following the disturbance. This definition suggests that resilience is bivariate, using resistance and recovery as quantifiable components (Hodgson et al., 2015; Yeung and Richardson, 2016). However, recent interests in non-equilibrium paradigm and alternative stable states suggest that, depending on the uniqueness of the stable state of the ecosystem, resilience may be interpreted in different ways. When the unique stable state exists, resistance is similar to the one in this thesis and describes the instantaneous impact of exogenous disturbance on system state (Hodgson et al., 2015; Yeung and Richardson, 2016). Meanwhile, recovery captures the endogenous processes that pull the disturbed system back towards its equilibrium. Recovery can be quantified using either the return time (we use this quantification in Chapter 4) - duration of the journey form disturbed to the stable state - or the rate of the returning process (we use this quantification in Chapter 2). Hodgson et al. (2015) suggested that when alternative stable states exist, then "latitude" can be used to describe the distance to a tipping point - a state past which the system will move to a new stable state - and "Precariousness" can be used to indicate the distance from the disturbed state to the nearest tipping point.

In this these, we only considered the situation of the unique stable system state. Therefore, we most likely included both the resistance and recovery of Holling's resilience.

The vast majority of research on ecological stability to date has, however, failed to address this inherent complexity and has been almost wholly confined to just single, or a few, stability components (Fig. 1.1a). Empirical studies have tended to focus on the variability of the key properties of ecosystems across time and space (Fig. 1.1b), such as their productivity and total biomass (Tilman, 1996; Tilman et al., 2006; Bai et al., 2004; Hautier et al., 2014), while most theoretical studies have examined asymptotic stability, i.e. the ability of the biological community to maintain a relatively stable state under (very) weak perturbations (Fig. 1.1b). However, a reliable evaluation of ecological stability requires a better understanding of its multidimensional nature, the relationships between its different components, and how these relationships are regulated by both inherent properties of ecosystems, such as the network structure and distribution of interspecific interaction strengths in the system, and external perturbations (Donohue et al., 2013).

Species live in a web of resources, mutualists, competitors, predators and other enemies (Montoya et al., 2006; Bascompte, 2009; Kéfi et al., 2012). All encounter a profusion of diverse perturbations in their environment, both natural and human-induced, that vary in their spatial extent, duration, frequency and intensity (Tylianakis et al., 2008; Miller et al., 2011; Pincebourde et al., 2012; MacDougall et al., 2013). These multifaceted disturbances precipitate a range of responses that can alter the many components of ecological stability and the relationships among them (Donohue et al., 2013). However, as mentioned above, most early studies have emphasised the complexity of the biological community itself, and overlooked the impact of perturbations. While theoretical studies have linked the intensity of perturbations to the time taken for the system to return to equilibrium, they are constrained by the need to maintain the mathematical tractability of linear dynamics in their systems by exploring the effects of only very weak perturbations. Strong natural phenomena including drought, flooding, extreme weather conditions, and human-induced disturbance such as overexploitation of biological resources, destruction of habitats, and introduced exotic species can exert a profound influence upon different components of ecological stability (Jentsch et al., 2009; Zhao and Running, 2010; Bellard et al.,
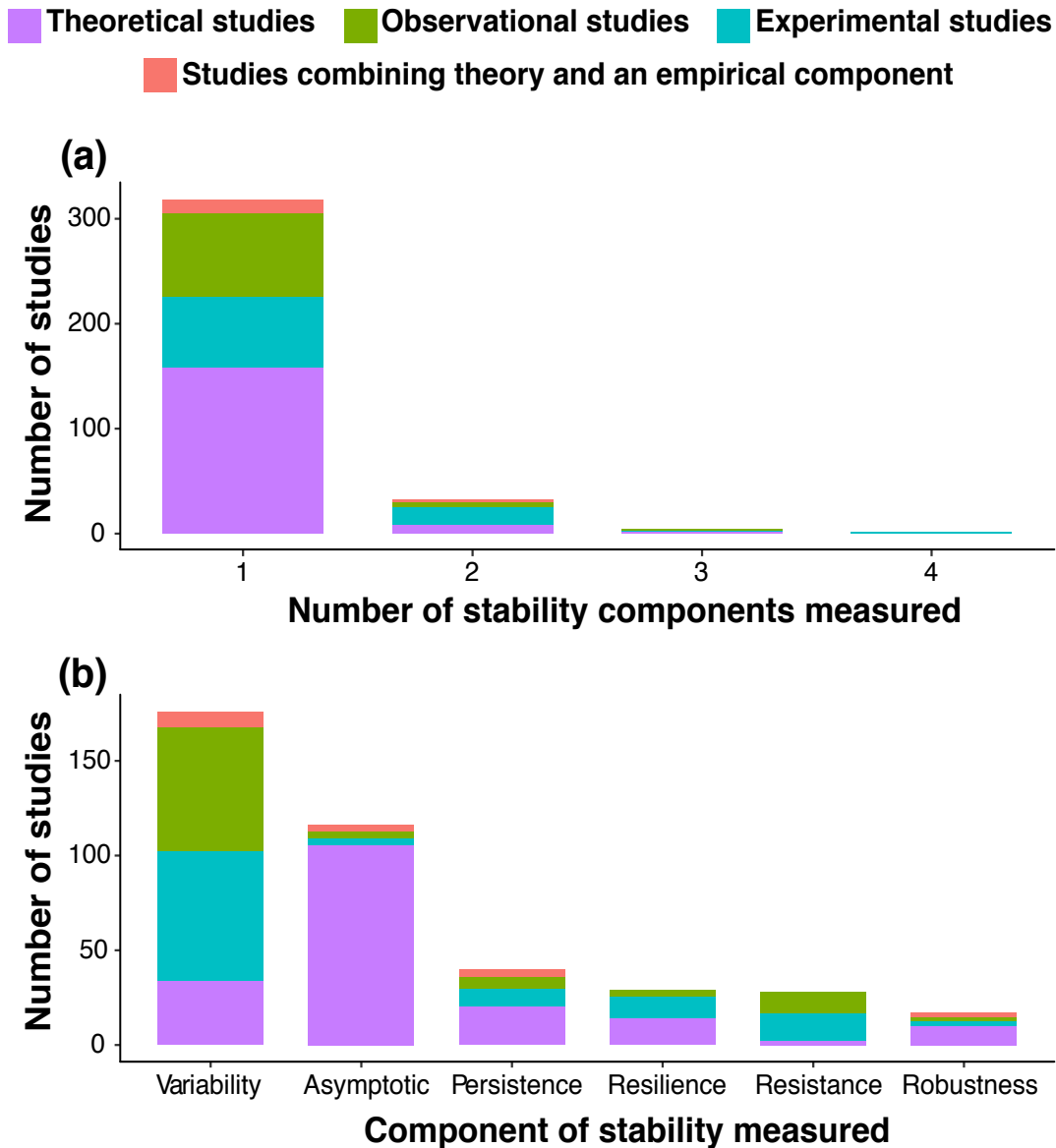
FIGURE 1.1: **Overview of studies of ecological stability.** To understand the differences in what theoreticians and empiricists study, Donohue et al. (including the author of this thesis, 2016) surveyed three high-impact multidisciplinary journals and four leading general ecology journals: *Nature*, *Science*, *PNAS*, *Ecology Letters*, *Ecology*, *Oikos* and *American Naturalist*. Using relevant search terms (*ecolog* stability*; *ecolog* resilience*; *ecolog* resistance*; *stability and diversity*), this yielded 894 papers, 354 of which measured ecological stability in one or more ways **(a)**. About half of these studies were purely theoretical, the other half empirical. Of the latter, there were nearly equal proportions of experimental and observational studies. Only 4% of studies combined both theory and empirical measurement. A further look into the stability components in these studies reveal a huge discrepancy between the components of stability studied in theoretical and empirical studies **(b)**.

2012; Cahill et al., 2013). However, we know little about how the different stability components trade off with one another under these intense perturbations (Schwarz et al., 2017).

Another form of perturbation that is often overlooked in studies of ecological stability is environmental stochasticity. Environmental stochasticity arises from externally derived uncertainty that affects populations regardless of size. Current models and experiments predicting ecological responses have typically applied static approaches that focus on mean environmental changes over gradients such as global warming and deforestation (Thompson et al., 2013) and fail to incorporate environmental stochasticity. Moreover, those that do tend to incorporate it as irregular uncertainty in environmental variation. However, environmental stochasticity has structure. The structure arises from correlated patterns of draws in the underlying distributions through time/space. Positive autocorrelation (i.e. red noise) occurs when successive events from a process are more likely to be similar to those nearby in time/space, whereas negative autocorrelation (i.e. blue noise) occurs when successive events are more likely to be dissimilar. Events can also exhibit no autocorrelation, termed white noise. Of these, red noise is most commonly observed in nature (Vasseur and Yodzis, 2004; Ruokolainen et al., 2009).

Exploring the underlying characteristics of environmental stochasticity such as its variance and spectral structure (Halley, 1996; Vasseur and Yodzis, 2004; Ruokolainen et al., 2009) can reveal the frequency and duration of extreme events (Easterling et al., 2000; Jentsch et al., 2009; Thompson et al., 2013; Kuparinen et al., 2014; Kayler et al., 2015), which may have more significant ecological consequences than averaged environmental changes alone. Until now studies involving both environmental stochasticity and ecological stability have almost exclusively focused on the effect of environmental stochasticity on population variability, persistence, and the consequent population extinction risk. Using theoretical models, these studies found that the predictable outcomes for population persistence depend on the interplay between population density dependence (i.e. compensatory dynamics) and the structure of the autocorrelation in environmental stochasticity (Lande, 1993; Sæther, 1997; Reuman et al., 2008; Ruokolainen et al., 2009). When scaling to communities, interspecific competition modulates the interactions between density dependence and autocorrelation in environmental stochasticity in complex ways

(Ruokolainen and Fowler, 2008). Only by incorporating community context - rather than summing up the component population-level patterns - can we predict how community diversity patterns respond to positive autocorrelation in environmental stochasticity. Using the competitive Lotka-Volterra model, Ruokolainen and Fowler (2008) found that the degree of synchrony in, versus independence of, species' responses to environmental variability played a key role. When each species responds independently (i.e. with low synchrony) to environmental variability, increasing positive autocorrelation of environmental stochasticity increases extinction risk (Ruokolainen and Fowler, 2008). Despite these important insights into the effect of environmental stochasticity on population and Community extinction patterns in coloured environments, knowledge of how environmental stochasticity regulates the multiple components of ecological stability, particularly those not directly related to extinction risks, is lacking.

In this thesis, I study how the predictability of different components of ecological stability and the relationships among these components are regulated by external disturbances in the form of single perturbation events and environmental stochasticity. To address these questions, I adopt both a theoretical simulation approach of food-web dynamics and an empirical analysis of data from a globally-distributed ecological experiment. To be simple and keep comparable with previous relevant studies (May, 1973; Pimm, 1982; Emmerson and Yearsley, 2004), theoretical models in this thesis adopted the equilibrium paradigm, assuming that ecosystems possess the capacity to return to its equilibrium after a perturbation by internal regulation through negative feedback mechanisms, such as intra- and interspecific competitions and consumer-resource interactions (DeAngelis and Waterhouse, 1987). In real nature, however, because of the disruptive feedbacks, fluctuating environment, and demographic and environmental stochasticity, ecosystems hardly maintain a stable state and present ongoing dynamics instead. When strong positive feedbacks in the ecosystem, the initial effect of the external perturbation may be amplified by the system itself, and lead to the gradual change of the system from its original stable states to another state. If there is a limit beyond which a system cannot return directly to its former state without strong external forces, this is termed a tipping point (Ives and Carpenter, 2007; Donohue et al., 2016). However, equilibrium models can still reveal the mechanisms that keep the species and functions of the ecosystem persistent in the face of perturbations and environmental variations.

1.2 STUDYING ECOLOGICAL STABILITY WITH ECOLOGICAL NETWORKS AND MODULES

Besides the multidimensionality of ecological stability and the multifaced nature of perturbations, another challenge in studying the dynamics and stability of ecosystems is the inherent complexity of the ecological network itself. Ecological networks are abstract representations of nature describing species diversity, trophic (i.e., feeding) and nontrophic (e.g., facilitation, mutualism) relationships between species, and flows of energy and nutrients or individuals within an ecosystem. Ecological networks are potentially difficult to understand because of their structural complexity, their dynamic nature (the number of nodes and edges frequently change through time), the diversity of types of links and nodes, the presence of nonlinear dynamics in the relationships between nodes and the fact that various network properties can often influence each other (Eklöf and Allesina, 2012).

In order to overcome the complexity of ecological networks, ecologists have tended to greatly simplify and deconstruct food webs (McCann and Gellner, 2012). A result of this simplification has been the development of the modular theory-the study of isolated subsystems, by assuming that a useful approach between the baroque complexity of the entire network and the bare bones of single and pairwise population dynamics is provided by close analyses of models of 'community modules' (Holt, 2002). Food webs are not random networks, and contain certain types of small connected modules with three or four species more often than expected by chance (Rossberg, 2012). Analyses of these modules may, at the very least, illuminate general processes and qualitative features of complex communities. For example, the food-chain module has received more attention than most of the other modules. Simple food chain models have helped clarify issues in the long-standing debate in ecology about the relative importance of natural enemies and resources in population regulation and stimulated interest in the interplay of primary production and trophic interactions in determining community structure and ecosystem function (Holt, 2002). Theoretical studies of community modules also clearly raised our consciousness about the potential importance of indirect interactions and weak interactions in regulating the dynamics and stability of ecosystems (Wootton, 1994; Holt, 2002).

By the facilitation of the community-module approach and some other network approaches, importance of the general network properties in regulating the stability of the ecological community have been identified. A central question in ecology is what network properties of ecosystems promote the long-term coexistence of numerous interacting species (May, 1973; Pimm, 1984; McCann et al., 1998; Montoya et al., 2006). The central concern is the relationship between the complexity and stability of the ecological network. The traditional view was that complexity, like many species and interactions between species, enhances stability (Odum, 1953; MacArthur, 1955), a view primarily based on observational studies of natural and experimental empirical systems. This view was, however, challenged in 1972 by Robert May (1972). May showed that an ecological network with randomly interacting species, resting at an equilibrium point, is inherently unstable if complex enough (i.e. high species number and/or high connectance between species). This study challenged other ecologists to try to find the mechanisms and ecological structures that promote the existence of large, complex natural ecosystems. Many studies have then been conducted to explore how the realistic, non-random interaction patterns in the community structures can stabilise ecological networks (de Ruiter et al., 1995; Allesina and Tang, 2012; Tang et al., 2014). Most of the theories found that many weak interactions with very few strong interactions can enhance the stability of the ecological network (McCann et al., 1998; Emmerson and Yearsley, 2004). This is, however, challenged by Allesina and Tang (2012). They extended May's findings and showed that predator-prey interactions are stabilising while mutualistic and competitive interactions are destabilising. Therefore, whether weak interactions enhance or decrease the stability of the ecological network depends on not only the interaction strength but also the interaction types (Mougi and Kondoh 2012). Recently, ecological networks in which parasitic and mutualistic links have been included have started appearing in the literature. The combination of different types of interaction would give a holistic view of ecological networks, although it would increase their complexity (Eklöf and Allesina, 2012).The topological characteristics of the ecological networks were also found to affect the stability of the ecosystems. Specifically, the existence of compartment (the group of highly interacting species) was found to enhance the stability of the communities, especially competitive communities (Moore and Hunt, 1988; Rozdilsky et al., 2004). The relationship between omnivory and stability has been another longstanding debate in ecology. Early theory predicted that omnivory would decrease the probability of food webs being

stable. However, the detailed study of food webs revealed that omnivory is actually ubiquitous across ecosystems and taxa (Kratina et al., 2012; Holyoak and Sachdev, 1998). Current efforts have therefore focused on identifying biological mechanisms that promote the persistence of food webs with omnivory. By synthesizing recent evidence, Kratina et al. (2012) conclude that omnivory stabilizes food webs when it occurs as life-history omnivory, when prey experience reduced predation rates due to refuges or adaptive antipredator defenses, and when omnivores interfere with each other or feed adaptively.

In this thesis, we quantified a total of six stability components including, resistance, resilience, invariability, ability to resist invasion, ability to resist extinction, and structural stability. Specifically, we quantified resistance, resilience, and invariability in Chapter 2. Resistance is the inverse of the degree to which a variable is changed following a perturbation; resilience is a measure of how fast a variable returns towards its equilibrium following a perturbation; and invariability is the inverse of the variance of a variable over time (Pimm, 1982; Donohue et al., 2016). So the resistance and resilience are actually two components of Holling's resilience (Holling, 1973). The resilience in this thesis is also referred as engineering resilience in some other literature (Hodgson et al., 2015). We quantified resistance and invariability in Chapter 3 by the same way as that in Chapter 2. However, because of the ongoing and non-negligible variation in the grassland ecosystems, we can not obtain a rigorous resilience and therefore we did not include resilience in Chapter 3. In addition to resistance and invariability, in Chapter 3 we also quantified the ability to resist invasion, ability to resist extinction, and structure stability, based on the species composition in the experimental plots. The ability of communities to resist species invasion was quantified as the reciprocal of the number of the species that were absent before experimental manipulation but present in the most recent sampling year after perturbation. The ability of communities to resist extinction was quantified as the reciprocal of the number of the species that were present within plots before experimental manipulation but absent in the most recent sampling year after perturbation. Structural stability is the ability of the community to maintain its original species composition after perturbations. This was defined as the reciprocal of community turnover, which was quantified as the mean Jaccard distance between the communities (after presence/absence transformation) over consecutive sampling years. In chapter 4, we quantified the extent of change, recovery time,

and variability, which are actually representatives of 'instability' and can be directly converted into the resistance, resilience, and invariability in Chapter 2. Therefore, our conclusions about the effect of environmental stochasticity on the predictability of the three 'instability' components are also equally applicable for the 'stability' components in Chapter 2.

In chapter 2 and Chapter 3, we focused on how external perturbations will change the correlation between stability components. We expect most of the six stability components in these two chapters to be positively correlated. We expect that resistance and invariability are strongly correlated. The relationship between resistance and invariability can be considered using their counterparts in Chapter 4, the extent of change and variability. The extent of change and variability can be considered the extreme value and variance of a data sample. Larger extreme values can be expected to appear in data samples with higher variance. Although we expect that a system has larger resistance to environmental variation and disturbances will recover faster than that susceptible to environmental variation, the relationship between them under strong perturbations is not clear, because large perturbation or strong environmental variations may keep the ecosystem away from its equilibrium and dominate by transient dynamics. Resistance and invariability are also expected to be positively correlated with the three stability components based on species composition. Communities with high temporal variability in abundance are expected to have low robustness due to an increased extinction risk in species with small population sizes (Pimm and Redfearn, 1988). Species extinction may provide niche space to facilitate invasion and potential strong competition from new species may lead to the loss of the local species. High rates of species invasion and extinction will inevitably increase the species turnover, i.e. structural stability in this thesis.

In the theoretical studies of Chapter 2 and Chapter 4, I adopted the modular approach.

1.3 RESEARCH OUTLINE

Chapter 2: Relationships among the various components of stability can vary in both nature and strength when systems are perturbed. Here, I investigate using theory the regulation by perturbation intensity of the relationships between stability components, and explore the underlying mechanisms of this regulation. By simulat-

ing the dynamics of food-webs following perturbations on the apex predator, I find that the predictability of individual stability components and the correlations between these components tend to decrease along an increasing gradient of perturbation intensity. Moreover, this pattern holds across numerous food-web modules that differ in their network structure. The increasing nonlinearity and consequent unpredictability of population dynamics induced by stronger perturbations may cause a decrease in the predictability of the stability components and their relationships. These results further emphasise why studies that focus on single forms of stability in isolation risk significantly underestimating the potential of perturbations to destabilise ecosystems.

Chapter 3: Here, I test the theoretical predictions of the research described in Chapter 2 by examining whether experimental perturbations weaken the relationships between multiple components of ecological stability in natural communities at the global scale. Using data from the globally-distributed Nutrient Network experiment, I compare relationships between stability components in unperturbed grassland plots with those that were perturbed either through enrichment with different nutrient combinations and/or reduction in grazing pressure. I find weaker relationships between stability components in perturbed plots relative to the controls, supporting the decoupling effect of perturbations suggested by my theory. Contrary to previous small-scale experiments, however, I find relatively weak correlations between stability components and therefore an overall high dimensionality of ecological stability. The weak stability relationships, together with the decoupling effect of perturbations, strengthens the need to evaluate the stability of ecosystems from a multi-perspective angle.

Chapter 4: Stochasticity is a core component of ecology, as it underlies key processes that structure and create variability in nature. Current models and experiments predicting ecological responses have typically applied static approaches that focus on mean environmental changes and fail to incorporate environmental stochasticity. Environmental stochasticity has structure, and examining the underlying structure such as the autocorrelation structure can improve the predictability of ecological models. Until now, most studies trying to build a link between ecological stability and environmental stochasticity have focused on how stochasticity affects the variability of populations and the resulting extinction risk. Knowledge of how structured environ-

mental stochasticity regulates the multiple components of ecological stability and its prediction is lacking. Here, I explore how the response and predictability of three key components of ecological stability - recovery time, resistance, and variability - are regulated by characteristics underlying the statistical distribution of environmental stochasticity, including its temporal autocorrelation, and the correlations between species responses to environmental noise. I found a significant discrepancy between the response of different stability components to environmental stochasticity and a big difference in their predictability. Overall, environmental reddening decreased recovery time and resistance and increased variability. Recovery time and resistance were much less predictable than variability in stochastic environments, and environmental reddening decreased the predictability of all the three components of stability. Considering that high and positive environmental autocorrelation (i.e. red noise) prevails in nature, these findings challenge the utility of models that overlook the structure of environmental stochasticity or incorporate it simply as white noise.

A short comparison of Chapter 2 and Chapter 4: Although both Chapter 2 and Chapter 4 use theoretical approaches by simulating the dynamics of the food-webs that are described by the Lotka-Volterra model, they differ in both the type of the perturbation conducted on the food webs and the quantification of the stability components. In Chapter 2, a single pulse perturbation is conducted only on the top species of the food-web for each simulation. While in Chapter 4, a single pulse perturbation together with environmental stochasticity - a series of "small" pulse perturbations - were conducted on each of the four species of the food-web for each simulation. In Chapter 2, the stability components include resistance (i.e. the inverse of the largest Euclidean distance between the perturbed food-web and the unperturbed food-web), resilience (i.e. the inverse of the log-transformed recovery time following the perturbation), and invariability (i.e. the inverse of the temporal variability of the total standardised density during recovery). While in Chapter 4, the stability components include the extent of change (i.e. the largest Euclidean distance between the perturbed food-web and the unperturbed food-web), recovery time, and variability (i.e. the temporal variability of the total standardised density during recovery). Therefore, Chapter 2 quantified stability components (larger value means being more stable) and Chapter 4 quantified instability components (larger value indicates being less stable).

Chapter 5: In this chapter, I draw together the findings of Chapters 2, 3 and 4 to discuss their overall implications and how the results of this thesis opens new avenues for research. I then discuss the limitations of my analyses, and suggest improvements for future studies. I also present some concluding thoughts on the utility of the multidimensional concept of ecological stability to improve the practice of ecosystem management and conservation.

1.4 ADDITIONAL WORK

In addition to the chapters enclosed in this thesis, I have also been involved in the following research during my PhD studies:

Donohue, I., Hillebrand, H., Montoya, J.M., Petchey, O.L., Pimm, S.L., Fowler, M.S., Healy, K., Jackson, A.L., Lurgi, M., McClean, D., O'Connor, N.E., O'Gorman, E.J., and **Yang, Q.** (2016). Navigating the complexity of ecological stability. *Ecology Letters*, 19, 1172-1185.
Contribution: I was involved with the conception, data collection and writing of this paper.

Donohue, I., Petchey, O.L., Kéfi, S., Génin, A., Jackson, A.L., **Yang, Q.**, O'Connor, N.E. (2017). Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. *Global Change Biology*, 23, 2962-2972.
Contribution: I was involved with the conception and data analysis of this paper.

Shi, P.L., Shen, H., Wang, W.J., **Yang, Q.**, Xie, P. (2016). Habitat-specific differences in adaptation to light in freshwater diatoms. *Journal of Applied Phycology*, 28, 227-239.
Contribution: I was involved with the conception and writing of this paper.

Shoemaker, L.G., Sullivan, L.L., Donohue, I., Cabral, J.S., Williams, R.J., Mayfield, M.M., Chase, J.M., Chu, C., Harpole, W.S., Huth, A., HilleRisLambers, J., James, A.R.M., Kraft, N.J.B., May, F., Muthukrishnan, R., Satterlee, S., Taubert, F., Wang, X., Wiegand, T., **Yang, Q.**, Abbott, K.C. Integrating Stochasticity into Community Ecology. Under review in Nature Ecology & Evolution.
Contribution: I was involved with the conception and writing of this paper.

Donohue, I., Coscieme, L., Gellner, G., **Yang, Q.**, Jackson, A.L., Kubiszewski, I., Costanza, R., McCann, K.S. Does reliance on fossil fuels undermine the resilience of economic networks? Under review in Nature sustainability.

Contribution: I was involved with the conception and data analysis of this paper.

PERTURBATION INTENSITY DETERMINES THE PREDICTABILITY OF ECOLOGICAL STABILITY

ABSTRACT

Even though the concept of ecological stability is fundamental to ecosystem conservation and management, we have remarkably little insight into its multidimensional nature or relationships between its individual components. This hinders significantly our capacity to manage the stability of ecosystems. Recent empirical research suggests that relationships between stability components vary in both strength and direction when systems are perturbed. However, the generality of this phenomenon and the mechanisms underpinning it are unknown. Here, we show that relationships between components of stability generally weaken - with stability thereby becoming more complex and difficult to predict - along a gradient of increasing perturbation intensity. This phenomenon occurs across a broad variety of network structures, driven by increasing prevalence of nonlinearity in community dynamics as perturbations intensify. These findings have profound implications for ability to predict the effects of perturbations on ecosystems and highlight the necessity for a multidimensional perspective when quantifying stability.

2.1 INTRODUCTION

Exploration of the factors that underpin ecological stability has comprised a central focus of both theoretical (May, 1972; Rooney et al., 2006; Allesina and Tang, 2012) and empirical (Fagan, 1997; Neutel et al., 2002; Donohue et al., 2013) research for decades. However, application of this understanding to the conservation and management of natural communities remains limited (Donohue et al., 2016). One particularly challenging aspect of stability is its complexity, arising from its multi-dimensionality. Ecological stability encapsulates multiple components - including asymptotic stability, variability, resistance, resilience and persistence (Pimm, 1984; Grimm and Wissel, 1997; Ives and Carpenter, 2007) - that together capture the different aspects of the dynamics of the system and its response to perturbations. However, lack of exploration of the multidimensional nature of ecological stability means that our ability to predict the overall stability of ecosystems or optimise it for different management and policy goals is at present extremely limited (Donohue et al., 2016).

The various components of stability are unlikely to be independent. This raises the possibility that the overall stability of the system may be predicted from one or a few of its individual components (Donohue et al., 2013). Theory (Harrison, 1979; Loreau, 1994; Tang et al., 2014) indicates that relationships between stability components are, however, not fixed, but may vary depending upon the structure of ecological networks and the response of species to environmental fluctuations. Results of recent experimental studies (Donohue et al., 2016; Dai et al., 2015) are consistent with this, revealing that relationships between stability components can change in both strength and nature when systems are perturbed. Indeed, these studies found that relationships between stability components consistently weakened, or decoupled, after strong experimental perturbations (respectively, after species removal and simultaneous exposure to multiple stressors). This means that stability became more complex and high-dimensional - and therefore more difficult to predict - after systems were perturbed. This not only amplifies the need for a multidimensional perspective on stability, but also implies that the largely one-dimensional focus ecologists have taken to date underestimates significantly the capacity for perturbations to destabilize ecosystems (Donohue et al., 2013). In spite of the profound implications of these findings for our understanding of - and our

ability to predict - the impacts of perturbations on ecosystems, we know little about the generality of this phenomenon or the mechanisms underpinning it.

There is significant disjoint between our theoretical understanding of ecological stability and what can be measured empirically in natural communities (Donohue et al., 2016). Many of the parameters that underpin theoretical models, such as the eigenvalues calculated from the interaction matrix that determine both asymptotic mathematical (Lyapunov) stability and resilience, are difficult to quantify using empirical data (Wootton and Emmerson, 2005). Moreover, our theoretical understanding of the mechanisms that underpin ecological stability is based almost exclusively on local stability analysis (Donohue et al., 2016). This theoretical framework suffers from the significant constraint that only the effects of extremely small perturbations can be considered, where the dynamics of the system are close enough to the equilibrium to be credibly linearized based on Taylor's Theorem (Pimm, 1982). This approach is not appropriate for analysing effects of large perturbations, following which nonlinear behaviours and transient dynamics may dominate (Hastings, 2004, 2010). In contrast, natural ecosystems are subject to a wide variety of frequently strong perturbations (Hughes et al., 2003; Post et al., 2013; Halpern et al., 2015; Donohue et al., 2017). This creates significant need to explore the effects of increases in perturbation intensity - where nonlinear dynamics are likely to become increasingly prominent - on ecological stability.

Here, we explore whether - and how - the complexity of ecological stability is modulated by the intensity of perturbations. We used simulated model food-webs to examine how the strength of relationships between three key components of ecological stability - resistance, resilience, and invariability (Fig. 2.1) - vary along a gradient from weak to strong perturbations. Resistance is the inverse of the degree to which a variable is changed following a perturbation; resilience is a measure of how fast a variable returns towards its equilibrium following a perturbation; and invariability is the inverse of the variance of a variable over time (Pimm, 1982; Donohue et al., 2016). We perturbed our model systems by reducing the densities of the apex predator in each food-web as a pulse perturbation and then quantified stability based on the responses of all other species in the system. We quantified these three components of stability empirically (Fig. 2.1) across a broad variety of four-species food-web modules (Table 2.1) - subnetworks of tightly interacting species that act as

the 'building blocks' of food-webs (Milo et al., 2002; Bascompte and Melián, 2005; Kondoh, 2008) - to explore the generality of our findings.

Specifically, we make the following hypotheses. We expect strong correlations between different stability components, as all of them are based on the same property of the ecosystem - the density of the populations. Moreover, as what Donohue et al. (2013) found, we hypothesize that stronger perturbations can decrease the correlation between different stability components and therefore increase the dimensionality of ecological stability. Under weak perturbations, the dynamics of the system are close enough to the equilibrium, the system can be credibly linearized (Pimm, 1982). The dynamics of the system are therefore more deterministic and predictable. For example, the system will follow an approximately "exponential" returning path within the "local stability" region. Under strong perturbations, the system dynamics cannot be credibly linearized anymore and the behavior of the system will be dominated by nonlinear dynamics, which leads to low predictability of stability components (Strogatz, 1994).

2.2 METHODS

2.2.1 *Food-web simulations*

We constructed sets of 14 distinct four-species food-web modules, covering a large range of different network structures that vary in both trophic complexity and connectance (Table 2.1), to explore the effects of perturbation intensity on relationships between stability components. We then constructed 1000 locally stable and biologically feasible individual food-webs within each set of food-web module structures (see below).

The dynamics of our simple food-webs are described by the general Lotka-Volterra system (Pimm and Lawton, 1977, 1978; Emmerson and Yearsley, 2004):

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^{n} a_{ij}N_j) \tag{2.1}$$

where i and j are the identity of species in the food web, n is the number of the species that interact directly with species i, N_i is the population density of species i, r_i is the intrinsic growth/decay rate (positive for basal species; otherwise negative), and a_{ij} is the interaction coefficient that describes the per capita effect of the jth

TABLE 2.1: **The food-web modules used in this study and their structural traits**

Modules	ID	No. trophic levels	No. basal species	No. omnivorous species	Connectance
	1	4	1	0	0.1875
	2	3	1	0	0.25
	3	3	2	0	0.1875
	4	2	3	0	0.1875
	5	2	2	0	0.25
	6	4	1	1	0.25
	7	3	2	1	0.25
	8	4	1	1	0.25
	9	4	1	1	0.25
	10	4	1	2	0.3125
	11	4	1	1	0.3125
	12	4	1	2	0.3125
	13	3	2	1	0.3125
	14	4	1	2	0.375

species on the growth/decay rate of the ith species (positive if it enhances population growth - the consumer-resource interaction, for example; negative if it causes decreases in density).

We parameterised the food-web model defined in (Equation 2.1) following Pimm & Lawton (1977, 1978) and Emmerson & Yearsley (2004). We first constructed the Jacobian matrix of interaction strength J, with its upper-triangular element J_{ij} ($j > i$) sampled randomly from the uniform distribution in the interval [-10, 0], its lower-triangular element J_{ji} sampled randomly from the uniform distribution of the interval [0, 0.1], and the intraspecific interactions of basal species J_{ii} from the interval [-1, 0]. The element of the Jacobian matrix represents the direct effect of a single individual of a focal species on the total population of another species at equilibrium (Wootton and Emmerson, 2005). These parameter values are consistent both with those used in previous theoretical studies (Pimm and Lawton, 1977, 1978; Emmerson and Yearsley, 2004), and those found in natural communities (de Ruiter et al., 1995; Wootton and Emmerson, 2005).

We assume that the equilibrium density of species conforms to the trophic pyramid, such that the density of consumers is lower than that of their resources (Pimm and Lawton, 1977; Woodward et al., 2005). The equilibrium density of species at the kth trophic level $N_i^*(k)$ was drawn randomly from a uniform distribution [$N(k)_{min}/m$, $N(k)_{max}/m$], where m is the number of species at the kth trophic level and $N(k)_{min}$ and $N(k)_{max}$ are, respectively, the smallest and largest expected total density for trophic level k. $N(k)_{min}$ was set arbitrarily at 1, 10, 100, and 1000 while $N(k)_{max}$ was set at 10, 100, 1000, and 10000 for, respectively, $k = 1, 2, 3,$ and 4. We were then able to calculate the interaction coefficient a_{ij} given $a_{ij} = J_{ij}/N_i^*$, and the intrinsic growth/decay rate r_i by $r = AN^*$, where $r_i \in r$, $a_{ij} \in A$, $N_i^* \in N^*$, following Emmerson & Yearsley (2004). We examined the eigenvalue of the Jacobian matrix and the intrinsic growth/decay rates within all food-webs to ensure they all met the criteria of both local stability and feasibility (Pimm and Lawton, 1977; Pimm, 1982; Emmerson and Yearsley, 2004). Every square matrix has special values called eigenvalues. An eigenvector of a square matrix **A** is a nonzero vector x such that for some number λ, we have the following: **Ax** = λ **x**, then we call λ an eigenvalue, and **x** an eigenvector. These special eigenvalues and their corresponding eigenvectors are frequently used in stability analysis, including the analysis of ecosystem stability.

Specifically, the real part of the eigenvalue can be used to characterize the behavior of the ecosystem departures from equilibrium. If all the real parts of the eigenvalues are negative, the system returns to the equilibrium, and if at least one of them is positive, the system departs from the equilibrium. The existence or lack of imaginary part of the eigenvalues provides information on how the system departs from the equilibrium or returns to the equilibrium. If there are no imaginary parts of the eigenvalues, the system directly and linearly shrinks to or expands from the quilibrium. If there are imaginary parts of the eigenvalues, the system oscillates away from the equilibrium or oscillates back to the equilibrium (Brassil, 2012). Criteria for food-webs to be considered feasible comprised: (1) the density of each species was positive when the food-web was at equilibrium; (2) the basal species had a positive intrinsic growth rate, and (3) non-basal species had a negative intrinsic decay rate (Emmerson and Yearsley, 2004).

2.2.2 *Stability measurement*

We examined the effect of perturbation intensity on relationships between different stability components by reducing the densities of the apex predator in each food-web as a single pulse perturbation. This was done factorially, with five levels of perturbation intensity (i.e. apex predator density reductions of 10%, 30%, 50%, 70%, and 90%) for every food-web (i.e. for all 1000 food-webs in all 14 modules). We simulated food-web dynamics numerically. All simulations started at time zero, i.e. the moment that the perturbation was conducted, until time 1000, with a time step of 0.1. The narrow time step used here enabled the simulated discrete time series to capture the detailed changes in the continuous dynamical system defined in (Equation 2.1).

We attributed equal importance to all species in the food-web when measuring stability. We avoided underestimating the importance of species at higher trophic levels (Pauly et al., 1998), which are usually at low densities, by standardising the population density of each species N_i by dividing it by their density at equilibrium N_i^* before calculating stability. In order to avoid confounding our measures of stability with the intensity of perturbations, we quantified all components of stability based only upon the standardised densities of the species that were not perturbed directly (i.e. all species except for the top predator in the system).

First, we identified the time point at which a perturbed food-web recovered to its equilibrium as the point after which the densities of all species were less than 1% away from their density at equilibrium (Fig. 2.1). We then calculated the Euclidean distance of the food-web from its equilibrium for every time step from the start of the simulation to the recovery point. Resistance was quantified as the inverse of the maximum Euclidian distance in this time period. We quantified resilience as the inverse of the log-transformed recovery time (i.e. the time duration between the point at which the impact of the perturbation was maximal to the point of recovery). We log-transformed the recovery time because of the exponential theoretical relationship between perturbation size and recovery time (Pimm, 1982). Invariability was quantified as the inverse of the temporal variability (measured as the coefficient of variation) of the total standardised density during the recovery period.

We quantified the strength of pairwise relationships between stability components from the stability properties of the 1000 replicate food-webs within each food-web module across each level of perturbation intensity. To unify the magnitude of the range of stability components and assign equal importance to each of them, we standardised all metrics of stability by subtracting their mean value and dividing by their standard deviation prior to quantification of relationships between them with Pearson correlation coefficients. We quantified changes in the overall dimensionality of ecological stability using the proportion of variance explained by the first axis (PC1) of a Principal Components Analysis (PCA) as a measure of the strength of overall multivariate relationship among stability components (Donohue et al., 2013). A higher proportion means that the relationships between stability components were stronger and, thus, that fewer principal axes capture greater variance in the stability matrix, and *vice versa*.

2.2.3 *Nonlinearity measurement*

The Lotka-Volterra model (Equation 2.1) becomes increasingly nonlinear following large perturbations because the instantaneous reduction in the density of the top species N_4 and the consequent change in other species N_i ($i \neq 4$) prevent the density-dependent effect $\sum_{j=1}^{n} a_{ij} N_j$ on species N_i from maintaining a relatively consistent value. Nonlinearity is likely to reduce the predictability of the system and even lead to chaotic dynamics (May, 1976; Sugihara and May, 1990). Therefore, nonlinear dynamics caused by large perturbations may cause a reduction in the

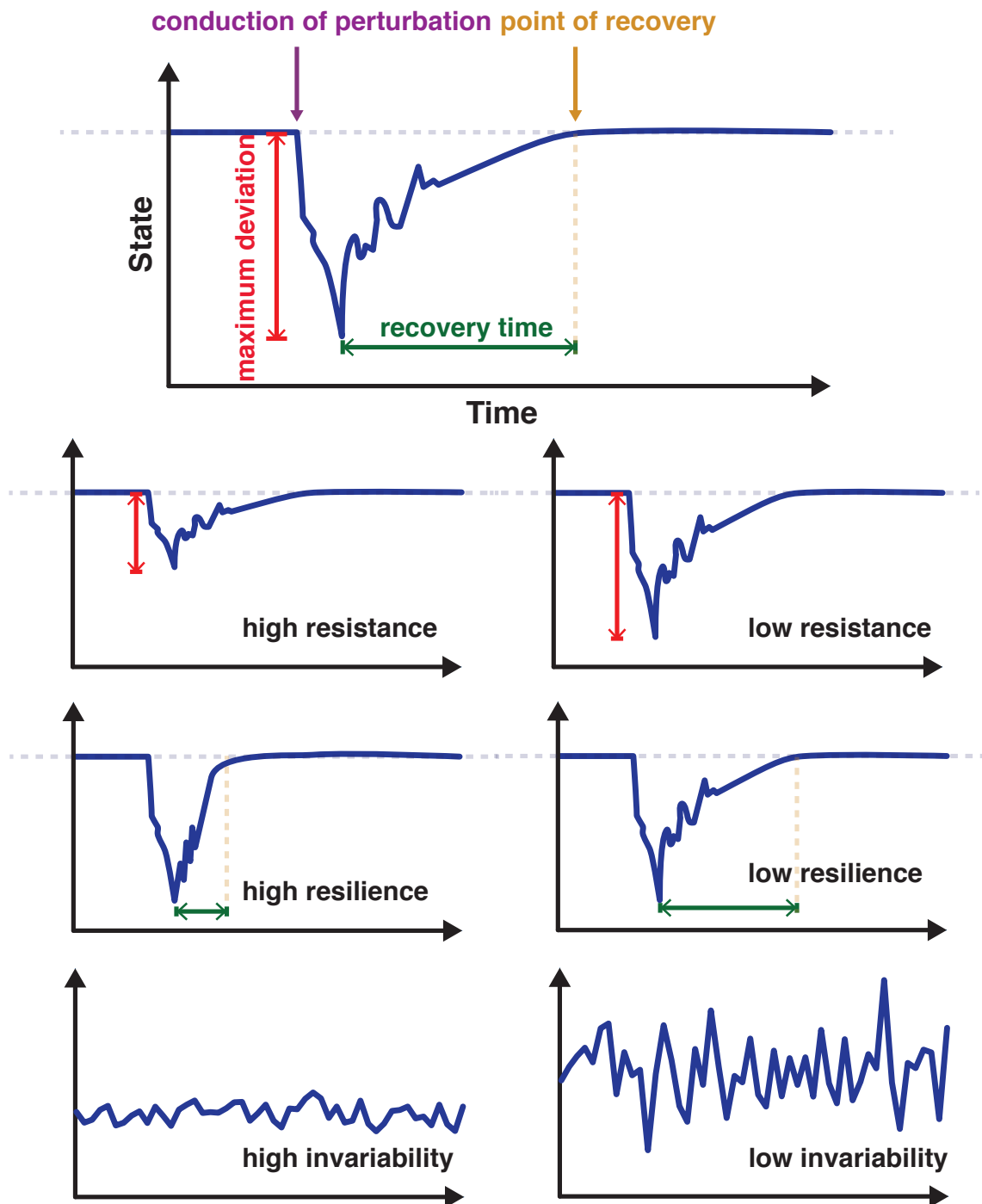FIGURE 2.1: **The measurement of ecological stability.** We quantified resistance as the inverse of the maximum deviation of the system from its equilibrium and resilience as the inverse of the log-transformed recovery time (i.e. the time taken for the system to recover from the maximum deviation to its equilibrium). Invariability was quantified as the inverse of the coefficient of variation over the period of recovery.

predictability of individual stability components and, thus, the relationship between them.

One of the most common approaches used to detect nonlinearity and chaos in dynamical systems is the Lyapunov component, which gives the average rate at which perturbation effects grow (positive Lyapunov component) or decay (negative Lyapunov component) (Ellner and Turchin, 1995). An alternative method uses the dimension embedding technique to quantify the probability that a system will recapture previous patterns in the future (Sugihara and May, 1990). While both methods have been applied successfully to empirical time series (Ushio et al., 2018; Grenfell et al., 1998), they are not appropriate for analysing the data produced by our simulations. This is because many food-webs in our study recovered very quickly following perturbation, which introduced time windows that were not only too short for their application, but also whose lengths differed from each other. Because of this, we developed a more straightforward method to quantify the nonlinearity of food-web dynamics in our simulated systems. For species i of a dynamical food-web, we first calculated the ratio of its density over adjacent time steps as $Q_i(t) = N_i(t+1)/N_i(t)$, and then calculated the coefficient of variation of this ratio across the period from perturbation to recovery [i.e. $CV_i = sd(Q_i)/mean(Q_i)$]. We then took this coefficient as the nonlinearity indicator of species i. For a purely linear system, $N_i(t+1)/N_i(t)$ is constant, so CV_i equals zero, and we can predict the future state of the system based on previous states. A large CV_i indicates that the ratio between densities at adjacent time steps varied largely which, in turn, indicates high unpredictability of the future state based on the current state. We can, for example, easily deduce $N_i(t+2)$ just based on $N_i(t+1)$ and $N_i(t)$ when the system is linear, but cannot obtain a reliable estimate of $N_i(t+2)$ when the system becomes increasingly nonlinear.

All data processing was done with R version 3.2.4 (R Core Team, 2016). Numerical simulation of Lotka-Volterra models was done with the **deSolve** package (Soetaert et al., 2010).

2.3 RESULTS

For clarity and to illustrate our findings, we focus initially on the dynamics of what is the simplest food-web module - the food chain (i.e. Module 1 in Table 2.1). We then

expand our focus to more complex network structures and explore the generality of our results across the 14 food-web modules (Table 2.1).
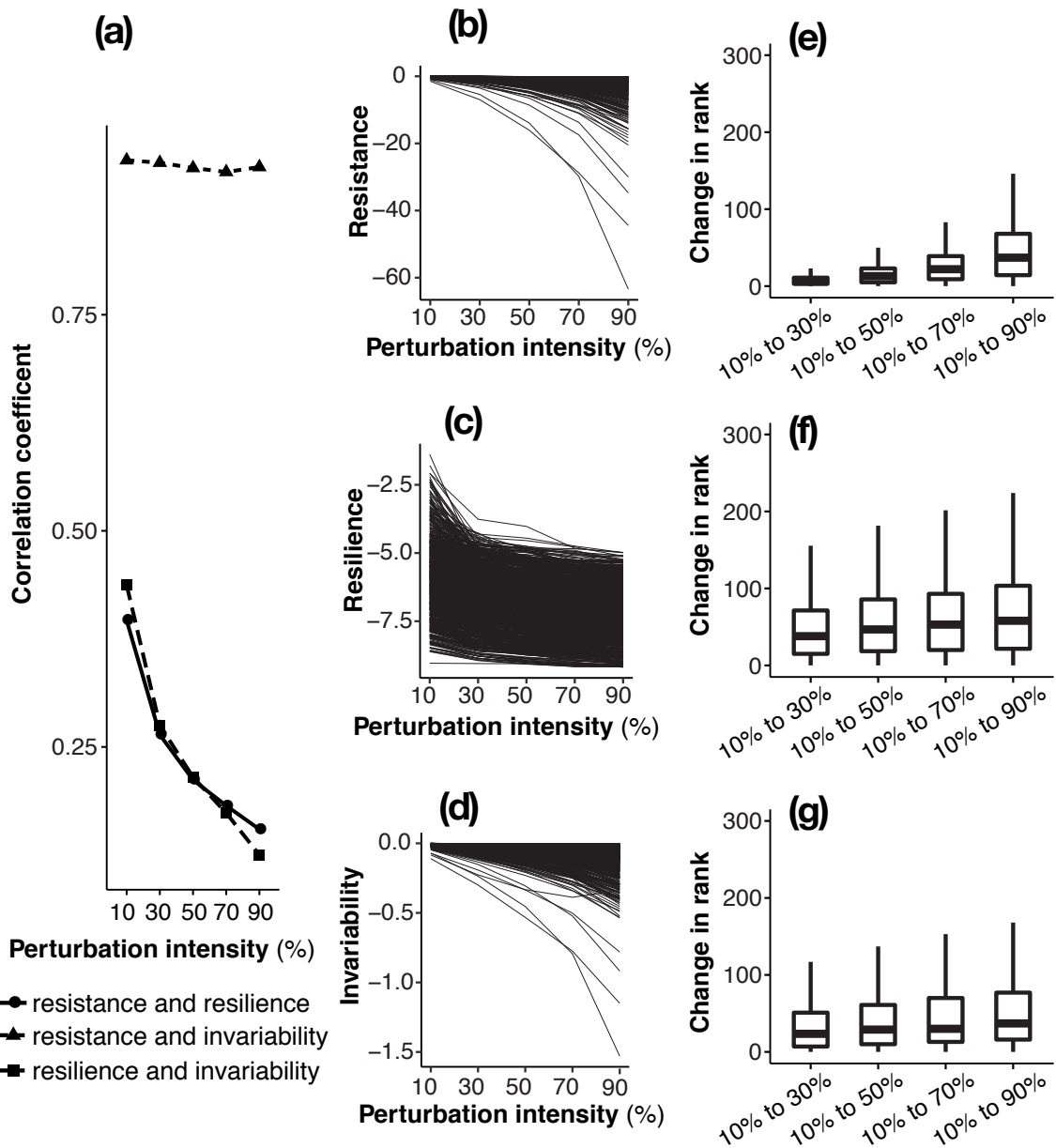
FIGURE 2.2: **Relationships among components of stability in the food-chain module** (i.e. Module 1; Table 2.1). **(a)** Reduction in the strength of pairwise correlations between stability components and patterns of change in **(b)** resistance, **(c)** resilience and **(d)** invariability with increasing perturbation intensity. Also shown are the extent of changes in the relative ranking of **(e)** resistance, **(f)** resilience and **(g)** invariability for individual food-webs as perturbation intensity increased. For each perturbation intensity, We marked the rank of the 1000 communities of the food-chain module by the value of stability components. Then we were able to calculate the change in the ranks of the communities along the increasing perturbation intensity. In Fig. 1(e-f), each box summarizes the change in the ranking of stability values of the communities. The larger change in the ranking indicates lower predictability.

This observed weakening in correlations between stability components as perturbation intensity increased was associated with both variation among the stability components in their patterns of response to increasing perturbation intensity (Fig. 2.2b-d) and increasingly large shifts in the relative ranking of food-webs in their individual stability properties (Fig. 2.2e-g). These latter shifts were associated with consistent and pervasive increases in the prevalence of nonlinear dynamics as perturbations intensified (Fig. 2.4), indicating that food-web dynamics became increasingly unpredictable as the strength of perturbations increased. Together, these results account for the observed overall decoupling of relationships between components of stability. Differences between individual food-webs in their multidimensional responses to perturbations were amplified as perturbations intensified, as a consequence of increased prevalence of nonlinearity in food-web dynamics. This led, in turn, to progressively greater decoupling of relationships between stability components as they became less predictable as perturbations intensified.
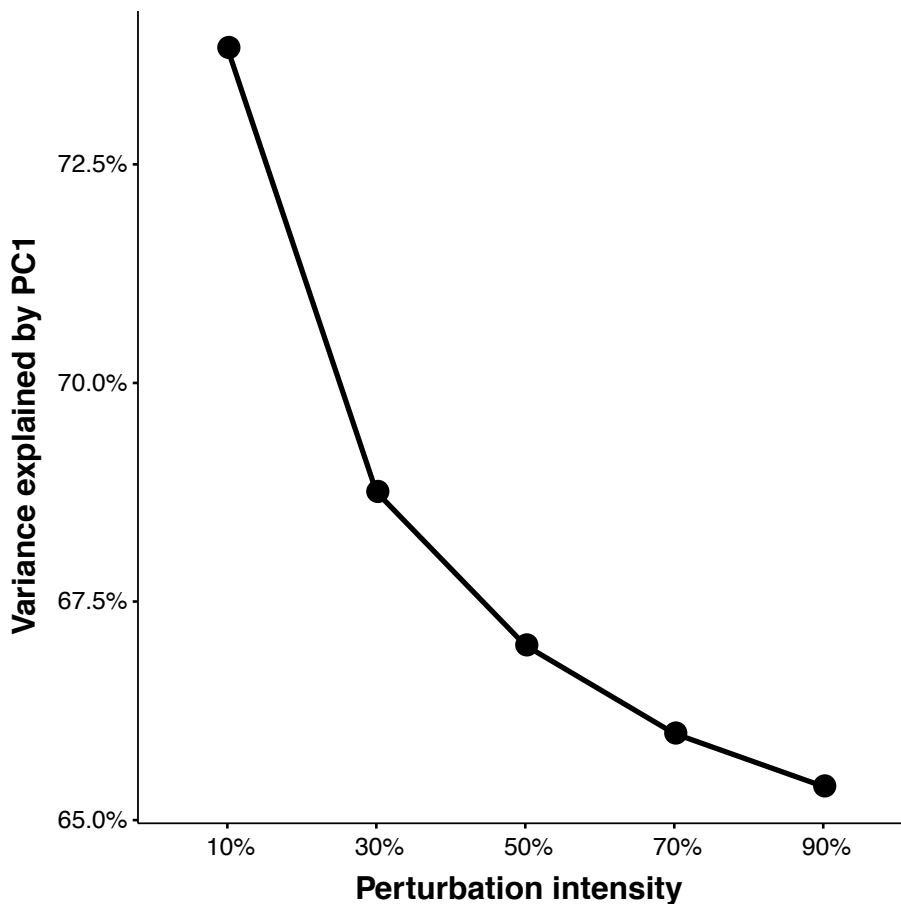
FIGURE 2.3: **Change in the strength of the overall relationship between stability components of the food-chain module** (i.e. Module 1; Table 2.1) with increasing perturbation intensity.
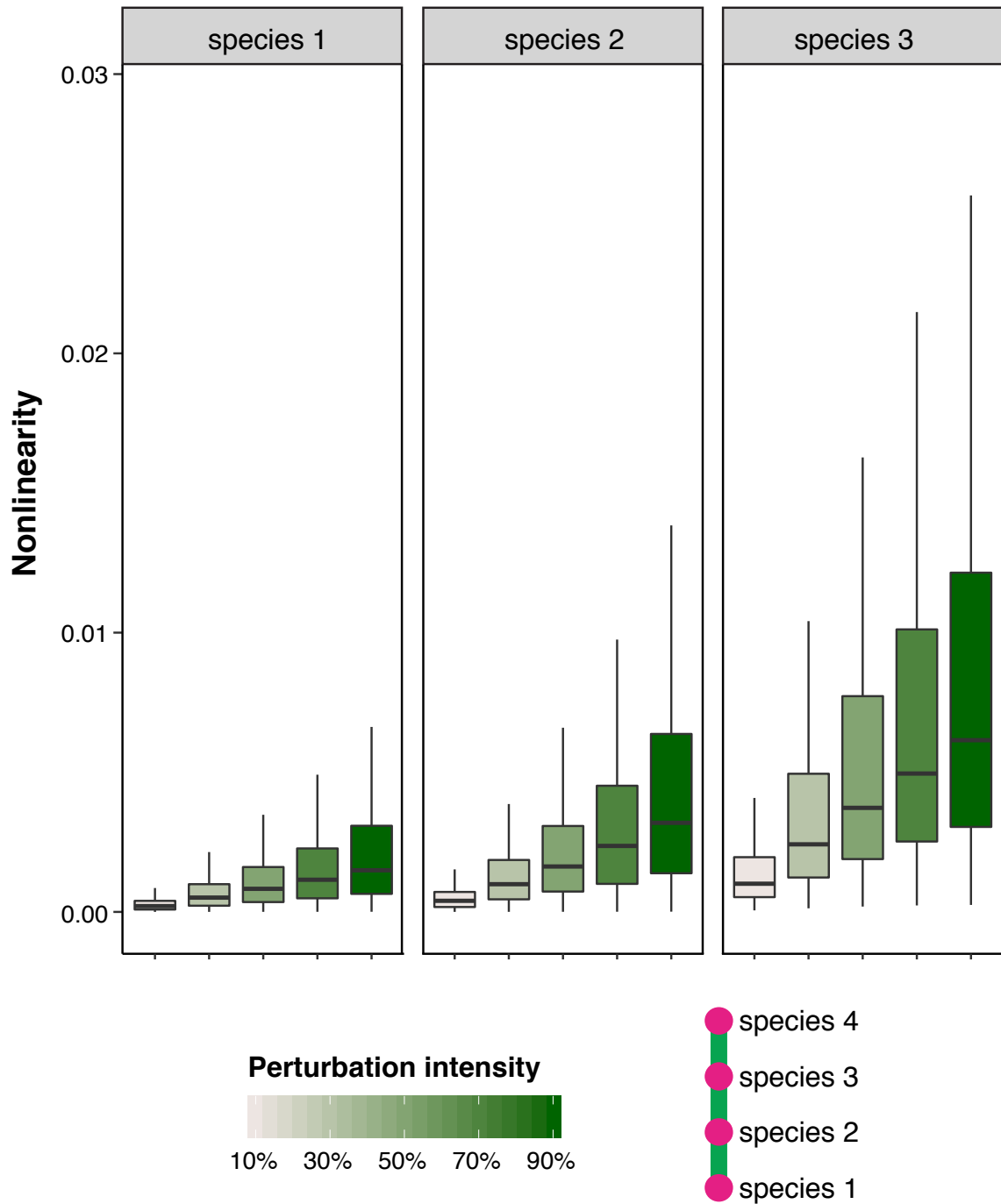
FIGURE 2.4: **The prevalence of nonlinearity in the dynamics of each of the unperturbed species in the food-chain module** (i.e. Module 1; Table 2.1) with increasing perturbation intensity.

The strength of pairwise relationships between resilience and both resistance and invariability was consistently reduced, both significantly and monotonically, with increasing intensity of perturbation to the food-chain module (Fig. 2.2a). Correlations between resistance and resilience decreased from 0.40 to 0.15, and between resilience and invariability from 0.44 to 0.13, as perturbation intensity increased from 10% to 90% removal of apex predator density. The consequent loss of predictive

power [measured as $1 - (R^2_{maximum.perturbation} / R^2_{minimum.perturbation})$, where R^2 was calculated from the linear regression between paired stability components] of using any one component of stability to predict another ranged between 84.8% and 91.8% as perturbation intensity went from relatively weak to strong. Although the correlation between resistance and invariability decreased only negligibly as perturbations intensified (Fig. 2.2a), the overall dimensionality of stability nonetheless decreased significantly and monotonically as perturbation intensity increased (Fig. 2.3).
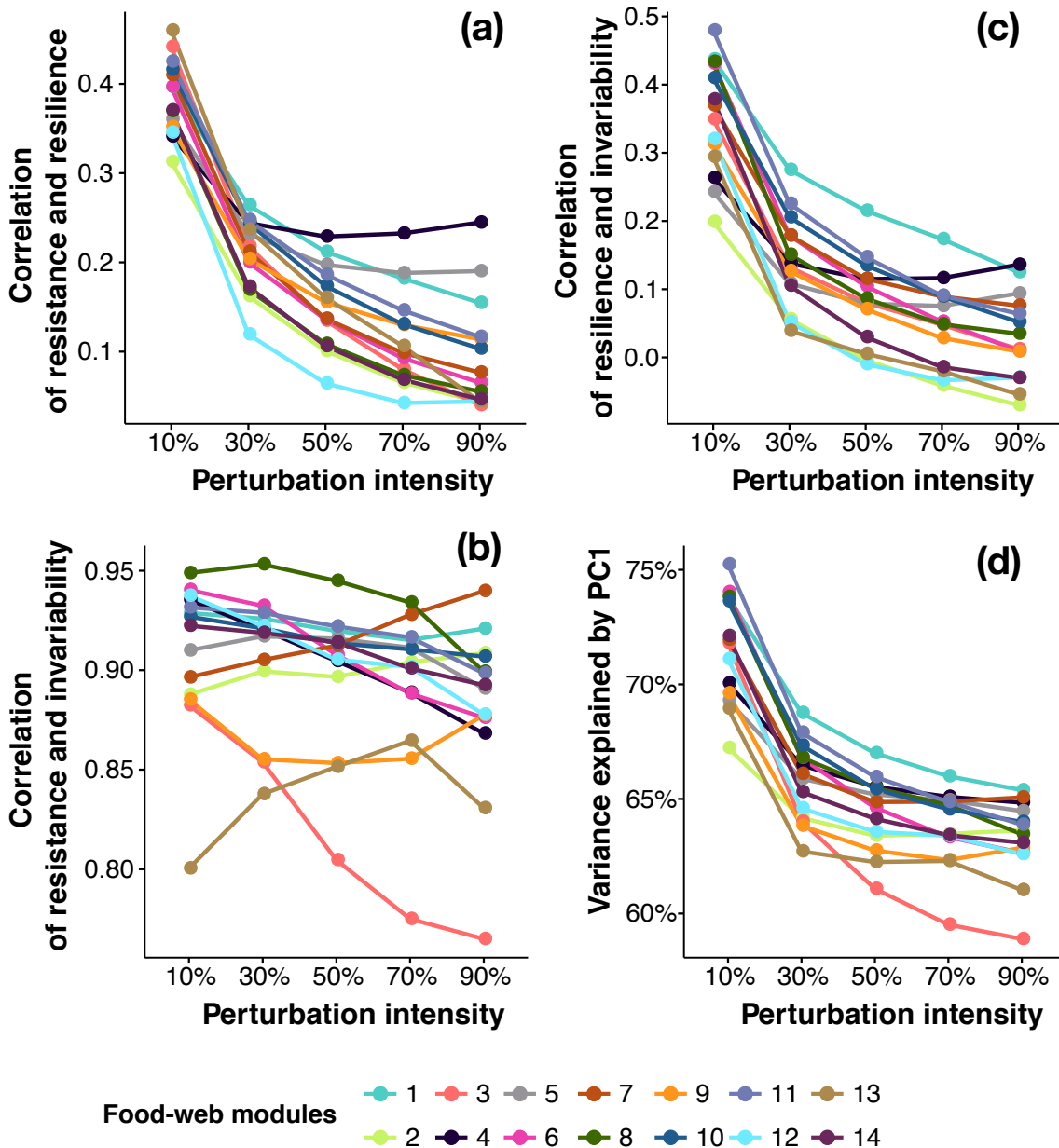
FIGURE 2.5: **The change in pairwise correlations** between **(a)** resistance and resilience, **(b)** resistance and invariability and **(c)** resilience and invariability, and **(d)** the strength of the overall multivariate relationship between stability components from the weakest perturbation to the strongest perturbation across all of the food-web modules analysed (see Table 2.1)

The trend towards decoupling of relationships between components of stability observed in the food-chain module in general holds across the other food-web modules analysed, especially for the pairwise relationships between resistance and resilience (Fig. 2.5a), and resilience and invariability (Fig. 2.5c), and for the overall multivariate relationship between stability components (Fig. 2.5d). All of the 14 modules we analysed showed a decreasing trend from the weakest perturbation to the strongest in these relationships. For all the food-web modules, the first two PC explained most of the variance in the stability metrics. Compared with PC1, PC2 showed an increasing trend along the increasing perturbation intensity (Fig. A.3). The decreasing curve of PC1 became flatter as the correlation coefficient approached a low value around the maximum perturbation intensity. Somewhat in contrast, correlations between resistance and invariability did not weaken universally across all of the modules we analysed - changes in the strength of this relationship with increasing perturbation strength were more variable than the other pairwise relationships examined. However, an overall weakening in the strength of this relationship was nonetheless observed in 11 out of 14 modules from the weakest to the strongest perturbations analysed. Consistent with results for the food chain module, both increasingly large shifts in the relative ranking of stability properties among food-webs (Fig. A.1) and increasing nonlinearity in population dynamics (Fig. A2) were observed across all of the 14 food-web modules analysed as perturbations intensified.

2.4   DISCUSSION

Our results demonstrate clearly that the dimensionality of ecological stability increases when perturbations are more intense. We found that pairwise correlations between the three stability components we quantified and their overall multivariate relationship in general weakened with increasing perturbation intensity. The fact that this pattern is consistent both with the findings of previous empirical studies from very different systems (Donohue et al., 2013; Dai et al., 2015) and across all of the food-web modules we analysed suggests that this is a general phenomenon across ecosystem types and network configurations. These results imply not only that ecological stability becomes more complex and difficult to predict as perturbations become increasingly intense, but also that the largely one-dimensional focus ecologists have taken to date (Donohue et al., 2016) underestimates significantly the true capacity for perturbations to destabilize ecosystems.

Reduction in the strength of the overall multivariate relationship between stability components was attributable primarily to changes in relationships between resilience and the other two stability components quantified. This suggests that resilience is particularly susceptible to changes in perturbation strength and becomes especially unpredictable as perturbations intensify. This contrasts with the assumption of most theoretical studies that perturbations decay at the asymptotic return rate, which is estimated by the eigenvalue of the Jacobian matrix at equilibrium, and is, therefore, constant. Moreover, the resilience is not correlated to the connectance of the network module, an indicator of network complexity (Fig. A4), providing further evidence for the low predictability of resilience. There are at least three forces likely responsible for pushing resilience away from this constant pattern and reducing its predictability. First, recovery time was measured as when the perturbation decayed to a critical value (0.01 in our study). The asymptotic return rate - a recovery rate based on long-term recovery - is not necessarily a proxy of the real recovery rate during this relatively short period (Arnoldi et al., 2016). Second, the discrepancy between the asymptotic return rate and real (or short-term) return rate is especially obvious when the food- web is reactive - the deviation from equilibrium will show an instantaneous increase instead of decay after perturbation, and the return rate is positive during the period of growing deviation (Neubert and Caswell, 1997; Tang and Allesina, 2014). Finally, and likely most importantly, strong perturbations enhanced nonlinearity and unpredictability in population dynamics. Given that resilience was determined primarily by the recovery of the slowest recovering species (see also Haegeman et al., 2016), this likely made it particularly susceptible to the unpredictability caused by strong perturbations.

Somewhat in contrast with the other pairwise relationships examined, relationships between resistance and invariability were generally relatively strong and less susceptible to changes in perturbation intensity. The relatively high correlation between these stability components may be a consequence of the fact that both were quantified using all species (excluding the species that was perturbed directly), whereas resilience was determined primarily by the species with slowest recovery speed. Though they were generally more variable than the other pairwise relationships examined, relationships between resistance and invariability weakened from the least to the most intense perturbations in 11 out of the 14 modules analysed. This indicates that decoupling was not driven only by reductions in the predictability of re-

silience. This finding is supported by our previous empirical results (Donohue et al., 2013), where, even though we did not quantify resilience, we nonetheless found that strong perturbations (in the form of species loss) caused significant decoupling of relationships between components of stability.

As expected (Pimm, 1984; Hastings, 2004, 2010), we found that increasing perturbation intensity was associated with greater prevalence of nonlinearity in population dynamics. This phenomenon was observed consistently across all species in all of the food-web modules. This indicates clearly that the consequent increased unpredictability of population dynamics (May, 1976; Sugihara and May, 1990) underpinned observed shifts in the relative ranking of stability properties among food-webs and weakened correlations between components of stability.

The observed weakening of relationships among components of stability was most significant when perturbations were weak to moderate. Such perturbations are more frequent than large perturbations in nature (White and Jentsch, 2001). This pattern was consistent across all the food-web modules analysed. Though our analyses focused only on four-species modules of intermediate complexity, many of these modules are ubiquitous in empirical networks, regardless of ecosystem type (Milo et al., 2002; Bascompte and Melián, 2005; Rip et al., 2010). Given the generality of our findings, it is very likely that the observed pattern of decoupling is maintained or perhaps even magnified when the modules are aggregated into systems of higher complexity. Taken together, these results imply that the decoupling of ecological stability by perturbations is likely a common and widespread phenomenon in natural systems. However, negligible weakening of relationships between stability components took place when perturbation intensity increased from moderate to strong. This suggests that the decoupling of stability is perhaps less prevalent in systems that are already highly perturbed, because relationships between components of stability are already very weak.

For simplicity, we explored the effects of a single pulse perturbation of varying intensity on the top predator in our food-web modules. Though such perturbations are common in nature (Estes et al., 2011), in natural communities all species are continually subject to diverse perturbations, both natural and human-induced, that vary not only in intensity but also in their spatial extents, periods, durations and frequencies (Tylianakis et al., 2008; Molinos and Donohue, 2010, 2011; Miller et al.,

2011; MacDougall et al., 2013; Donohue et al., 2016). These multifaceted disturbances likely precipitate a range of responses that alter the various components of stability and the relationships among them in diverse ways (Donohue et al., 2016). Future research - both theoretical and empirical - needs to explore not only how the various facets of disturbance influence components of ecological stability and the relationships among them, but also how the general context of the disturbance - the number and type of species it affects and how it affects them - determines ecological responses (Loreau and de Mazancourt, 2013).

In conclusion, we found that ecological stability becomes more complex and that overall ecological responses to perturbations become especially unpredictable as perturbation intensity increases. This has profound implications for our ability to conserve and manage ecosystems (Petchey et al., 2015) and emphasises the potential for perturbations to have unforeseen and undesirable consequences. As the impact of humanity on the biosphere continues to accelerate, these findings underscore the pressing need for a more comprehensive understanding of the multidimensional nature of ecological stability (Donohue et al., 2016) and highlight the necessity to take a multidimensional perspective for a more complete appreciation of the impacts of perturbations on ecosystems.

PERTURBATIONS INCREASE THE COMPLEXITY OF ECOLOGICAL STABILITY IN GLOBAL GRASSLANDS

ABSTRACT

Ecological stability is a complex and multifaceted concept, including components such as variability, resistance, resilience, persistence and robustness. Relationships among the various components of stability can vary in both strength and directionality when systems are perturbed. Theory developed in Chapter 2 of this thesis predicts that perturbations can weaken relationships between stability components. However, these predictions have not been rigorously tested. Here, we examine the decoupling effect of perturbations and the importance of environmental context using data from a globally-distributed grassland experimental network. Largely consistent with our predictions, we observed relatively weaker relationships between most pairs of stability components in perturbed treatments involving reduction of consumers compared with unmanipulated control plots. In contrast with previous small-scale experiments, however, we discovered relatively weak correlations between all stability components, even in the unmanipulated controls. Generally weak relationships between components of stability, together with the decoupling effect of perturbations on these relationships, highlight the necessity to quantify ecological stability under a multidimensional stability framework.

3.1 INTRODUCTION

The stability of ecosystems determines the reliability and sustainability of the goods and services provided by nature, with important ramifications for socio-economic development. We are living in an era of accelerating resource exploitation (Western, 2001; Halpern et al., 2008; Banks et al., 2015; Worm and Paine, 2016), significant climate change (Nemani et al., 2003; Zhao and Running, 2010) and dramatic biodiversity loss (Stuart et al., 2004; Cardinale et al., 2012; Hooper et al., 2012). An understanding of the mechanisms and drivers of ecological stability is critical for the sustainable management of natural resources. One of the greatest challenges in the study of ecological stability is its inherent multidimensionality. Ecological stability is touted as a complex and multifaceted concept, including components such as variability, resistance, resilience, persistence, and robustness (Pimm, 1984; Grimm and Wissel, 1997; Donohue et al., 2013, 2016). A complete understanding of the impacts of perturbations on ecosystems therefore requires evaluating these stability components simultaneously (Donohue et al., 2013, 2016).

In spite of the multidimensionality of ecological stability, most ecological research to date has focused on one or a few of those components in isolation (e.g. France and Duffy, 2006; Tilman et al., 2006; O'Gorman and Emmerson, 2009). Yet, the various components of stability are unlikely to be independent. For example, communities with high temporal variability in abundance are expected to have low robustness (the number of secondary extinctions caused by the initial loss of a species) due to an increased extinction risk in species with small population sizes (Pimm and Redfearn, 1988; Lande, 1993). The interrelatedness of different stability components raises the possibility that the overall stability of the system can be predicted from one or a few stability components. Theory predicts that the relationships between these stability components are, however, not fixed, but may be regulated by the structure of communities (Harrison, 1979; Loreau, 1994; Tang et al., 2014) and can be altered by external perturbations (Chapter 2). In Chapter 2 of this thesis, I used simulations to investigate the effect of the intensity of perturbations on the predictability of ecological stability for a large variety of communities. I found that stronger perturbations reduce the strength of relationships between different stability components, likely by increasing nonlinearity and unpredictability in the dynamics of their constituent populations. Furthermore, the observed weakening of correlations between stability components was consistent across communities of

different network structures. This suggests that this phenomenon may occur broadly in real ecosystems.

Results of some empirical studies are consistent with this prediction. In a manipulative field experiment on marine rocky shore communities, Donohue et al. (2013) found that relationships between stability components weakened after strong experimental perturbations caused by species removal. This is consistent with results of a laboratory microcosm experiment (Dai et al., 2015), where environmental conditions provoked a trade-off between different stability components of yeast populations and their correlation broke down when multiple drivers were changed simultaneously. However, notwithstanding the consistency of these patterns, the findings are from limited ecological contexts and need to be tested on much larger temporal and spatial scales. Moreover, it is unclear as to whether the extent to which this phenomenon occurs depends on the nature of the perturbation.

To address this, we examined the effect of different types of perturbations on the strength and nature of relationships between stability components at the global scale using data from a globally-distributed grassland experiment on herbaceous-dominated plant communities on six continents (Adler et al., 2011; Borer et al., 2014a). The grassland communities were perturbed in a variety of ways, both from the 'bottom-up' - through the addition of different nutrients and nutrient combinations - and from the 'top-down' through the reduction of herbivore grazing pressure. Both nutrient addition and fencing have been shown to affect the multiple stability components of different ecosystem properties. The effect of nutrient enrichment on the resistance of individual species and the ecosystem were broadly observed in terrestrial, freshwater, and marine ecosystems (Villagra et al., 2013; Lamberti-Raverot and Puijalon, 2012; D'Angelo and Wiedenmann, 2014). For example, nutrient enrichment changed the anatomical and biomechanical traits of two freshwater plant species by producing weaker stem tissues and thus increased the risk of plants to mechanical failure (Lamberti-Raverot and Puijalon, 2012). Nutrient enrichment has also been observed to affect the ecosystem variability (Isbell et al., 2013). Using the same dataset analyzed in this Chapter, Hautier et al. (2014) found that fertilization weakened the positive effect of diversity on the stability (quantified as the temporal invariability in the above-ground net primary production) of the grassland ecosystem. Using a 7-year field experiment, Yang showed that nutrient addition

increased both population and community variability (Yang et al., 2012). Nutrient addition can also lead to the change in the species composition of the ecosystem by affecting species persistence and species invasion (Liu and van Kleunen, 2017). In the well known long-term grassland experiment conducted at Cedar Creek Ecosystem Science Reserve in central Minnesota, Isbell et al. (2013) found that nutrient enrichment even led to the nonrandom loss of initially dominant native perennial C4 grasses. By comparing the responses of seven common alien, seven rare alien, nine common native and six rare native herbaceous plants to nutrient availability and fluctuations, Liu and van Kleunen found that alien plant species, in contrast to native plant species, benefited from a large nutrient pulse (Liu and van Kleunen, 2017). Grazing exclusion by fencing has also been found to affect multiple stability components. Fencing increased both the resistance and resilience of degraded alpine grasslands to grazing and to a changing climate in Tibetan Plateau (Wu et al., 2017). Despite the many recognized effects of nutrient addition and fencing on the individual stability components, how they affect the correlation between the stability components is not clear yet. Here we address this question in this Chapter.

3.2 METHODS

3.2.1 *Dataset and Data Selection*

We used data from the globally-distributed Nutrient Network (NutNet) grassland experiment, which includes 110 field sites in 25 countries on six continents at the time of writing (`https://nutnet.org/field_sites`). Each site is dominated by low-statured, primarily herbaceous vegetation and is representative of a particular grassland ecosystem (e.g. shortgrass steppe, tallgrass prairie, salt marsh, alpine tundra; Adler et al., 2011). In most cases, one site consists of three blocks representing different environmental gradients, and each block comprises ten 5×5 m plots. The ten plots are assigned different treatments in isolation. Three nutrient treatments (N, P, and K plus micronutrients) are crossed in a factorial design to generate eight treatment combinations (i.e. no nutrient control, +N, +P, +K, +NP, +NK, +PK, +NPK). A fencing treatment to restrict access of large aboveground mammalian herbivores and digging animals is crossed with the nutrient control and NPK treatments to generate two additional treatment combinations (i.e. +Fence, Fence+NPK; see Borer et al., 2014a for more details of the nutrient and fencing manipulations). For each plot, both aboveground biomass and the percentage of the sampling area

covered (area cover) are quantified annually at the peak total biomass season for each species. In this study, we used the area cover data alone since these data were collected at a higher taxonomic resolution than biomass. The measurement of area cover involves both living and dead plants. We used only the area cover data for living plants to quantify ecological stability. The sites differ in their experimental duration; only those sites with $\geqslant 4$ sampling years were included in this study. Moreover, only sites where all ten experimental treatments were present were used for analysis. This resulted in the analysis of data from 1,226 experimental plots from 41 sites (Fig. 3.1).
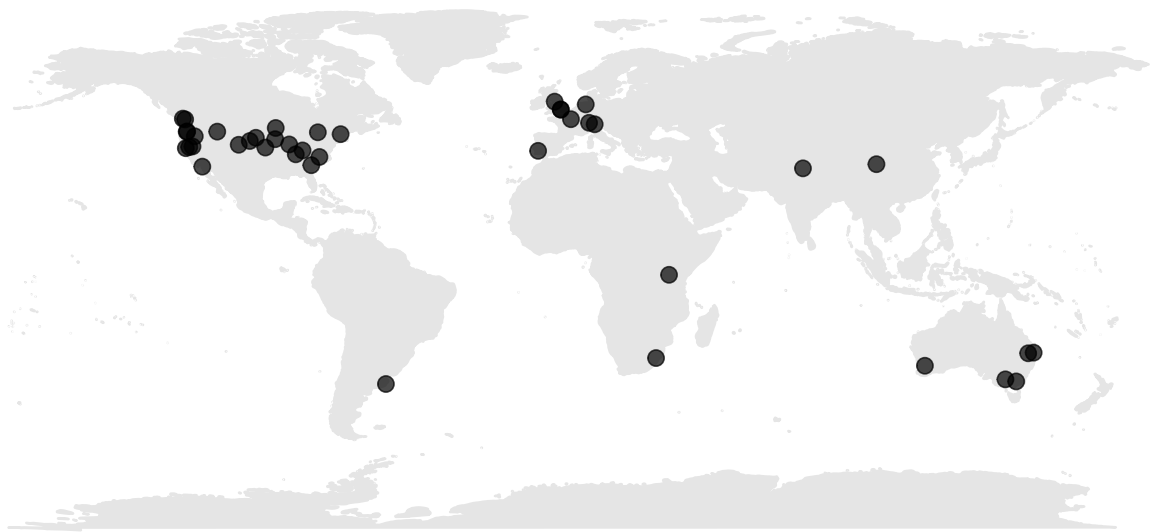
FIGURE 3.1: **Locations of the 41 NutNet sites that provided data for this study.**

3.2.2 *Stability Quantification*

To avoid underestimating the importance of rare species, all area cover data were $log_{10}(x+1)$-transformed prior to the quantification of ecological stability. For each experimental plot, we quantified five measures of ecological stability: invariability, the ability to resist invasion (ARI), the ability to resist extinction (ARE), resistance, and structural stability (SS). We define invariability as the ability of a community to maintain a relatively constant state (of biomass, abundance, coverage, etc.) in time or space. We measured invariability by first quantifying the temporal variability of total plant cover in each plot after detrending to avoid the potentially confounding effect of any positive or negative shifts in plant cover as the experiment progressed. We derived the standard deviation of the residuals from the linear regression of total

cover of each plot for each sampling year and divided this by the respective mean total cover to obtain the detrended temporal coefficient of variation (CV; Tilman et al., 2006). Invariability was then quantified as the squared reciprocal of the detrended temporal CV. The ability of communities to resist species invasion was quantified as the reciprocal of the number of the species that were absent before experimental manipulation but present in the most recent sampling year after perturbation. The ability of communities to resist extinction was quantified as the reciprocal of the number of the species that were present within plots before experimental manipulation but absent in the most recent sampling year after perturbation. Resistance was quantified as the inverse of the maximum Bray-Curtis distance of the community after experimental manipulation from its state prior to being perturbed. Structural stability is the ability of community to maintain its original species composition after perturbations. This was defined as the reciprocal of community turnover, which was quantified as the mean Jaccard distance between the communities (after presence/absence transformation) over consecutive sampling years.

3.2.3 *Statistical analysis*

We quantified the strength of pairwise relationships among stability components using Pearson correlation coefficients. Some of the 1226 experimental plots had no extinction ($n = 39$) or invasion ($n = 67$) of species, resulting in infinite values of ARI and ARE. These plots were therefore excluded from quantification of correlation coefficients involving either ARI or ARE.

We compared the overall multidimensional relationships of stability components in the different experimental treatments by quantifying the shape and orientation of their fitted ellipsoid convexes in multidimensional stability space, following the methods of Donohue et al. (2013). These analyses were done in five-dimensional space, one for each of the five components of stability measured. Specifically, we compared the distribution of relative semi-axis lengths of each dimension of the ellipsoids from each treatment (Fig. 3.2). Longer relative length of the dominant (first) semi-axis indicates lower dimensionality of stability and thus a stronger relationship between stability components, and *vice versa* (Donohue et al., 2013). Ellipsoids were constructed from the matrix of pairwise covariances between components of stability. All measures of stability were standardised by subtracting the means and then dividing by the standard deviation to remove differences in scales of measurement prior
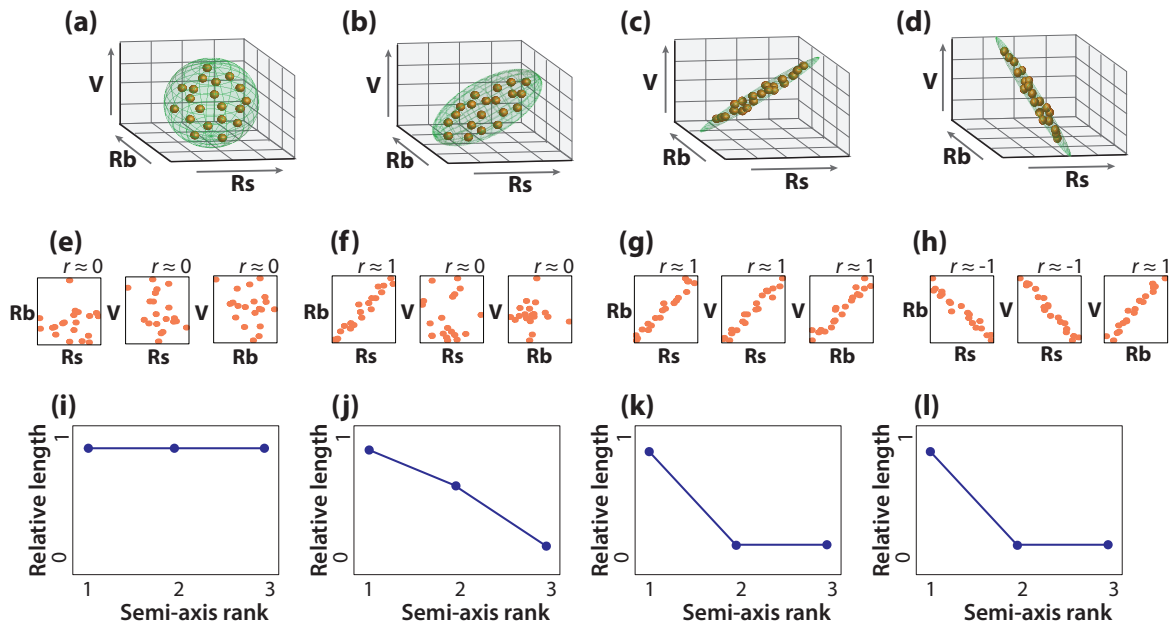
FIGURE 3.2: **Four scenarios illustrating a spectrum of possible relationships among three different dimensions of stability;** variability (V), resistance (Rs) and robustness (Rb) are used in this example, though in reality there will often be more than three components: **(a, e, i)** the three components of stability are independent, ecological stability is a relatively complex phenomenon with relatively high effective dimensionality; **(b, f, j)** two components of stability are strongly correlated and both independent of the third; **(c, g, k)** all measures of stability are strongly and positively correlated, ecological stability is a relatively simple phenomenon, with low effective dimensionality; **(d, h, l)** all measures of stability are strongly correlated, but some of those correlations are negative; ecological stability again has low effective dimensionality. The relationships among the three components of stability for the four scenarios are illustrated as ellipsoids in multidimensional stability space in **(a-d)** [**(a)** spherical, **(b)** 'frisbee'-shaped and **(c, d)** 'cigar'-shaped], which were constructed using the covariance matrix of stability measures; as sets of pairwise scatterplots in **(e-h)**, with associated Pearson correlation coefficients (*r*), and using the relative (to the dominant axis) lengths of ellipsoid semi-axes in **(i-l)**. The relative length of any ellipsoid semi-axis is proportional to the amount of variation along that axis, meaning that the distribution of relative lengths among axes defines the dimensionality and shape of the ellipsoid. Similarly, the volume of the ellipsoid describes the total variation in stability, while changes in ellipsoid orientation indicate shifts in the relative magnitude and/or form of correlations among stability measures. The orientation of the ellipsoid in **(c)** is orthogonal to that in **(d)** (i.e. the angle between the dominant eigenvectors of each ellipsoid is $90°$). This figure is adapted from Donohue et al. (2013).

to the construction of ellipsoids. The length of the semi-axis a_i was estimated by $a_i = \lambda_i^{0.5}$ ($i = 1, 2, 3, 4, 5$), where λ_i is the ith eigenvalue of the covariance matrix for a given treatment. We standardised each set of ellipsoidal semi-axis lengths by dividing by their maximum. By doing this, we set the relative length of the dominant semi-axis to 1. We tested the difference between the relative length of semi-axes from perturbed and control treatments with null distributions, which were generated by a series of permutation analyses, where we reassigned each observation to a treatment group randomly without replacement 10^4 times. In addition to examining differences in the strength of relationships between components of stability in the different experimental treatments, we also quantified differences in the nature of those relationships by comparing the orientation of the dominant semi-axis (i.e. the direction of the dominant eigenvector) in perturbed treatments with that of the control in a similar manner (Fig. 3.2). The smallest angle (ϑ) between the dominant eigenvectors ($\nu_{1,i}$ and $\nu_{1,j}$) of treatments i and j is a function of their dot product and the product of their norms by the equation

$$\vartheta = \arccos\left(\frac{\nu_{1,i} \cdot \nu_{1,j}}{(|\nu_{1,i}| * |\nu_{1,j}|)}\right) \tag{3.1}$$

The null distribution of angles between eigenvectors was created using the permuted null dataset and observed values compared against it to test for significance. As angles are inherently dyadic and positive, we used one-tailed tests to test for pairwise differences in orientation between treatments.

3.3 RESULTS

In general, pairwise correlations between different stability components were relatively weak (Fig. 3.3), particularly the correlations involving invariability and the ability to resist invasion. In the control plots without nutrient addition and fencing, only four of the ten pairs of stability component correlations (resistance-structural stability, resistance-ability to resist extinction, ability to resist extinction-structural stability, and structural stability-ability to resist invasion) were significantly ($P < 0.05$) correlated. When expanded to all treatments, only three pairs of stability component correlations (resistance-structural stability, resistance-ability to resist extinction, and ability to resist extinction-structural stability) were significantly correlated. These three correlations were lower in most treatments than that in the control, indicating a

decoupling effect of perturbations. The decoupling effect of perturbations was also found on the correlation between structural stability and ability to resist invasion, where this correlation is significant ($P < 0.05$) in the controls but not in the perturbed treatments. Contrary to our expectations, a few pairs of stability components correlations (structural stability-invariability, resistance-invariability, and ability to resist extinction-invariability) were higher in treatments than that in the control. These correlations are very weak in both the control and the treatment and increases in their values by the treatments are not strong enough to offset the decrease in the significant correlations mentioned above.

Perturbations also changed the nature of the relationships between components of stability (i.e. the orientation of the dominant axis of the multidimensional stability ellipsoid). Although these effects were not not statistically significant for most treatments, the ellipsoid from the plots that were enriched with both N and P were oriented significantly differently to those of the unmanipulated controls ($P < 0.05$, Fig. 3.5). In the unperturbed controls, the orientation of the stability ellipsoid was determined mainly by three stability components - resistance, structural stability, and ability to resist extinction, as the pairwise correlations between them were much stronger than the correlations between the other seven pairs of stability components (Fig. 3.3). These three correlations all decreased considerably in the NP treatment, while the correlation between structural stability and invariability and the correlation between resistance and ability to resist invasion increased. These shifts in correlations caused the observed shift in the orientation of the dominant axis of the stability ellipsoid of the NP treatment relative to that of the control. This is further verified by the PCA conducted on the stability metrics of each treatments (Fig. B1). From the loading values of PCA, the loadings on PC1 in NP treatment have opposite signs with that of the other treatments, indicating that they point to opposite directions.

3.4 DISCUSSION

Our results demonstrate clearly that external perturbations can decrease the strength and even change the nature of correlations between components of ecological stability in natural ecosystems. We found that pairwise correlations between the stability components we quantified and their overall multivariate relationship were in general weakened by experimental perturbations. This pattern is fully consistent with both our theoretical findings in Chapter 2 and the findings of previous empirical studies
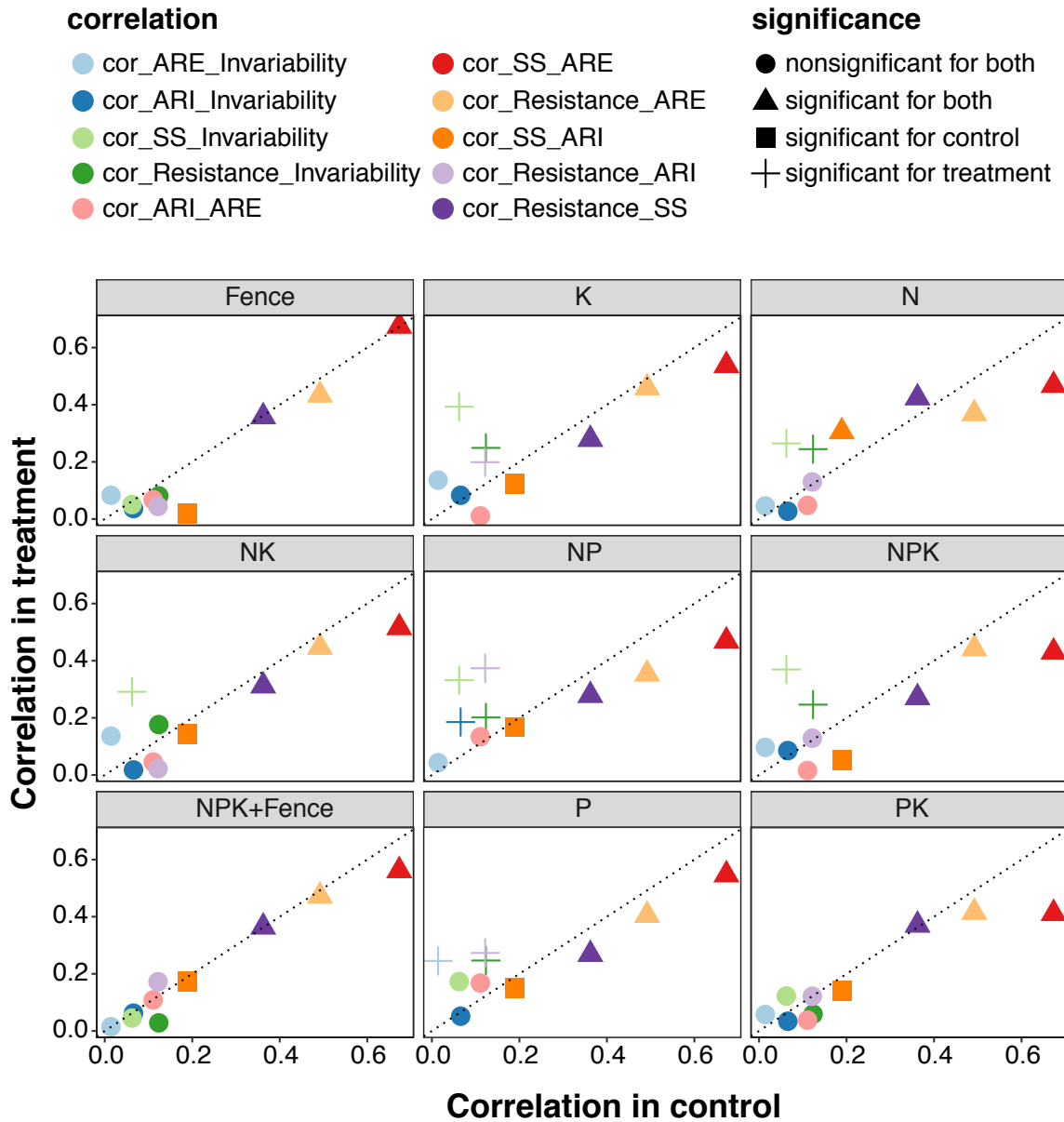
FIGURE 3.3: **Pairwise correlations between components of ecological stability in control and treatment plots.** Significant correlations in both the treatment and the control ($P < 0.05$) are indicated by triangles; correlations only significant in the controls are indicated by squares; correlations only significant in the perturbed treatments are indicated by the cross; correlations that are nonsignificant for both the treatment and the control are indicated by the circles. The dashed line is the identity line, where $y = x$.
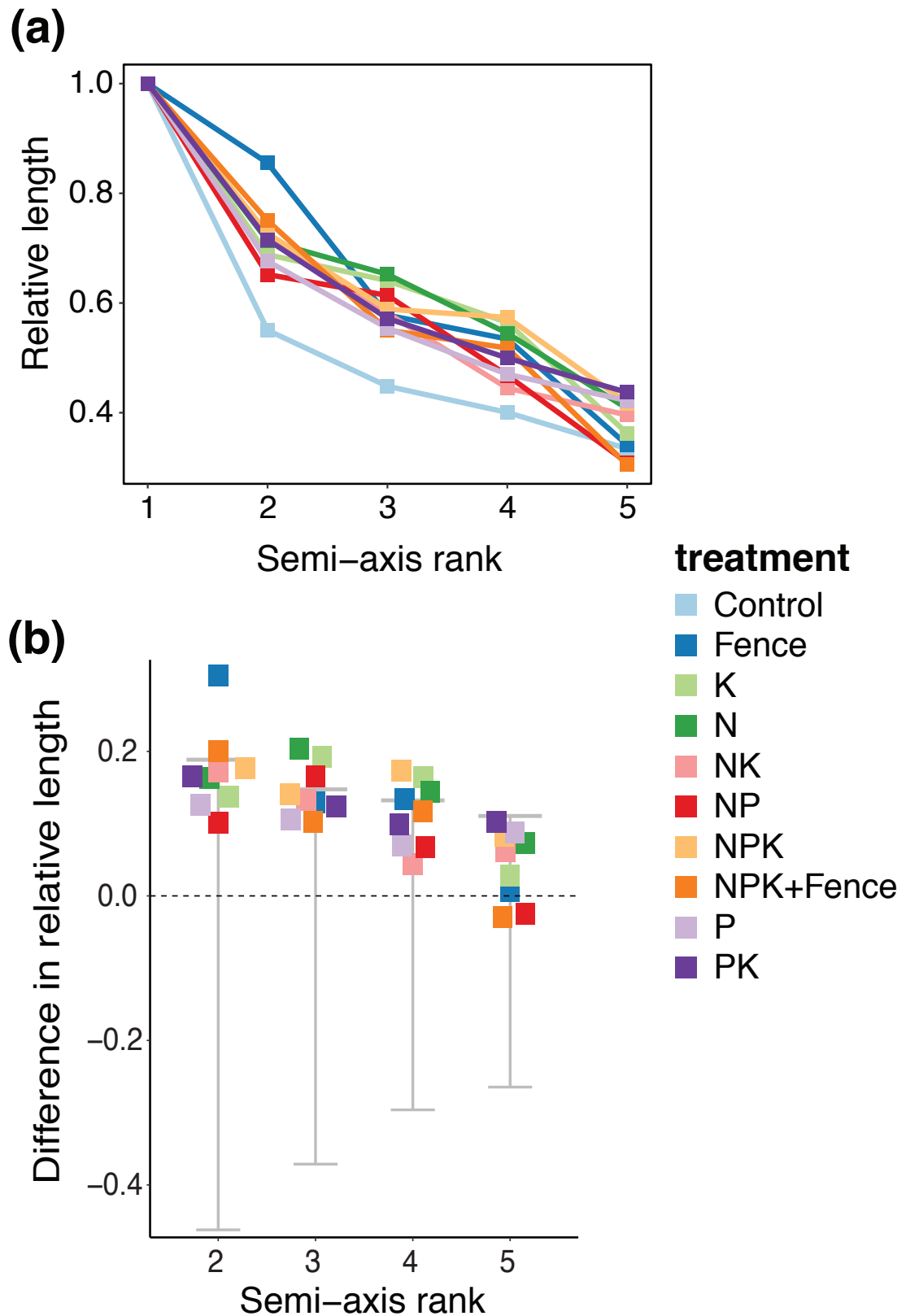
FIGURE 3.4: **(a) The relative length of semi-axes of multidimensional stability ellipsoids.** The x-axis indicates the rank (by length) of the semi-axis of the ellipsoid convex fitted for each treatment and the y-axis shows the relative length of the semi-axis, calculated as the real semi-axis length of the ellipsoid divided by the longest semi-axis length of the ellipsoid. **(b) Pairwise differences in relative semi-axis lengths for random permutations of the data (the 95% CI shown here) and points above the CI bar indicate significant pairwise differences.**
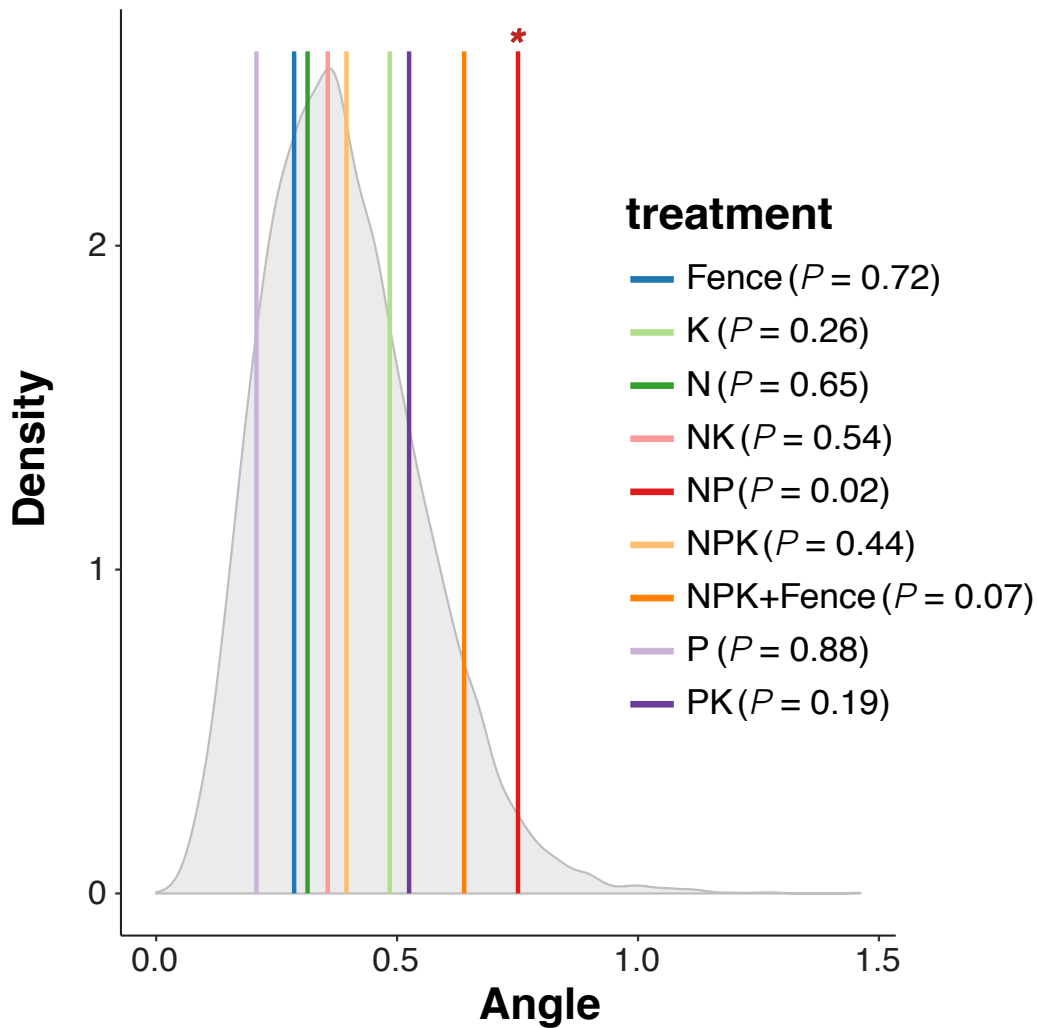
FIGURE 3.5: **Pairwise differences in the angle (in radians) between the dominant semi-axes (i.e. eigenvectors) of perturbed treatments compared with the control plots for random permutations of the data (grey density plot).** The observed angle between the dominant semi-axis of the treatment and that of the control are indicated by solid lines. Asterisk indicates statistical significance ($P < 0.05$).

from very different systems (Donohue et al., 2013; Dai et al., 2015), suggesting that this is a general phenomenon across ecosystem types. These results imply the largely one-dimensional focus ecologists have taken to date (Donohue et al., 2016) underestimates significantly the true capacity for perturbations to destabilize ecosystems.

A previous manipulative field experiment on marine rocky shore communities (Donohue et al., 2013) suggested that correlations between stability components in unperturbed communities were consistently strong and therefore that the overall dimensionality of ecological stability is low. However, in this study we observed generally weak correlations between stability components, particularly between invariability and invasion. This disparity may be because we used different experimental plots from different sites located across six continents to calculate correlations between stability components, whereas the analysis of marine shore communities used replicate plots with similar biotic and abiotic conditions. The NutNet sites vary significantly in ambient nutrient conditions, and therefore the addition of the same nutrient volumes may change the nutrient level and structure of these sites disproportionately. Further, the sites also differ considerably in species composition and diversity, which can largely influence the response of the components of ecological stability to perturbations (Wardle et al., 2000; Steiner et al., 2005; Leary et al., 2012). Moreover, the grassland sites are likely more closed systems relative to the coastal system, possibly affecting the estimation of extinctions and invasions distinctly. Finally, the NutNet data covered a much longer time window (at least four years, compared with 16 months), which likely involved significant changes in environmental conditions for some sites, which can greatly affect community stability.

The majority of, though not all, pairwise stability correlations were stronger in the control than in the perturbed treatments. This is consistent with the result of the overall multivariate relationship between stability components. The relative length of the dominant semi-axis of ellipsoid of the control was longer than that of all the perturbed treatments, suggesting stronger relationships between different components of ecological stability in the unmanipulated control plots. Perhaps most interestingly, the weakest overall multivariate relationships between stability components were found in the two treatments involving the reduction in consumer grazing (i.e. the Fence and NPK+Fence treatments). This is consistent with the perturbation we performed

in our theoretical study in Chapter 2, where the top species of the food-web was perturbed by reducing its density. Therefore, our overall results are consistent with our theoretical finding of the decoupling effect of perturbations on the dimensionality of ecological stability. However, due to the design of the NutNet experiment, we are not able to investigate the effect of perturbation strength. This may be improved in the future with more background data of eutrophic state and grazing pressure in these sites.

There was considerable variation in relationships between stability components across the different treatments, suggesting an importance of environmental context, which have not been addressed in previous studies (Donohue et al., 2013; Dai et al., 2015). The discrepancy between the effect size of nutrient addition and fencing on the relationships between stability components may be caused by the trade-off between the responses of different stability components to them. For example, in a previous study using the NutNet dataset, nutrient addition was found to more strongly affect species richness and biomass change than the Fence treatment and NPK+Fence treatment (Borer et al., 2014b). The trade-off between the responses of different stability components also raises the possibility that perturbations can change the nature of the overall relationship between different components of stability even when the strength of the overall relationship remains unchanged. For example, while adding both nitrogen and phosphorus didn't significantly decrease the strength of the overall relationship between different stability components (Fig. 3.4), it nonetheless caused a change in the nature of relationships, as indicated by a significant shift on the orientation of the dominant axis of the stability ellipsoid (Fig. 3.5).

The observed multidimensionality of ecological stability cautions against a focus on individual stability components in isolation, which is likely to underestimate the overall effects of perturbations on ecological stability (Donohue et al., 2013, 2016). Different natural systems encounter a large variety of perturbations that vary in their spatial extents, periods, durations, frequencies and intensities (Donohue et al., 2013; Tylianakis et al., 2008; Miller et al., 2011; Pincebourde et al., 2012; MacDougall et al., 2013; Donohue et al., 2016). The decoupling effect of perturbations on the relationship between the different components of ecological stability in this study further emphasizes the need to quantify ecological stability under a multidimensional framework (Donohue et al., 2013).

In this study, we quantified different components of ecological stability based on two ecosystem properties. We quantified resistance and invariability based on the area cover of the plant species, and estimated ARI, ARE, and SS by the species composition. While most pairwise correlations between these stability components were weak, three strong correlations were observed. Most interestingly, one strong stability correlation, resistance and ARE (Fig. 3.1), involved both ecosystem properties mentioned above. This implies that some stability components of different ecosystem properties can be strongly correlated. Here in this chapter, for simplicity, we quantified different stability components for the two ecosystem properties. In reality, the same stability components could be quantified for different ecosystem properties(e.g. biomass, productivity, and abundance). Whether the behavior of the same stability component is consistent between different ecosystem properties may depend on the trait of the species within the ecosystem. Species differ from one another in their resource use, environmental tolerances, and interactions with other species, such that species composition has a major influence on ecosystem stability. Theories predict that the aggregate properties of a community or ecosystem such as total productivity and total biomass can be maintained through the compensatory dynamics of different species in a variable environment (Yachi and Loreau, 1999; Gonzalez and Loreau, 2009; Loreau and de Mazancourt, 2013). For example, several long-term grassland experiments observed low temporal variation in the total biomass of the community but high variation in the population biomass (Bai et al., 2004; Tilman et al., 2006). We may expect that the same phenomenon occurs for abundance. However, the temporal variation of the total abundance is not necessarily at the same magnitude as but likely larger than that of the total biomass. This is more likely to happen when the biomass or body size of the multiple species largely differ from each other. For example, the loss of an individual of a large-size species may release space for multiple individuals of a small-size species, possibly leading to a considerable change in the total abundance. Future work considering not only the multidimensionality of ecological stability but also the difference between different ecosystem properties can provide a more detailed and thorough understanding of ecological stability, and help make more comprehensive plans and policy for the conservation of ecosystem functions.

THE PREDICTABILITY OF ECOLOGICAL STABILITY IN A NOISY WORLD

ABSTRACT

Environmental noise, or stochasticity, is a key determinant of ecological dynamics. While we have some appreciation of how environmental stochasticity can moderate the variability and persistence of populations, we know little about its effects on communities, particularly on its implications for the nature and predictability of their response to perturbations. Here, we found that different stability components showed distinct responding patterns to changing temporal autocorrelation of environmental noise. Increasing environmental autocorrelation stabilizes communities in some dimensions yet simultaneously destabilizes them in others. Specifically, increasingly positive autocorrelation (reddening) of environmental noise increases community recovery (resilience, a stability property) while at the same time increasing temporal variability and reducing resistance to perturbation (both signals of instability). In contrast to the difference in the response of different stability components, the predictability of all stability components decreases consistently as environmental noise reddens, with resistance and resilience being much more difficult to predict than variability. Our findings demonstrate the fundamental and indeed dominant role played by environmental stochasticity in determining the dynamics and stability of ecosystems and challenge the credibility of models that overlook it or simply incorporate it as white noise.

4.1 INTRODUCTION

Predicting how ecosystems will respond to global environmental change has become a central focus of ecological research (Davis et al., 1998; Bellard et al., 2012; Blois et al., 2013; Oliver et al., 2015; Petchey et al., 2015; Urban et al., 2016). Prediction of ecological responses typically involves the use of static approaches that focus on mean levels of environmental change, such as warming and deforestation (Thompson et al., 2013; Donohue et al., 2016). Most community approaches overlook environmental stochasticity, which introduces uncertainties and even when incorporated is usually considered as a random term. However, stochasticity has structure and comprises a key determinant of the dynamics and structure of ecosystems (May, 1973; Vellend, 2016, Shoemaker et al in review). Exploration of its underlying characteristics, such as its variance and spectral structure (Halley, 1996; Vasseur and Yodzis, 2004; Ruokolainen et al., 2009), reveals, for example, the frequency and duration of extreme events and can determine the variability and persistence of populations (Ripa and Heino, 1999; Easterling et al., 2000; Schiegg, 2003; Pike et al., 2004; Schwager et al., 2006; Ruokolainen et al., 2009; Jentsch et al., 2009; Thompson et al., 2013; Kuparinen et al., 2014; Kayler et al., 2015; Crone, 2016). However, in spite of its overarching influence on community dynamics, the role played by environmental stochasticity in moderating ecological responses to perturbations remains largely unknown.

Ecological stability is a multidimensional concept that tries to capture the different aspects of the dynamics of the system and its response to perturbations (Pimm, 1984; Donohue et al., 2016). The concept has been a central focus of ecological research for decades (**?**May, 1973; Pimm, 1984; Tilman et al., 2006; **?**; Donohue et al., 2013, 2016), and is fundamental to the conservation and management of natural resources (Donohue et al., 2016). The behaviour and predictability of different ecological stability components, such as the variability of communities in time and space, their resistance and their resilience - their capacity to, respectively, resist and recover from perturbations - likely depend strongly on the spatiotemporal range across which they are estimated (Sabo and Post, 2008). Stability components such as variability and persistence - the length of time a system maintains the same state before it changes in some defined way - are usually estimated from long-term dynamics and are therefore more likely to reflect key features of environmental stochasticity. In contrast, stability components determined within shorter time windows, such as those

that describe the responses of communities to distinct perturbations - resistance and resilience - are likely to be sensitive to the timing and duration of potential extreme events. This probably makes them less predictable. Nonetheless, their general response pattern can be still revealed by examining and averaging the stability of many similar systems experiencing the same environmental stochasticity.

Here, we explore how three key components of ecological stability - recovery time (a measure of resilience), extent of change (a measure of resistance; larger extent of change indicates weak resistance), and variability (Fig. C1) - are regulated by environmental stochasticity. Specifically, we use simulated model food-webs described by the general Lotka-Volterra system (Pimm and Lawton, 1977, 1978; Petchey et al., 2008) to examine both the nature and predictability of these stability responses along gradients of the key factors that characterise stochasticity - its temporal autocorrelation [i.e. its colour; Vasseur and Yodzis, 2004; Fowler and Ruokolainen, 2013] and the correlations in species responses to it (Ruokolainen and Fowler, 2008; Ruokolainen et al., 2009). We perturbed our model systems by reducing the densities of the apex predator in each food-web as a pulse perturbation. Given the significant disjoint between many theoretical measures of stability and what can be measured empirically (Donohue et al., 2016), we quantified all components of stability empirically across a broad variety of four-species food-web modules (Fig. C2) - subnetworks of tightly interacting species that act as the 'building blocks' of food-webs (Milo et al., 2002; Bascompte and Melián, 2005; Kondoh, 2008) - to explore the generality of our findings.

4.2 METHODS

4.2.1 *Food-web construction and simulations*

We constructed sets of 14 distinct four-species modules (Fig. C2) to cover a large range of different network structures that vary in both trophic complexity and connectance. We then constructed 100 individual communities within each set of module structures. The dynamics of our simple modules are described by the general Lotka-Volterra system (Pimm and Lawton, 1977, 1978; Petchey et al., 2008):

$$\frac{dN_i}{dt} = N_i(r_i + \sum_{j=1}^{n} a_{ij}N_j + \epsilon_i(t)) \qquad (4.1)$$

where i and j are the identity of species in the community, N_i is the population density of species i, r_i is the intrinsic growth/mortality rate (positive for basal species; otherwise negative), a_{ij} is the interaction coefficient that describes the per capita effect of the jth species on the growth/mortality rate of the ith species (positive if it enhances population growth - the consumer-resource interaction, for example; negative if it causes decreases in density) and $\epsilon_i(t)$ is the specific response to environmental stochasticity (see below).

We followed Petchey et al. (2008) to parameterize the models. We first set the growth rates of basal species to 1, and drew mortality rates of consumers randomly from the uniform distribution $[0, 0.001]$. We sorted the mortality rate so that the predator had lower rates than their prey, as species at higher trophic levels tend to be larger (Cohen et al., 2003) and large size generally leads to low mortality rate (Brown et al., 2004). The value of the per capita effect of the consumer on its resources a_{ij} was assigned depending on the number of resource species. When the consumer fed on only one species, a_{ij} was set to 0.5. Otherwise, a randomly chosen link was given one strong interaction coefficient (set to 0.4), and other links were assigned weak interactions and set to 0.1 divided by the number of the resources minus 1. This approach resulted in a skewed distribution of interaction strengths, which is commonly found in real ecological networks (Paine, 1992; Wootton and Emmerson, 2005). The per capita effect of the resource species on its consumer a_{ji} was calculated as a_{ij} times the conversion efficiency. We set the conversion efficiency of non-omnivory links to 0.2 and that of omnivory links to 0.02 by assuming that it takes more mass of the basal species (plants in most situations) than animal mass to produce one predator offspring (Petchey et al., 2008).

Using the interaction coefficient matrix A with entries a_{ij} and the vector R with entries of r_i, we estimated the density of species at equilibrium, N_i^*. At equilibrium, the per capita change rate of all species is zero, so $AN^* = -R$. Then, N^* can be solved $N^* = -A^{-1}R$, where A^{-1} is the inverse of matrix A. The equilibrium Jacobian interaction matrix J^* (also known as the community matrix) with entries J_{ij}, which is used to test the local stability of the constructed community (May, 1973), is calculated by $J_{ij} = a_{ij}N_i^*$ (see Fig. C3 for the distribution of the maximum real part of the eigenvalues of the community matrix of the communities). The process of parameterization continued until for each of the 14 food-web modules we

constructed 100 communities that satisfied the requirements of both local stability and feasibility (Gilpin, 1975; Jansen and Kokkoris, 2003; Emmerson and Yearsley, 2004). The equilibrium species density of communities generated by this method conformed to the pyramidal structure, with species of lower trophic levels being more abundant (Fig. C4).

4.2.2 *Environmental stochasticity*

The effect of environmental stochasticity was incorporated in the dynamical system of Equation 4.1 by the continuous variable $\epsilon_i(t)$, which represents the specific response to environmental stochasticity. $\epsilon_i(t)$ was obtained as a function of continuous time t by linearly interpolating the discrete variable $\epsilon_i(T)$, which is given by the autoregressive process (Ruokolainen and Fowler, 2008), as:

$$\epsilon_i(T+1) = k\epsilon_i(T) + \sigma\sqrt{1-k^2}\frac{\varphi(T) + \beta\omega_i(T)}{\sqrt{1-\beta^2}}$$

$$\beta = \sqrt{\frac{1-|\rho|}{|\rho|}}$$

(4.2)

where T is the discrete time point $(0, 1, 2...1000)$, k is the autocorrelation coefficient, and ρ is species response correlation, i.e. the correlation between all pairs of specific response ϵ_i. The terms $\varphi(T)$ and $\omega_i(T)$ are standard normal random components, where the former is consistent for all species and the latter differs between species. Parameter β is a scaling factor ensuring that noise variance remains independent of ρ. This method scales the noise time series to its asymptotical variance σ_i^2 independently of noise autocorrelation (Heino et al., 2000; Ruokolainen and Fowler, 2008). In our early test of the model, varying the value of σ_i^2 did not affect the conclusion of this study, so we set σ_i^2 to 0.05 for simplicity. We simulated a range of regimes of environmental stochasticity within a fully-crossed design using k and ρ. k was set to -0.8, -0.4, 0, 0.4, and 0.8, reflecting ranges in colour from blue through white to red, while ρ was set to 0.2, 0.5, and 0.8. The unique combination of stochasticity features all led to different stochasticity regimes determined by the random terms $\varphi(T)$ and $\omega_i(T)$. We produced 50 sets of $\varphi(T)$ and $\omega_i(T)$, and consider this as a factor of randomness. We applied them for each unique combination of stochasticity features to build 50 'replicated' regimes of environmental stochasticity for each individual food-web.

Most models comparing coloured environments with white noise assume implicitly that the normality of the noise time series is retained as its temporal autocorrelation changes from zero to either positive or negative values (e.g. Ripa and Heino, 1999; Greenman and Benton, 2005). However, Fowler and Ruokolainen (2013) showed that coloured series tend to deviate from the normal distribution when using an autoregressive approach to generate time series of environmental stochasticity, and this can underestimate extinction risks in red environments. Cohen et al. (1999) developed an approach, termed 'spectral mimicry', to generate coloured environmental series following a desired normal frequency distribution yet with the level of temporal autocorrelation of the original environmental stochasticity series. Therefore, for each regime of environmental stochasticity generated using the autoregressive process, we used spectral mimicry (Cohen et al., 1999) to generate another shape-controlled regime to test whether controlling the frequency distribution of the noise series modifies ecological stability responses and/or predictability (Fowler and Ruokolainen, 2013). Both the autoregressive method and spectral mimicry produced the desired gradient of temporal autocorrelation and species response correlation (Fig. C5 and Fig. C6).

4.2.3 *Ecological stability*

We simulated species dynamics for all food-webs in the stochastic environment with the locally stable equilibrium as the initial state value. We also simulated their dynamics with a 50% reduction in the equilibrium density of the species at the highest trophic level in each food-web module as the initial state value. Simulations of dynamics of both the 'unperturbed' and 'perturbed' community were run over 1000 time steps with a step length of 1. The time allowed almost all (> 99.9%) of the simulated communities to recover fully (Fig. C7).

The recovery time for each food-web simulation was quantified as the time when the difference between the 'unperturbed' and 'perturbed' community dynamics (Fig. C1a) reduced to a critical level (Fig. C1b). This corresponded to the first moment when the difference between the densities of all species in the perturbed and unperturbed communities were less than 0.01 and this difference was maintained for at least 50 timesteps to ensure convergence had been acheived. The maximum Euclidean distance between perturbed and unperturbed communities, which we measured at each simulation step, was used to measure resistance (Fig. C1c).

Increases in Euclidian distance correspond to reductions in resistance, and *vice versa*. We quantified variability as the standard deviation of the total density of the unperturbed community during the simulation time window divided by its mean (Fig. C1d).

4.2.4 *Random forest regression*

We examined the nature and predictability of stability responses using random forest regression at two analytical scales - from (1) individual replicate ($n = 50$) food-web simulations, which incorporates variation in responses of food-webs to distinct runs of stochastic noise described by identical autocorrelation, and (2) the mean stability response of the 50 noise replicates at each level of environmental stochasticity, which indicates the general response pattern at the level of each food-web. The random forest algorithm converges on an optimal solution from individual solutions of multiple trees (500 regression trees in this case) using bootstrapping and is non-parametric and not subject to distributional assumptions, compatible with categorical, ordinal, and continuous data simultaneously, invariant to outliers and capable of handling high-dimensional data and identifying and incorporating complex variable interactions (Evans et al., 2011). Random forest regression was therefore appropriate for analysis of our multiple-layer dataset given the skewed distribution and nonlinear responses of many of our stability components (e.g. Supplementary. Fig. 7) and the need to include both continuous and categorical variables as predictors. The importance of each predictor in the random forest is computed from permuting out-of-bag (OOB) data (When the training set for the a tree model in the random forest is drawn by sampling with replacement, the cases that are left out of the sample are called out of bag data) (Liaw et al., 2002). For each tree, the prediction (mean-squared) error on the out-of-bag portion of the data was recorded. The same was then done after permuting each of the predictors. The differences between the two are then averaged across all trees, and normalized by the standard deviation of the differences. The random forest regression model was conducted in R version 3.2.4 (R Core Team 2016) using the **ranger** library (Wright and Ziegler, 2017).

4.3 RESULTS

To illustrate our findings, we focus initially on the effect of temporal autocorrelation on the dynamics of one community from what is the simplest food-web module -

the food chain (i.e. Module 1 in Fig. C2). We then expand our focus to 100 such communities from each of 14 food-web modules to explore the generality of our results (Fig. C2).
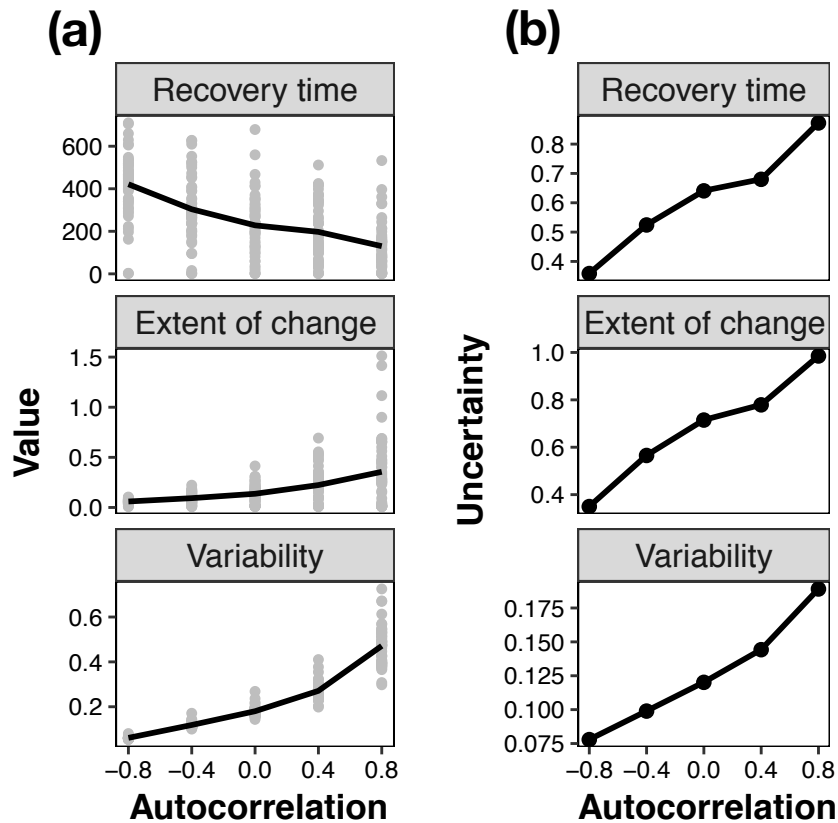

FIGURE 4.1: **Effect of the temporal autocorrelation of environmental noise on the various components of ecological stability in an example food chain community. (a)** Stability responses (recovery time, extent of change in community structure and variability) of a single community to replicate temporal patterns of environmental stochasticity along a gradient in temporal autocorrelation. Every point at each level of autocorrelation represents the stability response of one of the 50 noise replicates (distinct runs of stochastic noise described by identical autocorrelation) for the community. All responses are inversely related to stability (i.e. stability increases from the top to the bottom of the y-axis in every case). The solid line corresponds to the mean response for the community across noise replicates and, therefore, indicates the general response of each stability component to the temporal autocorrelation of environmental noise. For this illustrative example, the correlation of species responses to environmental fluctuations was set to 0.2 and stochasticity was generated using the autoregressive method rather than spectral mimicry. **(b)** Uncertainty in stability responses of the community to the temporal autocorrelation of environmental noise. This was quantified as the coefficient of variation (standard deviation divided by the mean) across the noise replicates. High uncertainty corresponds to low predictability of ecological stability.

Increased temporal autocorrelation of environmental stochasticity both stabilized and destabilized the example food chain along different dimensions of stability. In-

creasing autocorrelation from negative (blue) to positive (red) destabilized the community by increasing both density variability and the extent of change in community structure in response to perturbation (i.e. reducing resistance), yet simultaneously enhanced stability by reducing recovery time after perturbation (i.e. increasing resilience; Fig. 4.1a). In contrast, the uncertainty in all stability responses increased consistently with environmental reddening, indicating that higher temporal autocorrelation reduces the predictability of ecological stability (Fig. 4.1b). However, our measures of resistance and resilience were both considerably more uncertain - and thus less predictable - than variability across the simulated range of stochasticity, likely reflecting particular sensitivity of both resistance and resilience to random stochastic events over the relatively short time window over which they were quantified.

Results from the example food chain community were fully consistent with those not only from the other communities with the same module structure, but also with those from across all of the other modules examined (Fig. 4.2). In general, recovery time decreased while the extent of community change and variability both increased with environmental reddening (Fig. 4.2a). Further, the predictability of all components of stability decreased as environmental autocorrelation became increasingly positive, with recovery time and the extent of change displaying consistently higher uncertainty and lower predictability than variability (Fig. 4.2b).

The general response of all stability components analysed was highly predictable (random forest regression pseudo-R^2 values > 0.98 in every case; 4.3a). However, predictability of the specific responses of stability components to distinct runs of stochastic noise was significantly lower (regression pseudo-R^2 of recovery time, extent of community change and variability was reduced to, respectively, 0.42, 0.33 and 0.79; 4.3a). These reductions in predictability were particularly acute for resistance and resilience, consistent with the high uncertainty associated with these stability components in previous analyses (Fig. 4.1b and 4.2b).

The temporal autocorrelation of environmental stochasticity was the dominant predictor of both the general and specific responses of all stability components examined (Fig. 4.3b). In addition, a second component of environmental stochasticity - the correlation in species responses to environmental fluctuations - was also important for predicting the specific response of recovery time and variability, but
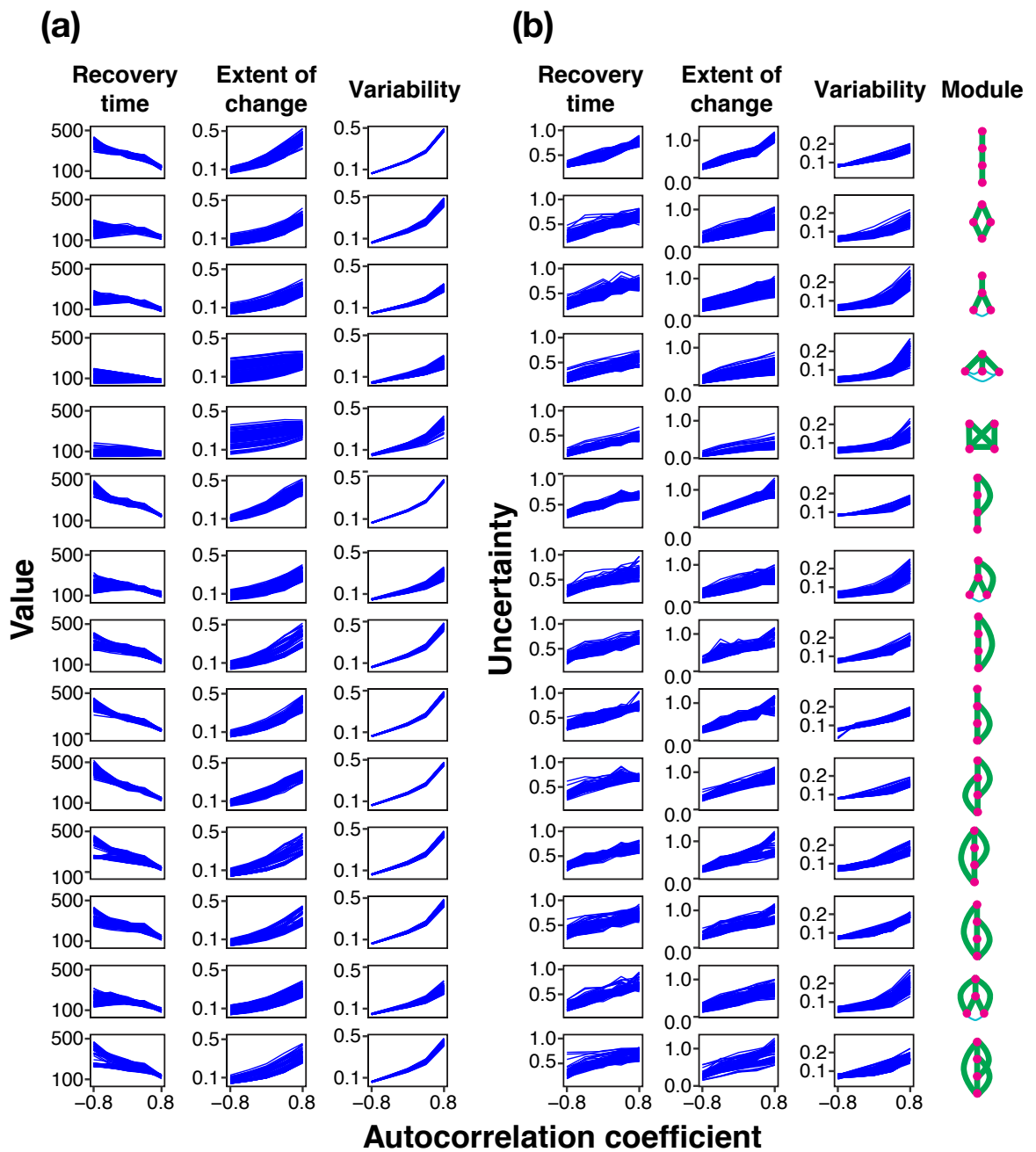
FIGURE 4.2: **General stability responses to changes in environmental autocorrelation across a diverse range of food-web modules.** The **(a)** general response of ecological stability components and **(b)** uncertainty in those general responses to the colour of environmental noise. Each solid blue line represents one of the 100 communities of a module.
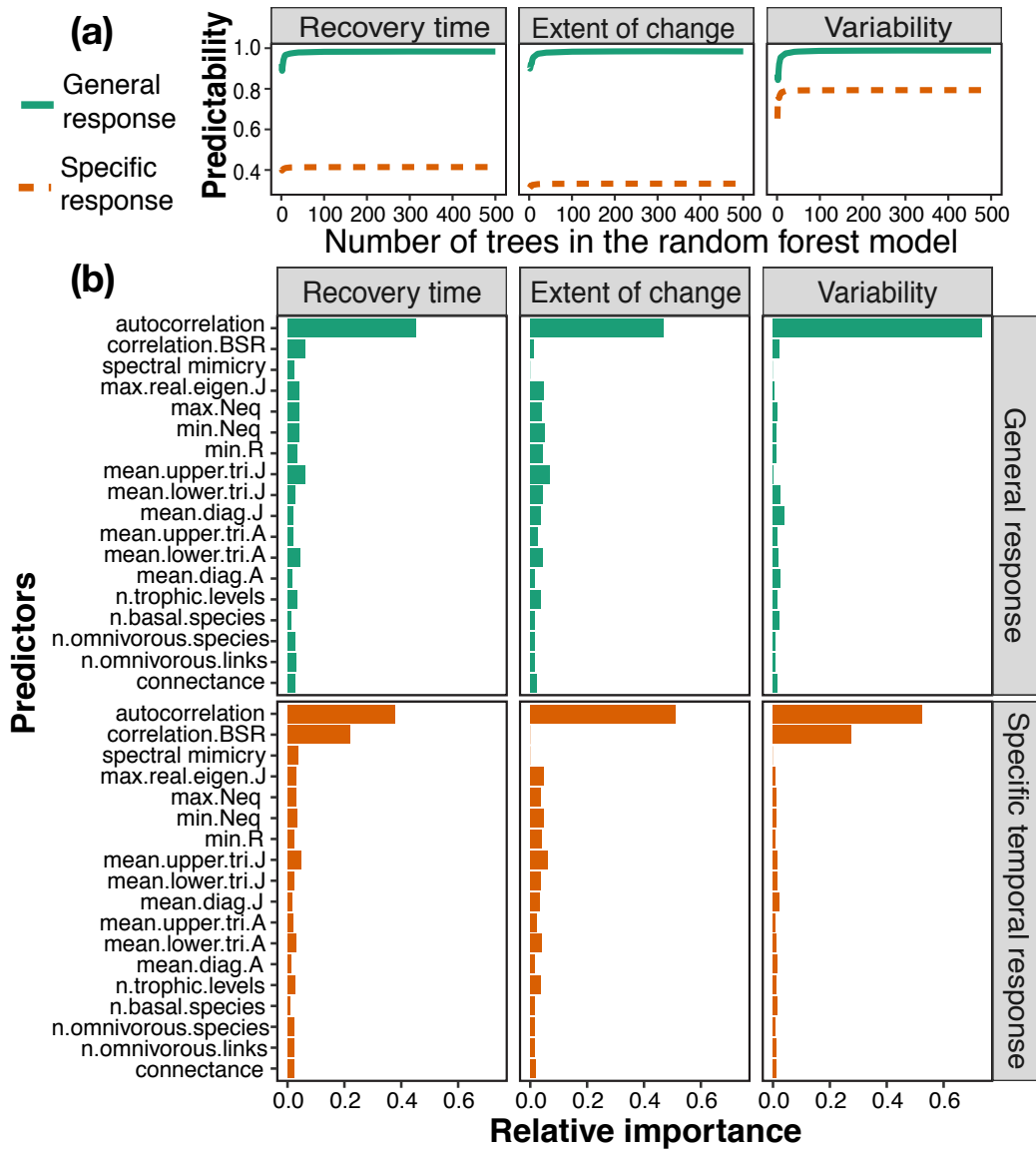
FIGURE 4.3: **The predictability of ecological stability in stochastic environments. (a)** Predictability (pseudo-R^2 of random forest regression models) of both the specific temporal response (i.e. incorporating variation in responses of food-webs to distinct runs of stochastic noise described by identical autocorrelation, $n = 2,100,000$) and the general response pattern (the mean stability response across noise replicates, $n = 42,000$) of stability components to environmental autocorrelation. **(b)** Relative importance of predictors of stability, calculated as the importance value of each predictor in random forest regression models divided by the sum of the importance of all predictors. The following predictors were included in the model: the autocorrelation coefficient of environmental stochasticity (autocorrelation), the correlation of species responses to environmental noise (correlation.BSR), whether envionmental noise series are controlled to be normally distributed using spectral mimicry (spectral.mimicry), the maximum real part of the eigenvalue of the community matrix (max.real.eigen.J), the maximum and minimum equilibrium species density (max.Neq and min.Neq), the slowest growth/decay rate of the community (min.R), the mean value of the upper triangular (mean.upper.tri.J) and lower triangular(mean.lower.tri.J) and diagonal (mean.diag.J) entries of the community matrix, the mean value of the upper triangular (mean.upper.tri.A) and lower triangular(mean.lower.tri.A) and diagonal (mean.diag.A) entries of the interaction coefficient matrix, food web connectance, the number of trophic levels (n.trophic.levels), basal species (n.basal.species), omnivorous species and links (n.omnivorous.species and n.omnivorous.links).
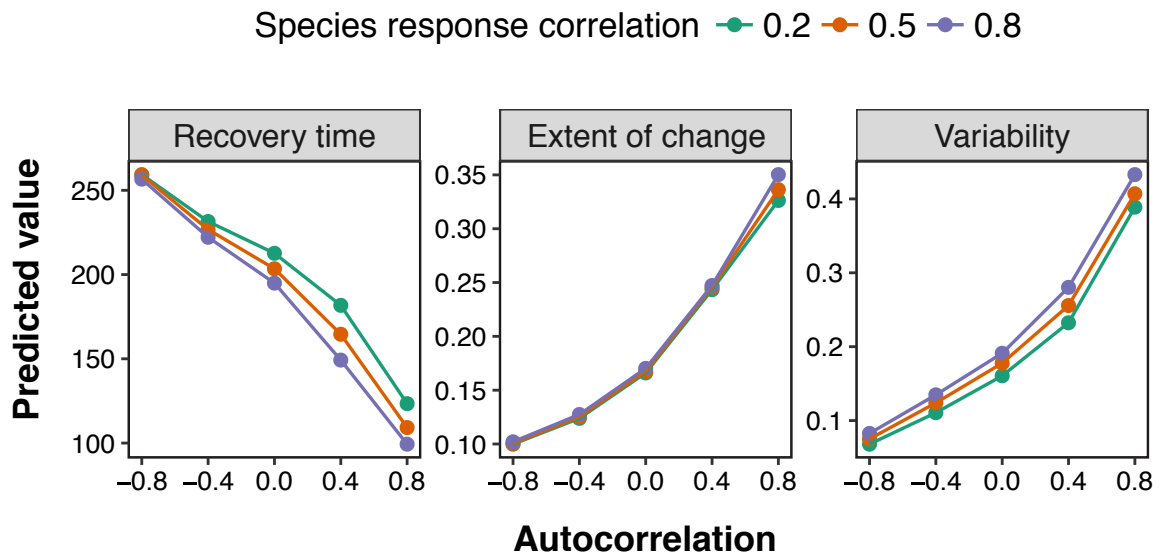
FIGURE 4.4: **Partial dependence of stability components on the temporal autocorrelation and correlation of species responses to environmental stochasticity.** The partial value was calculated as the mean of model predictions when fixing temporal autocorrelation and species response correlations to stochasticity.

not for the extent of community change (Fig. 4.3b). Strong correlations in species responses to environmental fluctuations stabililized communities by reducing variability and reducing the extent of community change in response to perturbation (though only marginally at high positive levels of temporal autocorrelation), yet simultaneously destabilized communities by increasing recovery time (Fig. 4.4). However, species response correlations had a far weaker effect on stability than temporal autocorrelation (Fig. 4.3 and Fig. 4.4) and contributed little to predicting the general response of any stability component.

Compared to environmental stochasticity, both community and module characteristics were of only minor importance to predicting stability (Fig. 4.3b). This suggests that the effects of temporal autocorrelation and species responses to environmental stochasticity are consistent irrespective of community structure. In contrast with expectations (Cohen et al., 1999; Fowler and Ruokolainen, 2013), controlling the shape of the frequency distribution of the stochasticity series by spectral mimicry was unimportant for predicting stability responses (Fig. 4.3b).

4.4 DISCUSSION

Although environmental stochasticity plays a critical role in determining the assembly, diversity, functioning, and evolution of ecological communities (Clark, 2003; Ruokolainen and Fowler, 2008; Ruokolainen et al., 2009; Clark, 2010), it has been treated as synonymous with fundamental unpredictability in many ecological studies (Shoemaker et al. in review). Our results show key aspects of environmental stochasticity - its temporal autocorrelation and correlations of species responses to it - regulate ecological stability responses in a predictive way. Further, environmental stochasticity was a far more important determinant of stability than characteristics of the communities. These findings highlight the potential of applying environmental stochasticity to illuminate our understanding of, and enhance significantly our capacity to predict, the ecological stability of communities.

We found that different stability components showed distinct responding patterns to changing temporal autocorrelation of environmental noise. Increasing environmental autocorrelation stabilize communities in some dimensions yet simultaneously destabilize them in others. The reddening of environmental noise reduced recovery time (i.e. increasing resilience), while simultaneously increasing both the extent of change in response to perturbation (i.e. reducing resistance) and variability. Moreover, these effects were amplified when correlations in species responses to environmental fluctuations were strong. In general, increasing environmental reddening amplifies the fluctuations in population density in under-compensatory single-species populations (Ripa and Heino, 1999; Laakso et al., 2004; Ruokolainen et al., 2009), as was the case in our study. Increases in the extent of change in response to perturbation and variability was probably a consequence of propagation of this enlarged population variance as stochasticity reddened. Further, the higher temporal variability of both populations and communities in red noise environments more rapidly supressed the effect of the initial perturbation, bringing the perturbed and unperturbed communities into more similar environmental scenarios with the same environmental stochasticity and a negligible perturbation size, and therefore reduced recovery time. Increasing correlations of species responses to environmental noise enhanced this effect further most likely by increasing species synchrony, which results in the community acting more like an individual population and reduces the buffering effect caused by species responding in more diverse ways to environmen-

tal fluctuations (Tilman, 1996; Loreau and de Mazancourt, 2013; Wang and Loreau, 2016).

Despite the trade-off that occurred among components of stability as temporal autocorrelation changed, their predictability decreased consistently as environmental noise reddened. Further, recovery time and resistance were much less predictabile than variability. This was probably a consequence of the difference in the time range across which they are quantified. Recovery time and resistance were quantified within a relatively short window, and were therefore more sensitive to the time and duration of individual extreme events, whereas variability was measured across the whole simulation time and was thus more likely to reflect the key features of the stochasticity regime. Further, recovery time and resistance were both obtained from single timepoints in the system dynamics, whereas variability was measured from the deviation and mean of the dynamics, which is likely to much more closely reflect stochastic structure. These findings highlight the challenges in predicting ecological stability and other ecological processes on small temporal and spatial scales.

The hierarchical nature of ecology provides a key challenge in predicting ecological stability in stochastic environments. For simplicity, we controlled the variance of environmental stochasticity at the same level, and assigned set levels of species response correlations to environmental fluctuations for all consumers and basal species. In nature, different species are experiencing different levels of stochasticity in multiple environmental factors all the time. These different types of environmental stochasticity scale up to affect ecosystem stability by propagation through the linear and nonlinear interactions between the other components of the system. Predicting the outcomes of these processes is a complex challenge. However, our findings demonstrate that incorporating key characteristics of environmental stochasticity into our models is an essential step towards improving prediction in ecological systems. Moreover, understanding how human activities and climate change modify the temporal and spatial autocorrelation of environmental noise is necessary to provide improved understanding and prediction of ecosystem stability.

GENERAL DISCUSSION

5.1 THE COMPLEXITY OF ECOLOGICAL STABILITY

One of the central goals of ecology is to understand the factors that determine the stability of biological communities under diverse perturbations in their environment (**?**Pimm, 1984; **?**; Ives and Carpenter, 2007; de Mazancourt et al., 2013; Donohue et al., 2013, 2016; Loreau and de Mazancourt, 2013). Ecological stability is really a metaconcept that integrates a wide range of different properties or components (Pimm, 1984; Donohue et al., 2013). An accurate evaluation of ecological stability requires a better understanding of its multidimensional nature. However, until now most research has focused on only a few of these components in isolation, and knowledge is scarce concerning the relationships between different components of ecological stability. Further, the links between ecological stability, external perturbations and the complexity of the biological community may be different for different stability components (Loreau, 2010). Natural systems suffer from diverse disturbances that vary in their spatial extents, periods, durations, frequencies and intensities (Tylianakis et al., 2008; Miller et al., 2011; Pincebourde et al., 2012; MacDougall et al., 2013). These multifaceted disturbances precipitate a range of responses that can alter the many components of ecological stability and the relationships among them (Donohue et al., 2016). With more intensive human interferences and significant climate change (Finney et al., 2000; Nemani et al., 2003; Araújo and Rahbek, 2006; Halpern et al., 2008; McMahon et al., 2011; Cahill et al., 2013; Lambers, 2015; Worm and Paine, 2016), it is of growing importance to investigate how these relationships are regulated by different types of external perturbations.

Throughout this thesis, Our results have shown how the different components of ecological stability can trade-off in their responses to external perturbations. Broadly, in Chapter 2 and Chapter 3, we demonstrated how external perturbations can weaken the strength of relationships between different stability components. In Chapter 4, The result showed that environmental stochasticity generates trade-offs between

different stability components. These results demonstrate that both the strength and the nature (or sign) of relationships among stability components change when communities are disturbed in different ways. This complexity has critical implications for our understanding of the impacts of disturbances on ecosystems. It means that restricting our focus to single measures of stability in isolation, or to amalgamated ones such as Holling's resilience (Holling, 1973), when they are used to reduce the multidimensional complexity of stability to a single dimension and its measurement to a single number, risks significantly underestimating the impacts of perturbations. It also risks incomplete understanding of the mechanisms that underpin the overall stability of ecosystems. The multidimensionality of ecological responses demands explicit multidimensional measurement of both disturbances and stability (Donohue et al., 2016).

Although the effect of external perturbations on the complexity of ecological stability is a focal point of this thesis, the different components of ecological stability and the relationships between them are determined collectively by the strength and type of perturbations, environmental context, and the complexity of the biological community itself. In Chapter 3, I found that the largest decrease in overall multivariate relationships between components of stability occurred in the two treatments involving consumer exclusion by fencing, rather than from nutrient addition. This suggests that the effects of the perturbations on the relationships between components of ecological stability also depend on the type of the perturbations. Depending on local environmental context and the traits of the species in the community (Petchey and Gaston, 2009; Grman et al., 2010), different stability components may respond distinctly to different types of perturbations (Donohue et al., 2013). For example, it is possible that in response to a drought, a plant community might retain biomass but lose biodiversity (May and McLean, 2007).

Ecosystems are hierarchical, and so is ecological stability. Only community-level stability was analysed in this thesis for simplicity. However, the stability components of biological communities may behave differently across different ecological scales. A classic example is the biodiversity-induced trade-offs between the temporal variability of populations and communities, where species diversity can simultaneously decrease population-level stability and increase community-level stability through compensatory dynamics between different populations (Tilman, 1996; Yachi and

Loreau, 1999; Bai et al., 2004; Tilman et al., 2006; Loreau and de Mazancourt, 2013). Even at the same ecological scale, species at different trophic levels may have different stability responses to external perturbations. For example, in most food-webs, species at higher trophic levels tend to have longer generation times (Cohen et al., 2003; Brown et al., 2004), and are therefore likely to recover more slowly from perturbations relative to species from lower trophic levels. A realistic assessment of ecological stability also needs to cover sufficiently broad spatiotemporal scales (Levin, 1992; Chave, 2013). This is especially necessary for those stability components that require large sample sizes. However, as shown in Chapter 4, these stability components are likely to be more predictable under environmental variation than the those that are quantified over finer spatiotemporal scales.

Our theoretical studies in Chapter 2 and Chapter 4 consider three components of ecological stability, including resistance, resilience, and variability, following Pimm's (1984) definitions. Of them, resistance and resilience are based on the assumption of the existence of a unique equilibrium in the biological community. However, more than a single stable state may exist in natural systems. In this case, the ecosystem can shift from one state to another, driven either by strong environmental forces or positive feedback from the ecosystem (Beisner et al., 2003; Suding et al., 2004; Aronson et al., 2004; Ives and Carpenter, 2007; Fletcher et al., 2014). If there is a limit beyond which a system cannot return directly to its former state, this is termed a tipping point (Scheffer et al., 2009; Hirota et al., 2011; Barnosky et al., 2012; Dakos and Hastings, 2013). Moreover, the species in communities are exposed to constant changes in their local environment. The time lag between adjacent disturbances may be so short that the community does not have sufficient time to return to its equilibrium. Instead, the community will stay far away from its equilibrium, and display transient dynamics (Hastings, 2001, 2004). Future research on how these non-traditional components of ecological stability act as an interactive function of the type, intensity, and duration of the environmental and biological driver is needed to increase understanding of the varying effects of driver presses, pulses, and stochasticity on ecosystem dynamics (Ratajczak et al., 2017).

5.2 FUTURE PROSPECTS

5.2.1 *Theoretical models*

Many theoretical and empirical studies have provided insights as to how ecological stability is determined by the richness and composition of species or functional groups (Steiner et al., 2005; Tilman et al., 2006, 2014; de Mazancourt et al., 2013; Loreau and de Mazancourt, 2013; Oliver et al., 2015), the type and strength of interactions (Huston, 1997; McCann et al., 1998; Emmerson and Yearsley, 2004; Allesina and Tang, 2012), and the network structure (e.g. connectance, nestedness, and modularity) of the biological community (Allesina and Tang, 2012; Grilli et al., 2016; van Altena et al., 2016). For simplicity, we used four-species food-web modules as the basic structure of the biological communities. Although these modules cover some of the most common building blocks of the real ecological networks (Milo et al., 2002; Bascompte and Melián, 2005; Kondoh, 2008), these models only consider one type of interspecific interaction - the consumer-resource interaction - and assume that the interaction coefficient (i.e. the per capita interaction strength) is constant.

This approach ignores some important biological details that are likely to affect how biological systems respond to environmental change, and oversimplify the complexity of ecosystems, where numerous species affect each other through multiple types of direct and indirect interactions (Sauve et al., 2016). Specifically, the models fail to consider: i) the configuration of different types of intraspecific and interspecific interactions (e.g. the resource-consumer interaction, intraguild predation, cannibalism, competition, facilitation, mutualism, and higher-order interactions) (Petchey et al., 1997; Brooker et al., 2008; Mougi and Kondoh, 2012; Cavieres et al., 2014; Lurgi et al., 2016; Sellman et al., 2016; Grilli et al., 2017; Godsoe et al., 2017; Fichtner et al., 2017); ii) the intraspecific variation caused by age, stage, sex, and previous history (Benton et al., 2006; Benton, 2012; Des Roches et al., 2017); iii) the density-dependent change in demographic rates and intraspecific and interspecific interaction coefficients (Sinclair and Pech, 1996; Coulson et al., 2001); and iv) the genetic, phenotypic, and behavioural adaptability of species in response to the stress caused by environmental change and the presence of other species (Schmitz et al., 1997; Ellner et al., 2001; Miner et al., 2005; Jones et al., 2009; Lee et al., 2010; Valdovinos et al., 2016). Incorporating these important biological details in

ecological models may help bridge the still significant gap between theory and the response of stability components in natural ecosystems to environmental drivers.

The simplicity of the models used in this thesis also arises from the exclusion of spatial dynamics. While the past two decades have seen great progress in understanding the mechanisms of ecosystem stability in local ecological systems, there is an urgent need to extend existing knowledge to larger spatial scales to match the scale of management and conservation (Wang and Loreau, 2014). New theoretical work may grasp the complexity of ecological stability and its relationship to multiple types of disturbances within a spatial framework by considering several factors. First, considering spatial heterogeneity between local patches and habitats (Stachowicz et al., 2008; Oliver et al., 2015). Second, considering the spatial autocorrelation of environmental drivers (Legendre, 1993; Koenig, 1999; Shurin et al., 2009). Third, considering the dynamics of adjacent individuals and populations that may be affected by the Moran and Neighbourhood Effects (Ranta et al., 1997; Koenig, 2002; Kim and Underwood, 2015). Fourth, attaching great importance to the dispersal and movement of species, in terms of their speed (Hill et al., 2002; Kneitel and Miller, 2003; Howeth and Leibold, 2010), direction (Altermatt et al., 2011), and distance (Johst et al., 2002; Débarre and Lenormand, 2011; Lesser and Jackson, 2013). Finally, and perhaps most importantly, to the study of the complexity of ecological stability, assessing various stability components at different spatial scales, from local through regional to global (Loreau et al., 2003; Wang and Loreau, 2014).

The inclusion of different types of interaction, biological and ecological flexibility and spatiotemporal heterogeneity will clearly increase the complexity of ecological models. However, it also provides a more holistic view of the dynamics of ecological networks. It is also likely that some of these factors can be incorporated in multiple candidate models. For example, the impact of species dispersal rates can be evaluated by the Levins Model and its successors (Hastings, 2010), Reaction-Diffusion Equations (Flather and Bevers, 2002), or Agent-Based Models (Grimm et al., 2005). Future work can test the generality of the biological and environmental drivers of ecological stability across alternative models, and compare the theoretical results of these models separately or collectively with the empirical findings.

5.2.2 *Integrating the complexity of stability into ecosystem management*

Ecosystem stability is the key indicator of ecosystem health and determines the reliability of the goods and services that nature offers to us. Many international bodies, including the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, broadly aspire to maintain or enhance ecological stability (Mace, 2014; Díaz et al., 2015; Lu et al., 2015; Donohue et al., 2016). Theories on ecological stability can provide valuable directions to protect species and conserve and restore ecosystems. However, as described in this thesis, ecological responses to environmental variations and human interferences are ineluctably complex. The successful application of knowledge of ecological stability to ecosystem management needs to systematically consider its multidimensionality, hierarchy, environmental context, and the input capacity of the management practice such as labour and investment.

To facilitate the application of theories of ecosystem stability to the practice of conservation and restoration, theorists, empiricists, policymakers, and executive bodies of ecosystem management must first speak the same language and use the same terms. By surveying policy targets and mission and vision statements of 42 key international agreements, organisations and agencies that are concerned primarily with the conservation and protection of nature, Donohue et al. (2016) found that there is, however, a great disparity between the terms used by decision-makers and ecologists. For example, the most common terms associated positively with stability were 'sustain' and 'sustainability'. And among the 14 other terms (including sustain/sustainable, conserve/conservation, safeguard, maintain, secure/security, protect, altered, constrain impacts, harmony, healthy, integrity, safety, survival, safe ecological limits) that occurred less frequently across the documents that were examined, only two - 'stabilise'/'stable' and 'resilience'/'resilient' - have clear ecological definitions. Therefore, policymakers and practitioners are advised to either use the same terminology as ecologists, or clearly and unambiguously elaborate upon the terms and measurement they use.

In spite of the widely different terminologies used by ecologists and policymakers and practitioners, the terms used in policy targets and statements could be associated in some way with at least one, and frequently more than one, component of ecological stability, implying that the multidimensionality of ecological stability is already integrated, even if unconsciously, in the language and targets of policy-

makers. Compared to policies, however, the practice of ecosystem management largely fails to consider the multidimensionality and hierarchy of ecosystem stability. For instance, taxonomic bias commonly exists in the practice of conservation and reintroduction (Clark and May, 2002; Seddon et al., 2005; Darwall et al., 2011; Roberts et al., 2016). Moreover, although the ecosystem is the carrier of multiple ecosystem functions and services, ecosystem restorations frequently fail to restore all lost ecological functions (Palmer et al., 2014). Perhaps funding agencies and practitioners should more equitably allocate research funds and practice efforts across the taxonomic spectrum, different types of ecosystem functions and services, and consider the scale and process of time and space. Both scientists and policy-makers need to recognise that the multidimensional nature of environmental change always requires a multidimensional assessment of ecological response. Different components of ecological stability and functioning are of not same importance and are not necessarily treated equally, depending on the type of ecosystem, ecological ethics, and their values for human society. A simple yet scientifically sound approach to quantify the overall stability of ecosystems is to integrate the multiple components of ecological stability with different weights assigned on them depending on the objective of the management and policy (Donohue et al., 2016).

5.3   CONCLUDING REMARKS

In this thesis, through both theoretical simulations and empirical analyses, I demonstrated the trade-offs between different stability components under both perturbations and environmental stochasticity. These findings highlight the importance of studying and managing ecological stability using a multidimensional framework.

Bibliography

Adler, P. B., E. W. Seabloom, E. T. Borer, H. Hillebrand, Y. Hautier, A. Hector, W. S. Harpole, L. R. O'Halloran, J. B. Grace, T. M. Anderson, et al. 2011. Productivity is a poor predictor of plant species richness. Science 333:1750–1753.

Allesina, S. and S. Tang. 2012. Stability criteria for complex ecosystems. Nature 483:205–208.

Altermatt, F., S. Schreiber, and M. Holyoak. 2011. Interactive effects of disturbance and dispersal directionality on species richness and composition in metacommunities. Ecology 92:859–870.

Araújo, M. B. and C. Rahbek. 2006. How does climate change affect biodiversity? Science 313:1396–1397.

Arnoldi, J. F., M. Loreau, and B. Haegeman. 2016. Resilience, reactivity and variability: A mathematical comparison of ecological stability measures. Journal of Theoretical Biology 389:47–59.

Aronson, R. B., I. G. Macintyre, C. M. Wapnick, and M. W. O'Neill. 2004. Phase shifts, alternative states, and the unprecedented convergence of two reef systems. Ecology 85:1876–1891.

Bai, Y., X. Han, J. Wu, Z. Chen, and L. Li. 2004. Ecosystem stability and compensatory effects in the inner mongolia grassland. Nature 431:181–184.

Banks, N. C., D. R. Paini, K. L. Bayliss, and M. Hodda. 2015. The role of global trade and transport network topology in the human-mediated dispersal of alien species. Ecology Letters 18:188–199.

Barnosky, A. D., E. A. Hadly, J. Bascompte, E. L. Berlow, J. H. Brown, M. Fortelius, W. M. Getz, J. Harte, A. Hastings, P. A. Marquet, et al. 2012. Approaching a state shift in earth/'s biosphere. Nature 486:52–58.

Bascompte, J. 2009. Mutualistic networks. Frontiers in Ecology and the Environment 7:429–436.

Bascompte, J. and C. J. Melián. 2005. Simple trophic modules for complex food webs. Ecology 86:2868–2873.

Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. Frontiers in Ecology and the Environment 1:376–382.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Benton, T. 2012. Individual variation and population dynamics: lessons from a simple system. Philosophical Transactions of the Royal Society of London B: Biological Sciences 367:200–210.

Benton, T. G., S. J. Plaistow, and T. N. Coulson. 2006. Complex population dynamics and complex causation: devils, details and demography. Proceedings of the Royal Society of London B: Biological Sciences 273:1173–1181.

Blois, J. L., P. L. Zarnetske, M. C. Fitzpatrick, and S. Finnegan. 2013. Climate change and the past, present, and future of biotic interactions. Science 341:499–504.

Borer, E. T., W. S. Harpole, P. B. Adler, E. M. Lind, J. L. Orrock, E. W. Seabloom, and M. D. Smith. 2014a. Finding generality in ecology: a model for globally distributed experiments. Methods in Ecology and Evolution 5:65–73.

Borer, E. T., E. W. Seabloom, D. S. Gruner, W. S. Harpole, H. Hillebrand, E. M. Lind, P. B. Adler, J. Alberti, T. M. Anderson, J. D. Bakker, et al. 2014b. Herbivores and nutrients control grassland plant diversity via light limitation. Nature 508:517–520.

Brassil, C. E. 2012. Stability analysis. Pages 680–686 *in* Encyclopedia of theoretical ecology. University of California Press.

Brooker, R. W., F. T. Maestre, R. M. Callaway, C. L. Lortie, L. A. Cavieres, G. Kunstler, P. Liancourt, K. Tielbörger, J. M. Travis, F. Anthelme, et al. 2008. Facilitation in plant communities: the past, the present, and the future. Journal of Ecology 96:18–34.

Brose, U., R. J. Williams, and N. D. Martinez. 2006. Allometric scaling enhances stability in complex food webs. Ecology Letters 9:1228–1236.

Brown, J. H., J. F. Gillooly, A. P. Allen, V. M. Savage, and G. B. West. 2004. Toward a metabolic theory of ecology. Ecology 85:1771–1789.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, O. Warsi, et al. 2013. How does climate change cause extinction? Proceedings of the Royal Society of London B: Biological Sciences 280:rspb20121890.

Cardinale, B. J., J. E. Duffy, A. Gonzalez, D. U. Hooper, C. Perrings, P. Venail, A. Narwani, G. M. Mace, D. Tilman, D. A. Wardle, et al. 2012. Biodiversity loss and its impact on humanity. Nature 486:59–67.

Cavieres, L. A., R. W. Brooker, B. J. Butterfield, B. J. Cook, Z. Kikvidze, C. J. Lortie, R. Michalet, F. I. Pugnaire, C. Schöb, S. Xiao, et al. 2014. Facilitative plant interactions and climate simultaneously drive alpine plant diversity. Ecology Letters 17:193–202.

Chave, J. 2013. The problem of pattern and scale in ecology: what have we learned in 20 years? Ecology Letters 16:4–16.

Clark, J. A. and R. M. May. 2002. Taxonomic bias in conservation research. Science 297:191–192.

Clark, J. S. 2003. Uncertainty and variability in demography and population growth: a hierarchical approach. Ecology 84:1370–1381.

Clark, J. S. 2010. Individuals and the variation needed for high species diversity in forest trees. Science 327:1129–1132.

Cohen, J. E., T. Jonsson, and S. R. Carpenter. 2003. Ecological community description using the food web, species abundance, and body size. Proceedings of the National Academy of Sciences 100:1781–1786.

Cohen, J. E., C. M. Newman, A. E. Cohen, O. L. Petchey, and A. Gonzalez. 1999. Spectral mimicry: a method of synthesizing matching time series with different fourier spectra. Circuits, systems, and Signal Processing 18:431–442.

Costanza, R., R. d'Arge, R. De Groot, S. Farber, M. Grasso, B. Hannon, K. Limburg, S. Naeem, R. V. O'neill, J. Paruelo, et al. 1997. The value of the world's ecosystem services and natural capital. Nature 387:253–260.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. Morgan, J. Pemberton, T. H. Clutton-Brock, M. Crawley, and B. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in soay sheep. Science 292:1528–1531.

Crone, E. E. 2016. Contrasting effects of spatial heterogeneity and environmental stochasticity on population dynamics of a perennial wildflower. Journal of Ecology 104:281–291.

Dai, L., K. S. Korolev, and J. Gore. 2015. Relation between stability and resilience determines the performance of early warning signals under different environmental drivers. Proceedings of the National Academy of Sciences 112:10056–10061.

Dakos, V. and A. Hastings. 2013. Editorial: special issue on regime shifts and tipping points in ecology. Theoretical Ecology 6:253–254.

D'Angelo, C. and J. Wiedenmann. 2014. Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Current Opinion in Environmental Sustainability 7:82–93.

Darwall, W. R., R. A. Holland, K. G. Smith, D. Allen, E. G. Brooks, V. Katarya, C. M. Pollock, Y. Shi, V. Clausnitzer, N. Cumberlidge, et al. 2011. Implications of bias in conservation research and investment for freshwater species. Conservation Letters 4:474–482.

Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998. Making mistakes when predicting shifts in species range in response to global warming. Nature 391:783–786.

De Angelis, D. L. 1975. Stability and connectance in food web models. Ecology 56:238–243.

de Mazancourt, C., F. Isbell, A. Larocque, F. Berendse, E. Luca, J. B. Grace, B. Haegeman, H. Wayne Polley, C. Roscher, B. Schmid, et al. 2013. Predicting ecosystem stability from community composition and biodiversity. Ecology Letters 16:617–625.

de Ruiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257.

DeAngelis, D. L. and J. Waterhouse. 1987. Equilibrium and nonequilibrium concepts in ecological models. Ecological Monographs 57:1–21.

Débarre, F. and T. Lenormand. 2011. Distance-limited dispersal promotes coexistence at habitat boundaries: reconsidering the competitive exclusion principle. Ecology Letters 14:260–266.

Des Roches, S., D. M. Post, N. E. Turley, J. K. Bailey, A. P. Hendry, M. T. Kinnison, J. A. Schweitzer, and E. P. Palkovacs. 2017. The ecological importance of intraspecific variation. Nature Ecology & Evolution 2:57–74.

Díaz, S., S. Demissew, J. Carabias, C. Joly, M. Lonsdale, N. Ash, A. Larigauderie, J. R. Adhikari, S. Arico, A. Báldi, et al. 2015. The ipbes conceptual framework - connecting nature and people. Current Opinion in Environmental Sustainability 14:1–16.

Donohue, I., H. Hillebrand, J. M. Montoya, O. L. Petchey, S. L. Pimm, M. S. Fowler, K. Healy, A. L. Jackson, M. Lurgi, D. McClean, et al. 2016. Navigating the complexity of ecological stability. Ecology Letters 19:1172–1185.

Donohue, I., O. L. Petchey, S. Kéfi, A. Génin, A. L. Jackson, Q. Yang, and N. E. O'Connor. 2017. Loss of predator species, not intermediate consumers, triggers rapid and dramatic extinction cascades. Global Change Biology 23:2962–2972.

Donohue, I., O. L. Petchey, J. M. Montoya, A. L. Jackson, L. McNally, M. Viana, K. Healy, M. Lurgi, N. E. O'Connor, and M. C. Emmerson. 2013. On the dimensionality of ecological stability. Ecology Letters 16:421–429.

Easterling, D. R., G. A. Meehl, C. Parmesan, S. A. Changnon, T. R. Karl, and L. O. Mearns. 2000. Climate extremes: observations, modeling, and impacts. Science 289:2068–2074.

Eklöf, A. and S. Allesina. 2012. Ecological networks. Pages 470–478 *in* Encyclopedia of theoretical ecology. University of California Press.

Ellner, S. and P. Turchin. 1995. Chaos in a noisy world: new methods and evidence from time-series analysis. The American Naturalist 145:343–375.

Ellner, S. P., E. McCauley, B. E. Kendall, C. J. Briggs, P. R. Hosseini, S. N. Wood, A. Janssen, M. W. Sabelis, P. Turchin, R. M. Nisbet, et al. 2001. Habitat structure and population persistence in an experimental community. Nature 412:538–543.

Emmerson, M. and J. M. Yearsley. 2004. Weak interactions, omnivory and emergent food-web properties. Proceedings of the Royal Society of London B: Biological Sciences 271:397–405.

Estes, J. A., J. Terborgh, J. S. Brashares, M. E. Power, J. Berger, W. J. Bond, S. R. Carpenter, T. E. Essington, R. D. Holt, J. B. Jackson, et al. 2011. Trophic downgrading of planet earth. Science 333:301–306.

Evans, J. S., M. A. Murphy, Z. A. Holden, and S. A. Cushman. 2011. Modeling species distribution and change using random forest. Pages 139–159 *in* Predictive species and habitat modeling in landscape ecology. Springer.

Fagan, W. F. 1997. Omnivory as a stabilizing feature of natural communities. The American Naturalist 150:554–567.

Fichtner, A., W. Härdtle, Y. Li, H. Bruelheide, M. Kunz, and G. Oheimb. 2017. From competition to facilitation: how tree species respond to neighbourhood diversity. Ecology Letters 20:892–900.

Finney, B. P., I. Gregory-Eaves, J. Sweetman, M. S. Douglas, and J. P. Smol. 2000. Impacts of climatic change and fishing on pacific salmon abundance over the past 300 years. Science 290:795–799.

Flather, C. H. and M. Bevers. 2002. Patchy reaction-diffusion and population abundance: the relative importance of habitat amount and arrangement. The American Naturalist 159:40–56.

Fletcher, M.-S., S. W. Wood, and S. G. Haberle. 2014. A fire-driven shift from forest to non-forest: evidence for alternative stable states? Ecology 95:2504–2513.

Fowler, M. S. and L. Ruokolainen. 2013. Confounding environmental colour and distribution shape leads to underestimation of population extinction risk. PloS one 8:e55855.

France, K. E. and J. E. Duffy. 2006. Diversity and dispersal interactively affect predictability of ecosystem function. Nature 441:1139–1143.

Gilpin, M. E. 1975. Stability of feasible predator-prey systems. Nature 254:137–139.

Godsoe, W., N. J. Holland, C. Cosner, B. E. Kendall, A. Brett, J. Jankowski, and R. D. Holt. 2017. Interspecific interactions and range limits: contrasts among interaction types. Theoretical Ecology 10:167–179.

Gonzalez, A. and M. Loreau. 2009. The causes and consequences of compensatory dynamics in ecological communities. Annual Review of Ecology, Evolution, and Systematics 40:393–414.

Greenman, J. and T. Benton. 2005. The impact of environmental fluctuations on structured discrete time population models: resonance, synchrony and threshold behaviour. Theoretical Population Biology 68:217–235.

Grenfell, B., K. Wilson, B. Finkenstädt, T. Coulson, S. Murray, S. Albon, J. Pemberton, T. Clutton-Brock, and M. Crawley. 1998. Noise and determinism in synchronized sheep dynamics. Nature 394:674.

Grilli, J., G. Barabás, M. J. Michalska-Smith, and S. Allesina. 2017. Higher-order interactions stabilize dynamics in competitive network models. Nature 548:210–213.

Grilli, J., T. Rogers, and S. Allesina. 2016. Modularity and stability in ecological communities. Nature Communications 7:12031.

Grimm, V., E. Revilla, U. Berger, F. Jeltsch, W. M. Mooij, S. F. Railsback, H.-H. Thulke, J. Weiner, T. Wiegand, and D. L. DeAngelis. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science 310:987–991.

Grimm, V. and C. Wissel. 1997. Babel, or the ecological stability discussions: an inventory and analysis of terminology and a guide for avoiding confusion. Oecologia 109:323–334.

Grman, E., J. A. Lau, D. R. Schoolmaster, and K. L. Gross. 2010. Mechanisms contributing to stability in ecosystem function depend on the environmental context. Ecology Letters 13:1400–1410.

Haegeman, B., J.-F. Arnoldi, S. Wang, C. de Mazancourt, J. M. Montoya, and M. Loreau. 2016. Resilience, invariability, and ecological stability across levels of organization. bioRxiv .

Halley, J. M. 1996. Ecology, evolution and 1f-noise. Trends in Ecology & Evolution 11:33–37.

Halpern, B. S., M. Frazier, J. Potapenko, K. S. Casey, K. Koenig, C. Longo, J. S. Lowndes, R. C. Rockwood, E. R. Selig, K. A. Selkoe, et al. 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. Nature Communications 6:7615.

Halpern, B. S., S. Walbridge, K. A. Selkoe, C. V. Kappel, F. Micheli, C. D'agrosa, J. F. Bruno, K. S. Casey, C. Ebert, H. E. Fox, et al. 2008. A global map of human impact on marine ecosystems. Science 319:948–952.

Harrison, G. W. 1979. Stability under environmental stress: resistance, resilience, persistence, and variability. The American Naturalist 113:659–669.

Hastings, A. 2001. Transient dynamics and persistence of ecological systems. Ecology Letters 4:215–220.

Hastings, A. 2004. Transients: the key to long-term ecological understanding? Trends in Ecology & Evolution 19:39–45.

Hastings, A. 2010. Timescales, dynamics, and ecological understanding. Ecology 91:3471–3480.

Hautier, Y., E. W. Seabloom, E. T. Borer, P. B. Adler, W. S. Harpole, H. Hillebrand, E. M. Lind, A. S. MacDougall, C. J. Stevens, J. D. Bakker, et al. 2014. Eutrophication weakens stabilizing effects of diversity in natural grasslands. Nature 508:521–525.

Heino, M., J. Ripa, and V. Kaitala. 2000. Extinction risk under coloured environmental noise. Ecography 23:177–184.

Hill, M. F., A. Hastings, and L. W. Botsford. 2002. The effects of small dispersal rates on extinction times in structured metapopulation models. The American Naturalist 160:389–402.

Hirota, M., M. Holmgren, E. H. Van Nes, and M. Scheffer. 2011. Global resilience of tropical forest and savanna to critical transitions. Science 334:232–235.

Hodgson, D., J. L. McDonald, and D. J. Hosken. 2015. What do you mean, 'resilient'? Trends in Ecology & Evolution 30:503–506.

Holling, C. S. 1973. Resilience and stability of ecological systems. Annual Review of Ecology and Systematics 4:1–23.

Holt, R. D. 2002. Community modules. Pages 333–349 *in* Multitrophic Interactions in Terrestrial Ecosystems. Blackwell Science.

Holyoak, M. and S. Sachdev. 1998. Omnivory and the stability of simple food webs. Oecologia 117:413–419.

Hooper, D. U., E. C. Adair, B. J. Cardinale, J. E. Byrnes, B. A. Hungate, K. L. Matulich, A. Gonzalez, J. E. Duffy, L. Gamfeldt, and M. I. O'Connor. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. Nature 486:105–108.

House, C. M., Z. Lewis, D. J. Hodgson, N. Wedell, M. D. Sharma, J. Hunt, and D. J. Hosken. 2013. Sexual and natural selection both influence male genital evolution. PLoS One 8:e63807.

Howeth, J. G. and M. A. Leibold. 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. Ecology 91:2727–2741.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. Jackson, J. Kleypas, et al. 2003. Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933.

Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. Oecologia 110:449–460.

Isbell, F., P. B. Reich, D. Tilman, S. E. Hobbie, S. Polasky, and S. Binder. 2013. Nutrient enrichment, biodiversity loss, and consequent declines in ecosystem productivity. Proceedings of the National Academy of Sciences 110:11911–11916.

Ives, A. R. and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58–62.

Jansen, V. A. and G. D. Kokkoris. 2003. Complexity and stability revisited. Ecology Letters 6:498–502.

Jentsch, A., J. Kreyling, J. Boettcher-Treschkow, and C. Beierkuhnlein. 2009. Beyond gradual warming: extreme weather events alter flower phenology of european grassland and heath species. Global Change Biology 15:837–849.

Johst, K., R. Brandl, and S. Eber. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos 98:263–270.

Jones, L. E., L. Becks, S. P. Ellner, N. G. Hairston, T. Yoshida, and G. F. Fussmann. 2009. Rapid contemporary evolution and clonal food web dynamics. Philosophical Transactions of the Royal Society of London B: Biological Sciences 364:1579–1591.

Kayler, Z. E., H. J. De Boeck, S. Fatichi, J. M. Grünzweig, L. Merbold, C. Beier, N. McDowell, and J. S. Dukes. 2015. Experiments to confront the environmental extremes of climate change. Frontiers in Ecology and the Environment 13:219–225.

Kéfi, S., E. L. Berlow, E. A. Wieters, S. A. Navarrete, O. L. Petchey, S. A. Wood, A. Boit, L. N. Joppa, K. D. Lafferty, R. J. Williams, et al. 2012. More than a meal - integrating non-feeding interactions into food webs. Ecology Letters 15:291–300.

Kim, T. N. and N. Underwood. 2015. Plant neighborhood effects on herbivory: damage is both density and frequency dependent. Ecology 96:1431–1437.

Kneitel, J. M. and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of sarracenia purpurea inquilines. The American Naturalist 162:165–171.

Koenig, W. D. 1999. Spatial autocorrelation of ecological phenomena. Trends in Ecology & Evolution 14:22–26.

Koenig, W. D. 2002. Global patterns of environmental synchrony and the moran effect. Ecography 25:283–288.

Kondoh, M. 2008. Building trophic modules into a persistent food web. Proceedings of the National Academy of Sciences 105:16631–16635.

Kratina, P., R. M. LeCraw, T. Ingram, and B. R. Anholt. 2012. Stability and persistence of food webs with omnivory: is there a general pattern? Ecosphere 3:1–18.

Kuparinen, A., D. M. Keith, and J. A. Hutchings. 2014. Increased environmentally driven recruitment variability decreases resilience to fishing and increases uncertainty of recovery. ICES Journal of Marine Science 71:1507–1514.

Laakso, J., V. Kaitala, and E. Ranta. 2004. Non-linear biological responses to environmental noise affect population extinction risk. Oikos 104:142–148.

Lambers, J. H. R. 2015. Extinction risks from climate change. Science 348:501–502.

Lamberti-Raverot, B. and S. Puijalon. 2012. Nutrient enrichment affects the mechanical resistance of aquatic plants. Journal of Experimental Botany 63:6115–6123.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. The American Naturalist 142:911–927.

Leary, D. J., J. M. Rip, and O. L. Petchey. 2012. The impact of environmental variability and species composition on the stability of experimental microbial populations and communities. Oikos 121:327–336.

Lee, H. H., M. N. Molla, C. R. Cantor, and J. J. Collins. 2010. Bacterial charity work leads to population-wide resistance. Nature 467:82–85.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74:1659–1673.

Lesser, M. R. and S. T. Jackson. 2013. Contributions of long-distance dispersal to population growth in colonising pinus ponderosa populations. Ecology Letters 16:380–389.

Levin, S. A. 1992. The problem of pattern and scale in ecology: the robert h. macarthur award lecture. Ecology 73:1943–1967.

Liaw, A., M. Wiener, et al. 2002. Classification and regression by randomforest. R News 2:18–22.

Liu, Y. and M. van Kleunen. 2017. Responses of common and rare aliens and natives to nutrient availability and fluctuations. Journal of Ecology 105:1111–1122.

Loreau, M. 1994. Material cycling and the stability of ecosystems. The American Naturalist 143:508–513.

Loreau, M. 2010. From populations to ecosystems: Theoretical foundations for a new ecological synthesis. Princeton University Press.

Loreau, M. and C. de Mazancourt. 2013. Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. Ecology Letters 16:106–115.

Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. Proceedings of the National Academy of Sciences 100:12765–12770.

Lu, Y., N. Nakicenovic, M. Visbeck, and A. Stevance. 2015. Policy: Five priorities for the un sustainable development goals. Nature 520:432–433.

Lurgi, M., D. Montoya, and J. M. Montoya. 2016. The effects of space and diversity of interaction types on the stability of complex ecological networks. Theoretical Ecology 9:3–13.

MacArthur, R. 1955. Fluctuations of animal populations and a measure of community stability. Ecology 36:533–536.

MacDougall, A. S., K. S. McCann, G. Gellner, and R. Turkington. 2013. Diversity loss with persistent human disturbance increases vulnerability to ecosystem collapse. Nature 494:86–89.

Mace, G. M. 2014. Whose conservation? Science 345:1558–1560.

May, R. and A. R. McLean. 2007. Theoretical ecology: principles and applications. Oxford University Press.

May, R. M. 1972. Will a large complex system be stable? Nature 238:413–414.

May, R. M. 1973. Stability and complexity in model ecosystems. Princeton university press.

May, R. M. 1976. Simple mathematical models with very complicated dynamics. Nature 261:459–467.

McCann, K. and G. Gellner. 2012. Food chains and food web modules. Pages 288–294 *in* Encyclopedia of theoretical ecology. University of California Press.

McCann, K., A. Hastings, and G. R. Huxel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794–798.

McMahon, S. M., S. P. Harrison, W. S. Armbruster, P. J. Bartlein, C. M. Beale, M. E. Edwards, J. Kattge, G. Midgley, X. Morin, and I. C. Prentice. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends in Ecology & Evolution 26:249–259.

Miller, A. D., S. H. Roxburgh, and K. Shea. 2011. How frequency and intensity shape diversity–disturbance relationships. Proceedings of the National Academy of Sciences 108:5643–5648.

Milo, R., S. Shen-Orr, S. Itzkovitz, N. Kashtan, D. Chklovskii, and U. Alon. 2002. Network motifs: simple building blocks of complex networks. Science 298:824–827.

Miner, B. G., S. E. Sultan, S. G. Morgan, D. K. Padilla, and R. A. Relyea. 2005. Ecological consequences of phenotypic plasticity. Trends in Ecology & Evolution 20:685–692.

Molinos, J. G. and I. Donohue. 2010. Interactions among temporal patterns determine the effects of multiple stressors. Ecological Applications 20:1794–1800.

Molinos, J. G. and I. Donohue. 2011. Temporal variability within disturbance events regulates their effects on natural communities. Oecologia 166:795–806.

Montoya, J. M., S. L. Pimm, and R. V. Solé. 2006. Ecological networks and their fragility. Nature 442:259–264.

Moore, J. C. and H. W. Hunt. 1988. Resource compartmentation and the stability of real ecosystems. Nature 333:261.

Mougi, A. and M. Kondoh. 2012. Diversity of interaction types and ecological community stability. Science 337:349–351.

Nemani, R. R., C. D. Keeling, H. Hashimoto, W. M. Jolly, S. C. Piper, C. J. Tucker, R. B. Myneni, and S. W. Running. 2003. Climate-driven increases in global terrestrial net primary production from 1982 to 1999. Science 300:1560–1563.

Neubert, M. G. and H. Caswell. 1997. Alternatives to resilience for measuring the responses of ecological systems to perturbations. Ecology 78:653–665.

Neutel, A.-M., J. A. Heesterbeek, and P. C. de Ruiter. 2002. Stability in real food webs: weak links in long loops. Science 296:1120–1123.

Odum, E. P. 1953. Fundamentals of ecology. Saunders Philadelphia.

O'Gorman, E. J. and M. C. Emmerson. 2009. Perturbations to trophic interactions and the stability of complex food webs. Proceedings of the National Academy of Sciences 106:13393–13398.

Oliver, T. H., M. S. Heard, N. J. Isaac, D. B. Roy, D. Procter, F. Eigenbrod, R. Freckleton, A. Hector, C. D. L. Orme, O. L. Petchey, et al. 2015. Biodiversity and resilience of ecosystem functions. Trends in Ecology & Evolution 30:673–684.

Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. Nature 355:73–75.

Palmer, M. A., K. L. Hondula, and B. J. Koch. 2014. Ecological restoration of streams and rivers: shifting strategies and shifting goals. Annual Review of Ecology, Evolution, and Systematics 45:247–269.

Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres. 1998. Fishing down marine food webs. Science 279:860–863.

Petchey, O. L., A. Eklöf, C. Borrvall, and B. Ebenman. 2008. Trophically unique species are vulnerable to cascading extinction. The American Naturalist 171:568–579.

Petchey, O. L. and K. J. Gaston. 2009. Effects on ecosystem resilience of biodiversity, extinctions, and the structure of regional species pools. Theoretical Ecology 2:177–187.

Petchey, O. L., A. Gonzalez, and H. B. Wilson. 1997. Effects on population persistence: the interaction between environmental noise colour, intraspecific competition and space. Proceedings of the Royal Society of London B: Biological Sciences 264:1841–1847.

Petchey, O. L., M. Pontarp, T. M. Massie, S. Kéfi, A. Ozgul, M. Weilenmann, G. M. Palamara, F. Altermatt, B. Matthews, J. M. Levine, et al. 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters 18:597–611.

Pike, N., T. Tully, P. Haccou, and R. Ferrière. 2004. The effect of autocorrelation in environmental variability on the persistence of populations: an experimental test. Proceedings of the Royal Society of London B: Biological Sciences 271:2143–2148.

Pimm, S. and J. H. Lawton. 1978. On feeding on more than one trophic level. Nature 275:542–544.

Pimm, S. L. 1982. Food Webs. Springer.

Pimm, S. L. 1984. The complexity and stability of ecosystems. Nature 307:321–326.

Pimm, S. L. and J. Lawton. 1977. Number of trophic levels in ecological communities. Nature 268:329–331.

Pimm, S. L. and A. Redfearn. 1988. The variability of population densities. Nature 334:613–614.

Pincebourde, S., E. Sanford, J. Casas, and B. Helmuth. 2012. Temporal coincidence of environmental stress events modulates predation rates. Ecology Letters 15:680–688.

Post, E., U. S. Bhatt, C. M. Bitz, J. F. Brodie, T. L. Fulton, M. Hebblewhite, J. Kerby, S. J. Kutz, I. Stirling, and D. A. Walker. 2013. Ecological consequences of sea-ice decline. Science 341:519–524.

R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing Vienna, Austria.

Ranta, E., V. Kaitala, J. Lindström, and E. Helle. 1997. The moran effect and synchrony in population dynamics. Oikos 78:136–142.

Ratajczak, Z., P. D'Odorico, S. L. Collins, B. T. Bestelmeyer, F. I. Isbell, and J. B. Nippert. 2017. The interactive effects of press/pulse intensity and duration on regime shifts at multiple scales. Ecological Monographs 87:198–218.

Rejmanek, M. and P. Starỳ. 1979. Connectance in real biotic communities and critical values for stability of model ecosystems. Nature 280:311–313.

Reuman, D. C., R. F. Costantino, R. A. Desharnais, and J. E. Cohen. 2008. Colour of environmental noise affects the nonlinear dynamics of cycling, stage-structured populations. Ecology Letters 11:820–830.

Rip, J. M., K. S. McCann, D. H. Lynn, and S. Fawcett. 2010. An experimental test of a fundamental food web motif. Proceedings of the Royal Society of London B: Biological Sciences 277:1743–1749.

Ripa, J. and M. Heino. 1999. Linear analysis solves two puzzles in population dynamics: the route to extinction and extinction in coloured environments. Ecology Letters 2:219–222.

Roberts, B. E., W. E. Harris, G. M. Hilton, and S. J. Marsden. 2016. Taxonomic and geographic bias in conservation biology research: a systematic review of wildfowl demography studies. PloS one 11:e0153908.

Rooney, N., K. McCann, G. Gellner, and J. C. Moore. 2006. Structural asymmetry and the stability of diverse food webs. Nature 442:265–269.

Rossberg, A. 2012. Food webs. Pages 294–301 *in* Encyclopedia of theoretical ecology. University of California Press.

Rozdilsky, I. D., L. Stone, and A. Solow. 2004. The effects of interaction compartments on stability for competitive systems. Journal of Theoretical Biology 227:277–282.

Ruokolainen, L. and M. S. Fowler. 2008. Community extinction patterns in coloured environments. Proceedings of the Royal Society of London B: Biological Sciences 275:1775–1783.

Ruokolainen, L., A. Linden, V. Kaitala, and M. S. Fowler. 2009. Ecological and evolutionary dynamics under coloured environmental variation. Trends in Ecology & Evolution 24:555–563.

Sabo, J. L. and D. M. Post. 2008. Quantifying periodic, stochastic, and catastrophic environmental variation. Ecological Monographs 78:19–40.

Sæther, B. E. 1997. Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. Trends in Ecology & Evolution 12:143–149.

Sauve, A. M., C. Fontaine, and E. Thébault. 2016. Stability of a diamond-shaped module with multiple interaction types. Theoretical Ecology 9:27–37.

Scheffer, M., J. Bascompte, W. A. Brock, V. Brovkin, S. R. Carpenter, V. Dakos, H. Held, E. H. Van Nes, M. Rietkerk, and G. Sugihara. 2009. Early-warning signals for critical transitions. Nature 461:53–59.

Schiegg, K. 2003. Environmental autocorrelation: curse or blessing? Trends in Ecology & Evolution 18:212–214.

Schmitz, O. J., A. P. Beckerman, and S. Litman. 1997. Functional responses of adaptive consumers and community stability with emphasis on the dynamics of plant-herbivore systems. Evolutionary Ecology 11:773–784.

Schwager, M., K. Johst, and F. Jeltsch. 2006. Does red noise increase or decrease extinction risk? single extreme events versus series of unfavorable conditions. The American Naturalist 167:879–888.

Schwarz, B., A. D. Barnes, M. P. Thakur, U. Brose, M. Ciobanu, P. B. Reich, R. L. Rich, B. Rosenbaum, A. Stefanski, and N. Eisenhauer. 2017. Warming alters energetic structure and function but not resilience of soil food webs. Nature Climate Change 7:895–900.

Seddon, P. J., P. S. Soorae, and F. Launay. 2005. Taxonomic bias in reintroduction projects 8:51–58.

Sellman, S., T. Säterberg, and B. Ebenman. 2016. Pattern of functional extinctions in ecological networks with a variety of interaction types. Theoretical Ecology 9:83–94.

Shurin, J. B., K. Cottenie, and H. Hillebrand. 2009. Spatial autocorrelation and dispersal limitation in freshwater organisms. Oecologia 159:151–159.

Sinclair, A. and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75:164–173.

Soetaert, K., T. Petzoldt, and R. W. Setzer. 2010. Solving differential equations in r: package desolve. Journal of Statistical Software 33:1–25.

Stachowicz, J. J., M. Graham, M. E. Bracken, and A. I. Szoboszlai. 2008. Diversity enhances cover and stability of seaweed assemblages: the role of heterogeneity and time. Ecology 89:3008–3019.

Steiner, C. F., Z. T. Long, J. A. Krumins, and P. J. Morin. 2005. Temporal stability of aquatic food webs: partitioning the effects of species diversity, species composition and enrichment. Ecology Letters 8:819–828.

Strogatz, S. H. 1994. Nonlinear dynamics and chaos: with applications to physics, biology, chemistry, and engineering. CRC Press.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19:46–53.

Sugihara, G. and R. M. May. 1990. Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. Nature 344:734–741.

Tang, S. and S. Allesina. 2014. Reactivity and stability of large ecosystems. Frontiers in Ecology and Evolution 2:21.

Tang, S., S. Pawar, and S. Allesina. 2014. Correlation between interaction strengths drives stability in large ecological networks. Ecology Letters 17:1094–1100.

Thompson, R. M., J. Beardall, J. Beringer, M. Grace, and P. Sardina. 2013. Means and extremes: building variability into community-level climate change experiments. Ecology Letters 16:799–806.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology 77:350–363.

Tilman, D., F. Isbell, and J. M. Cowles. 2014. Biodiversity and ecosystem functioning. Annual Review of Ecology, Evolution, and Systematics 45:471–493.

Tilman, D., P. B. Reich, and J. M. Knops. 2006. Biodiversity and ecosystem stability in a decade-long grassland experiment. Nature 441:629–632.

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

Urban, M., G. Bocedi, A. Hendry, J. B. Mihoub, G. Pe'er, A. Singer, J. Bridle, L. Crozier, L. De Meester, W. Godsoe, et al. 2016. Improving the forecast for biodiversity under climate change. Science 353:aad8466.

Ushio, M., C.-h. Hsieh, R. Masuda, E. R. Deyle, H. Ye, C.-W. Chang, G. Sugihara, and M. Kondoh. 2018. Fluctuating interaction network and time-varying stability of a natural fish community. Nature 554:360.

Valdovinos, F. S., B. J. Brosi, H. M. Briggs, P. Moisset de Espanés, R. Ramos-Jiliberto, and N. D. Martinez. 2016. Niche partitioning due to adaptive foraging reverses effects of nestedness and connectance on pollination network stability. Ecology Letters 19:1277–1286.

van Altena, C., L. Hemerik, and P. C. de Ruiter. 2016. Food web stability and weighted connectance: the complexity-stability debate revisited. Theoretical Ecology 9:49–58.

Vasseur, D. A. and P. Yodzis. 2004. The color of environmental noise. Ecology 85:1146–1152.

Vellend, M. 2016. The theory of ecological communities. Princeton University Press.

Villagra, M., P. I. Campanello, L. Montti, and G. Goldstein. 2013. Removal of nutrient limitations in forest gaps enhances growth rate and resistance to cavitation in subtropical canopy tree species differing in shade tolerance. Tree Physiology 33:285–296.

Wang, S. and M. Loreau. 2014. Ecosystem stability in space: α, β and γ variability. Ecology Letters 17:891–901.

Wang, S. and M. Loreau. 2016. Biodiversity and ecosystem stability across scales in metacommunities. Ecology Letters 19:510–518.

Wardle, D. A., K. I. Bonner, and G. M. Barker. 2000. Stability of ecosystem properties in response to above-ground functional group richness and composition. Oikos 89:11–23.

Western, D. 2001. Human-modified ecosystems and future evolution. Proceedings of the National Academy of Sciences 98:5458–5465.

White, P. S. and A. Jentsch. 2001. The search for generality in studies of disturbance and ecosystem dynamics. Pages 399–450 *in* Progress in botany. Springer.

Woodward, G., B. Ebenman, M. Emmerson, J. M. Montoya, J. M. Olesen, A. Valido, and P. H. Warren. 2005. Body size in ecological networks. Trends in Ecology & Evolution 20:402–409.

Wootton, J. T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics 25:443–466.

Wootton, J. T. and M. Emmerson. 2005. Measurement of interaction strength in nature. Annual Review of Ecology, Evolution, and Systematics 36:419–444.

Worm, B. and R. T. Paine. 2016. Humans as a hyperkeystone species. Trends in Ecology & Evolution 31:600–607.

Wright, M. N. and A. Ziegler. 2017. ranger: A fast implementation of random forests for high dimensional data in c++ and r. Journal of Statistical Software 77:1–17.

Wu, J., Y. Feng, X. Zhang, S. Wurst, B. Tietjen, P. Tarolli, and C. Song. 2017. Grazing exclusion by fencing non-linearly restored the degraded alpine grasslands on the tibetan plateau. Scientific Reports 7:15202.

Yachi, S. and M. Loreau. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. Proceedings of the National Academy of Sciences 96:1463–1468.

Yang, H., L. Jiang, L. Li, A. Li, M. Wu, and S. Wan. 2012. Diversity-dependent stability under mowing and nutrient addition: evidence from a 7-year grassland experiment. Ecology Letters 15:619–626.

Yeung, A. C. and J. S. Richardson. 2016. Some conceptual and operational considerations when measuring 'resilience': a response to hodgson et al. Trends in Ecology & Evolution 31:2–3.

Zhao, M. and S. W. Running. 2010. Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. science 329:940–943.
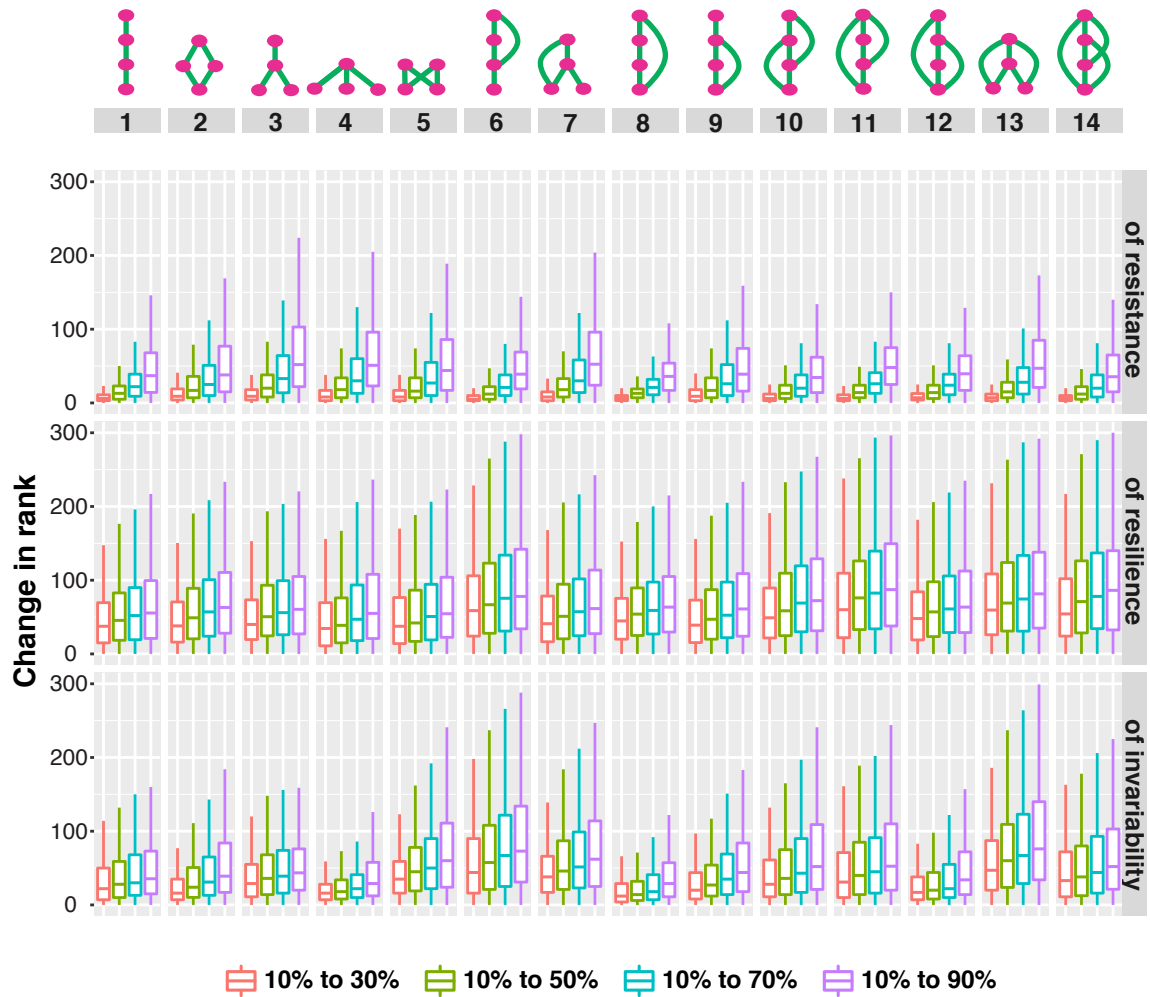
SUPPLEMENTARY INFORMATION TO CHAPTER 2

FIGURE A.1: **The extent of changes in the ranking of resistance, resilience and invariability for individual food-webs as perturbation intensity increased.** Numbers above the graph indicate the food-web modules used in this study.
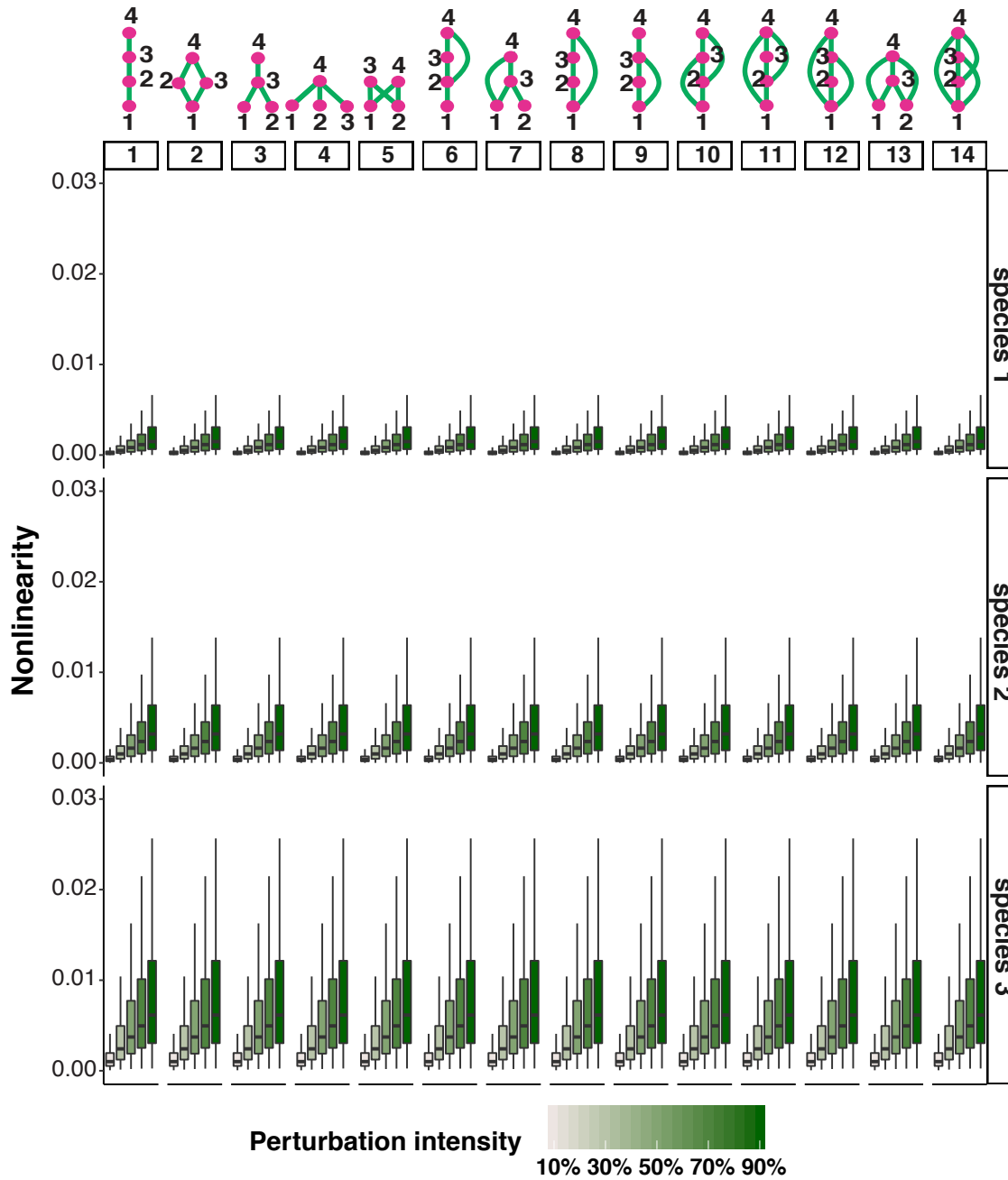
FIGURE A.2: **The prevalence of nonlinearity in the dynamics of each of the unperturbed species in all of the 14 modules with increasing perturbation intensity.** Numbers aside the node of each food-web module indicate the identity of the species.
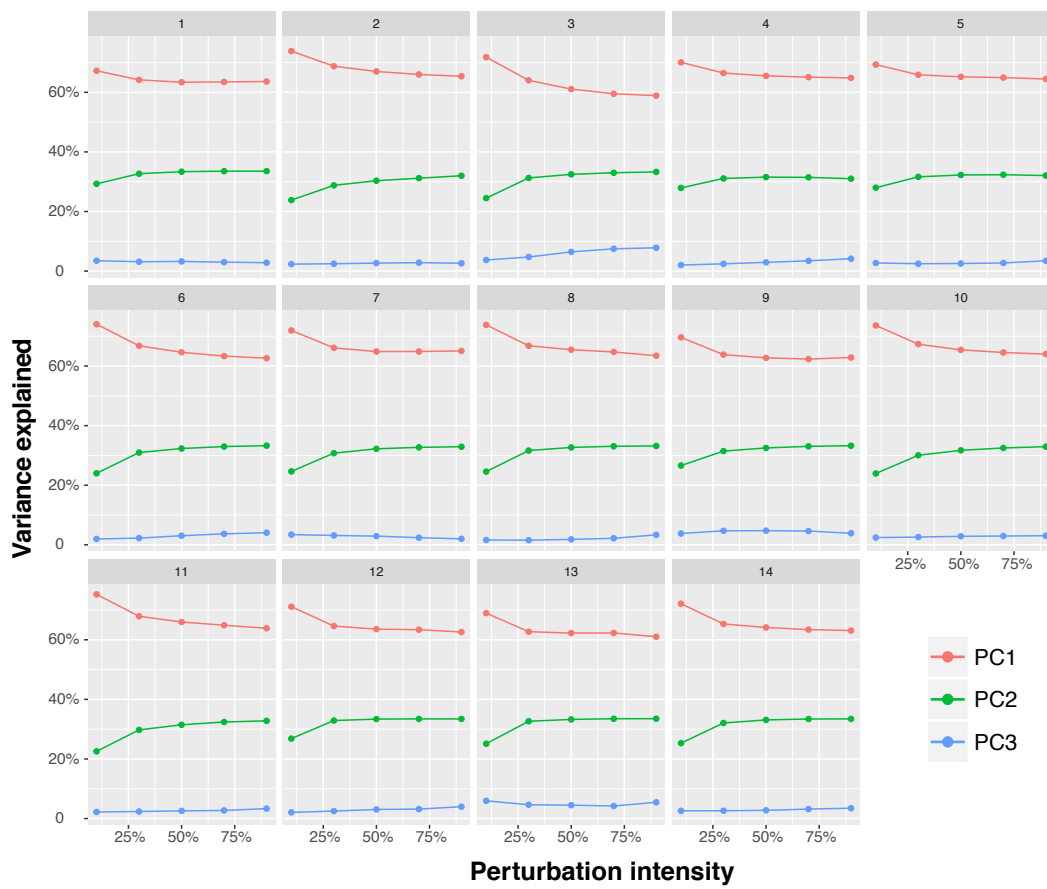
FIGURE A.3: **Variance in stability metrics explained by each PC.** The number at the top of each plot represents the ID of the food-web module.
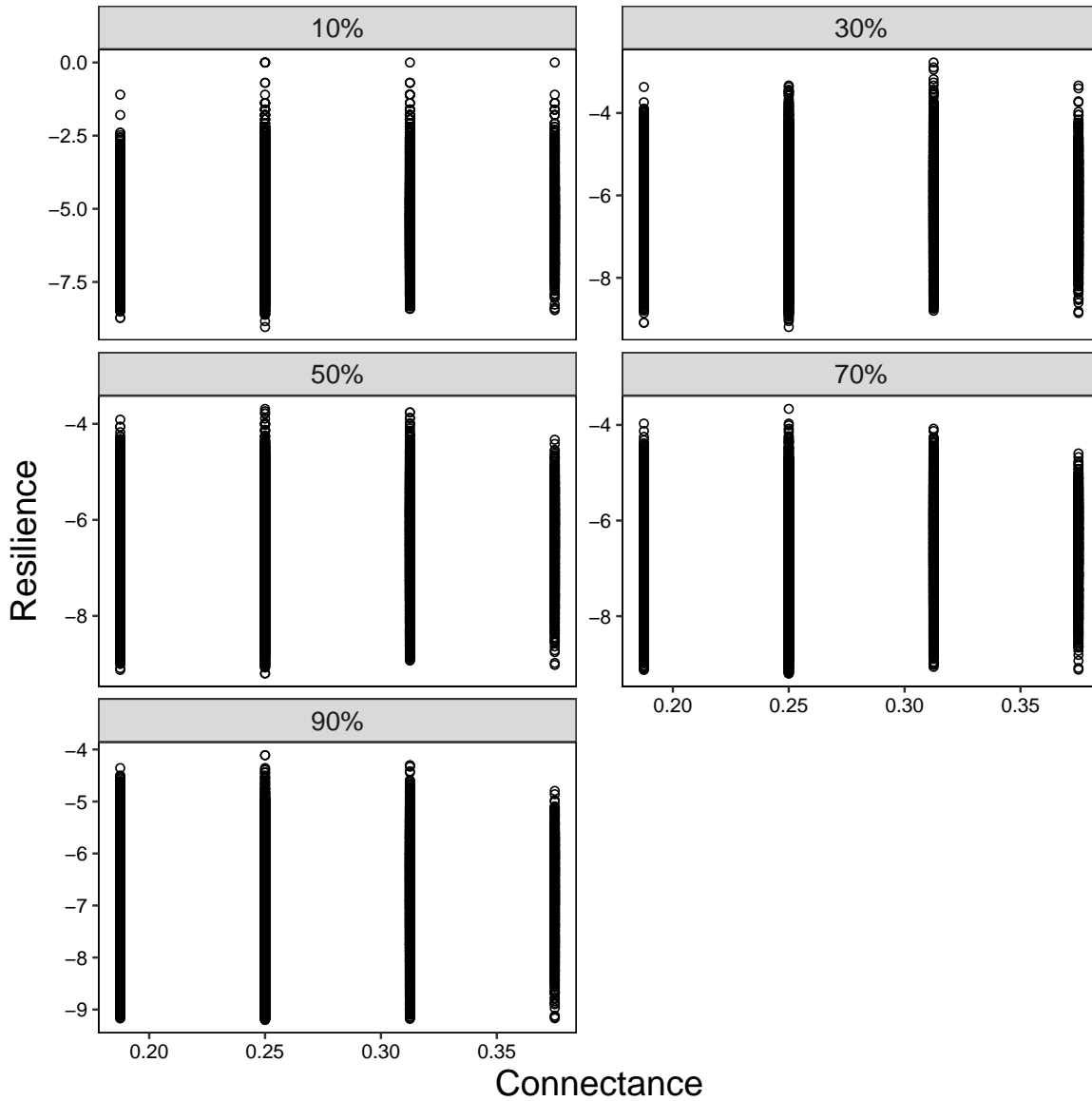
FIGURE A.4: **The relationship between resilience and connectance.** Each point indicates a single community. The percentage value above each plot represent the level of the perturbation strength. Connectance is quantified as l/s^2, where l is the number of the interaction links between species, and s is the number of species.

SUPPLEMENTARY INFORMATION TO CHAPTER 3
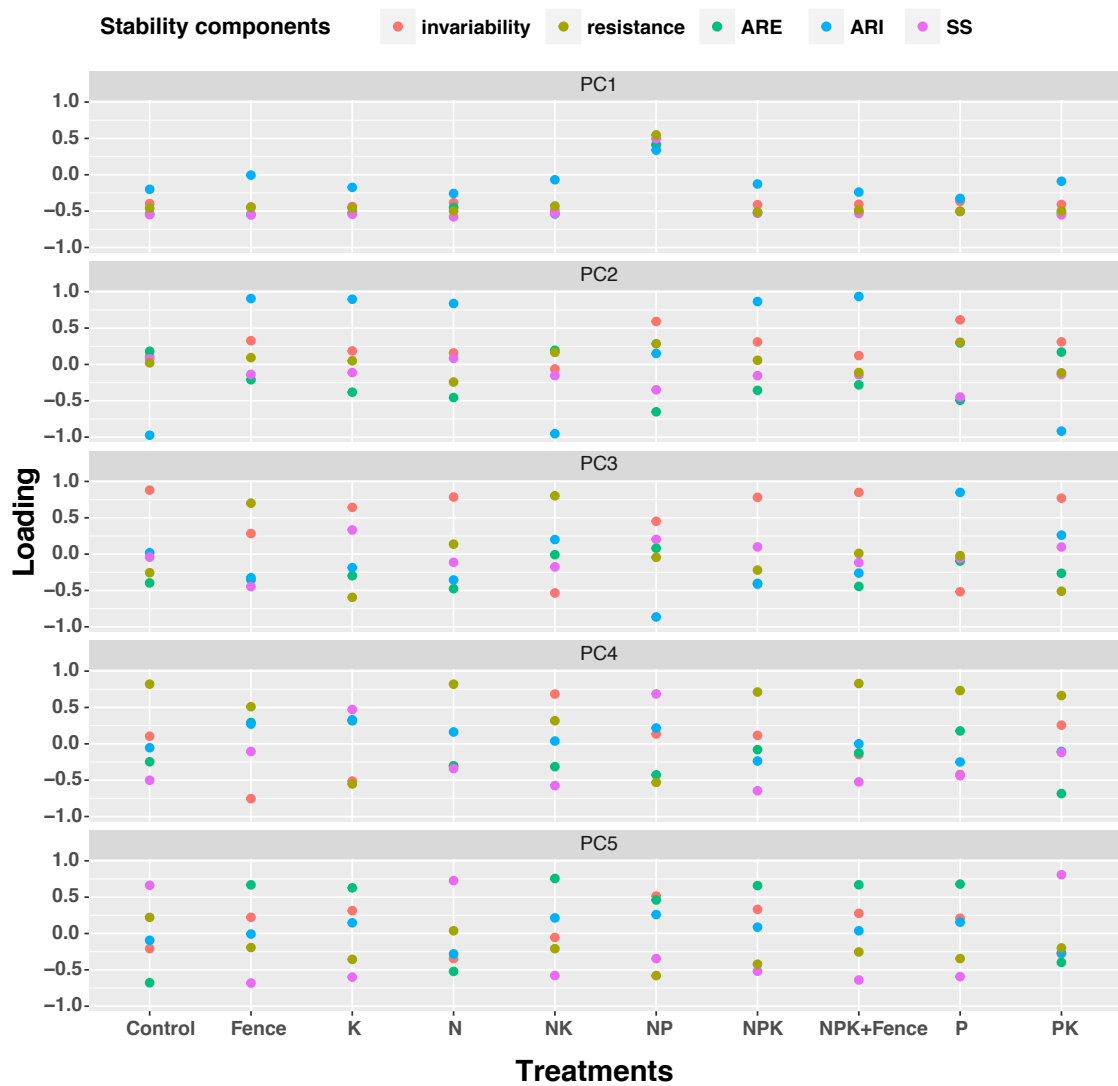
FIGURE B.1: **loadings of Principal Component Analysis (PCA) on the stability metrics of NutNet**

SUPPLEMENTARY INFORMATION TO CHAPTER 4
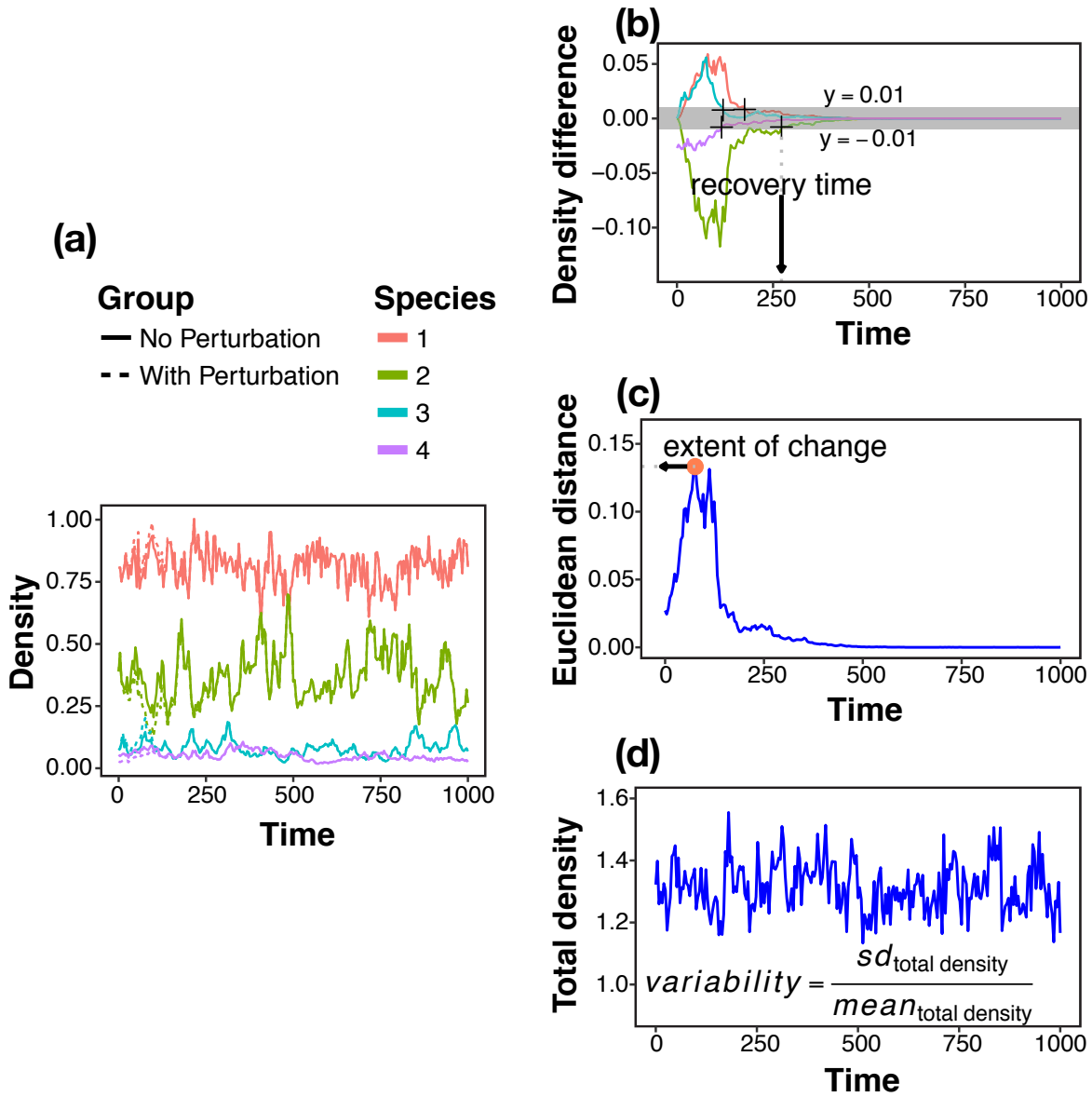
FIGURE C.1: **Quantification of ecological stabilities.** **(a)** A typical example of community dynamics. **(b)** The species density difference between the perturbed and unperturbed community at each simulation timestep. Recovery time was quantified as the moment when the species density difference is smaller than 0.01 for all the species. **(c)** The extent of change of the community was quantified as the largest Euclidean distance between the perturbed and the unperturbed community. **(d)** Variability was quantified as the standard deviation of the total density of the unperturbed community divided by its mean value.
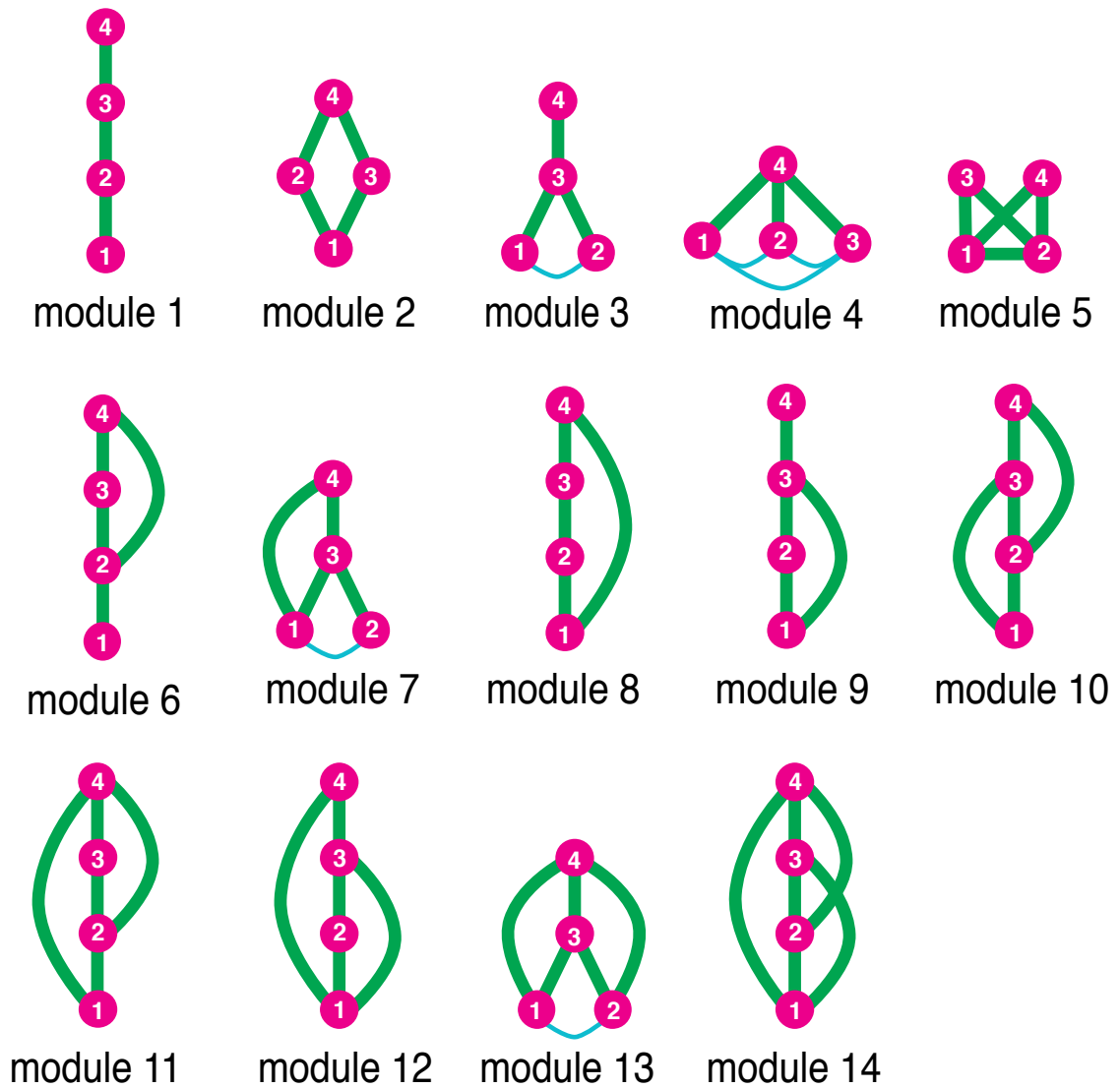
FIGURE C.2: **Food-web modules used in this study.** Pink points represent different species, with lower points as the resource and the upper points as the consumer. Green curves indicate the consumer-resource interaction. Cyan curves represent the competition between basal species.
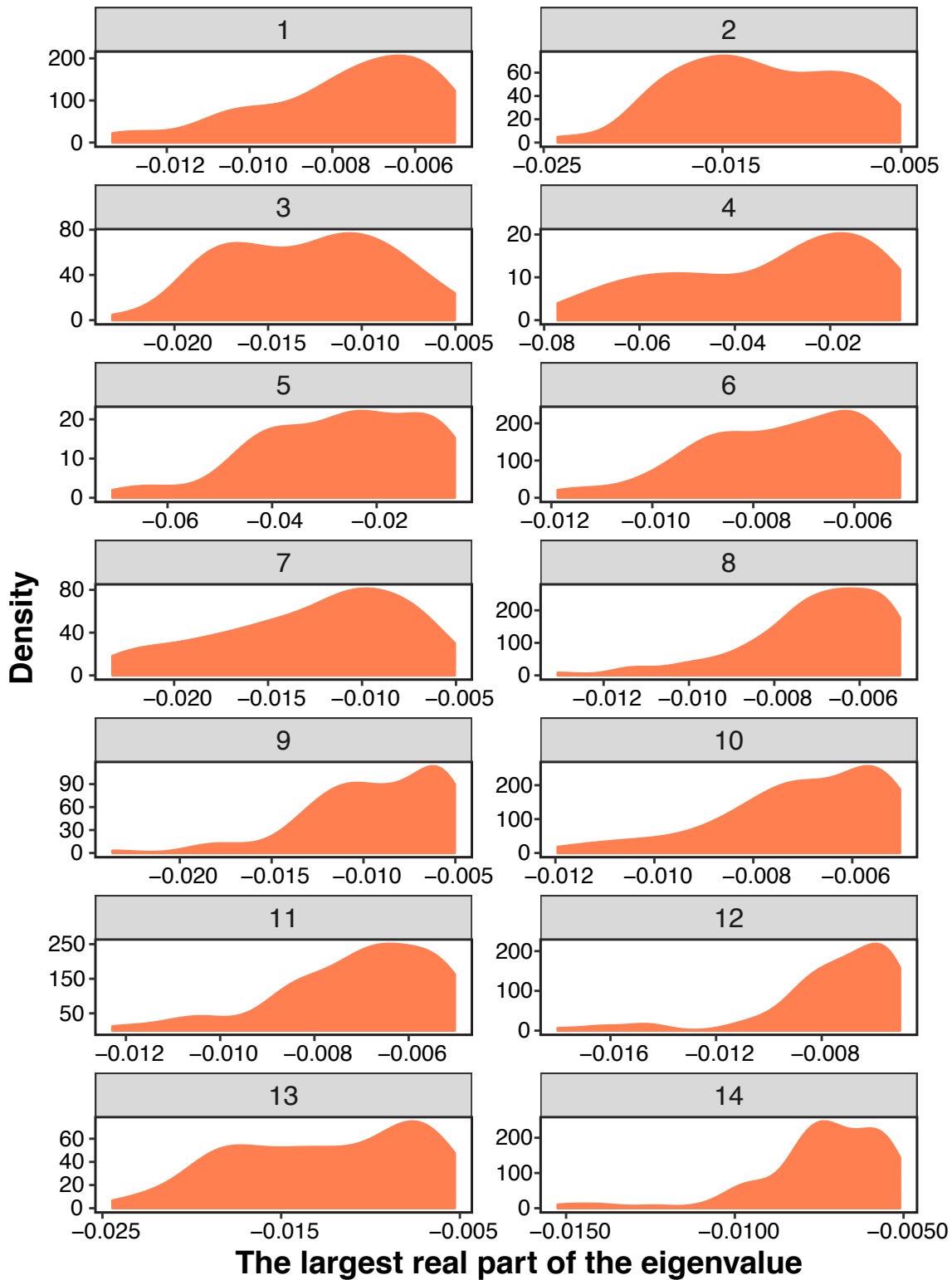
FIGURE C.3: **The distribution of the maximum real part of the eigenvalues of the community matrix of the constructed communities.** Numbers in the shaded area indicate the identity of the modules in Fig. B.2.
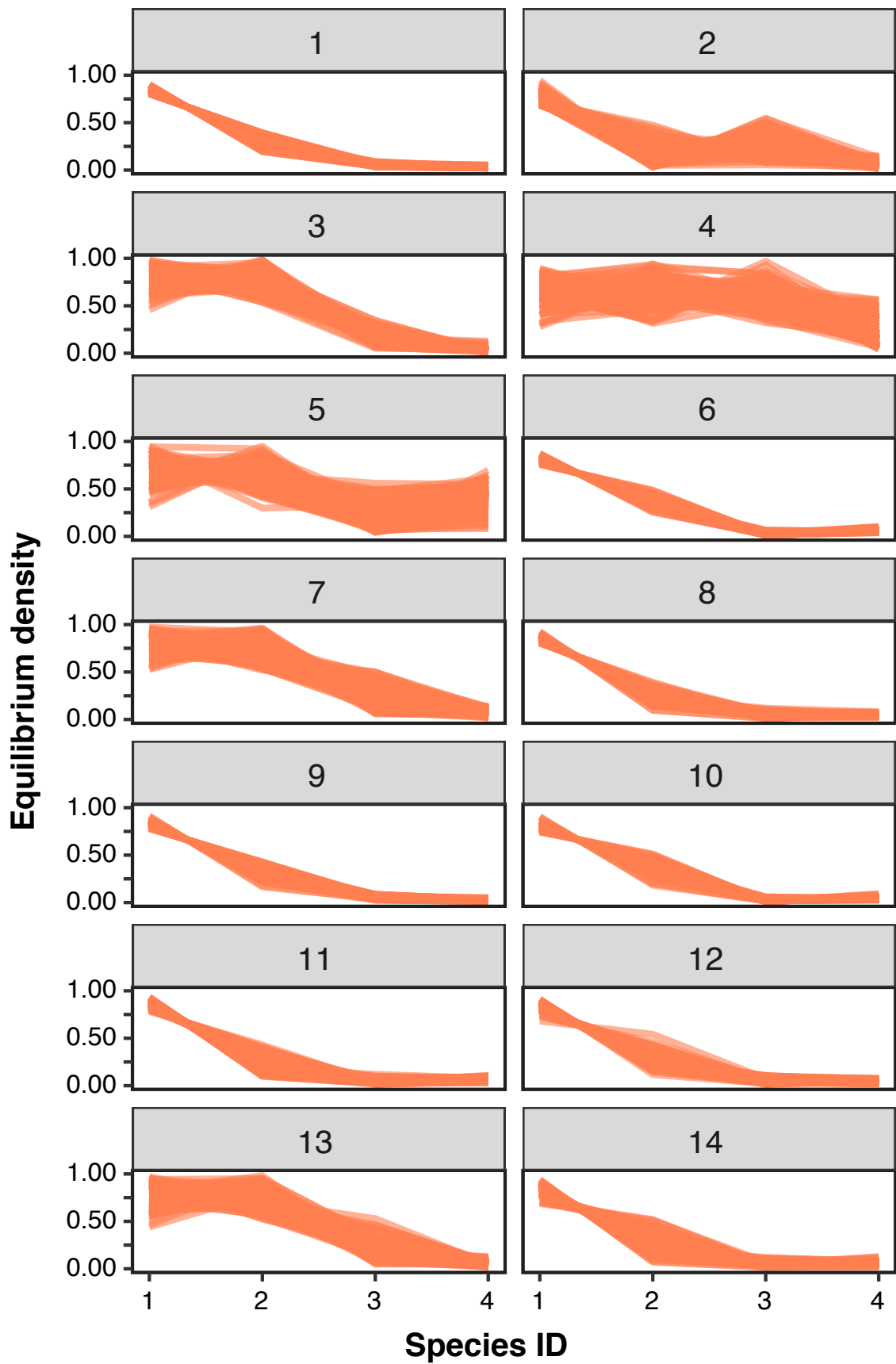
FIGURE C.4: **The equilibrium density of each species of the communities.** Numbers in the shaded area indicates the identity of the modules in Fig. B.2. Numbers along the x-axis represent the species identity that is marked on the module node.
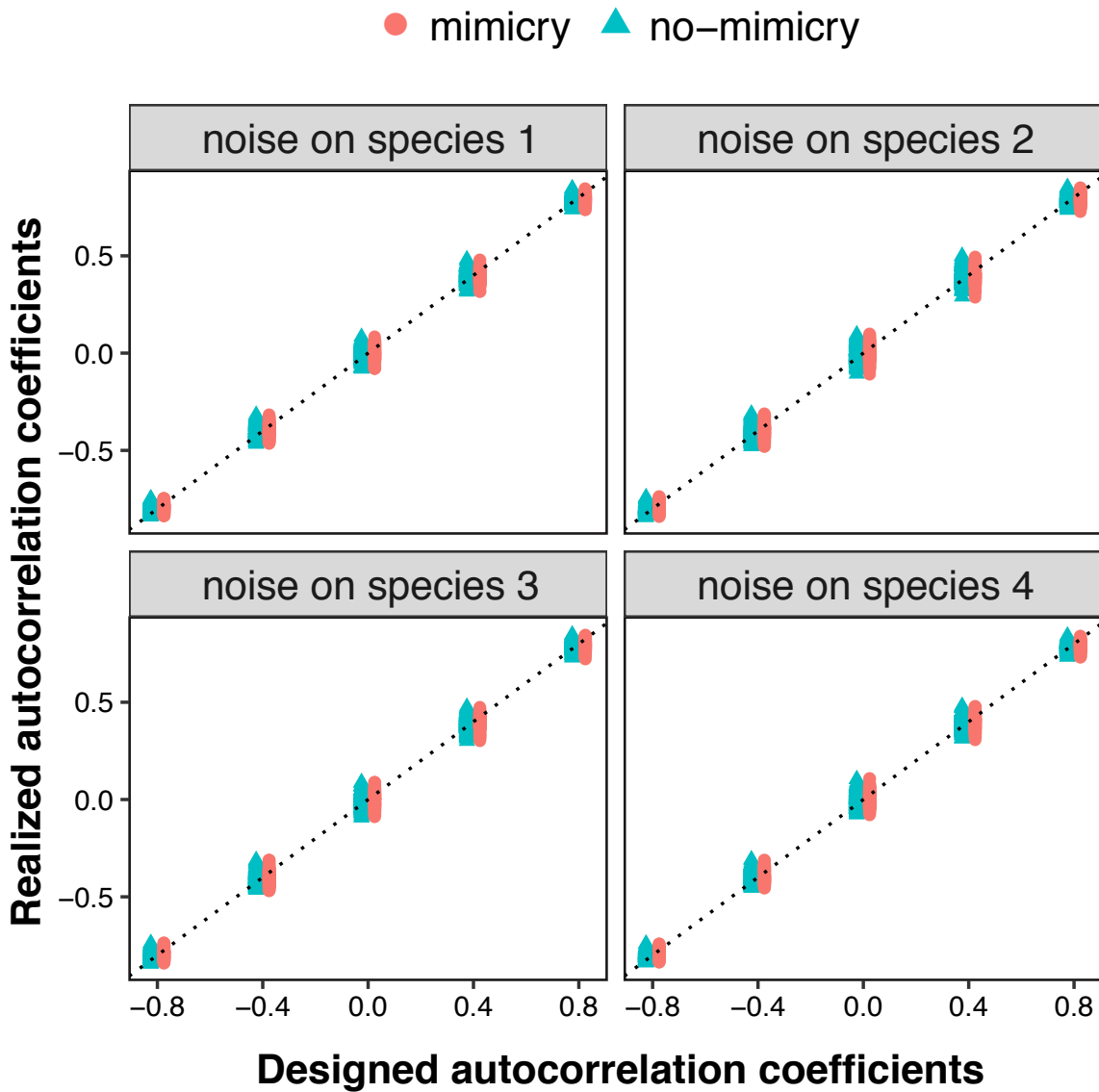
FIGURE C.5: **The realized temporal autocorrelation of the environmental stochasticity time series generated by the autoregressive method (no-mimicry) and that generated by spectral mimicry (mimicry).** The dashed line is the identity line where $x = y$.
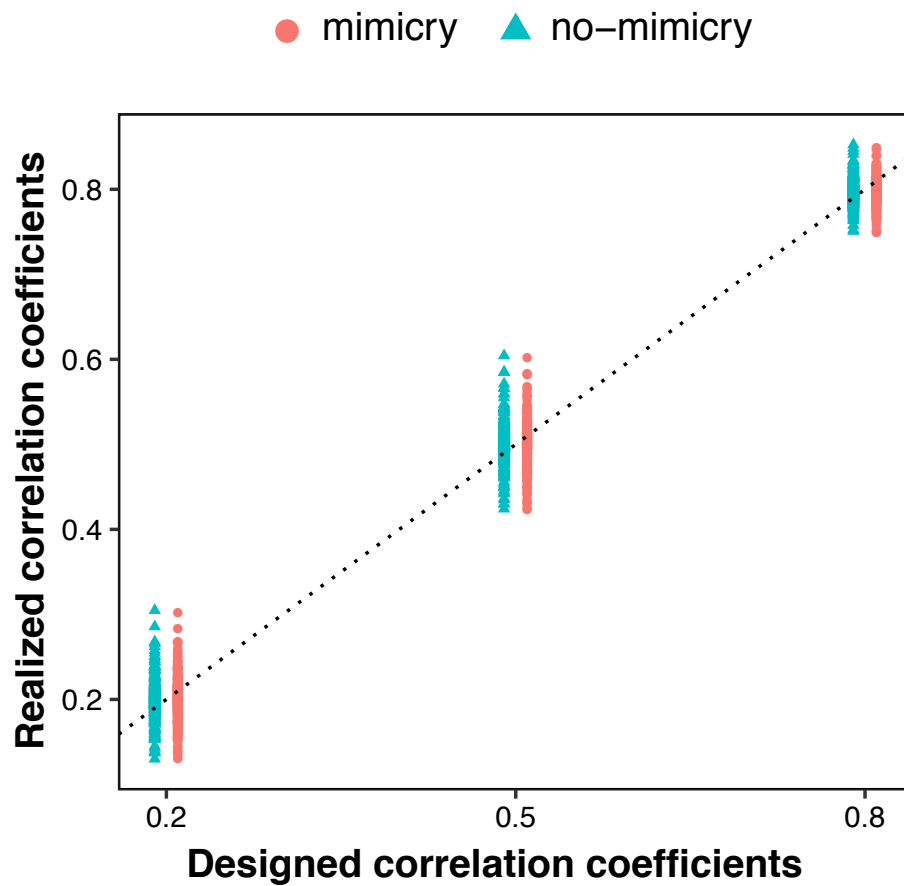
FIGURE C.6: **The realized species response correlation generated by the autoregressive method (no-mimicry) and that generated by spectral mimicry (mimicry).** The dashed line is the identity line where $x = y$.
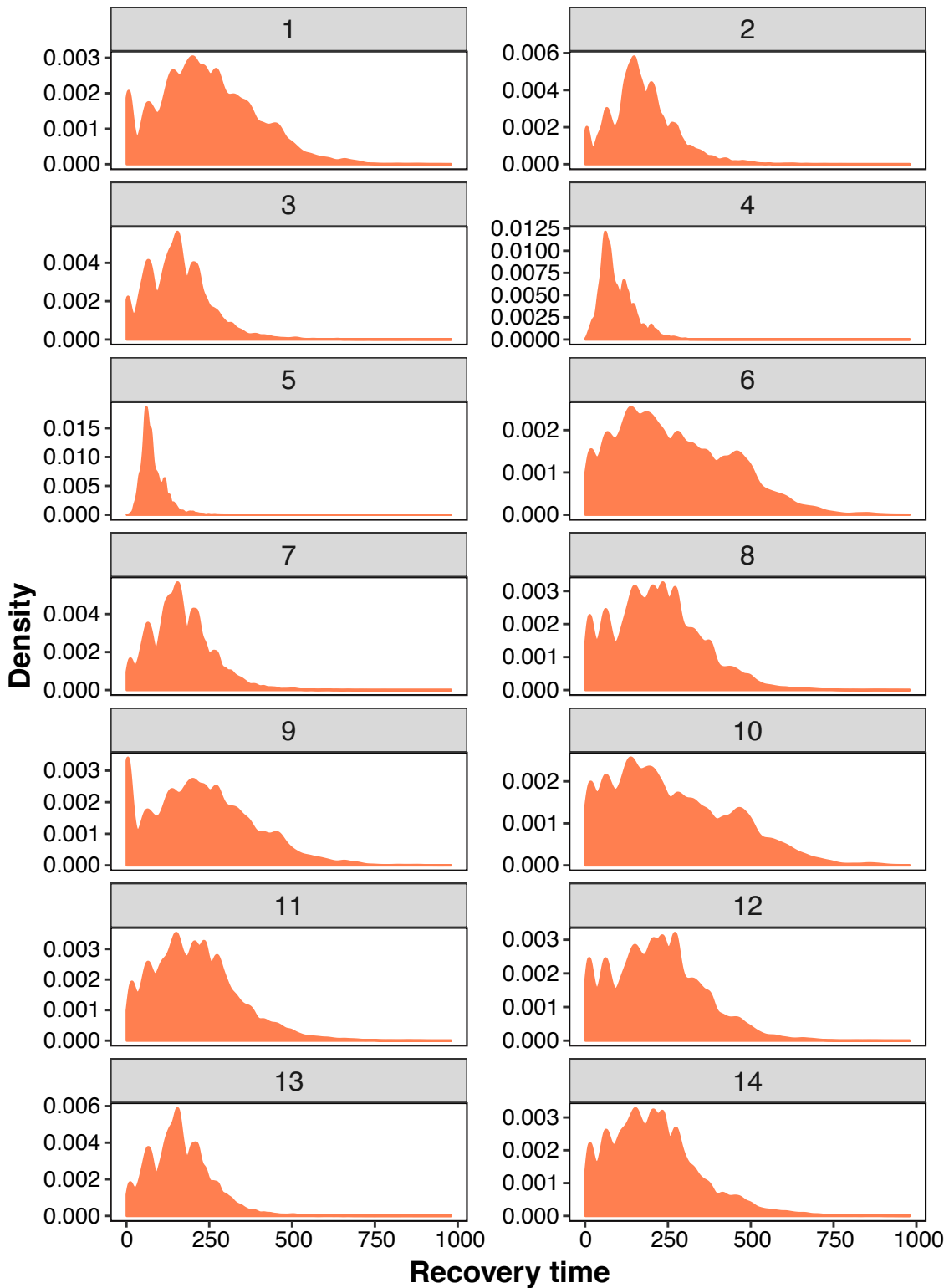
FIGURE C.7: **The distribution of recovery time.** Numbers in the shaded area indicate the identity of the modules in Fig. B.2.