

The stability of ecosystems under global environmental change

BY

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DECLARATION

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SUMMARY

Through global environmental change, humans are modifying the planet at an unprecedented rate and scale, triggering the ongoing biodiversity and climate crises. Ecological stability and the consistency of nature's contributions to people are fundamental to the continued sustainability of human societies. Stability is a complex and multidimensional concept including components such as variability in time and space and the resistance to and recovery from disturbances. Global change has the potential to destabilise ecosystems, but the form and strength of the relationship between different global change drivers and dimensions of stability remains understudied, precluding general or mechanistic understanding. Here, I combine theory, a field experiment, and observational data from a high-resolution acoustic monitoring network to reveal the potential for multiple global change drivers to erode multidimensional ecological stability. Critically, I also show how biodiversity and natural habitats can buffer the destabilising effects of global environmental change on ecosystems and soundscapes, providing vital insurance against disturbance. In an era characterised by unrelenting global change and intensifying disturbance regimes, my results provide a key step towards a generalisable understanding—and ultimately management—of the stability of ecosystems and their contributions to human wellbeing.

In loving memory of
Dr Aoibheann Gaughran

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“The living beings of the jungle have their own way of expressing the life that manifests through them. The set of songs is like a symphony, which took millions of years to write. It’s a unique and priceless creation, which we cannot let be destroyed or disappear.”

Dider Lacaze, *Sacha Warmi Foundation*
courtesy of Alice Eldridge (2021)

The work in this thesis is made possible through the guardianship of lands by numerous local peoples. Firstly, as a visitor to Ireland (Éire), and particularly as an English resident of Dublin (Baile Átha Cliath), I acknowledge my privilege in the pursuit of higher education at Trinity College, and thank the Irish people both past and present who have made my time in Ireland possible. In Chapter 2, I use data from the web-of-life database, collected by innumerable researchers across all continents of earth; I thank the local peoples from which these data were collected.

I was privileged to work in Japan for much of my PhD. As such, I am indebted to the present-day Japanese people, and particularly my local collaborators in Hokkaido and Okinawa. For Chapter 3, I conducted fieldwork in Tomakomai (苫小牧) and visited Hokkaido University in Sapporo (札幌) on the island of Hokkaido (北海道). Hokkaido (formerly Yezo) is land belonging traditionally to the Ainu (蝦夷) people before colonisation by Japanese settlers, and the name Tomakomai derives from the Ainu words *to* (marsh) and *makomai* (river which goes into the depths of the mountain). I am grateful for the stewardship of the land by the Ainu people and to the staff at the Tomakomai experimental forest for their work maintaining the forest field site. My data from Chapters 4 and 5 comes from the island of Okinawa (沖縄本島). Okinawa is the historic capital of the kingdom of the Ryūkyūs (琉球 in Okinawan) before colonisation by Japanese settlers and the U.S. occupation following World War II. I am grateful to the Ryūkyūan people (琉球民族) and the present day people of Okinawa for their custodianship of the island and its surrounding seas. 苫小牧と沖縄の土地をどうもうありがとうございます。

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TABLE OF CONTENTS

Declaration	i
Summary	ii
Land Acknowledgements	iv
Acknowledgements	v
Table of Contents.....	vii
List of Figures.....	x
List of Tables	xii
Chapter 1 General Introduction	1
1.1 Disturbance regimes in ecological systems	1
1.2 Ecological stability: the core framework for understanding disturbance impacts	3
1.3 Measuring global change impacts in complex systems	5
1.4 Outline of this thesis	7
1.5 Additional work.....	10
Chapter 2 Universal scaling of robustness of ecosystem services to species loss.....	11
2.1 Summary.....	12
2.2 Introduction	12
2.3 Methods.....	17
2.3.1 Boolean model for the robustness of ecosystem service supply....	17
2.3.2 Analysis of empirical networks	18
2.4 Results.....	20
2.5 Discussion	23
Chapter 3 Predators mitigate the destabilising effects of heatwaves on multitrophic stream communities	26
3.1 Summary.....	27
3.2 Introduction	27
3.3 Methods.....	29

3.3.1	Study location and experimental system.....	29
3.3.2	Experimental design	30
3.3.3	Heatwave implementation.....	31
3.3.4	Algae biomass and composition	32
3.3.5	Macroinvertebrate communities and ecosystem processing	33
3.3.6	Data analyses	33
3.4	Results.....	35
3.5	Discussion	42
Chapter 4 Utility of acoustic indices for ecological monitoring in complex sonic environments.....		
4.1	Summary.....	47
4.2	Introduction	47
4.3	Methods	49
4.3.1	Study location and experimental system.....	49
4.3.2	Aural inventory	50
4.3.3	Acoustic index processing.....	51
4.3.4	Statistical analyses.....	52
4.4	Results.....	53
4.4.1	Acoustic index performance	54
4.4.2	Acoustic index sensitivity.....	57
4.5	Discussion	59
Chapter 5 Land use shapes ecological resilience to typhoons		
5.1	Summary.....	65
5.2	Introduction	65
5.3	Methods	67
5.3.1	Acoustic monitoring and typhoon impact.....	67
5.3.2	Geographic analyses.....	70
5.3.3	Data analyses	71
5.4	Results.....	78
5.4.1	Acoustic indices	78

LIST OF FIGURES

Figure 2.1 The principles of my approach to measuring the robustness of ecosystem services to species loss.....	14
Figure 2.2 A Boolean model for ecosystem services	15
Figure 2.3 Universal behaviour of the robustness of ecosystem service supply as a function of network fragility	20
Figure 2.4 Robustness of ecosystem service supply and network fragility in empirical networks.....	22
Figure 3.1 Experimental design and timeline	30
Figure 3.2 Effects of predation and heatwaves on total algal biomass and its temporal and spatial variability	37
Figure 3.3 Effects of predation and heatwaves on algal structure and compositional variability	39
Figure 3.4 Effects of predation and heatwaves on macroinvertebrate community composition, density, and leaf litter processing	41
Figure 4.1 Pairwise relationships between acoustic indices	54
Figure 4.2 Acoustic index performance.....	56
Figure 4.3 Sensitivity of acoustic indices to extraneous sonic conditions	58
Figure 5.1 Example of my acoustic time series	68
Figure 5.2 Measuring soundscape stability from passive acoustic monitoring time series.....	72
Figure 5.3 Relative variable importance of land use predictors of soundscape stability.....	79
Figure 5.4 Relationships between land use and multiple dimensions of NDSI stability.....	81
Figure 5.5 Effects of typhoons and land use on NDSI spatial variability	83
Figure 5.6 Relationships between land use and stability of bird species detections.....	84
Figure 5.7 Bird detection spatial variability through time	85
Figure A.1 Relationships between simulated robustness of ecosystem service supply quartiles and analytically-estimated network fragility	125
Figure A.2 Robustness uncertainty is greatest at intermediate network fragility	125
Figure A.3 Redundancy of a random Boolean function	129
Figure A.4 Justification behind using the logical AND function	130

Figure B.1 Water temperatures during heatwaves in my experimental mesocosms.....	131
Figure B.2 Predator extinctions increase macroinvertebrate taxon richness..	133
Figure C.1 Visualisation of best performing models of acoustic index ~ richness relationships.....	146
Figure C.2 Seasonal sensitivity of acoustic indices to anthropophony.....	147
Figure C.3 Seasonal sensitivity of acoustic indices to geophony	148
Fig. C.4 Seasonal sensitivity of acoustic indices to insect noise	149
Figure D.1 Extent of change for bird species detections with different error tolerances.....	150
Figure D.2 Comparison of moving average window sizes	151
Figure D.3 Comparison of recovery time baseline methods	152
Figure D.4 Comparison of recovery window sizes	153
Figure D.5 Illustrative example of resilience time series	153
Figure D.6 Effects of land use on multiple dimensions of NDSI _{Bio} stability..	156
Figure D.7 Effects of land use on multiple dimensions of NDSI _{Anthro} stability	157
Figure D.8 Effects of land use on multiple dimensions of ADiv stability	158
Figure D.9 Effects of land use on multiple dimensions of H stability	159
Figure D.10 Effects of land use on multiple dimensions of M stability.....	160
Figure D.11 Effects of typhoons and land cover on NDSI _{Bio} spatial variability	161
Figure D.12 Effects of typhoons and land cover on NDSI _{Anthro} spatial variability	162
Figure D.13 Effects of typhoons and land cover on ADiv spatial variability ..	163
Figure D.14 Effects of typhoons and land cover on H spatial variability.....	164
Figure D.15 Effects of typhoons and land cover on M spatial variability	165
Figure D.16 Stability of all bird detections across sites	166
Figure D.17 Land cover features and locations of study sites	167

LIST OF TABLES

Table 3.1 Summary of the effects produced by the heatwaves and predator presence on each response variable.....	36
Table 4.1 Recommendations for acoustic index use under different sonic conditions	61
Table 5.1 Components of ecological stability measured in this study, methods of their measurement and interpretation.....	75
Table 5.2 Summary of land use variables included in the set of closely competing models.....	78
Table B.1 Experimentally-induced heatwave properties and range of observed current and projected future heatwaves.....	132
Table B.2 List of variables analysed in this study.....	132
Table B.3 Model outputs for ANOVA and PERMANOVA tests of treatment effects on all response variables.....	134
Table B.4 Contribution of the three algal functional groups to the Bray-Curtis dissimilarity between predator treatments.....	135
Table B.5 Contribution of the three algal functional groups to the Bray-Curtis dissimilarity between heatwave treatments	136
Table B.6 Macroinvertebrate taxa contributing most to the Bray-Curtis dissimilarity between heatwave and predator treatments	137
Table C.1 Sonic conditions under which the performance of my focal acoustic indices was examined	138
Table C.2 The acoustic indices used in this study, their calculation method and interpretation	139
Table C.3 Model selection results for acoustic index ~ measured richness relationship.....	144
Table D.1 List of variables analysed in this study	154

CHAPTER 1 | GENERAL INTRODUCTION

“The highest function of ecology is understanding consequences.”

Dr. Liet-Kynes, *Dune* (1965).

1.1 DISTURBANCE REGIMES IN ECOLOGICAL SYSTEMS

A central tenet of modern ecology is that both biotic and abiotic disturbances can influence the composition, functioning, and stability of ecosystems, frequently with far-reaching societal consequences. Such disturbances are typically characterised along a few key axes. Since the introduction of the terms by Bender *et al.* (1984), disturbances are now commonly classified either as a discrete shock (that is, pulse) or a sustained alteration (press). For example, pulse disturbances include wildfires, storms, and extreme climatic events (Hidasi-Neto *et al.* 2012; Stockwell *et al.* 2020), or pulses of nutrients or other resources (Yang *et al.* 2008), while press disturbances include species extinctions and introductions (Wardle *et al.* 2011; Dirzo *et al.* 2014), changes to population densities (Montoya *et al.* 2009), and habitat modifications such as clear cutting or urban development (Nakagiri *et al.* 2001; Devictor *et al.* 2007). When assessing the impact of disturbances on ecological systems, researchers consider disturbance properties such as their intensity and duration (Ratajczak *et al.* 2017), or measure their cumulative intensity over time (*e.g.*, Laufkötter *et al.* 2020), which accounts for the rate of change (Hobday *et al.* 2016; Pinek *et al.* 2020). As well as their duration, disturbances have a temporal signal of change, often referred to as autocorrelation or stochasticity (Wolkovich *et al.* 2014; Yang *et al.* 2019; Shoemaker *et al.* 2020), and a spatial extent over which they impact species and ecological processes (Gladstone-Gallagher *et al.* 2019). Taken together, the press/pulse categorisation (*sensu* Bender *et al.* 1984) and various disturbance properties including intensity, duration, and spatial extent, present a useful framework for considering the consequences of disturbance in ecological systems.

There is now broad consensus that we have entered the Anthropocene—a period dominated by human alterations to ecosystems and natural processes (Corlett 2015). Human-induced changes are increasingly exposing species and communities to novel disturbances or altering the dynamics of natural disturbance regimes (Newman 2019). Disturbance dynamics, in turn, represent a key knowledge gap precluding the achievement of global sustainability goals

(Mastrángelo *et al.* 2019). For example, anthropogenically-induced climate change is increasing not only the intensity and duration of extreme climatic events (*e.g.*, heatwaves), but also their frequency, because of changes to both temperature means and variances (Planton *et al.* 2008; Stott 2016). Human activity is simultaneously destroying, fragmenting, and polluting natural habitats (Fahrig 2003; Ziegler *et al.* 2009; Buxton *et al.* 2017; Daskalova *et al.* 2020; Olivier *et al.* 2020), changing species distributions through introductions of non-native species and climate-related range shifts (Parmesan & Yohe 2003; Wardle *et al.* 2011; Burrows *et al.* 2014; Seebens *et al.* 2018), and is driving species to extinction at rates far in excess of background levels (Pimm *et al.* 2006, 2014; De Vos *et al.* 2015; Humphreys *et al.* 2019). Species extinctions typically do not occur randomly, with anthropogenic activity driving sequential losses, particularly of habitat specialists (Burivalova *et al.* 2014), species at higher trophic levels (Pauly *et al.* 1998; Estes *et al.* 2011), larger-bodied species (Cardillo *et al.* 2005), and phylogenetically or functionally distinct species (Purvis *et al.* 2000; Petchey *et al.* 2008; Sobral *et al.* 2016). At the global scale, such non-random extinctions result in systematic biodiversity change representing increasing species turnover and a global biotic homogenisation (Dornelas *et al.* 2014, 2019; Magurran *et al.* 2015). These high turnover rates lead in turn to no-analog communities and novel ecosystems (Dornelas & Madin 2020), hindering the predictive capacity of ecological forecasts.

Disturbances can also interact across time and space, further modifying natural disturbance regimes and exposing ecological communities to multiple stressors simultaneously (Zarnetske *et al.* 2012; Bowler *et al.* 2019; Birk *et al.* 2020). Human-induced changes to the temporal dynamics of disturbance regimes is resulting in multi-pulse disturbances, where a system is exposed to multiple pulse disturbances in short succession (Fugère *et al.* 2020; Jackson *et al.* 2021). Moreover, disturbances can have lasting legacies on ecological dynamics and functioning, with disturbance responses persisting long after the disturbance itself has ceased, or emerging only after a time lag (Kuussaari *et al.* 2009; Wearn *et al.* 2012; Miller *et al.* 2021). Such legacies may also interact with subsequent disturbances to exacerbate or dampen disturbance impacts. For example, ecological memory can reduce disturbance impact when ecosystems are primed against the signal of disturbance (Hughes *et al.* 2019; Fugère *et al.* 2020; Jackson *et al.* 2021). Conversely, if recovery from a previous disturbance is incomplete, further disturbances may amplify their impact non-additively (*e.g.*, Stockwell *et al.* 2020). The properties and type of disturbance can further modify how ecosystem structure and function responds to disturbance (García Molinos &

Donohue 2011; Radchuk *et al.* 2019), leading to complex interactions between disturbances. Interactions between press and pulse disturbances are particularly insidious; whether exposure to press disturbances modify the impact of pulse disturbances is an understudied topic in disturbance ecology but is increasingly relevant in face of continued systematic planetary change in the form of press disturbances (*e.g.*, habitat conversion, climate change, and species extinctions). For example, the potential for species extinctions to compound the effects of climate change or extreme events on ecosystems is gaining increased attention (Zarnetske *et al.* 2012; O'Connor *et al.* 2015; Kordas *et al.* 2017; White *et al.* 2018; Rasher *et al.* 2020). Interactions between disturbances are thus highly context-dependent but are critical to a mechanistic understanding of how ecosystems respond to disturbance in the Anthropocene.

1.2 ECOLOGICAL STABILITY: THE CORE FRAMEWORK FOR UNDERSTANDING DISTURBANCE IMPACTS

There are myriad ways for disturbances to affect ecosystems. Many studies have measured the response of within-site species richness (that is, alpha-diversity) to global environmental change (Estes *et al.* 2011; McGill *et al.* 2015; Chase *et al.* 2019), while others have focused on dissimilarity in community composition among sites (beta-diversity; Baselga 2010; Dornelas *et al.* 2014; Magurran *et al.* 2015). Still others consider how disturbance affects the diversity of species' functional traits (that is, functional diversity; Suding *et al.* 2008; Bjorkman *et al.* 2018) or evolutionary histories (phylogenetic diversity; Purvis *et al.* 2000; Sol *et al.* 2017), or biomass or abundance, at both the species and community level (Dirzo *et al.* 2014; Lichtenberg *et al.* 2017; Ross *et al.* 2018b). Compositional change may result from a range of mechanisms including changes to species richness, evenness, and dominance, with a recent synthesis finding that global change drivers affect these underlying mechanisms equally (Avolio *et al.* 2021). These myriad disturbance impacts can propagate through food webs causing cascading extinctions (Barnes *et al.* 2017; Donohue *et al.* 2017) and affecting ecosystem functioning and the supply of the vital ecosystem services on which human societies depend (Worm *et al.* 2006; Hector & Bagchi 2007; Mori *et al.* 2013; Oliver *et al.* 2015a, 2015b; Smale *et al.* 2019; Brauman *et al.* 2020; Ross *et al.* 2021a). The response of species and communities to disturbance is therefore a critical determinant of ecosystem structure and functioning, and the

concept of *ecological stability* provides a unifying framework for characterising such responses.

Ecological stability has been a core focus of ecologists since the 1950s when interest in the relationship between diversity and stability first arose (McCann 2000). A series of observations led figures such as Robert MacArthur and Charles Elton to propose that more diverse communities were more stable in their ability to resist invasions or of the magnitude of their oscillations (Odum 1953; MacArthur 1955; Elton 1958). Later, Robert May used randomly structured model communities to show that diversity *per se* did not increase linear stability, but rather decreased it (May 1973; see also Pimm & Lawton 1978; Yodzis 1981). In the 1990s, early results from the Cedar Creek long-term biodiversity experiment—the first of its kind—showed that biodiversity tended to dampen the variability of community, but not population, biomass (Tilman & Downing 1994; Tilman 1996; Tilman *et al.* 1996). Together, these decades of theoretical and empirical work revealed that biodiversity is only the “*passive recipient*” (McCann 2000), through which underlying ecological mechanisms drive the positive diversity-stability relationships generally observed in naturally assembled communities (Ives & Carpenter 2007; Downing *et al.* 2014; Craven *et al.* 2018; Wang *et al.* 2021; but see Jacquet *et al.* 2016; Pennekamp *et al.* 2018). Since May’s (1973) foundation that diversity alone is insufficient to explain empirically observed positive diversity-stability relationships, various driving mechanisms have been proposed (McCann 2000; Loreau *et al.* 2021). Proposed mechanisms include: interaction strengths (Yodzis 1981; McCann *et al.* 1998) or mixtures of interaction types (Mougi & Kondoh 2012; Hammill *et al.* 2015); redundancy within functional groups (Naeem & Li 1997; Biggs *et al.* 2020); nestedness of food webs (Thebault & Fontaine 2010); trophic flexibility and food web rewiring (Kondoh 2003; Edwards *et al.* 2013); asynchrony of biomass in time (Craven *et al.* 2018; Sasaki *et al.* 2019) or space (Loreau *et al.* 2003; Wang & Loreau 2016); and the diversity of responses to disturbance, termed *response diversity* (Suding *et al.* 2008; Mori *et al.* 2013; Pennekamp *et al.* 2018). Overall, there is consensus that, in variable environments, more diverse systems will exhibit more stable (that is, less variable) aggregate ecosystem properties through time, as declines in species abundance or performance will be offset by neutral or positive responses of other species or phenotypes (reviewed by Loreau *et al.* 2021). Together, these ideas encapsulate the insurance effect of biodiversity (Yachi & Loreau 1999)—that biodiversity both enhances and stabilises ecosystem functioning.

One challenge with the study of ecological stability is inconsistency in its definition and measurement. Ecologists have long recognised that there is no single agreed-upon definition of stability (Lewontin 1969; Pimm 1984; Grimm & Wissel 1997). This perhaps results from the different approaches theoreticians and empiricists have taken when measuring stability (Donohue *et al.* 2016). Theoreticians typically focus on asymptotic stability (May 1972; Thebault & Fontaine 2010; Allesina & Tang 2012) or resilience (Pimm & Lawton 1977; Okuyama & Holland 2008; Suweis *et al.* 2013) of multi-species population dynamics, in terms of displacement of a system from, and return to, a basin of attraction (Walker *et al.* 2004). On the other hand, observational studies focus mostly on population or community variability through time (Pimm & Redfearn 1988; Inchausti & Halley 2001; Ives *et al.* 2008), while experimentalists generally consider compositional or functional responses to some manipulation or perturbation (Tilman *et al.* 2006; O’Gorman & Emmerson 2009; Carpenter *et al.* 2011; Hautier *et al.* 2014; Baert *et al.* 2016; Donohue *et al.* 2017). The multidimensional nature of ecological stability—with its many components and methods of measurement—is now widely appreciated (Donohue *et al.* 2013, 2016; Domínguez-García *et al.* 2019; Kéfi *et al.* 2019; Ross *et al.* 2021c), with recent theoretical and empirical work considering multiple dimensions of stability simultaneously (Arnoldi *et al.* 2016; Garnier *et al.* 2017; Hillebrand *et al.* 2018; Radchuk *et al.* 2019; Yang *et al.* 2019; White *et al.* 2020a, 2020b; Clark *et al.* 2021). Moreover, studies of ecological stability now commonly consider both functional (*e.g.*, biomass) and compositional stability (Donohue *et al.* 2013; Baert *et al.* 2016; Hillebrand & Kunze 2020; White *et al.* 2020b; see also Magurran *et al.* 2018). Despite the wealth of literature on multiple aspects of ecological stability, no consistent pattern has emerged regarding how global environmental change might erode ecological stability (Ives & Carpenter 2007), perhaps due to the limitations of studying stability in theory and practice.

1.3 MEASURING GLOBAL CHANGE IMPACTS IN COMPLEX SYSTEMS

Just as theoretical studies are limited by the assumptions inherent to their models, experimental studies of ecological stability are limited by the complexity of the system that can be practically and ethically manipulated. McCann (2000) wrote: “*the complexity of whole ecological communities...cannot manifest itself in experiments that focus on single trophic levels.*” Indeed, many of the seminal experimental manipulations focusing on stability were conducted in low-diversity

systems with sessile species at a single trophic level (Tilman & Downing 1994; Tilman *et al.* 1997, 2006). Even recent stability experiments (*e.g.*, García-Palacios *et al.* 2018; Pennekamp *et al.* 2018) still typically include fewer than 30 species with limited numbers of interactions. The question remains then as to how best to scale up these results to complex multitrophic systems, and whether results from low-diversity systems are meaningful simplifications of natural ecosystems (Kéfi *et al.* 2019; Clark *et al.* 2021). One option to solve this issue is to use complex models capable of examining a range of extinction scenarios (Yang *et al.* 2019; Zhao *et al.* 2019; Ross *et al.* 2021a). Alternatively, experimental manipulations embedded in well-characterised food webs (*e.g.*, Paine 1966; Fausch *et al.* 2002) or replicated across multiple ecoregions (*e.g.*, Borer *et al.* 2020; Seabloom *et al.* 2021) give important context to results (Seibold *et al.* 2018). Finally, high-resolution multispecies observational time series (*e.g.*, Dornelas *et al.* 2018) provide insight into natural community dynamics and stability in complex systems (Gotelli *et al.* 2017; Ushio *et al.* 2018), though such data are hard to come by.

Recent advances in automation hold promise for mechanistic understanding of disturbance and stability via continuous biodiversity monitoring (Keitt & Abelson 2021). Developments in data acquisition, storage, and processing have led to Passive Acoustic Monitoring (PAM) approaches—so called because recorders can collect data autonomously—increasingly being adopted for a wide array of ecological applications and conservation management (Lomolino *et al.* 2015; Deichmann *et al.* 2018; Gasc *et al.* 2018; Burivalova *et al.* 2019a, 2019b; Elise *et al.* 2019; Sethi *et al.* 2020a, 2020b; Duarte *et al.* 2021; Keitt & Abelson 2021). Despite its increasing popularity, there remains considerable debate surrounding methodological best practice in PAM studies, for example in terms of survey design (Desjonquères *et al.* 2020; Sugai *et al.* 2020), data visualisation (Gage & Axel 2014; Towsey *et al.* 2014), and the utility of a suite of acoustic indices for rapidly summarising the soundscape when applied in a management context (Gasc *et al.* 2015; Bradfer-Lawrence *et al.* 2019; Ross *et al.* 2021b). Regardless, PAM is now widely accepted as a useful addition to the environmental monitoring toolkit (Gibb *et al.* 2019; Desjonquères *et al.* 2020; Guan *et al.* 2021). Critically, PAM has several advantages over traditional survey techniques, including being less cost- and labour-intensive (Gibb *et al.* 2019), more scalable (sampling across spatial scales and at high temporal resolution; Gottesman *et al.* 2018; de Camargo *et al.* 2019; Sueur *et al.* 2019; Francomano *et al.* 2020), and able to detect complex community interactions by monitoring multiple taxonomic groups simultaneously (Skalak *et al.* 2012; Seibold *et al.*

2018). In turn, information-rich biodiversity time series can help identify the mechanisms underpinning ecological patterns (Wolkovich *et al.* 2014; Moreno-Mateos *et al.* 2020), and PAM studies can help reveal the impacts of global change in complex ecosystems (Gasc *et al.* 2018; Burivalova *et al.* 2021; Gottesman *et al.* 2021).

1.4 OUTLINE OF THIS THESIS

Throughout this thesis, I consider the combined impact of several elements of global environmental change on multidimensional ecological stability. I combine theory (Chapter 2; Ross *et al.* 2021a), an experiment embedded within a well-resolved ecosystem (Chapter 3), and observational acoustic time series data from a high-resolution landscape-scale sensor network (Chapters 4 and 5; Ross *et al.* 2021b), to measure ecological stability under global environmental change.

First, in Chapter 2, I ask how species extinctions affect the supply of ecosystem services, with an explicit focus on redundancy in species contributions to ecosystem functioning and service supply (Ross *et al.* 2021a). I explored the insurance effect of biodiversity (Yachi & Loreau 1999) using a Boolean framework to measure the robustness of service supply to sequential species extinctions (a series of press perturbations). I found that robustness scales with a simple mathematical property based on the distribution of species and their functional traits in bipartite networks—a metric I term *network fragility*. I then tested the theoretical prediction that species extinctions should predictably affect ecosystem service robustness based on network fragility by simulating species extinctions on >250 empirical real-world bipartite networks from the web-of-life database. Remarkably, I found that results from the empirical networks closely matched my theoretical prediction, and that remaining uncertainty is due to properties of the networks such as the dispersion of species and traits, and the type of ecosystem service being considered. These results demonstrate the potential for measuring stability of ecosystem services using a Boolean framework and allow characterisation of the contribution of individual species to ecological stability (Ross *et al.* 2021a).

In Chapter 3, I ask whether species extinctions (press perturbations) modify the responses of multitrophic aquatic communities to heatwaves (pulse perturbations). I conducted an aquatic mesocosm experiment in the field (Ross *et al.* 2022), embedded in a well-characterised food web in Hokkaido, Japan (Fausch *et al.* 2002; Marcarelli *et al.* 2020), with multitrophic communities

exposed to heatwaves at current and projected future intensities in the presence and absence of a common predatory sculpin (Yagami & Goto 2000; Miyasaka *et al.* 2003). I measured the functional (biomass) and compositional variability of benthic macroalgal communities in time and space, using a factorial design to test for heatwave-by-predator interactions. I found that heatwaves destabilised algal communities by homogenising them in space. However, predators buffered the destabilising effects of heatwaves through trophic control of macroinvertebrate herbivores. Moreover, many of the heatwave impacts I observed emerged only after the heatwaves had passed; heatwaves left legacies on total algal biomass, functional temporal variability, and the structure of macroalgal and macroinvertebrate communities. Together, my results demonstrate the contribution of a single species (*Cottus nozawae*) to ecological stability, underscoring the importance of conserving trophic structure and the integrity of biological communities. Moreover, I highlight the considerable potential for species extinctions to amplify the impacts of climate change and extreme events on ecosystems (Ross *et al.* 2022).

In Chapter 4, my focus shifts towards the use of high-resolution acoustic time series as rich datasets on which to test questions about the impacts of global change on vocalising animal communities and soundscapes. Ecologists now often use a suite of acoustic indices to synthesise the sonic environment (reviewed by Sueur *et al.* 2014). Such indices are generally reported to well represent some aspect of the biology of an ecosystem, either by ground-truthing acoustic indices with point counts (*e.g.*, Mammides *et al.* 2017) or through aural inventories, which directly count the richness of biological audio signals in recordings and compare these results to acoustic indices (*e.g.*, Buxton *et al.* 2018a). In this chapter, I use acoustic data collected as part of the Okinawa Environmental Observation Network (OKEON) in Okinawa, Japan (Ross *et al.* 2018a), and report the results of the largest aural inventory ever conducted (Ross *et al.* 2021b). I tested the performance of 11 commonly used acoustic indices—that is, whether indices approximate the richness of biological signals contained in audio recordings—across a range of potentially confounding sonic conditions, including the presence and absence of insect stridulations, audible wind or rain, and human-related sounds. Whereas most studies avoid the sonic conditions tested here, I demonstrate the potential for acoustic indices to reflect richness across the full range of conditions inherent to Okinawa’s sonic environment. I identified well- and poor-performing indices in response to both sonic press (*e.g.*, insect noise, anthropophony) and pulse (*e.g.*, inclement weather) perturbations, and

make practical recommendations for acoustic index use based on study design (Ross *et al.* 2021b).

In Chapter 5, I assess the potential for human land use (a press perturbation) to modify the stability of soundscapes in response to typhoons (a multi-pulse perturbation). Using >770,000 minutes of acoustic data from the OKEON project (Ross *et al.* 2018a), I measured multiple components of the stability of six acoustic indices, based on recommendations from Chapter 4 (Ross *et al.* 2021b), in response to two extreme weather events from the 2018 typhoon season. I measured typhoon impact on acoustic index values, as well as on the numbers of bird detections of several key species—measured via supervised machine learning algorithms (Ross *et al.* 2018a)—to understand how typhoons affect species and soundscapes (Lynch 1991; Chevalier *et al.* 2019; Gottesman *et al.* 2021) in different land use contexts. Across OKEON's 24 field sites, my data represent a range of land cover types including forest, scrubland, agriculture, and urban areas. I measured eight components of ecological stability, including the spatial and temporal variability of soundscapes, their overall change, and their resilience and reactivity to typhoons. My results reveal that land use moderates the impact of typhoons on the stability of soundscapes. Specifically, I found that soundscapes from areas with natural land use, and particularly pre-climax scrubland, were the most resistant to typhoons, and that landscape-scale stability was driven largely by the range of responses to typhoons across unforested and agricultural sites compared with forested sites which tended to respond homogeneously across space. Bird species detections showed similar patterns, whereby typhoon responses were species-specific and seemingly mirrored spatial variability in detections. These results again highlight spatial variability as an important mechanism driving responses to extreme events (Chapter 3), underscoring the importance of natural habitat in insuring ecosystems against disturbance (Gibson *et al.* 2011).

The final chapter of my thesis (Chapter 6) ties together the results of Chapters 2-5, to draw general conclusions about the impact of global environmental change on ecological stability. I discuss the negative impact of global change on ecological stability, and the range of possible mechanisms driving my observations, with a focus on spatial insurance and response diversity. I conclude that while global environmental change has the capacity to erode multiple dimensions of ecological stability, biodiversity and natural habitats play a critical role in buffering ecosystems against perturbations, one that will only increase in importance as the Anthropocene progresses.

1.5 ADDITIONAL WORK

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

Ross S.R.P-J., Friedman N.R., Janicki J., Economo E.P. (2019). A test of trophic and functional island biogeography theory with the avifauna of a continental archipelago. *Journal of Animal Ecology* **88**, 1392-1405.

DOI: 10.1111/1365-2656.13029

Contribution—I co-led the conceptualisation, analysis, and writing of this paper.

Ross S.R.P-J., Hita Garcia F., Fischer G., Peters M.K. (2018b). Selective logging intensity in an East African rain forest predicts reductions in ant diversity. *Biotropica* **50**, 768-778.

DOI: 10.1111/btp.12569

Contribution—I led the analysis and writing of this paper.

Ross S.R.P-J., O'Connell D.P., Bolgan M., Deichmann J.L., Desjonquères C., Gasc A., Phillips J.N., Sethi S.S., Wood C.M., Burivalova Z. (In Preparation). A fresh look at fundamental ecological questions with acoustic methods. Invited submission by *Functional Ecology*.

Contribution—I co-organised a symposium on this topic for the Annual Meeting of the British Ecological Society (Online, 2020) and co-led the conceptualisation and writing of this paper.

Ross S.R.P-J., Suzuki Y., Kondoh M., Suzuki K., Villa Martín P., Dornelas M. (2021c). Illuminating the intrinsic and extrinsic drivers of ecological stability across scales. *Ecological Research* **36**, 364-378.

DOI: 10.1111/1440-1703.12214

Contribution—I co-organised a symposium on this topic for the Annual Meeting of the Ecological Society of Japan (Kobe, 2019) and co-led the conceptualisation and writing of this paper.

CHAPTER 2 | UNIVERSAL SCALING OF ROBUSTNESS OF ECOSYSTEM SERVICES TO SPECIES LOSS

THIS CHAPTER IS PUBLISHED AS:

Ross S.R.P-J.[†], Arnoldi J-F.[†], Loreau M., White C.D., Stout J.C., Jackson A.L., Donohue I. (2021). Universal scaling of robustness of ecosystem services to species loss. *Nature Communications* **12**, 5167.

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[†]Equal contributions

AUTHOR CONTRIBUTION:

I co-led this study with Jean-François Arnoldi who developed the models and theoretical framework with Andrew Jackson. I conceived the ideas, co-designed the study, and interpreted the results. Jean-François, Andrew, and I produced the figures, and I led the writing of the manuscript with Ian Donohue. Though I use the *I* pronoun for consistency among chapters, the analytics presented in this chapter were performed primarily by Jean-François Arnoldi and Andrew Jackson.

2.1 SUMMARY

Ensuring reliable supply of services from nature is key to the sustainable development and well-being of human societies. Varied and frequently complex relationships between biodiversity and ecosystem services have, however, frustrated our capacity to quantify and predict the vulnerability of those services to species extinctions. Here, I use a qualitative Boolean modelling framework to identify universal drivers of the robustness of ecosystem service supply to species loss. These drivers comprise simple features of the networks that link species to the functions they perform that, in turn, underpin a service. Together, they define what I call network fragility. Using data from >250 real ecological networks representing services such as pollination and seed-dispersal, I demonstrate that network fragility predicts remarkably well the robustness of empirical ecosystem services. I then show how to quantify contributions of individual species to ecosystem service robustness, enabling quantification of how vulnerability scales from species to services. My findings provide general insights into the way species, functional traits, and the links between them together determine the vulnerability of ecosystem service supply to biodiversity loss.

2.2 INTRODUCTION

Ecosystem services—ecological structures, functions or processes that directly or indirectly contribute to human wellbeing (Costanza *et al.* 2017)—provide a plethora of benefits to humanity (Costanza *et al.* 1997; Mace *et al.* 2012). Through current global environmental change, humans are driving species to extinction at rates hundreds to thousands of times in excess of background (Pimm *et al.* 2014; De Vos *et al.* 2015; Humphreys *et al.* 2019). Such extinctions compromise the capacity of ecosystems to reliably provide the goods and services upon which human societies depend (Hooper *et al.* 2005; Worm *et al.* 2006; Cardinale *et al.* 2012; Isbell *et al.* 2015a, 2015b; Oliver *et al.* 2015a, 2015b; Smale *et al.* 2019; Reilly *et al.* 2020). The mechanisms through which ecosystem services collapse—that is, when they are either no longer being supplied or have declined to the point that they are no longer utilised by people (that is, are no longer in demand)—remain elusive, however, and vary with both ecological and social context (Tscharntke *et al.* 2005; Kaiser-Bunbury *et al.* 2010; Hautier *et al.* 2014; Duncan *et al.* 2015; Oliver *et al.* 2015b; Dee *et al.* 2017; Mastrángelo *et al.* 2019). Consequently, we have only a rudimentary understanding of the vulnerability of many, perhaps all, ecosystem services to species loss (Worm *et al.*

2006; Isbell *et al.* 2015a; Mace *et al.* 2015; Donohue *et al.* 2016; Smale *et al.* 2019; Greenop *et al.* 2021). Certainly, different services vary in their vulnerability (Carpentier *et al.* 2021; Keyes *et al.* 2021), but we lack general rules that might explain these differences.

Here, I develop and test a simple model to measure and predict the robustness of ecosystem service supply to species loss. I take a purely qualitative perspective, where species are either present or absent and an ecosystem service is provided or not (Figs. 2.1a, 2.2a). I focus on the implications of species removal and aim to understand how functional redundancy and species richness combine to buffer ecological processes against biodiversity loss (Yachi & Loreau 1999; Pillar *et al.* 2013; Feit *et al.* 2019). I limit my scope to the supply of ecosystem services, and do not address here the extent or dynamics of human demand for those services. On the other hand, my approach could be applied to any emergent, high-level ecosystem process, not necessarily considered (or recognised) as a service.

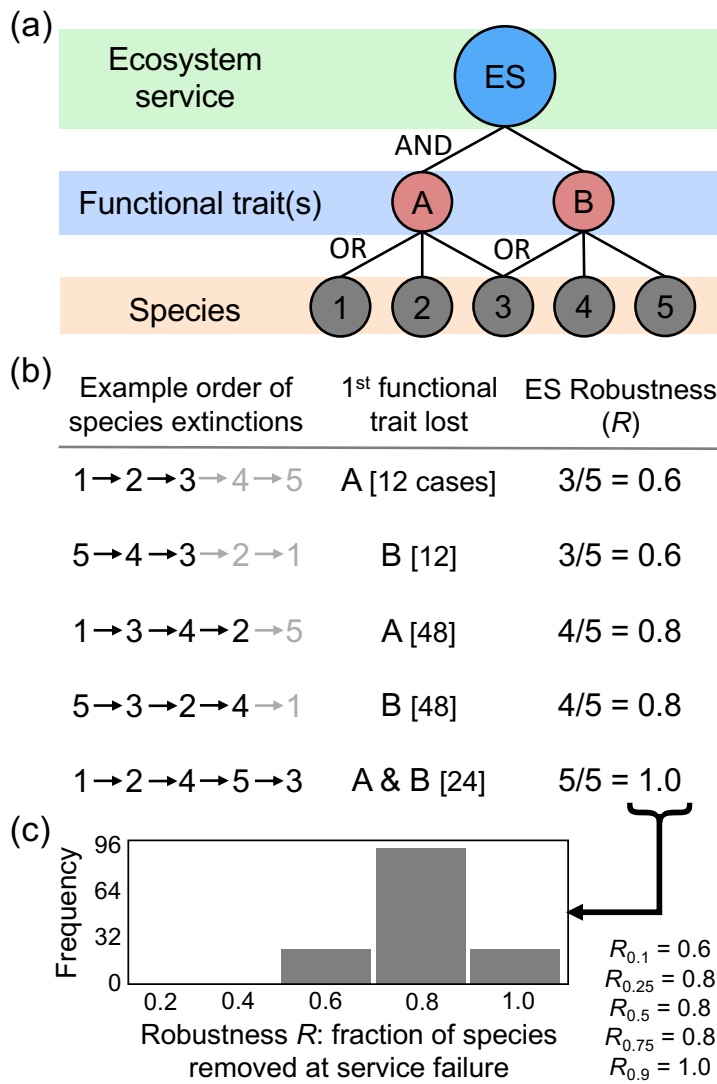


Figure 2.1 | The principles of my approach to measuring the robustness of ecosystem services to species loss. (a) I use a qualitative framework (see 2.3 Methods for a detailed description) whereby species [1-5 in this example] are linked to their functional traits [A & B] and are either present or absent from a community (Fig. 2.2). An ecosystem service [ES] is supplied only when all underpinning functional traits are present in the community (the Boolean function AND; see 2.3 Methods and Appendix A for justification). (b) As species are removed sequentially from the system, a functional trait is present until all species connected to that trait are lost. In this way, species losses are tolerated (the Boolean function OR) until a unique functional trait has been lost. ‘Example order of species extinctions’ presents illustrative examples of the sequential removal of the species in (a), with sequences in grey indicating extinctions after service failure. ‘1st functional trait lost’ is the identity of the unique functional trait [A and/or B] first lost from the system—which, under my framework, necessarily causes service loss—with [n cases] indicating the number of extinction sequences for which this result is obtained [reflected also in the histogram (c)]. I measure ‘ES Robustness (R)’ as the fraction of species removals required to bring about loss of a service for each extinction sequence. (c) This results in a distribution of robustness R values, representing the fraction of species loss tolerated across all extinction scenarios. This distribution of R

values can be described via its percentiles [denoted with subscript c] with, for example, the median robustness [$R_{0.5}$] here equating to 0.8. That is, in 50% of extinction scenarios in this hypothetical example, 4/5 or fewer species extinctions are required to cause service failure.

I use Boolean functions to model a robust-vulnerable continuum (Salski 2006) of ecosystem services (Fig. 2.2). At one extreme is the logical AND function, where every species is essential to the supply of an ecosystem service. In this case, even the loss of a single species will result in service failure, owing to a complete lack of functional redundancy (Ehrlich & Mooney 1983). At the other extreme, all species are fully substitutable and only a single species is then needed to supply a service. In this case, the ecosystem service equates to the logical OR function, where full redundancy among species promotes robust service supply even in the face of multiple species extinctions (Ehrlich & Mooney 1983; Yachi & Loreau 1999; Winfree & Kremen 2009).

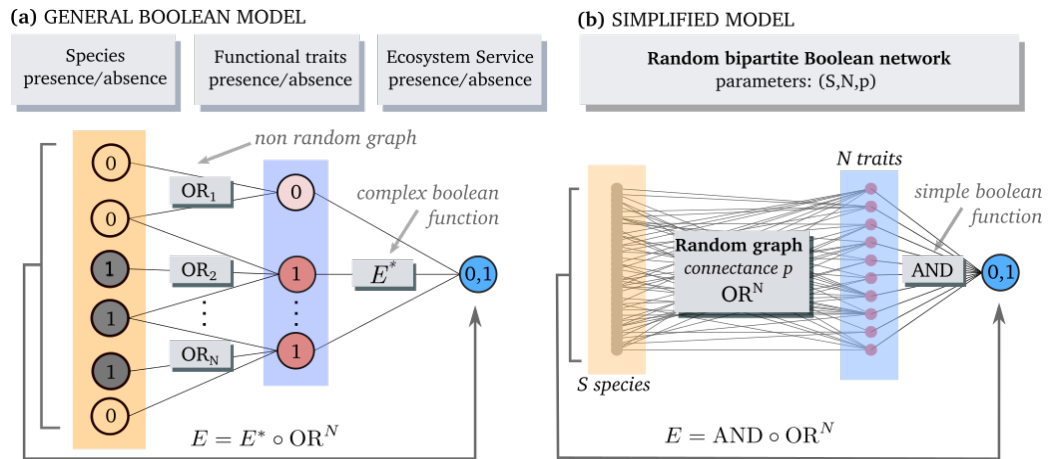


Figure 2.2 | A Boolean model for ecosystem services. (a) I view an ecosystem service as a Boolean function E over the presence/absence configurations of S species (leftmost column). I distinguish species from their N functional traits (middle column). The configuration of any trait n is defined by the logical OR function over the S_n species that share that trait. This amounts to writing E as the composition $E = E^* \circ OR^N$, which should aim to remove as much functional redundancy as possible from the auxiliary function E^* over trait configurations. (b) I simplify my model further by (i) considering random species-to-trait associations with connectance p , and (ii) choosing the logical AND function for E^* [that is, the least redundant function, which I show (in Appendix A.3) is representative of a random choice across the space of all Boolean functions]. In this model (see 2.3 Methods for full description), one can deduce analytical expressions for the percentiles of the distribution (considering all possible extinction sequences) of robustness of ecosystem service supply R : the fraction of species loss leading to loss of service supply.

For a given ecosystem service, rather than consider a particular model of extinction scenarios, I instead consider all possible extinction sequences simultaneously (Fig. 2.1b). I study the entire distribution of robustness, defined as the fraction of extinctions—along all extinction scenarios—sufficient to bring about the loss of supply of the ecosystem service (Fig. 2.1c). Services that can, along most extinction sequences, tolerate a high number of extinctions before they collapse are the most robust. I assume that the supply of a service requires species that have particular traits—phenotypic attributes that direct niche exploitation—whose presence drive all of the various ecological processes that are necessary to underpin provision of the service (Duncan *et al.* 2015; Díaz *et al.* 2007). Though many traits, such as body mass, occur along a continuous spectrum (Petchey & Gaston 2002; Petchey *et al.* 2004; Díaz *et al.* 2007), for simplicity I focus here only on whether or not a given species possesses a particular trait (Maseyk *et al.* 2017). I consider traits purely in a functional sense (Ehrlich & Mooney 1983), understood here as the capacity of a species to perform a particular functional role required for the ecosystem service to be provided (Maseyk *et al.* 2017). As such, traits are functional features that can be shared among species, as can be visualised by drawing, for a given service, a bipartite network linking species to traits (Dee *et al.* 2017; Figs. 2.1a, 2.2, but note that one could, in principle, refine the notion of traits by decomposing species into populations and differentiating traits within species).

Under these simplifying assumptions (Schröter *et al.* 2021), I reveal the universal drivers of the robustness distribution of any ecosystem service to species loss (see 2.3 *Methods*). I show that any percentile of the robustness distribution is driven by a synthetic parameter that I call network fragility. Network fragility combines simple features of the species-to-traits bipartite network—the numbers of species, functional traits and links between them—that together determine the fraction of species loss that can be tolerated before ecosystem service failure. I then go on to show how my results, based on properties of random bipartite networks, can be applied to non-random ecological networks representing real-world ecosystem services, such as plant pollination and seed-dispersal.

2.3 METHODS

2.3.1 BOOLEAN MODEL FOR THE ROBUSTNESS OF ECOSYSTEM SERVICE SUPPLY

I view the supply of an ecosystem service as a Boolean function E over the presence/absence configurations of S species

$$E: \{0,1\}^S \rightarrow \{0,1\} \quad (1)$$

I consider here only the presence and absence of species, though one could replace species with individuals to explore population-level contexts. Ecosystem service provision is also considered as binary—a service is either provided or it is not. Though these assumptions clearly simplify reality (Schröter *et al.* 2021), they nonetheless provide the foundation from which general insights applicable to real ecosystems can be developed, as I will show.

I am interested in the robustness $R(E)$ of supply of a given ecosystem service E . That is, the distribution—considering all possible extinction sequences—of the fraction of species extinctions that leads to loss of ecosystem service supply. Robustness is maximal and reduced to a single number if the service is lost only when all species are extinct [$R(E) \equiv 1$], and minimal and reduced to a single number if any species extinction is sufficient to cause service failure [$R(E) \equiv 1/S$]. More formally, if I consider all extinction scenarios, R is a distribution over the range $\left[\frac{1}{S}, 1\right]$. This distribution encodes the complex topology of species presence-absence configurations over which an ecosystem service is supplied. Considering the proportion of extinctions (rather than the absolute number) that result in service failure allows us to compare across systems of different species richness. It also leads to a notion of ecosystem service robustness that relates directly to the expected time to service loss, given a mean species extinction rate (Appendix A.2).

Next, I distinguish species from their N potential functional traits that relate to the ecosystem service of interest. I model functional redundancy by determining the configuration of trait n with the Boolean function OR over the configuration space of the S_n species that share this trait (Fig. 2.2a). Thus, a trait is present until all species that have this trait are extinct. If I denote OR_n as the extension of the OR function over the S_n species that share a given trait to the whole species configuration space (that is, a partial OR function), I have a mapping from S species configurations to N traits configurations:

$$\text{OR}^N = \text{OR}_1 \times \dots \times \text{OR}_N: \{0,1\}^S \rightarrow \{0,1\}^N \quad (2)$$

The state of the ecosystem service E is then determined by an auxiliary Boolean function $E^*: \{0,1\}^N \rightarrow \{0,1\}$ over trait configurations. In other words, I factorize E as the composition

$$E = E^* \circ \text{OR}^N: \{0,1\}^S \rightarrow \{0,1\}^N \rightarrow \{0,1\} \quad (3)$$

This factorization is always possible, since by choosing $N = S$ one could always make OR^N into a trivial mapping where each species has a unique trait and take $E^* \equiv E$. To be useful, however, this factorization should aim at having the lowest number of distinct functional traits relative to the service, thus removing as much functional redundancy as possible from the auxiliary function E^* .

To derive generic drivers of the robustness of ecosystem service supply, I need to define a universe of ecosystem services rich enough to be representative of real ecosystem services, yet simple enough to permit an analytical treatment of their robustness. Based on my factorization (Equation 3), there are two parts to the problem, and I make simplifying assumptions for both. I start by defining a universe of species-to-traits mapping. A simplifying choice is to assume the species-to-traits network to be a random graph with connectance p . I then need a model for the auxiliary function E^* . A natural choice, given my treatment of the species-to-trait association, would be to pick E^* at random and uniformly over the set of all 2^{2^N} possible Boolean functions over trait configurations. However, I can make a much simpler choice at a low cost in behavioural complexity. In terms of robustness of ecosystem service supply, I find (by drawing the auxiliary function E^* at random uniformly over the set of all Boolean functions of $\{0,1\}^N$; Appendix A.3) that assuming the AND function (that is, the least redundant function) for E^* is representative of the outcome of a random choice. Thus, I now have, for any choice of S , N , and p , a random set (the random component is in the species-to-trait graph, Fig. 2.2b) of ecosystem services of the form

$$E = \text{AND} \circ \text{OR}^N: \{0,1\}^S \rightarrow \{0,1\}^N \rightarrow \{0,1\} \quad (4)$$

This then allows us to derive an analytic form for the robustness of ecosystem service supply (Appendix A.1).

2.3.2 ANALYSIS OF EMPIRICAL NETWORKS

For my analysis of empirical networks, I downloaded all 258 available bipartite webs from the Web of Life ecological networks dataset (<http://www.web-of-life.es>), which comprised Anemone-Fish ($n = 17$), Host-Parasite ($n = 51$), Plant-Ant ($n = 4$), Plant-Pollinator ($n = 148$) and Seed-Disperser ($n = 34$) networks. I

removed three networks that comprised only a single trait (that is, where all species connected to the same single interaction partner), and four that showed no variation in the number of species per trait (of which the latter were all Anemone-Fish webs), leaving 251 networks for analysis. I converted the count-based association matrix to binary so that connections between species and traits were either present or absent. In these networks, the ‘traits’ are also species. For example, I view pollinators as the species that provide for the presence of a plant (Reilly *et al.* 2020), which is a web-level trait. These web-level traits then underpin the provision of the overall pollination service, which I consider here to be the pollination of all plants in the network. That is, for there to be an arbitrarily-defined pollination service for this ecosystem (Winfree *et al.* 2018), I demand that all plants (traits) are present so that if one plant is lost, then the pollination service is lost. In contrast, the pollinators themselves are compensable for a given plant (trait) and so species loss is tolerated if there remains another species to pollinate that plant (Memmott *et al.* 2004). Similarly, I have chosen to view the networks as trait-species such that seed-disperser refers to plant species as the trait and disperser as the species that provides for that trait. That these networks really are or are not ecosystem services, or whether some species would go extinct together due to interactions (Kaiser-Bunbury *et al.* 2010; Carpentier *et al.* 2021), is not relevant for my purpose. I simply use these empirical networks as a rich set of non-random example networks on which to showcase the relevance of my theory beyond random networks (Carpentier *et al.* 2021).

For each of the binary bipartite webs, I calculated network fragility f_c and dispersion-corrected network fragility f_c^* using, respectively, Equations (5) and (7). Connectance p was estimated as $L/(S \times N)$, where L is the number of links. The distribution of robustness of ecosystem service supply R was then determined by simulation, whereby species were selected at random and removed sequentially until a trait (and hence the service; Appendix A.3), was lost and R was then quantified as the proportion of species lost until service collapse (Fig. 2.1). By simulating sequential extinctions and measuring robustness as a distribution in this way, my model encompasses all possible combinations of extinction orders, which is critical given the non-random nature of species extinctions in real ecosystems (Purvis *et al.* 2000; Gross & Cardinale 2005; Estes *et al.* 2011).

2.4 RESULTS

In my framework, an ecosystem service E consists of N required functional traits shared between S species, with p characterising the connectance of the species-to-traits network (Fig. 2.2). I note $R(E)$, the distribution of robustness, that is, the distribution of the fraction of species loss along all extinction sequences that lead to ecosystem service failure (Fig. 2.1c). For random species-to-traits networks, I find that the c^{th} percentile $R_c(E)$ of R —the value R_c such that a fraction c of extinction sequences leads to service failure when losing less than $S \times R_c$ species (Fig. 2.1c)—takes the analytic form (if $q = 1 - p$; Appendix A.1)

$$R_c(E) = 1 - f_c; \text{ where } f_c = \frac{\log\left(1 - (1-q^S)e^{-\frac{c}{N}}\right)}{S \log q} \quad (5)$$

The statistics of $R(E)$ are, therefore, driven entirely by a family of parameter values (f_c), comprising measures of what I call network fragility. In particular, the median value for robustness of ecosystem service supply corresponds to $f_{0.5}$ (Fig. 2.3a). The width of the distribution of $R(E)$ is maximal at intermediate values of $f_{0.5}$ and decreases as the number of traits N increases (Fig. 2.3b). This means that the robustness of ecosystem service supply to species loss is at its most predictable at both low and high values of network fragility and when the service is underpinned by many functional traits.

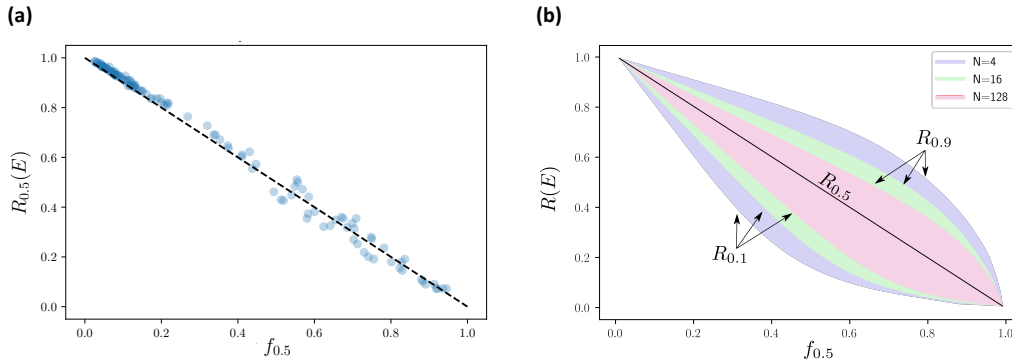


Figure 2.3 | Universal behaviour of the robustness of ecosystem service supply as a function of network fragility. (a) For 125 random ecosystem services of the form shown in Fig. 2.2, I uniformly sampled 5 values for species richness S between 10 and 200, 20 for functional traits N between 10 and 100, and 10 for connectance p between 0 and 0.5, and for each considered 600 extinction scenarios leading to a loss of service, drawn uniformly over the set of all possible extinction sequences. I see that the median robustness of ecosystem service supply (that is, $R_{0.5}(E)$) in my simplified Boolean model behaves as a simple decreasing linear function of median network fragility ($f_{0.5}$). (b) For three values of number of traits (that is, $N = 4, 16$, and 128) and random values of number of species S and connectance p , I used the analytical formula in Equation (5) to

draw the contours of the bulk of the robustness distribution (that is, 10th to 90th percentiles) as a function of $f_{0.5}$, the value of fragility associated with median robustness. I see that, at fixed N , the percentiles can be expressed as functions of $f_{0.5}$, with the largest spread at intermediate values of network fragility. At fixed fragility, increasing the number of traits N reduces the width of the distribution.

Next, I examine whether the one-to-one relationship between network fragility and the statistics of robustness of ecosystem service supply is universal, that is, valid beyond random species-to-traits association networks. To do this, I considered 251 real empirical bipartite networks from the Web of Life ecological networks database, representing a variety of ecosystem services, including, for example, pollination and seed-dispersal (see 2.3 *Methods*). I measured network fragility for each network directly from the numbers of species, traits, and links it comprises. To measure the robustness of ecosystem service supply, I simulated random extinction sequences leading to the loss of at least one functional trait (for example, the loss of pollination of at least one plant species following pollinator species extinctions; see 2.3 *Methods* and Appendix A.1), and replicated this process 1000 times to give a numerical estimate of the distribution of R for each service represented by each empirical network. In addition, I computed the variance in the number of species per trait, $\mathbb{V}(S_n)$, which I compared to a null expectation, $\mathbb{V}_0(S_n)$, if the species-to-traits network were random (for a random network with connectance p , $\mathbb{V}_0(S_n) = S_{pq}$). I then defined dispersion d as

$$d = \frac{\mathbb{V}(S_n)}{\mathbb{V}_0(S_n)} \quad (6)$$

so that $\log_{10}(d)$ gives a measure of deviation from randomness, vanishing if the observed variance is that of a random network, is negative if the variance is smaller, and positive if it is larger.

I found that network fragility explains well the robustness of ecosystem services in the empirical networks I examined (Spearman $\rho = -0.64$ for $c = 0.5$; Fig. 2.4a). However, overdispersion (that is, $\log_{10}(d) > 0$) led systematically to lower robustness of ecosystem service supply than predicted, whereas underdispersion ($\log_{10}(d) < 0$) had the opposite effect. Correcting network fragility (f_c^*) to then account for the deviation from randomness of the species-to-trait network (Fig. 2.4b), where

$$f_c^* = f_c + \lambda_c f_c (1 - f_c) \log_{10}(d), \text{ for } \lambda_c > 0 \quad (7)$$

improved the relationship with robustness of ecosystem service supply considerably (Spearman $\rho = -0.89$ for $c = 0.5$; Fig. 2.4c) and captures well its universal properties (Figs. 2.4c, 2.4d, & Fig. A.1). Moreover, I confirmed that uncertainty in ecosystem service robustness in the empirical networks was greatest at intermediate values of network fragility (Fig. A.2), as predicted by my analytical model (Fig. 2.3b). Variance among the different types of empirical networks in my analysis (Fig. 2.4d) suggests that there may be further nuances in the structure of those networks that contribute to their robustness to species loss beyond the universal characteristics I describe. However, these unknown drivers play a minor role in comparison to network fragility.

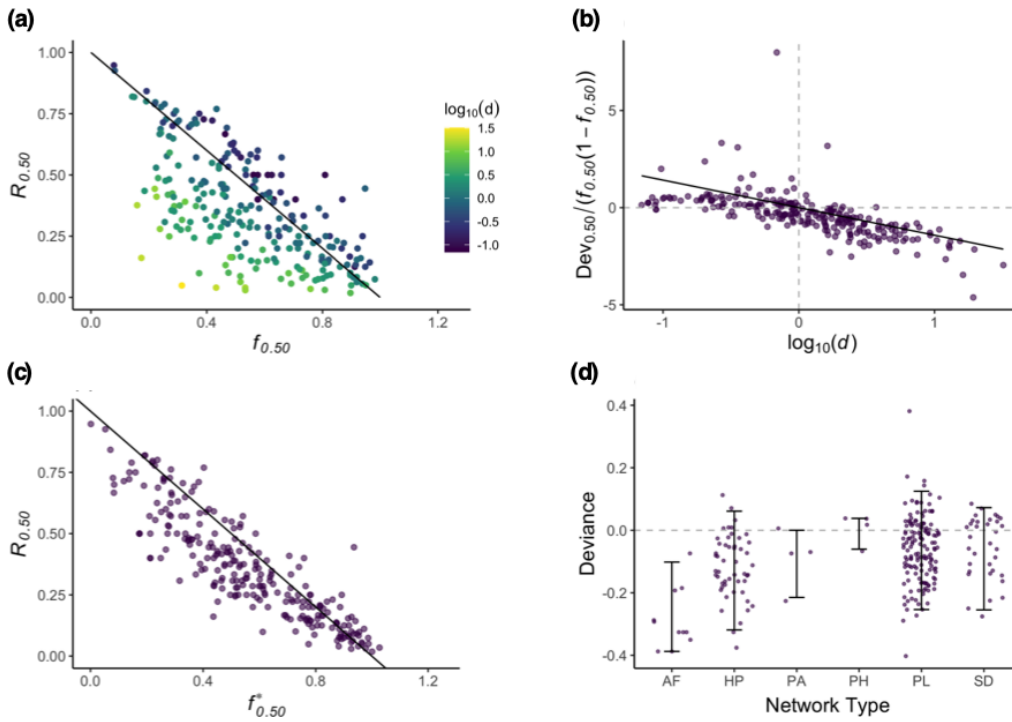


Figure 2.4 | Robustness of ecosystem service supply and network fragility in empirical networks. **a** The relationship between simulated robustness of ecosystem service supply ($R_c = R_{0.5}$) and analytically-estimated network fragility ($f_c = f_{0.5}$) for 251 empirical networks from the Web of Life follows the linear approximation $R_c = 1 - f_c$. Colour indicates network dispersion ($\log_{10}(d)$). **b** The residuals off the linear prediction $R_c = 1 - f_c$ correlate with $\log_{10}(d)$, which I model as $(R_c - 1 + f_c)/(f_c(1 - f_c)) = \lambda_c \log_{10}(d)$, where, for the case of $R_{0.5}$, $\lambda_{0.5} = -1.42$. **c** Correcting network fragility for dispersion according to $f_c^* = f_c + \lambda_c \log_{10}(d)$ yields an even closer relationship with robustness of ecosystem service supply. **d** Residuals from $R_{0.5} - f_{0.5}^*$ by network type show that my model captures well the universal properties, where AF = anemone-fish ($n = 10$), HP = host-parasite ($n = 51$), PA = plant-ant ($n = 4$), PH = plant-herbivore ($n = 4$), PL = pollination ($n = 148$), and SD = seed dispersal ($n = 34$). Error bars show the 5th and 95th quantiles of the data.

Whereas the distribution of robustness reflects the complex topology of species presence-absence configurations over which a given ecosystem service is supplied, network fragility can be evaluated directly from the most basic features of species-to-traits associations—the numbers of species, functional traits that underpin the service, and links between them. This local nature of network fragility therefore allows us to study its behaviour under any specific species extinction scenario. This crucial property allows us to quantify the contribution of any given species or combination of species to the robustness of ecosystem service supply. I can, for example, ask how much network fragility f_c^* would increase if species i were lost? The loss of a species with L_i traits will obviously reduce richness $S \rightarrow S - 1$, but it will also affect connectance as

$$p \rightarrow p - p \left(\frac{L_i}{L} - \frac{1}{S} \right) \quad (8)$$

Naturally, the species with the most links will reduce connectance, and therefore increase network fragility, the most. Species loss may, however, also affect dispersion d via its effect on the variance in the number of species per trait $\mathbb{V}(S_n)$. If I define $\overline{S_{n_i}}$, the mean number of species that have the same traits as species i , and $\overline{S_n} = L/N$ the mean number of species per trait, I get that (approximately)

$$\mathbb{V}(S_n) \rightarrow \mathbb{V}(S_n) + 2\overline{S_n}(\overline{S_n} - \overline{S_{n_i}}) \frac{L_i}{L} \quad (9)$$

Thus, dispersion (and, therefore, network fragility) increases the most if $\overline{S_{n_i}}$ is small compared to $\overline{S_n}$, that is, if the traits of species i are uncommon. It is, thus, those species that are generalist providers of multiple uncommon traits that contribute the most to the robustness of ecosystem service supply. This is an intuitive statement, but my theory makes it a quantitative measure, integrating precisely the relevant features of the service that a given species contributes to.

2.5 DISCUSSION

My model reveals how species richness and trait generality combine to determine the robustness of ecosystem service supply to the loss of species. Moreover, by also enabling quantification of the contribution of individual species to the robustness of ecosystem service supply, the model comprises a general tool for predicting and managing the vulnerability of ecosystem service provision (or,

indeed, any ecological process) in the face of rapid and ongoing global environmental change.

My theory predicts that extinction scenarios targeting species that possess multiple uncommon traits will likely lead to more rapid collapse of ecosystem service supply. That is, a species with unique links in a bipartite species-to-traits network is more likely to contribute substantially to robustness (Dee *et al.* 2019). As a network transitions via sequential extinctions from a starting point of high robustness, it will, however, pass through a window at intermediate network fragility where uncertainty in robustness is maximal. Thus, increasing network fragility via loss of species (or loss of their functional roles) not only reduces the robustness of service supply, but also increases the uncertainty surrounding predictions of ecosystem service loss in the face of uncertain species extinction scenarios.

The theory I present comprises a highly simplified representation of nature—my model assumes that ecosystem services are either provided or not and that the loss of a single unique functional trait causes ecosystem service provision to cease. The latter assumption may seem to be overly conservative, yet I show (Appendix A.3) that it captures well the robustness of randomly generated services. In addition, I did not consider either species abundances—which did not stabilise crop pollination services in a previous study (Winfrey & Kremen 2009)—or intraspecific trait variation, which often supports ecosystem service supply (Des Roches *et al.* 2021). Such detailed knowledge could, however, easily be incorporated in my model by replacing species with populations or even individuals. The resulting network representation of the service would then become highly complex (Dee *et al.* 2017). Importantly, however, my notion of network fragility would still apply and, because of its simplicity, would remain tractable. All in all, my abstractions of natural systems enabled us to gain general insights into biodiversity-ecosystem services relationships, taking a significant step forward in our understanding of the stability of ecosystem service provision in the face of widespread biodiversity loss.

Though biodiversity is foundational to the sustained supply of ecosystem services, ecological factors alone do not determine their overall vulnerability (Lafuite *et al.* 2017). Ecosystem services are linked intrinsically to human valuation (Costanza *et al.* 1997, 2017; Schröter *et al.* 2021), and shifts in their value can play an overarching and even dominant role (Costanza *et al.* 2014; Wyborn *et al.* 2020). The overall vulnerability of ecosystem services may, therefore, depend on the stability of human values to an even greater extent than on biodiversity. Models linking the ecological and social aspects of ecosystem

services, and the interactions between them, are, therefore, fundamental to understanding how ecosystem services will respond to future changes (Hooper *et al.* 2005; Isbell *et al.* 2015a; Bodin *et al.* 2019; Mastrángelo *et al.* 2019; Wyborn *et al.* 2020). This delineates a challenge for future research: how can we best integrate the robustness of ecosystem service supply with the various drivers of human valuation and demand? My modelling framework serves as a stepping-stone in that direction.

By enabling identification of the key species that contribute to the robustness of ecosystem service supply, my theory provides a focus for management efforts that require consideration of the conservation value of individual species (Petchey & Gaston 2002; Worm *et al.* 2006; Palumbi *et al.* 2009; Isbell *et al.* 2015a; Maseyk *et al.* 2017; Fanin *et al.* 2018; Dee *et al.* 2019; White *et al.* 2020b). Focusing on the contribution of individual species to robustness and the vulnerability of those species to extinction through their life histories, interactions, and functional traits (Díaz *et al.* 2007; Mace *et al.* 2008; Moreno-Mateos *et al.* 2020; Carpentier *et al.* 2021; Keyes *et al.* 2021) will enable empirical quantification of how vulnerability scales from species through to ecosystem services (Kaiser-Bunbury *et al.* 2010; Oliver *et al.* 2015a; Dee *et al.* 2017; Fanin *et al.* 2018; Smale *et al.* 2019; Greenop *et al.* 2021). Ultimately, such a shift will provide a far richer and mechanistic understanding of the sustainability of nature's contributions to people under global environmental change.

CHAPTER 3 | PREDATORS MITIGATE THE DESTABILISING EFFECTS OF HEATWAVES ON MULTITROPHIC STREAM COMMUNITIES

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AUTHOR CONTRIBUTION:

I designed the study, conducted the experiment with help from all coauthors, including implementing the heatwave, aided by Atsushi Okuda and Jackson Johnstone. I collected the data, identified the macroinvertebrates, analysed the data, produced the figures, and led the writing of the manuscript with input from all coauthors. Jorge García Molinos performed the climate model downscaling and I interpreted the results. Jorge García Molinos, Osamu Kishida, Atsushi Okuda, and many local collaborators constructed the experimental system, for which I remain deeply indebted to them.

3.1 SUMMARY

Amidst the global extinction crisis, climate change will expose ecosystems to more frequent and intense extreme climatic events, such as heatwaves. Yet, whether predator species loss—a prevailing characteristic of the extinction crisis—will exacerbate the ecological consequences of extreme climatic events remains largely unknown. Here, we show that the loss of predator species can interact with heatwaves to moderate the compositional stability of ecosystems. We exposed multitrophic stream communities, with and without a dominant predator species, to realistic current and future heatwaves and found that heatwaves destabilised algal communities by homogenising them in space. However, this happened only when the predator was absent. Additional heatwave impacts on multiple aspects of stream communities, including changes to the structure of algal and macroinvertebrate communities, as well as total algal biomass and its temporal variability, were not apparent during heatwaves and emerged only after the heatwaves had passed. Taken together, our results suggest that the ecological consequences of heatwaves can amplify over time as their impacts propagate through biological interaction networks, but the presence of predators can help to buffer such impacts. These findings underscore the importance of conserving trophic structure, and highlight the potential for species extinctions to amplify the effects of climate change and extreme events.

3.2 INTRODUCTION

Increases in the frequency and intensity of extreme climatic events are reshaping ecological communities globally (Parmesan *et al.* 2000; Kreyling *et al.* 2011; Wernberg *et al.* 2013; Harris *et al.* 2018; Smale *et al.* 2019), a trend that is predicted to become even more acute as the century progresses (Easterling *et al.* 2000; Oliver *et al.* 2018a; Fischer *et al.* 2021). The problem is particularly pertinent to freshwater ecosystems because of the narrower thermal safety margins of aquatic ectotherms relative to their terrestrial counterparts (Sunday *et al.* 2012; Comte & Olden 2017; Pinsky *et al.* 2019). For example, more than 30% of 463 European freshwater species already exceed their preferred thermal temperatures within their current distribution ranges (Kärcher *et al.* 2019). Consequently, as the climate warms, there is increasing potential for aquatic ecosystems to undergo temperature-driven biodiversity change, including species redistributions and extinctions (Wernberg *et al.* 2013; Fussmann *et al.* 2014;

García Molinos *et al.* 2016; Comte & Olden 2017; Waldock *et al.* 2018; Inagaki *et al.* 2020). Such biodiversity change is highly likely to disrupt their capacity to provide many vital ecosystem processes, functions, and services (Chapter 2; Worm *et al.* 2006; Oliver *et al.* 2015b; Pecl *et al.* 2017; Smale *et al.* 2019; Chen *et al.* 2020; Bernhardt & O'Connor 2021; Ross *et al.* 2021a).

Biodiversity change across the globe is a non-random process (Purvis *et al.* 2000; Gross & Cardinale 2005; Estes *et al.* 2011; Chen *et al.* 2020; Gerhard *et al.* 2020). Of particular concern is trophic downgrading, whereby species extinctions follow a pattern of systematic community disassembly starting from the highest trophic levels, as a result of the larger body sizes, metabolic demands, and resource requirements of apex predators (Estes *et al.* 2011; Tanentzap *et al.* 2020). Loss of predator species, in turn, often triggers trophic cascades and a wave of secondary extinctions (Nakano *et al.* 1999; Donohue *et al.* 2017), further modifying ecosystem structure and function (Chen *et al.* 2020), increasing the vulnerability of key ecosystem processes (Ross *et al.* 2021a), and undermining the overall stability of the system (Donohue *et al.* 2013; White *et al.* 2018). A defining characteristic of global environmental change is that ecological communities are exposed to multiple anthropogenic stressors simultaneously (Birk *et al.* 2020; Bowler *et al.* 2020), forming a complex backdrop against which species extinctions occur. One particularly important research question is the extent to which biotic and abiotic drivers of biodiversity change interact (Zarnetske *et al.* 2012; O'Connor & Donohue 2013; O'Connor *et al.* 2015; Kordas *et al.* 2017; White *et al.* 2018; Rasher *et al.* 2020). Within this question, the capacity of individual species to confer resistance to future climate change remains understudied, particularly for aquatic systems (Kordas *et al.* 2017; Goldenberg *et al.* 2018; Nagelkerken *et al.* 2020; Rasher *et al.* 2020). While the ecological consequences of climate change and species extinctions have primarily been considered independently, there is clear potential for species extinctions to compound the effects of climate change on ecosystems (Kishi *et al.* 2005; Post & Pedersen 2008; Kordas *et al.* 2017; Rasher *et al.* 2020).

To date, manipulative experiments exploring the effects of future climate change on ecological communities have relied largely on Global Circulation Model projections that do not represent adequately the climatic conditions at the local scales of relevance to the systems being manipulated (Korell *et al.* 2020). The consequent scale mismatch limits the representativeness of predictions of ecological responses to climate change. Here, I use present and future local temperature data, extracted from, respectively, a local weather station and a highly-resolved (5-km) regional climate model, to test experimentally whether

trophic downgrading moderates the response of an exceptionally well-resolved multitrophic cold temperate stream community (Fausch *et al.* 2002; Marcarelli *et al.* 2020) to simulated heatwaves in Tomakomai, northern Japan. I used flow-through mesocosms connected to a nearby stream, thus enabling continuous dispersal of microbes, algae and invertebrates both into and out of the experimental system, to test whether and how the functional and compositional responses of benthic algal and macroinvertebrate communities to simulated heatwaves were modified in the presence and absence of *Cottus nozawae*, a freshwater sculpin and common apex predator in the system (Konishi *et al.* 2001; Miyasaka *et al.* 2003; Kishi *et al.* 2005; Marcarelli *et al.* 2020). My experimental heatwaves comprised two levels: a lower intensity (+2.76 °C mean temperature increase) heatwave representative of a current local heatwave, and a higher intensity (+6.06 °C) heatwave, representing future extreme events as inferred from the local temperatures projected by the regional climate model towards the end of the century. For both heatwave treatments, I simulated realistic temperature dynamics before, during, and after the heatwaves based on local long-term records and future projections. I tested for treatment effects both during and after the heatwaves to separate their immediate impacts from their longer-lasting effects and reveal legacy impacts of heatwaves on multiple aspects of my experimental stream communities (Fugère *et al.* 2020; Jacquet & Altermatt 2020; Miller *et al.* 2021).

3.3 METHODS

3.3.1 STUDY LOCATION AND EXPERIMENTAL SYSTEM

My experiment (Fig. 3.1) ran for 50 days (10 July - 29 August 2019), using streamside mesocosms (Piggott *et al.* 2015) installed adjacent to a section of the Horonai Stream, a forested headwater stream that runs past the Tomakomai Experimental Forest field station in Hokkaido, Japan (42°43'N, 141°36'E). The experimental system comprised 48 flow-through mesocosms (volume 3.5 L), allowing near-natural immigration and emigration of algae, microorganisms, and invertebrates from and to the stream. A Kawamoto GS3-C pump fed three header tanks with stream water, each of which gravity-fed 16 mesocosms. After flowing through the mesocosms, water drained back into the stream downstream of the pump intake. One of the main advantages of this system is its potential to support natural community dynamics (*e.g.*, colonisation, predation), with conditions such as temperature, light, and water chemistry all mirroring those in the nearby

stream (Piggott *et al.* 2015). The total flow rate into the mesocosms throughout the duration of the experiment was maintained at $2.09 \pm 0.05 \text{ L min}^{-1}$ (mean $\pm$ SE).

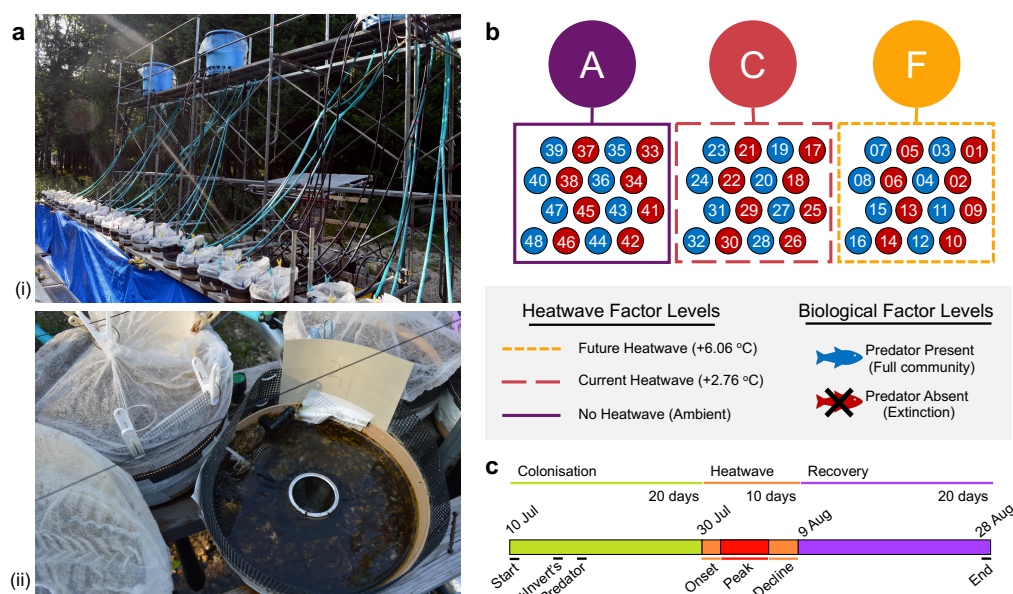


Figure 3.1 | Experimental design and timeline. (a) Photos of (i) the experimental set-up consisting of 48 flow-through aquatic mesocosms, and (ii) an individual mesocosm, post-colonisation of algae and macroinvertebrates. (b) Treatment design for my biological and heatwave factors and their levels. Mesocosms are numbered 1-48 and either comprise the full community including a predatory sculpin (*Cottus nozawae*) [24 blue circles], or the community minus *C. nozawae* [24 red circles]. Mesocosms were either heated to reflect future [F] climate conditions (mean = +6.06°C), current [C] climate conditions (mean = +2.76°C) or were kept in ambient conditions [A]. See Table B.1 for further details of the heatwave conditions. (c) Timeline for the experiment beginning 10 July when water began flowing and ending 28 August when water flow was terminated. The experiment comprised 20 days of colonisation, 10 days of heating including 5 days at peak heat intensity, and 20 days of ambient conditions following the heating period. My predation treatments were applied from 17 July [Predator]. Heatwave onset began on 30 July when leaf packs were also added to the mesocosms. Heatwave peak intensity ran 1-6 August [Peak] and was reduced to ambient by 9 August [Decline]. On Day 5, macroinvertebrate colonisation was supplemented with a kick-sample [+Invert's]. Daily algal measurements began on 18 July, immediately after [Predator], and continued until flow stopped and all samples were removed on 28 August [End]. Photos: S.R.P-J.R.

3.3.2 EXPERIMENTAL DESIGN

My experimental design comprised two factors—predation and heatwave intensity—with, respectively, two (presence/absence of fish predators) and three (ambient temperatures, current, and future heatwaves) levels (Fig. 3.1). Each of

the resulting six experimental treatments was replicated eight times. Each 3.5 L mesocosm (25 cm external diameter and 6 cm inner outflow ring; see Piggott *et al.* 2015) contained 1 L volume of substrate taken from the shallow riverbed downstream, and I allowed representative algal and macroinvertebrate communities to establish for 20 days before implementing experimental heatwaves. On Day 5, I supplemented natural colonisation of each mesocosm with invertebrates collected from the stream with a standardised 2-minute kick sample with a 1 mm mesh pond net. This was done to facilitate colonisation of poorly dispersing taxa that might be underrepresented in natural drift through the inflow pipe (*e.g.*, annelids, *Tipula* crane fly larvae) and to ensure that all mesocosms had an invertebrate community which was, as far as possible, representative of the natural stream community (Marcarelli *et al.* 2020).

My predation treatments began on Day 7 with the addition of a single freshwater sculpin (*Cottus nozawae*) to half of the mesocosms (Fig. 3.1c). *Cottus nozawae* (ハナカジカ in Japanese) is a temperature-sensitive (Yagami & Goto 2000; Kishi *et al.* 2005) dominant predatory benthic fish in the Horonai Stream (Goto & Nakano 1993), accounting for ~30% of total fish abundance (R. Futamura, unpublished data). *Cottus nozawae* forages on exposed benthic prey on the streambed (Yamamoto *et al.* 1988), consuming primarily amphipods (*e.g.*, *Sternomoera yezoensis*) but also Ephemeroptera, Oligochaeta, and others (Marcarelli *et al.* 2020). Single individuals of *Cottus nozawae* were allocated randomly to mesocosms and varied in length from 54-79 mm (mean $\pm$ SE: 66.71 $\pm$ 16.4 mm).

3.3.3 HEATWAVE IMPLEMENTATION

On Day 20, I began the application of the heatwave treatment, which comprised three levels: a higher intensity (mean = +6.06 °C) heatwave based on future climate conditions; a lower intensity (mean = +2.76 °C) heatwave based on current climate conditions; and an ambient (control) temperature treatment (Fig. B.1). I regulated water temperature in two header tanks by mixing stream water heated at 37 °C using a Rinnai RUX-A2400W-E series gas boiler and 140 V series controller with unheated stream water via valve-regulated intakes. I monitored temperatures manually and adjusted intake ratios every hour to maintain the desired temperatures for each treatment (Table B.1).

To produce locally relevant heatwaves for the region, I used the daily mean temperature series for the present time (1995-2017) and future projections (2076-2096), extracted from, respectively, the Tomakomai weather station

(42.62°N, 141.55°E; ~6 km from the experimental site) and the 5-km grid cell containing the experimental site (cell centroid 42.68°N, 141.11°E) from the dynamical downscaling non-hydrostatic regional climate model NHRCM05 (Sasaki *et al.* 2011), corresponding to the simulation experiment Global Warming Projection V9 performed by the Japan Meteorological Agency for the IPCC RCP8.5 high-emissions scenario (Moss *et al.* 2010). Heatwaves for each period were then estimated using the approach recommended by Hobday *et al.* (2016) and implemented by the *RMarineHeatwaves R* package (ver 0.16.1, Smit *et al.* 2018). Briefly, heatwaves, defined as a discrete prolonged anomalously warm event in a given location, were characterised as events with at least 5 consecutive days with mean daily temperatures above the 10% of temperatures recorded during that time of year for the whole series (Hobday *et al.* 2016). The definition of a heatwave is therefore contextual to the time of the year as the intensity threshold is seasonally adjusted (I used the default recommended 5 days duration before and after each focal day in the series). From the set of all detected heatwaves, I extracted those for the summer season (June-September) coincident with my experimental period and used their properties (Table B.1) to inform the heatwaves implemented in my experiment. Detected heatwaves differed in their intensity as well as onset and decline rates between current and future periods, but not in their duration properties (Current median = 7.5 days, Future = 5.5 days, Mann Whitney Test: $U = 134.5$, $p = 0.245$; Table B.1). Accordingly, I set the same total duration for my current and future experimental heatwaves, with a consistent 2-day onset followed by 5 days at peak intensity and a 3-day decline, resulting in a total duration of 10 days of heating (experimental days 20-30 inclusive; Fig. B.1). I thus achieved the intended experimental realism (Korell *et al.* 2020) by reproducing the current and future local conditions associated with the observed and projected heatwaves at the Tomakomai experimental site.

3.3.4 ALGAE BIOMASS AND COMPOSITION

I placed three identical terracotta tiles (45 x 45 mm) in each mesocosm on Day 1 to allow for natural colonisation and continued accrual of algae during the 20-day establishment phase of the experiment. I measured benthic algal biomass and composition from the surface of each tile daily using a BenthosTorch fluorometer (BBE Moldänke GmbH, Schwentinental, Germany) to quantify the total periphytic chlorophyll *a* concentration as a proxy for algal community biomass (Steinman *et al.* 2007; Cardinale 2011), as well as that of diatoms, cyanobacteria, and green algae separately (Kahlert & McKie 2014). Due to breakage, only a single tile was measured in two mesocosms where predators were present (one

under future heatwaves and one under current heatwaves). Before assessing algal community composition, I Hellinger-transformed the matrix of chlorophyll *a* concentrations of each algal group, since this transformation is insensitive to abundance (it does not give high weights to rare taxa; Legendre & Gallagher 2001), and then generated dissimilarity matrices using the Bray-Curtis dissimilarity index.

3.3.5 MACROINVERTEBRATE COMMUNITIES AND ECOSYSTEM PROCESSING

On Day 20, just before experimental heating began, I added a leaf litter decomposition pack (Benfield 2007) to each mesocosm to measure leaf litter processing by microbes and macroinvertebrates. Leaf packs were constructed from polyethylene nets (mesh size 3 mm) and contained ~ 3.5 g (mean $\pm$ SE: 3.45 ± 0.01 g) of dried oak leaves (*Quercus crispula*), a dominant tree along the Horonai stream. To estimate background rates of microbial decomposition, I also placed bags of smaller mesh size (~ 0.1 mm) in each mesocosm to prevent access by macroinvertebrates. Each of these bags contained ~ 0.5 g (mean $\pm$ SE: 0.5 ± 0.01 g) dried *Q. crispula* leaves. Leaf packs were in place for a total of 29 days (that is, until the end of the experiment; Fig. 3.1), incorporating both the heatwave and subsequent recovery period. I then calculated macroinvertebrate leaf shredding rates as the change in the dry mass of the leaf pack before and after the experiment, corrected for expected microbial decomposition using a microbial degradation factor calculated as the proportion of dry mass lost in each microbial leaf bag (Benfield 2007).

On Day 50, I destructively sampled all mesocosms to quantify the density (total abundance m^{-3}) and taxon richness of macroinvertebrates. Macroinvertebrates collected from the mesocosms were sorted from the mesocosm substrate, preserved in 90% ethanol, and identified subsequently to the highest taxonomic resolution practicable.

3.3.6 DATA ANALYSES

I calculated the temporal and spatial variability of both total biomass (functional variability) and the composition (compositional variability) of algal communities over two time periods, one encompassing the heatwave peak (5 days) and the other the post-heatwave recovery period (20 days). Functional stability represents the stability of ecosystem processes, such as biomass production or decomposition, performed by particular organism groups (Hillebrand *et al.* 2018). I calculated functional temporal variability as the coefficient of variation (that is,

the standard deviation divided by the mean) of total chlorophyll *a* concentrations in each mesocosm (from daily mean values on algal colonisation tiles) across each time period, where higher temporal variability corresponds to less stable biomass through time (Tilman *et al.* 2006; Ives & Carpenter 2007).). In dynamic systems such as streams, temporally stable chlorophyll production (that is, algal productivity) indicates consistency in energy production capacity, a foundational ecosystem function (Steinman *et al.* 2007). I calculated functional spatial variability as the coefficient of variation among the three algal tiles within each mesocosm (Hunter *et al.* 2019) on days 27 and 50 to capture treatment effects on spatial variability on, respectively, the final day of peak heating before the start of the receding limb of the heatwave and on the final day of the 20-day post-heatwave recovery period (Fig. 3.1). In contrast to temporal variability, higher functional spatial variability is stabilising, as spatial asynchrony in biomass enhances stability by providing spatial insurance through patch dynamics (Loreau *et al.* 2003; Leibold *et al.* 2004).

Compositional variability of algal communities was quantified from Bray-Curtis dissimilarity matrices calculated from algal biomass data (Baert *et al.* 2016; White *et al.* 2020b). I measured compositional temporal variability for each mesocosm as the mean Euclidean distance from each date to the mesocosm-specific date-averaged centroid (White *et al.* 2020b) for both the 5-day heatwave peak and the 20-day recovery period, with higher temporal variability (that is, higher mean Euclidean distances) equating to less stable community composition through time (that is, lower temporal stability; Hillebrand *et al.* 2018). I measured compositional spatial variability as the mean Euclidean distance between each mesocosm and their treatment-specific centroid (that is, for all eight replicates under a given treatment) to produce treatment-level estimates for spatial variability (White *et al.* 2020b). As with functional stability, higher compositional spatial variability is associated positively with stability, owing to the stabilising role of asynchrony in ecosystem dynamics (Loreau *et al.* 2003; Leibold *et al.* 2004), whereas homogenisation of community biomass or composition in space is destabilising (Olden *et al.* 2004; Donohue *et al.* 2009; Wang *et al.* 2021). To explore whether my measurements were confounded by shifts in mean values over time or in space, I detrended my measurements of variability following Tilman *et al.* (2006). Results for detrended data were consistent with those for non-detrended data, so I present here analyses of non-detrended data only.

I tested the effects of predator presence and heatwaves on algal communities over two time periods: during the five days of peak heatwave exposure, and at the end of the experiment following 20 days of post-heatwave

recovery after cessation of the heatwaves. In contrast, analyses of macroinvertebrate communities and leaf litter decomposition were done only at the end of the experiment. Analyses were done with analysis of variance (ANOVA) for univariate responses, after ensuring data homoscedasticity (via $\log_{10}$ -transformation where needed; Table B.2), and with permutational multivariate analysis of variance (PERMANOVA), based on Bray-Curtis dissimilarity matrices, for multivariate responses. The contribution of individual macroinvertebrate taxa or algal groups to treatment differences was quantified using similarity percentage (Simpser) analysis (Clarke 1993). Post-hoc comparisons among levels of significant terms were done with Tukey HSD tests for univariate analyses, and with pairwise multilevel comparisons with Bonferroni correction in the *pairwiseAdonis* *R* package (ver 0.4, Martinez Arbizu 2020) for multivariate analyses. All statistical analyses were conducted in *R* (ver 4.0.2, R Core Team 2020) using packages *orddom* (ver 3.1, Rogmann 2013) and *vegan* (ver 2.5-6, Oksanen et al. 2019).

3.4 RESULTS

During the heatwave period, I found no effects of my heatwave or predator treatments on the biomass (ANOVA, $p > 0.05$; Fig. 3.2a), functional temporal variability (ANOVA, $p > 0.05$; Fig. 3.2b), or functional spatial variability (ANOVA, $p > 0.05$; Fig. 3.2c) of algal communities (Table B.3). However, the presence of fish predators modified the structure of algal community composition (PERMANOVA, $F_{1,42} = 9.67$, $p < 0.001$; Fig. 3.3a; Table B.4) and interacted significantly with heatwaves to modify both the temporal (ANOVA, $F_{2,42} = 3.33$, $p = 0.046$; Fig. 3.3b) and spatial (ANOVA, $F_{2,24} = 6.65$, $p = 0.005$; Fig. 3.3c) variability of algal community composition during the heatwave period. Though post-hoc tests for compositional temporal variability were inconclusive (Tukey HSD, $p_{\text{adj}} > 0.05$), I found that predators stabilised the mesocosms exposed to current, but not future, heatwaves, by increasing the compositional spatial variability of their algal communities relative to ambient conditions (Tukey HSD, $p_{\text{adj}} = 0.05$; Table 3.1).

Table 3.1 | Summary of the effects produced by the heatwaves and predator presence on each response variable measured during heatwaves and at the end of the recovery period following the heatwaves. Where a significant ($p < 0.05$) treatment effect is reported for heatwave (HW_{Amb} = ambient, HW_{Cur} = current, HW_{Fut} = future) or predator (P_{Pres} = present, P_{Abs} = absent) treatments or their interaction ($HW:P$), significance level is marked (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$, ^ = $p < 0.1$) and corresponding levels for the statistically significant contrasts resulting from post hoc Tukey HSD/Bonferroni tests are shown. Vertical arrows represent an increase (↑) or decrease (↓) in relevant treatment level. Where pairwise comparisons are not explicit ('vs'), contrasts are for all relevant treatment levels. Horizontal arrows represent compositional shifts.

Response	Period	HW	P	HW:P	Contrast
Benthic algae					
Total biomass	Heatwave	N.S.	N.S.	N.S.	
Funct. temporal var.		N.S.	N.S.	N.S.	
Funct. spatial var.		N.S.	N.S.	N.S.	
Composition		N.S.	***	^	$P_{Abs} \leftarrow$
Comp. temporal var.		N.S.	N.S.	*	Inconclusive
Comp. spatial var.		N.S.	N.S.	**	$HW_{Cur}:P_{Pres} \uparrow$ vs $HW_{Amb}:P_{Pres}$
Benthic algae					
Total biomass	Recovery	***	***	N.S.	$HW_{Fut} \uparrow$; $P_{Abs} \downarrow$
Funct. temporal var.		***	*	N.S.	$HW_{Fut} \downarrow$; $P_{Abs} \uparrow$
Funct. spatial var.		N.S.	N.S.	N.S.	
Composition		**	N.S.	N.S.	$HW_{Fut} \rightarrow$ vs HW_{Amb} ; $HW_{Cur} \rightarrow$ vs HW_{Amb}
Comp. temporal var.		^	N.S.	N.S.	
Comp. spatial var.		N.S.	N.S.	**	$HW_{Cur}:P_{Abs} \downarrow$ vs $HW_{Amb}:P_{Abs}$; $HW_{Fut}:P_{Abs} \downarrow$ vs $HW_{Amb}:P_{Abs}$
Macroinvertebrate					
Composition	Recovery	*	***	N.S.	$HW_{Fut} \leftarrow$ vs HW_{Amb} ; $P_{Abs} \leftarrow$
Richness		N.S.	*	N.S.	$P_{Abs} \uparrow$
Density		N.S.	***	N.S.	$P_{Abs} \uparrow$
Leaf decomposition					
Macroinvert. shredding	Recovery	N.S.	***	N.S.	$P_{Abs} \uparrow$
Microbial degradation		N.S.	N.S.	N.S.	

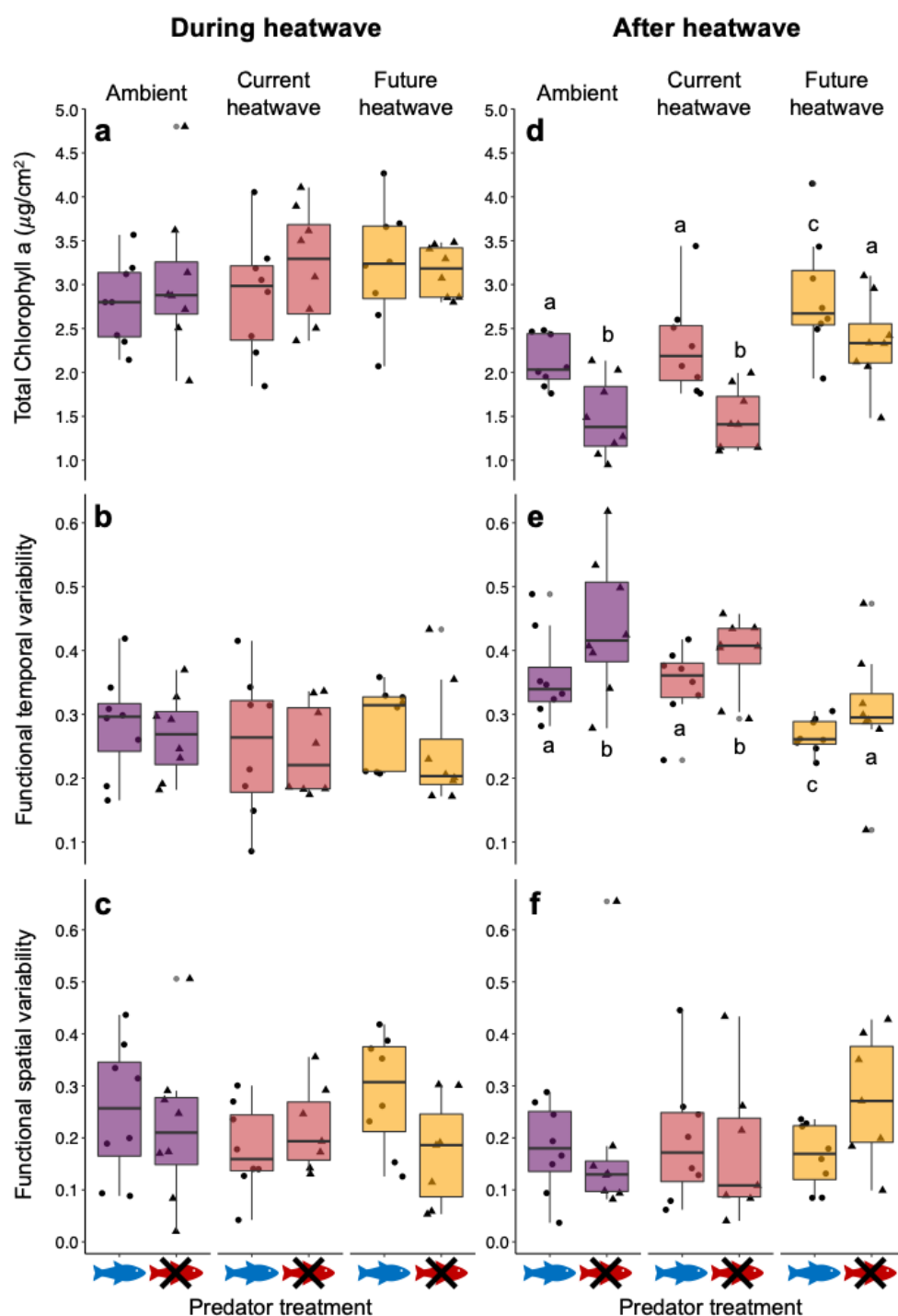


Figure 3.2 | Effects of predation and heatwaves on total algal biomass and its temporal and spatial variability during (a-c) and after (d-f) heatwaves. (a, d) Total chlorophyll *a* ($\mu\text{g cm}^{-2}$) and its corresponding (b, e) temporal and (c, f) spatial variability in my experimental mesocosms (a-c) during the five-day peak heatwave period (days 22-27 inclusive) and (d-f) over the 20-day post-heatwave recovery period (days 30-50 inclusive). Results for total chlorophyll *a* and functional spatial variability were measured at the final day of each period, whereas functional temporal variability was measured throughout the two time periods (over 5 and 20 days, respectively). Boxplots represent the range (box = median and interquartile range) of values across the eight mesocosm replicates by treatment in the presence or absence of predatory fish [X-axis] under (from left to right) the ambient,

current heatwave (+2.76 °C), and projected future heatwave (+6.06 °C) treatments. Significant ($p < 0.05$) pairwise contrasts (see Table 3.1) are denoted with superscript/subscript letters.

I found legacy effects of my experimental heatwaves that persisted after 20 days of post-heatwave recovery on algal biomass and functional variability. At the end of the experiment, total algal biomass was significantly higher in mesocosms under heatwave treatments (ANOVA, $F_{2,42} = 13.2$, $p < 0.001$; Fig. 3.2d), with projected future heatwaves yielding higher algal biomass than both current heatwaves and ambient temperatures (Tukey HSD, $p_{\text{adj}} < 0.001$ in both cases; Table 3.1). Heatwaves also reduced the functional temporal variability of algal communities during the post-heatwave recovery period (ANOVA, $F_{2,42} = 9.46$, $p < 0.001$; Fig. 3.2e), which was lowest under projected future heatwaves (Tukey HSD, $p_{\text{adj}} < 0.001$ and $= 0.008$ for ambient conditions and current heatwaves; Table 3.1). The presence of predators caused a trophic cascade by the end of the experiment, increasing the total biomass of algal communities (ANOVA, $F_{1,42} = 22.1$, $p < 0.001$; Fig. 3.2d). Predators also stabilised the mesocosm communities by decreasing their functional temporal variability (ANOVA, $F_{1,42} = 6.06$, $p = 0.018$; Fig. 3.2e). Though both predator presence and heatwaves affected algal biomass and temporal variability, their interaction was not significant in either case (ANOVA, $p > 0.05$; Table 3.1). I found no main or interactive treatment effects on functional spatial variability 20 days after the heatwave (ANOVA, $p > 0.05$; Fig. 3.2f).

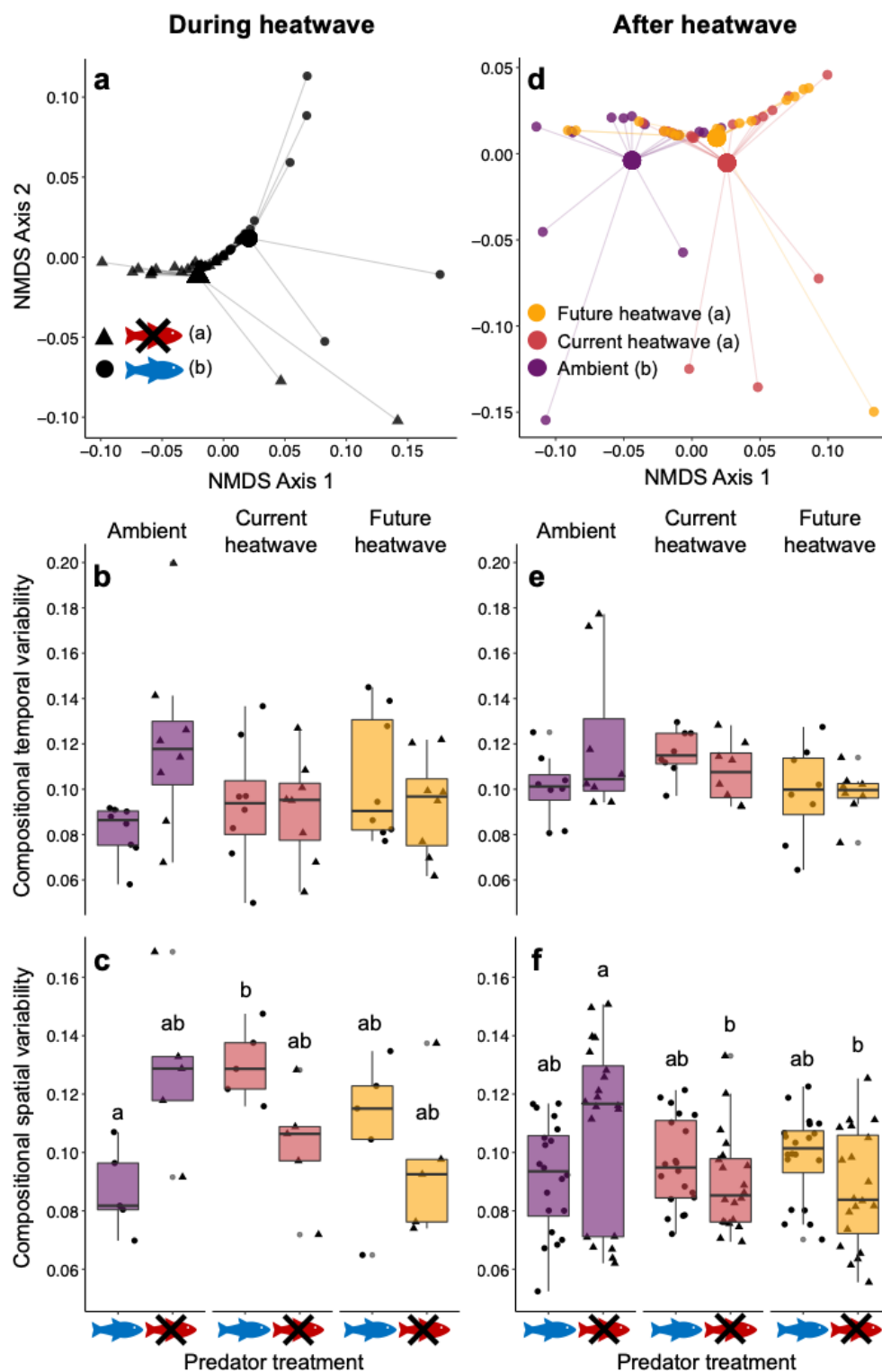


Figure 3.3 | Effects of predation and heatwaves on algal structure and compositional variability during (a-c) and after (d-f) heatwaves. (a, d) Nonmetric multidimensional scaling (NMDS) ordinations of algal community composition in mesocosms belonging to the different (a) predator (stress = 0.021) and (d) heatwave (stress = 0.045) treatments. Only significant ($p < 0.05$) treatment effects are shown in each case (see Table 3.1). Large points represent treatment level centroids for significant treatment effects, whereas small points represent algal communities within individual mesocosms. (b, e) Temporal and (c, f) spatial variability in algal composition. Panels (a-c) correspond to the 5-day peak

heatwave (days 22-27 inclusive), while (d-f) are for the 20-day post-heatwave recovery period (days 30-50 inclusive). Boxplots represent the range (box = median and interquartile range) of values across 8 mesocosms (b, e) or across days (c, f) within each treatment in the presence or absence of predatory fish [X-axis] under (from left to right) the ambient, current heatwave (+2.76 °C), and projected future heatwave (+6.06 °C) treatments. Significant ($p < 0.05$) pairwise contrasts (Table 3.1) are denoted with superscript/subscript letters.

Heatwaves left legacy effects on algal community structure (PERMANOVA, $F_{2,42} = 5.74$, $p = 0.001$; Fig. 3.3d), which, at the end of the experiment, differed in ambient temperature treatments relative to that following both current (Bonferroni, $p_{\text{adj}} = 0.003$) and future ($p_{\text{adj}} = 0.006$) heatwaves. In both cases, treatment differences were driven primarily by reductions in cyanobacteria biomass after heatwaves (Table B.5). While the effect of heatwaves on compositional temporal variability during the post-heatwave recovery period was not statistically significant at the $p < 0.05$ level (ANOVA, $F_{2,42} = 2.73$, $p = 0.077$; Fig. 3.3e), there was a significant interaction between predator and heatwave treatments on compositional spatial variability (ANOVA, $F_{2,114} = 5.88$, $p = 0.004$; Fig. 3.3f). Specifically, predators negated the destabilising effect of heatwaves on spatial variability; in the absence of predators, compositional spatial variability was lower under both current (Tukey HSD, $p_{\text{adj}} = 0.032$) and future ($p_{\text{adj}} = 0.012$) heatwaves, but there was no difference among heatwave treatments when predators were present ($p_{\text{adj}} > 0.05$; Table 3.1).

Heatwaves also modified the structure of macroinvertebrate communities (PERMANOVA, $F_{2,46} = 2.19$, $p = 0.031$; Fig. 3.4a), leading to communities that were exposed to the higher intensity (*i.e.*, future heatwaves) being significantly different from those under ambient conditions ($p_{\text{adj}} = 0.033$). Differences in community composition were driven mainly by increases in the densities of Chironomidae in mesocosms that experienced heatwaves (Table B.6a). The presence of my focal predatory fish also restructured macroinvertebrate communities significantly (PERMANOVA, $F_{1,46} = 7.25$, $p < 0.001$; Fig. 3.4b), particularly by increasing densities of orthocladiid chironomids and reducing those of the mayfly *Baetis thermicus* and amphipod *Sternomoera yezoensis* (Table B.6b). Regardless of heatwave treatment, both the taxon richness (ANOVA, $F_{1,42} = 5.96$, $p = 0.019$; Fig. B2) and density (ANOVA, $F_{1,42} = 31.4$, $p < 0.001$; Fig. 3.4c) of benthic macroinvertebrates were significantly higher in the absence of predators. This, in turn, resulted in higher rates of leaf litter processing (ANOVA, $F_{1,42} = 13.5$, $p < 0.001$; Fig. 3.4d) when predators were absent. Heatwaves or their

interactive effects had, however, no effect on macroinvertebrate richness, density, or leaf litter decomposition, including microbial degradation (Tables 3.1 and B3).

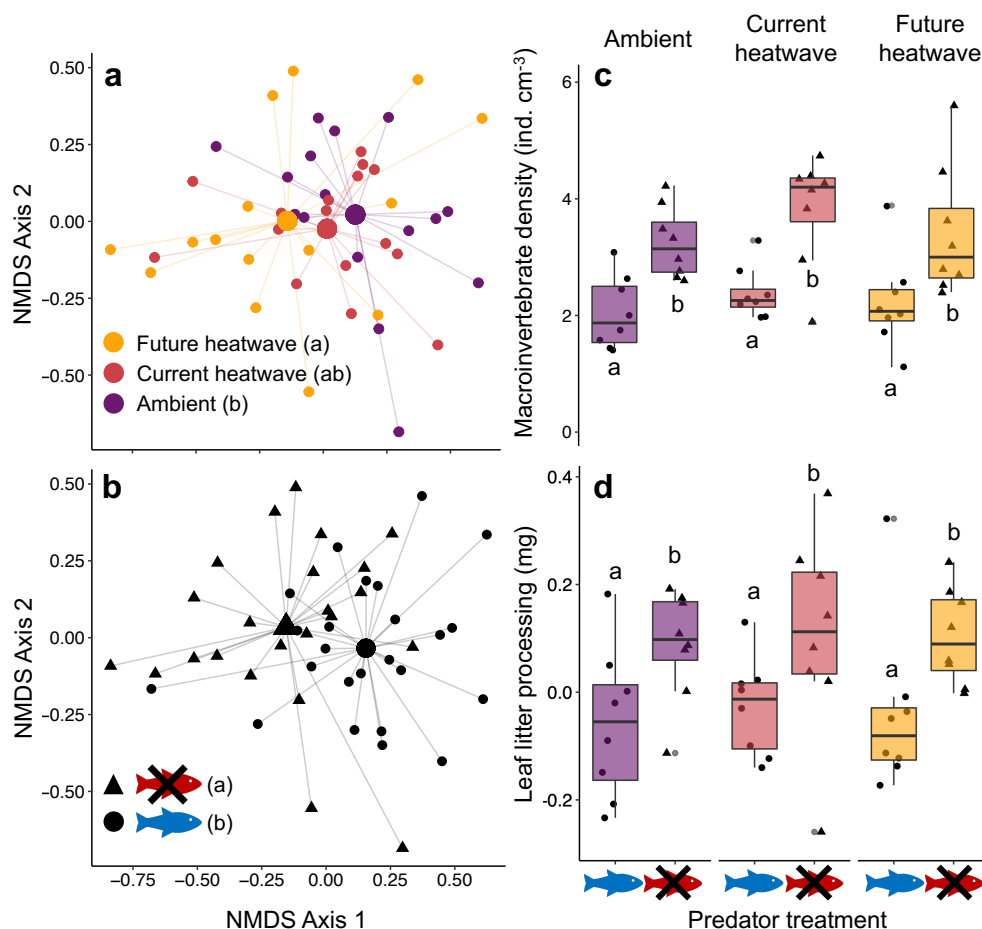


Figure 3.4 | Effects of predation and heatwaves on macroinvertebrate community composition, density, and leaf litter processing at the end of the experiment. (a-b) Nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate community composition in mesocosms belonging to the different (a) heatwave and (b) predator treatments (stress = 0.166). Large points represent treatment-level centroids and small points represent individual mesocosm communities. (c) Macroinvertebrate density (individuals cm⁻³) and (d) leaf litter processing by macroinvertebrates, the latter calculated as the mesocosm-specific change in leaf mass after correcting for microbial degradation (where negative values represent interactions between macroinvertebrates and microbes [Kominoski *et al.* 2011], reducing proportional microbial degradation in large versus small leaf packs). Boxplots represent the range (box = median and interquartile range) of values across mesocosms within treatments in the presence or absence of predatory fish [X-axis] under (from left to right) the ambient, current heatwave (+2.76 °C), and projected future heatwave (+6.06 °C) treatments. Significant ($p < 0.05$) pairwise contrasts (Table 3.1) are denoted with superscript/subscript letters.

3.5 DISCUSSION

My results demonstrate that predators can help to mitigate the destabilising effects of heatwaves on stream ecosystems. In the absence of predatory sculpin, heatwaves homogenised the composition of algal communities in space. However, where present, my focal predator buffered mesocosms against these negative heatwave impacts. The presence of fish predators also reduced macroinvertebrate densities, which, in turn, suppressed leaf litter processing. Taken together, these results suggest that the predator moderated heatwave impacts and modified ecosystem functioning via a classical trophic cascade (Konishi *et al.* 2001; Kishi *et al.* 2005; Donohue *et al.* 2017; Rasher *et al.* 2020). Though my experimental design does not allow us to explicitly identify the mechanisms underpinning the patterns I observed, they nonetheless suggest strongly that the stabilising effect of predators on algal communities exposed to heatwaves was an indirect consequence of the effects of the predators on their macroinvertebrate prey. Primary consumers can buffer producer assemblages against the effects of warming in terrestrial and marine systems (Post & Pedersen 2008; Kordas *et al.* 2017). For example, Kordas *et al.* (2018) found that a key mechanism driving this pattern in rocky intertidal communities was the action of herbivores modifying the spatial variability of algal community structure. My findings suggest predator effects on spatial variability occur indirectly through their effects on macroinvertebrate herbivores, highlighting the importance of both direct and indirect ecological interactions in providing resistance against heatwaves and climate warming more generally (Zarnetske *et al.* 2012; Kordas *et al.* 2017; Goldenberg *et al.* 2018; see also Beauchesne *et al.* 2021).

Heatwaves left lasting effects on both macroinvertebrate composition and algal biomass in my experimental system, even though many of their impacts were not apparent during or even at the end of the heatwaves themselves. However, after 20 days of post-heatwave recovery, mesocosms exposed to future heatwaves had higher total biomass and lower temporal variability of algal biomass, and had modified algal and macroinvertebrate communities. If heatwave impacts on algal communities were indeed mediated by macroinvertebrates—as suggested by my finding of predator effects on macroinvertebrate richness, abundance, and community structure—the observed lag in heatwave effects on algal biomass and structure is likely a consequence of the time taken for heatwave impacts to propagate through the food web (Konishi *et al.* 2001; Donohue *et al.* 2017). The fact that both heatwave and predator effects on algal communities were found at the end of the experiment, even though they were less apparent during and immediately following the heatwaves, implies that the consequences of heatwaves

for aquatic communities can be considerable even if not immediately detectable, with the potential for legacy effects to compound the impact of prior stressors over longer timescales (Jackson *et al.* 2021) or insidious effects of press perturbations such as background warming becoming obvious only when interacting with additional stressors (*e.g.*, Rasher *et al.* 2020). My results underscore the fundamental role of scale in understanding variability (Clark *et al.* 2021), including the pitfalls of not considering transience or legacy effects when interpreting the ecological consequences of extreme climatic events (Downing *et al.* 2008; Waldock *et al.* 2018; Miller *et al.* 2021; Ross *et al.* 2021c).

Though the predatory sculpin altered both the structure and variability of algal community composition during and after the heatwave, its presence took longer to affect functional variability and algal biomass. This suggests a difference in the time taken for heatwaves to affect functional versus compositional stability, and supports the notion that the drivers of functional and compositional stability are largely independent of one another (Baert *et al.* 2016; Magurran *et al.* 2018; Hillebrand & Kunze 2020; Jacquet & Altermatt 2020). It is also consistent with the recent finding that individual species provide complex and frequently contrasting contributions to different dimensions of ecological stability (White *et al.* 2020b). Further work examining the temporal scales of relevance when measuring functional versus compositional stability will help achieve a process-based understanding of disturbance and recovery through a multidimensional lens (Donohue *et al.* 2013; Baert *et al.* 2016; Hillebrand *et al.* 2018; Hillebrand & Kunze 2020).

As extreme events become more frequent and intense in future (Easterling *et al.* 2000; Oliver *et al.* 2018a), complex disturbance regimes will likely unfold (Eveleens *et al.* 2019; Jacquet & Altermatt 2020; Miller *et al.* 2021). Both disturbance regimes and their legacies can moderate the impact of subsequent disturbance events (García Molinos & Donohue 2011; Mrowicki *et al.* 2016; Eveleens *et al.* 2019; Fugère *et al.* 2020; Miller *et al.* 2021). The ecological impacts of heatwaves may, therefore, be compounded if recovery from a previous disturbance is incomplete (*e.g.*, Stockwell *et al.* 2020). Alternatively, ecological memory may prime ecosystems against repeated disturbances, attenuating their impact or facilitating community rescue (Fugère *et al.* 2020; Miller *et al.* 2021; Jackson *et al.* 2021). That said, even communities exposed to frequent climate extremes may exhibit temperature-driven biodiversity change under increasingly severe disturbance regimes (*e.g.*, Harris *et al.* 2018). A key next step is thus to test experimentally the consequences of increasingly complex disturbance regimes and repeated heatwaves for the functional and compositional stability of

multitrophic communities (Eveleens *et al.* 2019; Kéfi *et al.* 2019; Jacquet & Altermatt 2020; Stockwell *et al.* 2020; Jackson *et al.* 2021; Miller *et al.* 2021).

I used predictions from the IPCC RCP8.5 high-emission scenario to inform my future projected heatwaves. RCP8.5 represents a worst-case emission scenario, with previous warming experiments mostly manipulating temperatures less severe than those changes predicted under RCP8.5 (Korell *et al.* 2020). My results may therefore represent an extreme case, and I am unable to say with certainty whether predators would play similar stabilising roles under future heatwaves constructed based on more moderate emission stabilisation scenarios (RCP6.0-2.6). Nevertheless, CO₂ emissions are currently tracking RCP8.5 projections (Schwalm *et al.* 2020). Despite RCP8.5 being quite an extreme scenario, projections for the end of the century based on RCP8.5 may yet represent a plausible future (Schwalm *et al.* 2020). My finding that several heatwave effects, particularly on algal biomass and macroinvertebrate community structure, were weaker or not detectable under current heatwaves underscores the importance of avoiding extreme warming scenarios by enforcing strict climate change mitigation policies. Locally-informed climate change experiments, such as mine, considering a range of future climate scenarios are essential to provide much more realistic predictions of the likely ecological impacts of climate change (Korell *et al.* 2020).

As with all field-based ecological experiments, my study is limited in scope by its temporal scale. Beyond the 20 days of post-heatwave monitoring that I conducted, there may have been even longer-lasting legacies of heatwaves on community composition, functioning, and/or stability that were not detected within the timeframe of my measurements (Downing *et al.* 2008; Marcarelli *et al.* 2020; Clark *et al.* 2021; Ross *et al.* 2021c). For example, Downing *et al.* (2008) found that asynchrony among zooplankton taxa occurred only at time periods >80 days in response to recurring nutrient pulses, while synchrony dominated at shorter time scales and in constant environments. Marcarelli *et al.* (2020) also reported differences in the magnitude and direction of both direct and indirect trophic interactions in the Horonai stream food web through time, revealing scale-dependent top-down control of macroinvertebrates by predatory fish (including *C. nozawae*). Taken together, these results suggest the role of predators in mitigating heatwave impacts may be more pronounced over longer timescales. Alternatively, heatwave legacies may dissipate over longer time scales (*e.g.*, over months compared to weeks), as transient dynamics converge to long-term system dynamics post-disturbance (Hastings *et al.* 2018). Nevertheless, the fact that I found interactions between sculpin and heatwaves highlights the importance of

top-down control in the Horonai system, even over relatively short time scales, such as in my experiment.

The size of my experimental units also limited the capacity of my experiment to mimic the full complexity of the Horonai stream ecosystem (Yamamoto *et al.* 1988; Goto & Nakano 1993; Marcarelli *et al.* 2020), and the limited availability of microclimatic refugia in my mesocosm systems may have over-exposed macroinvertebrates and sculpin to heat stress compared to the natural stream (Isaak *et al.* 2016). Even so, the natural immigration and dispersal of algae, microorganisms, and invertebrates in the experimental system and continuous exposure to natural environmental fluctuations for the duration of the experiment increased considerably the realism of my experimental communities relative to a closed system. It is also possible that immigration from the stream may have dampened the effects of heating on my multitrophic communities (Leibold *et al.* 2004; Fugère *et al.* 2020), since individuals from the regional species pool upstream would not have been exposed to the heatwave until dispersal into my experimental system. Were that the case, the potential for temperature-driven biodiversity change on the stream system could be considerably greater than suggested by my experiment (Konishi *et al.* 2001; Kishi *et al.* 2005; Wernberg *et al.* 2013; Fussmann *et al.* 2014; García Molinos *et al.* 2016; Waddock *et al.* 2018; Inagaki *et al.* 2020).

By revealing that predators can mitigate the destabilizing effects of heatwaves on multitrophic stream communities, this study adds to a growing body of literature exploring the contribution of individual species to the stability of communities, ecosystem functioning, and service supply (Chapter 2; Worm *et al.* 2006; Post & Pedersen 2008; Oliver *et al.* 2015a; Kordas *et al.* 2017; White *et al.* 2018, 2020b; Smale *et al.* 2019; Gerhard *et al.* 2020; Ross *et al.* 2021a). As climate change increases the frequency and intensity of extreme climatic events such as heatwaves (Oliver *et al.* 2018a), predators may play a key role in tempering the ecological consequences of such extremes through both their direct and indirect effects on food webs (Kishi *et al.* 2005; Rasher *et al.* 2020). Further, our results highlight the potential for human impacts on predators to interact with other elements of global environmental change, worsening the consequences of trophic downgrading on ecosystems (Estes *et al.* 2011; Rasher *et al.* 2020). I conclude that much greater focus should be given to biotic multipliers of climate change and the role of community structure and biotic interactions in regulating ecological responses to extreme climatic events (Zarnetske *et al.* 2012; Rasher *et al.* 2020).

CHAPTER 4 | UTILITY OF ACOUSTIC INDICES FOR ECOLOGICAL MONITORING IN COMPLEX SONIC ENVIRONMENTS

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AUTHOR CONTRIBUTION:

I designed the study, conducted the aural inventory, analysed the data, produced
the figures, and led the writing of the manuscript with input from all coauthors.

4.1 SUMMARY

With the continued adoption of passive acoustic monitoring as a tool for rapid and high-resolution ecosystem monitoring, ecologists are increasingly making use of a suite of acoustic indices to summarise the sonic environment. Though these indices are often reported to well represent some aspect of the biology of an ecosystem, the degree to which they are confounded by various extraneous sonic conditions is largely unknown. I conducted an aural inventory across 23 field sites in Okinawa to identify the number of unique animal sounds present in recordings. Using these values of ‘measured richness’, I then examined how the performance of 11 commonly-used acoustic indices varied across a range of sonic conditions (including in the presence and absence of insect stridulations, audible wind or rain, and human-related sounds). My analysis identified both well- and poor-performing acoustic indices, as well as those that were particularly sensitive to sonic conditions. Only two indices reflected measured richness across the full range of sonic conditions examined. A few indices were relatively insensitive to extraneous sonic conditions, but no index correlated with measured richness when masked by sound from broadband stridulating insects. My results demonstrate considerable sensitivity of most commonly used acoustic indices to confounding sonic conditions, highlighting the challenges of working with large acoustic datasets collected in the field. I make practical recommendations for acoustic index use based on study design, with the aim of identifying the suite of acoustic indices with greatest utility as indicators for rapid biodiversity monitoring and management of the world’s natural soundscapes.

4.2 INTRODUCTION

The nascent field of ecoacoustics focuses on the properties and dynamics of biological sound while considering the acoustic environment in which sound is produced (Servick 2014; Sueur & Farina 2015). The field extends bioacoustics by shifting away from identifying individual species and their vocal properties (*e.g.*, Aide *et al.* 2013) towards quantifying the ‘soundscape’—the suite of all observable sounds produced in an ecosystem (Pijanowski *et al.* 2011a, 2011b). Ecoacoustics is rooted in the idea that all vocalising animals compete for niche space in the sensory environment (Krause 1987). Since acoustic space is limited, animals must partition the soundscape across temporal and frequency domains to be heard (Slabbekoorn 2018; Marín-Gómez *et al.* 2020). This, in turn, means that soundscapes can represent ecosystem condition, since more diverse systems

should exhibit increasingly structurally complex and diverse use of acoustic space (Dumyahn & Pijanowski 2011; van der Lee *et al.* 2020). Accordingly, soundscapes are often considered a proxy for various facets of ecological communities, including their diversity (Gasc *et al.* 2013; Harris *et al.* 2016; Mammides *et al.* 2017), abundance (Boelman *et al.* 2007; Pieretti *et al.* 2011; Buxton *et al.* 2018c), and biomass (Elise *et al.* 2019).

With recent advances in recording, processing and data-storage technology, passive acoustic monitoring is becoming increasingly tractable on even a moderate research budget (Gibb *et al.* 2019). Acoustic monitoring approaches have several advantages over traditional survey techniques, including their ability to produce data on a fine temporal scale (Ross *et al.* 2018a), capture long-term trends (Sueur *et al.* 2019), include or target rare species (Znidarsic *et al.* 2020), and facilitate surveys of remote or challenging environments (Burivalova *et al.* 2019a). Accordingly, there is growing interest in using soundscapes to ask ecological questions (Lomolino *et al.* 2015; Deichmann *et al.* 2018; Sugai *et al.* 2018; Burivalova *et al.* 2019b) and in establishing acoustic recording protocols to monitor changes in the soundscape through time and space (Gasc *et al.* 2018; Ross *et al.* 2018a; Sueur *et al.* 2019; Sethi *et al.* 2020b).

Since the development of ecoacoustics as a field, there has been a proliferation of acoustic indices that aim to characterise the ecology of a system (Pieretti *et al.* 2011; Kasten *et al.* 2012; Sueur *et al.* 2014). Most such indices work by summing or contrasting the acoustic power within different frequency ranges. Sueur *et al.* (2014) reviewed the range of indices for summarising the soundscape, while recognising that there is never likely to be a single value that accurately represents all levels of local or regional biodiversity. Although some acoustic indices may correlate—positively or negatively—with species richness (Depraetere *et al.* 2012; Jorge *et al.* 2018), inconsistencies in these relationships (Bradfer-Lawrence *et al.* 2020) have led to concerns over their broad applicability across taxa and habitats (Mammides *et al.* 2017; Gibb *et al.* 2019).

However, soundscapes are rich in information beyond biological signals that indicate the presence of particular animals. For example, soundscapes may provide information on landscape or habitat structure (Fuller *et al.* 2015; Burivalova *et al.* 2019b), the presence of particular weather conditions or storms (Sánchez-Giraldo *et al.* 2020), background levels of anthropogenic noise and its change (Gill *et al.* 2017), or the presence and identity of atypical sounds such as illegal logging activity (Sethi *et al.* 2020b). Moreover, soundscapes include valuable information on the phenology (*e.g.*, Oliver *et al.* 2018b), and temporal dynamics of vocalising animals (Gottesman *et al.* 2018; Marín-Gómez *et al.*

2020), including disruptive broadband insect choruses (Hart *et al.* 2015). Although this study focuses on the ability of acoustic indices to act as proxies for biodiversity, I acknowledge the myriad ways soundscapes and acoustic indices provide information beyond merely acting as biodiversity indicators.

The ability of acoustic indices to reflect some facet of biodiversity (that is, their *performance*) may be sensitive to a range of conditions. For example, human-related sounds ('anthropophony,' Kasten *et al.* 2012), interfere with animal communication, particularly in the lower frequency range, and several acoustic indices may consequently perform poorly in urban areas (Fairbrass *et al.* 2017). Similarly, soniferous insects, particularly stridulating orthopterans and cicadas, can mask other animal sounds with their broadband choruses (Hart *et al.* 2015). Sonic conditions such as these could, therefore, decouple acoustic indices from the biology they supposedly represent. Consequently, there is a need to examine the change in performance (henceforth *sensitivity*) of different acoustic indices to a broad range of sonic contexts in order to identify a best performing index or suite of indices across these conditions with utility for biodiversity monitoring (Harris *et al.* 2016; Eldridge *et al.* 2018).

Here, I test the performance of 11 commonly used acoustic indices across a range of sonic conditions. My aim is to identify whether particular indices outperform others as biodiversity indicators across contexts. I use an aural inventory approach to manually count unique biotic sound types (similar to vocalising species richness) from audio samples collected as part of the OKEON Churamori Project, comprising more than 13,800 minutes of recordings from across the island of Okinawa, Japan (Ross *et al.* 2018a). I use these data to compare the performance—measured as the strength of relationships (positive or negative) with richness—of acoustic indices across three sets of sonic conditions, namely in the presence and absence of each of anthropophony, soniferous insects, and geophony (wind, rain *etc.*). Based on my findings, I then provide guidance on which indices are likely to perform well for a given study, and I make recommendations for future acoustic surveys to make best use of acoustic indices as indicators of biodiversity.

4.3 METHODS

4.3.1 STUDY LOCATION AND EXPERIMENTAL SYSTEM

This study was part of the OKEON Churamori Project (Okinawa Environmental Observation Network; OKEON 美ら森プロジェクト) in Okinawa, the largest

island of the Ryukyu archipelago, Japan. OKEON uses a suite of complementary monitoring techniques to monitor Okinawa's ecosystems in space and time. At each of the project's 24 field sites, representing the full range of land cover types on the island, a Song Meter SM4 recorder (Wildlife Acoustics Inc., Concord, MA, USA) has been installed on a tree at approximately breast height (~1.3m), since at least February 2017 (Ross *et al.*, 2018a). These devices are used to record sound at default gain settings (+16 dB) with two omnidirectional microphones. Recorders are programmed on a recording schedule of 10-min at the beginning of each hour and half-hour (*i.e.*, 10-min on, 20-min off). Data are saved in stereo WAVE format at a sampling rate of 48-kHz to an SD card, which is collected on a two-week field rotation schedule when batteries and SD cards are replaced. Data are then archived with the Okinawa Institute of Science and Technology's high-performance computing centre.

Overall, Okinawa presents a challenging sonic environment in which to monitor biological sound. Okinawa's North-South urbanisation gradient results in considerably more anthropophony in the South than in the forested North of the island (Ross *et al.* 2018a). Geophony is common from late summer through winter, particularly during rainy season and typhoon season, when Okinawa often experiences heavy winds and rain in short bursts. Summer soundscapes are dominated by cicada choruses during daytime and stridulating orthopterans at night. Anuran choruses are common year-round, but peak during breeding season (usually winter-spring but breeding season varies by species). Okinawa has a rich avifauna (McWhirter *et al.* 1996), including several species endemic to the Northern Yanbaru forest (Itô *et al.* 2000) and migratory species such as the Ruddy Kingfisher (*Halcyon coromanda*) and Grey-faced Buzzard (*Butastur indicus*). Nocturnal Ryukyu Flying Foxes (*Pteropus dasymallus*) are also common across the island, including in urban areas. Most field sites are within audible distance of a road (Ross *et al.* 2018a), and some recordings include daily tests of the typhoon warning system. Commercial aeroplane traffic and military activity (including aircraft noise and occasional audible gunshots) make additional contributions to the anthropogenic component of Okinawa's soundscape (Cox 2010).

4.3.2 AURAL INVENTORY

I conducted an aural inventory by selecting 64 recordings of 10-min duration from each of 23 OKEON field sites (Ross *et al.* 2018a); one site was excluded due to a mismatch in the temporal extent of available data. To ensure recordings were equally representative of both seasons and time-of-day at each site, they were

selected from the middle month of each of Okinawa's seasons (January, April, July, and October), from four dates within each season (the 5th, 10th, 15th and 20th of each month), and at each of four times of day (midnight, midday, and two samples that aimed to capture dawn and dusk choruses at sunrise and sunset, respectively). Dawn chorus times were adjusted seasonally using the closest recording before the observed sunrise time for each season, and after observed sunset for the dusk chorus. This resulted in a total of 13,860-min of continuous audio data across all sites.

I counted the number of unique biotic sound types (animal sounds including birds, insects, frogs, geckos *etc.*) in each 10-minute recording (following Depraetere *et al.* 2012; Machado *et al.* 2017). This aural inventory approach comprised listening to recordings while visually inspecting spectrograms produced via Fast Fourier Transformation (window size = 256) in Kaleidoscope Pro (ver 5.1.8; Wildlife Acoustics Inc., Concord, MA, USA). Biotic sound-type richness—henceforth ‘measured richness’—was quantified as the number of distinct sound-types corresponding to unique species based on their spectral properties and cross-referenced with appropriate databases to prevent over-splitting sound classes (*e.g.*, www.xeno-canto.org).

For each recording, I noted the presence or absence of three distinct sonic conditions (Table C.1). If there was audible human-related sound in the recording, I marked the recording as anthropophony present. I also noted the presence or absence of audible geophony (*e.g.*, wind, rain) in each recording. Finally, if the recording contained audibly stridulating soniferous insects, I marked the recording as insects present. Note that this classification includes both broadband sounds produced by nocturnal orthopterans and the sonically disruptive cicada activity characteristic of Okinawa's summertime, though these categories can be separated by time-of-day. The total biodiversity of a system includes stridulating insects, but these insects contribute ambient long-duration broadband sound to the soundscape rather than transient animal signals such as birdsong (Hart *et al.* 2015), justifying inclusion of insect sounds both as biotic signal and as a potentially confounding sonic condition.

4.3.3 ACOUSTIC INDEX PROCESSING

For each 10-minute recording, I calculated a number of commonly used acoustic indices (Table C.2) in *R* (ver 4.0.0, R Core Team, 2020) using the *seewave* (ver 2.1.6, Sueur *et al.* 2008a) and *soundecology* (ver 1.3.3, Villanueva-Rivera & Pijanowski 2018) packages. These indices were acoustic complexity (ACI, Pieretti *et al.* 2011); acoustic diversity (ADiv) and acoustic evenness (AEve, Villanueva-

Rivera *et al.* 2011); the bioacoustic index (BioA, Boelman *et al.* 2007), and the related acoustic entropy (H) and temporal entropy indices (H_t , Sueur *et al.* 2008b); acoustic richness (ARic) and the median of the amplitude envelope (M, Depraetere *et al.* 2012); and the normalised difference soundscape index (NDSI), calculated by combining two component indices which I also analysed separately, anthropophony ($NDSI_{Anthro}$) and biophony ($NDSI_{Bio}$, Kasten *et al.* 2012). Though various subsets of these indices have been related previously to species richness estimated with point counts in the field or via an aural inventory approach (Table C.2), no study I am aware of has examined such a comprehensive set of indices across the broad range of sonic conditions considered here (Bradfer-Lawrence *et al.* 2020).

4.3.4 STATISTICAL ANALYSES

I first constructed a correlation matrix from all 11 acoustic indices to determine how suites of indices may provide congruent or distinct information about the soundscape. I then tested the performance of the various acoustic indices by relating each index (Table C.2) to the measured richness for each sound recording across all sites and sonic conditions ($n = 1,386$). To test the significance of relationships with richness, I fitted generalised linear mixed models (GLMMs) and used a model selection approach to choose from a full model that included the effect of site-specific measured richness on acoustic index values, while accounting for the influence of site and time-of-day as random effects. Models were produced using a beta distribution in the glmmTMB package (ver 1.0.1, Brooks *et al.* 2017). The beta distribution allows my models to cope with a range of data distributions including zero-inflation (Ferrari & Cribari-Neto 2004). In all cases, I used the Akaike Information Criterion (AIC) to assess model fit, and model simplification was based on maximum likelihood estimation to allow comparison of models with different fixed-effects structures. I assessed the support for each model component in the best fitting model by comparing AIC and using likelihood ratio tests to indicate the significance of model term removal. I measured performance as the model slope of the acoustic index ~ measured richness relationship, with the t-statistic of the model slope indicating whether the slope differs from zero. Larger absolute model slopes represent stronger relationships with measured richness, but I opted to preserve information on the direction (positive or negative) of this relationship by including the sign of the relationship in index performance values.

Acoustic index values vary considerably among indices and are often skewed, so I normalised values by dividing by their maximum for each index except

NDSI (Bradfer-Lawrence *et al.* 2020); NDSI is bounded -1 to 1 and so was scaled instead using $(\text{NDSI} + 1)/2$ (Fairbrass *et al.* 2017). I treated measured richness as a site-specific property by using the mean of all measured richness values per site in my GLMMs. Hence, richness was a zero-bounded continuous variable rather than a value per recording (Bradfer-Lawrence *et al.* 2020).

Seasonal patterns of animal activity may obscure the relationship between acoustic indices and measured richness if ephemeral animal sounds do not make the greatest contribution to the soundscape (Hart *et al.* 2015). I therefore additionally fitted all GLMMs with the interaction between season and measured richness as a fixed effect. To account for site-specific differences in seasonal richness changes, measured richness was taken as the mean richness per site per season. Since the interaction effect of season was always included in the best performing model (Table C.3), I assessed performance of acoustic indices for each season separately.

To establish whether there were certain indices that consistently outperformed others across my chosen range of sonic conditions, I fitted GLMMs between acoustic indices and richness as above, again with site and time-of-day as random effects, but with an interaction effect for each of the three sets of focal sonic conditions (Table C.1). I measured performance as the model slope for the relationship between each acoustic index (Table C.2) and measured richness in the absence of my three potentially confounding sonic conditions (Table C.1). To quantify the sensitivity of each index to the various sonic conditions, I took the inverse of the absolute change in model slope in the presence and absence of a sonic condition as a measure of whether the relationship between indices and measured richness improves or declines in its presence. I used the inverse of absolute slope change because doing so produces intuitive sensitivity scores which increase as acoustic indices are more affected by a sonic condition. Using t-statistics, I noted whether model slopes differed from zero in the presence of each sonic condition, regardless of the index's sensitivity to the condition. Finally, to determine whether the sensitivity of acoustic indices varied across seasons, I constructed the same GLMMs but with a three-way interaction between measured richness, each sonic condition in turn, and season (Appendix C.1.2).

4.4 RESULTS

I found two suites of positively correlated acoustic indices (Fig. 4.1). One comprised NDSI, NDSI_{Bio} , BioA, ADiv, and H which positively correlated and

AEve and $\text{NDSI}_{\text{Anthro}}$ which also positively correlated but were negatively related to the aforementioned indices (Fig. 4.1). The remaining indices (that is, ARic, H_t , ACI, and M) were largely independent of each other, though ARic and H_t correlated positively (Fig. 4.1).

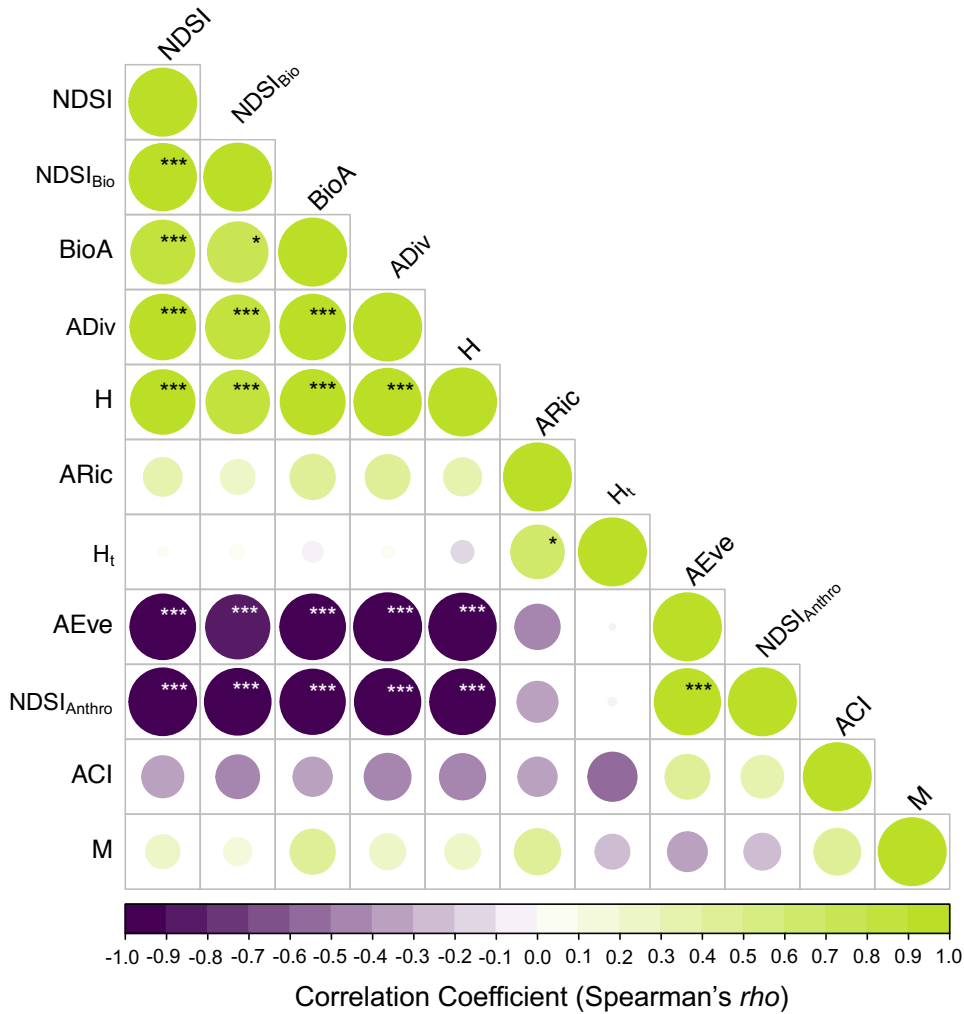


Figure 4.1 | Pairwise relationships between acoustic indices. Size and colour of circles represents the correlation coefficient (Spearman's ρ) between pairs of acoustic indices. Significance level of pairwise correlations is represented with * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.005$). I found one main suite of positively correlating indices, comprising NDSI, NDSI_{Bio} , BioA, ADiv, H, AEve, and $\text{NDSI}_{\text{Anthro}}$.

4.4.1 ACOUSTIC INDEX PERFORMANCE

When considering the full range of sonic conditions included in my study, and ignoring seasonality, most acoustic indices performed poorly, and did not reflect measured richness (Fig. 4.2). In fact, only H_t was associated significantly with richness ($t = -2.01$, $P = 0.044$) irrespective of conditions, though the performance

of ARic, which had the greatest absolute model slope, was bordering on statistical significance ($t = -1.95$, $P = 0.051$).

For all indices, the best performing model always included the interaction effect of season on measured richness (Table C.3). For a given season the identity of the best performing index varied, with some indices performing better in particular seasons (Fig. 4.2B, C.1). ARic and H_t still performed best overall, with significant relationships during spring and autumn for both indices, plus for winter in the case of H_t . During winter, $NDSI_{Anthro}$ and $NDSI_{Bio}$ were, respectively, positively ($t = 2.2$, $P = 0.028$) and negatively ($t = -2.45$, $P = 0.014$) related to measured richness, while ACI related positively to measured richness in spring ($t = 2.51$, $P = 0.012$). Only one index, H, was significantly related to measured richness during summer ($t = 1.97$, $P = 0.049$; Fig. 4.2B).

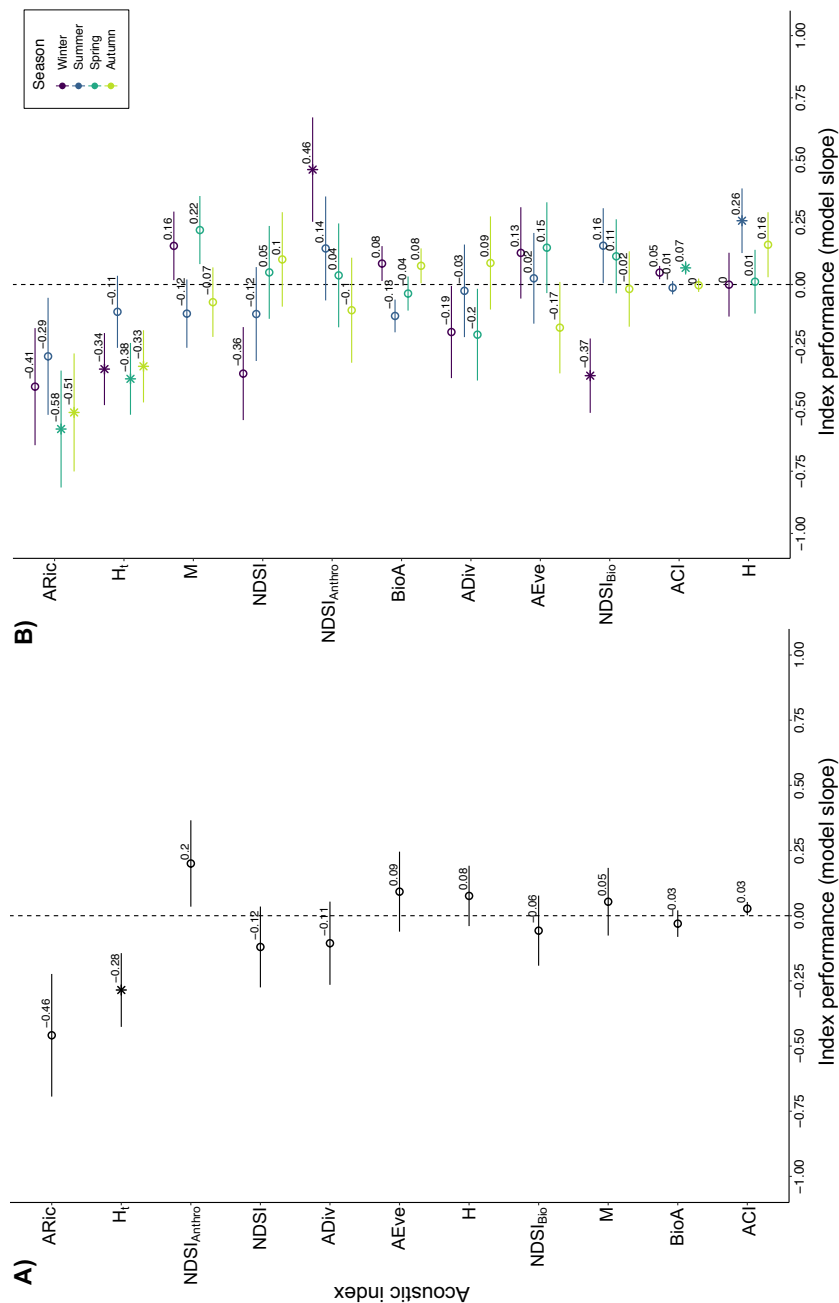


Figure 4.2 | Acoustic index performance. Performance (that is, the model slope of the acoustic index ~ mean site-level measured richness relationship) across all data (A) and separated by season (B). Values further from 0 indicate stronger relationships. Asterisks represent significant model slopes (two-sided test, $P = 0.05$). Indices are ordered top-bottom by absolute model slope values.

4.4.2 ACOUSTIC INDEX SENSITIVITY

There were only a few cases for which the underlying index ~ richness relationship was significant in the presence of my potentially confounding sonic conditions. The performance of H_t increased and the index remained significantly related to richness in both the presence of geophony (slope = -0.3, $t = -2.12$, $P = 0.034$) and anthropophony (slope = -0.29, $t = -2.09$, $P = 0.037$). The performance of ARic also increased in the presence of anthropophony (ARic ~ richness slope = -0.49, $t = -2.01$, $P = 0.044$). However, none of my acoustic indices were ever related significantly to measured richness in the presence of insect noise ($P > 0.05$). None of the remaining indices had index ~ richness relationships that differed significantly from zero in the presence of anthropophony, geophony or insect noise, even if their performance increased in the presence of one of these sonic conditions (Fig. 4.3).

I found consistent results across indices in their sensitivities to different sonic conditions. Three indices (ADiv, AEve, BioA) showed a significant decrease in absolute model slope when anthropophony was present, and three (BioA, ARic, M) performed significantly worse in the presence of geophony. Conversely, six indices (ACI, H_t , $NDSI_{Anthro}$, AEve, ARic, M) had significantly lower absolute model slopes in the presence of insect noise, while H performed significantly better in the presence than in the absence of insect noise ($t = 3.65$, $P < 0.001$, Fig. 4.3). However, H still did not correlate with measured richness when insect noise was present (slope = 0.18, $t = 1.2$, $P = 0.23$).

None of the acoustic indices in this study were affected significantly by all three sonic conditions. The performance of both $NDSI$ and $NDSI_{Bio}$ was not sensitive to the presence of any of my focal sonic conditions ($P > 0.05$; Fig. 4.3). Moreover, I found that season influenced the sensitivity rankings of indices and the identity of the sonic conditions to which many indices were most sensitive (Fig. C.2-C.4). However, some indices (*e.g.* ACI) were notably less affected by season than others.

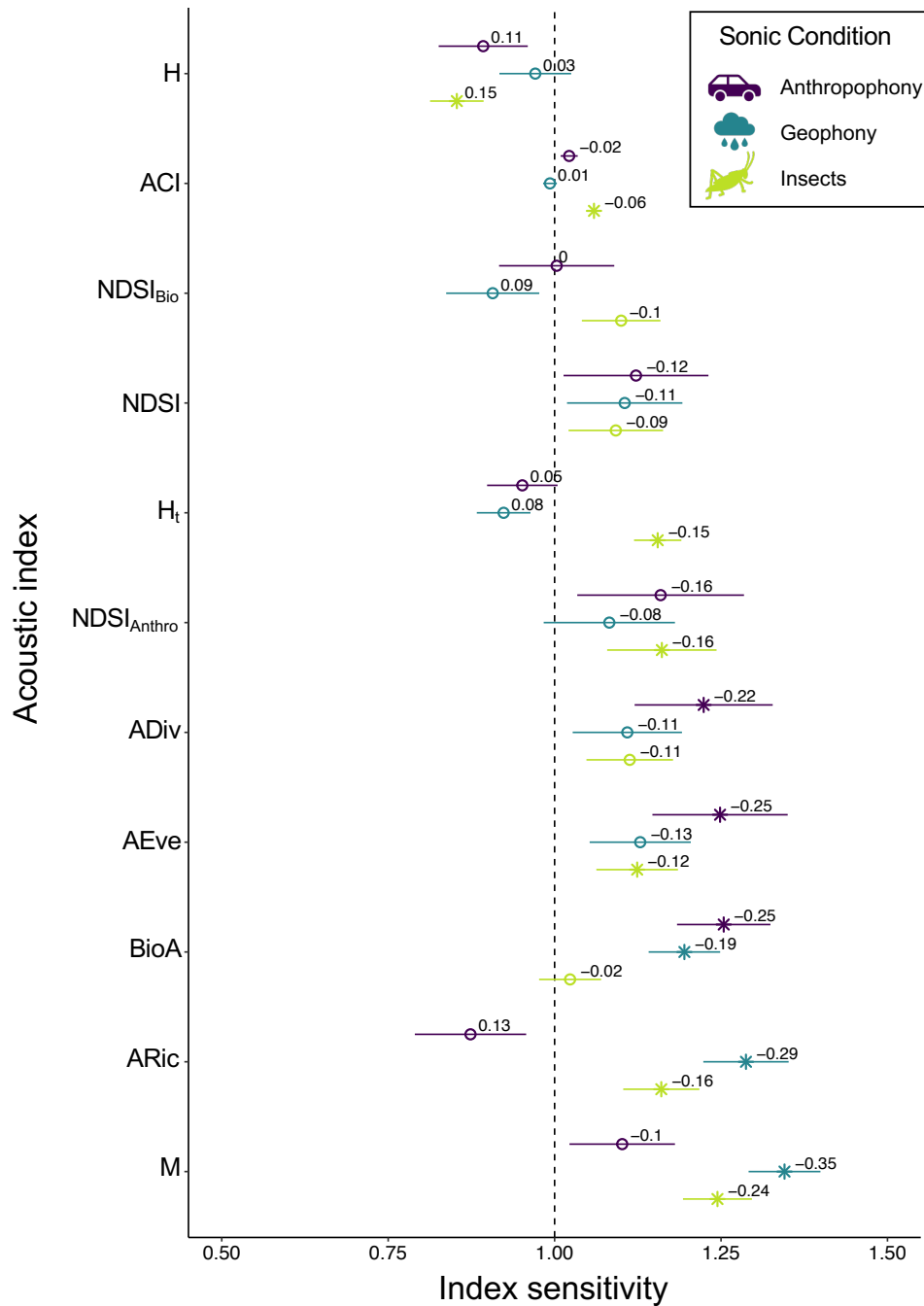


Figure 4.3 | Sensitivity of acoustic indices to extraneous sonic conditions. Sensitivity is the inverse of the absolute difference in model slope (that is, change in performance) of the acoustic index ~ mean site-level measured richness relationship between models where my three focal sonic conditions are absent (baseline) versus present. Sensitivity values below one indicate an increase in the strength of the model slope (performance improves), while values above one indicate a decrease in model slope (performance declines) under a given sonic condition—that is, in the presence of audible anthropophony (purple), geophony (turquoise) and broadband insects (lime green). Asterisks represent significant differences between model slopes (two-sided test, $P = 0.05$) based on t -statistics. Indices are ordered top-bottom by sensitivity values.

4.5 DISCUSSION

My study addresses the utility of different acoustic indices in reflecting a meaningful facet of biodiversity (that is, ‘measured richness’) across sonic conditions. I found that acoustic richness (ARic) and the temporal entropy index (H_t) outperformed other indices in terms of their relationship with measured richness. I also identified indices that were relatively insensitive to confounding sonic conditions (H , NDSI, NDSI_{Bio}). Practical users of these indices should take into consideration their performance across a relevant range of sonic conditions. When designing acoustic studies, researchers should tailor the selection of appropriate biodiversity facet(s) and sonic conditions to include in models to study design (Gasc *et al.* 2013, 2018; Hart *et al.* 2015; Harris *et al.* 2016). These may differ from my chosen conditions, particularly when considering aquatic soundscapes for example (Gottesman *et al.* 2018; van der Lee *et al.* 2020). Consideration of both performance and sensitivity across sonic conditions when selecting acoustic indices will be particularly important as ecoacoustics shifts increasingly towards answering questions of broad ecological interest (Lomolino *et al.* 2015; Gasc *et al.* 2018; Sueur *et al.* 2019).

I found that H_t was related negatively to richness, consistent with other tests of this index (Buxton *et al.* 2018a; Eldridge *et al.* 2018). Acoustic richness was also related negatively to measured richness here and elsewhere (Mammides *et al.* 2017; but see Depraetere *et al.* 2012). Other studies testing the performance of acoustic indices have not typically considered such a broad range of sonic conditions and land cover types as my study, likely contributing to the inconsistencies among studies testing the performance of particular acoustic indices (Fuller *et al.* 2015; Fairbrass *et al.* 2017; Machado *et al.* 2017; Mammides *et al.* 2017; Eldridge *et al.* 2018; Zhao *et al.* 2019; Bradfer-Lawrence *et al.* 2020). My finding of a few well-performing indices is then particularly noteworthy given that my models included a range of confounding sonic conditions most often excluded in studies testing the performance of acoustic indices (Harris *et al.* 2016; Buxton *et al.* 2018a).

Acoustic indices were related significantly to measured richness in only three cases. Despite its high sensitivity to insect stridulations and to geophony both here and elsewhere (Depraetere *et al.* 2012), ARic performed well in the presence of anthropogenic sound. This may be a product of ARic’s calculation method; acoustic richness is a function of both M and temporal entropy (Depraetere *et al.* 2012), and anthropophony is typically associated with temporally invariable low-frequency patterns in the soundscape (Pieretti *et al.* 2011). H_t was significantly related to measured richness under two sonic

conditions. H_t correlated with richness in the presence of geophony, but to my knowledge, the performance of H_t has not been tested previously under these conditions; the index was developed and tested by Sueur *et al.* (2008b) after applying a high-pass filter to remove the sonic effects of wind. H_t also performed well in the presence of anthropophony, and Depraetere *et al.* (2012) note that H_t was not affected by anthropogenic background noise in their study. Both NDSI and $NDSI_{Bio}$ were insensitive to the three sonic focal conditions, likely because NDSI compares a ratio of acoustic energy in high frequency to low frequency bands, making it relatively insensitive to broadband sounds of evenly distributed amplitude across frequencies, while $NDSI_{Bio}$ excludes frequency bands associated with anthropophony (Kasten *et al.* 2012).

When conducting an aural inventory, long-duration broadband insect sounds contribute both signal and noise to the soundscape (Hart *et al.* 2015). Insect noise consistently reduced the performance of all acoustic indices, with only BioA being insensitive to, though not related significantly to, richness in the presence of broadband insect stridulations. Eldridge *et al.* (2018) suggested that BioA is robust to insect noise because it is calculated across a limited range of frequency bands, largely excluding confounding effects of high frequency insects noise and low frequency anthropophony and geophony. I also found seasonal effects on both the performance and sensitivity of many acoustic indices, with H being least sensitive to seasonality (see also Mammides *et al.* 2017), though the generality of seasonal differences in acoustic index performance is doubtful; seasonal effects likely depend on features of the acoustic environment determined by landscape configuration and vocalising species composition (Fuller *et al.* 2015; Deichmann *et al.* 2018; Burivalova *et al.* 2019b; Sethi *et al.* 2020b).

Several acoustic indices have been proposed as being particularly capable of accounting for potentially confounding sonic conditions (Pieretti *et al.* 2011; Kasten *et al.* 2012; Fairbrass *et al.* 2017; Eldridge *et al.* 2018). For example, I found that ACI was insensitive to most background sounds with the exception of insect noise (see also Pieretti *et al.* 2011; Eldridge *et al.* 2018). However, its poor performance makes ACI a poor indicator of species richness (Mammides *et al.* 2017). Of the indices designed to be insensitive to anthropophony—ACI, ADiv, BioA, NDSI, and its component indices (see Fairbrass *et al.* 2017)—biophony ($NDSI_{Bio}$) was most robust to anthropogenic noise.

Though many indices did not reflect measured richness in my study, their robustness to sonic conditions (*e.g.*, BioA's robustness to insect noise, or biophony's low sensitivity to anthropophony) makes them candidate ecological indicators should it be demonstrated that such indices reflect well a meaningful

facet of biodiversity or habitat quality (Gasc *et al.* 2013; Elise *et al.* 2019). Until such time, the burden of proof remains on individual ecoacoustic studies to choose acoustic indices that can be interpreted meaningfully. Taken together, H_t , $ARic$, and perhaps also $NDSI$, or $NDSI_{Anthro}$ may be the most suitable indicators of richness under the full range of sonic conditions included in this study (Table 4.1). In the case of H_t , this index fulfilled both desirable conditions: 1) it correlates with richness, and 2) performs comparatively well across the range of sonic conditions tested, though it remains sensitive to insect noise. In exceptional circumstances, such as with heavy cicada activity, it may be preferable to use a less correlated but robust index in the face of a particular disturbance (Table 4.1), but I recommend cautioned interpretation of results in such cases.

Table 4.1 | Recommendations for acoustic index use under different sonic conditions. Recommended acoustic indices based on the results of this study and others when handling audio data including different conditions: presence of geophony, anthropophony, broadband insect stridulations, or study designs including different seasons. All/unknown is when not specifically considering any of the above conditions, but all may be present in the study design, hence the recommendations in this category are conservative recommendations for where sonic conditions are highly variable.

Study Conditions	Recommended Indices	Details
All/unknown	H_t , $ARic$, $NDSI_{Anthro}$, $NDSI$	Across all sonic conditions, H_t and $ARic$ performed best, followed by $NDSI_{Anthro}$. $NDSI$ performed less well but was insensitive to all three sonic conditions. Bradfer-Lawrence <i>et al.</i> (2020) found that species rich sites exhibit temporally variable soundscapes, and I observed this pattern in my study.
Anthropophony	H_t , $ARic$, $NDSI_{Bio}$	$ARic$ and H_t were related significantly to richness in the presence of anthropophony in my study and in that of Depraetere <i>et al.</i> (2012). $NDSI_{Bio}$ was insensitive to anthropophony here and elsewhere (Kasten <i>et al.</i> 2012; Fairbrass <i>et al.</i> 2017).
Geophony	H_t , ACI	H_t was related significantly to richness in the presence of geophony in my study. ACI was insensitive to geophony here and in Sánchez-Giraldo <i>et al.</i> (2020), but did not correlate with richness.
Broadband Insects	$BioA$	$BioA$ was least sensitive to insect stridulations in my study. Eldridge <i>et al.</i> (2018) found $BioA$ largely ignores high-frequency insect noise.
Multiple Seasons	H_t , $ARic$, $NDSI$, H	H_t and $ARic$ did not differ largely between seasons in their performance. $NDSI$ was not significantly affected by any sonic conditions when considering seasons. I found H was fairly robust to seasonality, as did Mammides <i>et al.</i> (2017). NB: seasonal effects likely differ among studies.

As the suite of acoustic indices available for ecologists to rapidly summarise audio recordings continues to grow, there will no doubt be continued debate surrounding the existence of a single best index (Sueur *et al.* 2014). Yet this accumulation of indices may also lead to redundancy. I found that several of the acoustic indices most common in the literature, including my two best performing indices (ARic and H_t), were highly correlated. However, redundancy is unlikely since acoustic indices often relate to different aspects of the overall soundscape (Bradfer-Lawrence *et al.* 2019). Equally, indices may reflect different features of ecological communities and their dynamics. I have focused on the richness of biological sounds, but acoustic indices may reflect additional dimensions of biodiversity including abundance, evenness, and functional or phylogenetic diversity (Pieretti *et al.* 2011; Gasc *et al.* 2013; Harris *et al.* 2016; Mammides *et al.* 2017; Elise *et al.* 2019).

The proliferation of ecoacoustic research brings with it an abundance of methodological refinement (Bradfer-Lawrence *et al.* 2019) and scores of new acoustic indices (Sueur *et al.* 2014). To remedy the disparity among previous studies, Bradfer-Lawrence *et al.* (2020) suggested considering species richness to be an emergent site-level characteristic in studies of acoustic index performance. In doing so, they revealed consistent soundscape patterns across indices, whereby sites with higher species richness had more uneven soundscapes (Bradfer-Lawrence *et al.* 2020). I find support for this pattern with two indices not included in their study: H_t and ARic. H_t was related negatively to measured richness, meaning that as site-level species richness increases, the temporal evenness of the soundscape decreases (Sueur *et al.* 2008b). Further, since acoustic richness values are a ranked function of both temporal entropy and the median of the amplitude envelope (M; Depraetere *et al.* 2012), the decrease in acoustic richness I observed with increased site-level richness likely reflects an increase in soundscape amplitude rather than in evenness. Overall, I can thus infer that sites with higher richness of vocalising species exhibit more structurally complex (less even) but more acoustically active (louder) soundscapes (Dumyahn & Pijanowski 2011; Bradfer-Lawrence *et al.* 2020). Remaining discrepancies between the results of many previous studies considering acoustic index performance may result from their sensitivity to particular sonic conditions (Harris *et al.* 2016; Eldridge *et al.* 2018). Indeed, my finding that most acoustic indices did not relate significantly to species richness—even when accounting for data distribution and zero-inflation—is likely a consequence of both seasonality and the wider range of sonic conditions considered in this study than in previous

tests of acoustic index performance (Harris *et al.* 2016; Buxton *et al.* 2018a; Bradfer-Lawrence *et al.* 2020).

Though we often lack the basic knowledge of species occurrences needed to interpret ecoacoustic results in a meaningful way (Machado *et al.* 2017), my methodological framework considering both performance and sensitivity to a range of relevant sonic conditions should facilitate appropriate and targeted use of acoustic indices. I thus recommend ground truthing acoustic indices for a given context to better interpret results, as I have described. I conclude that, with suitable guiding principles such as those outlined here (Table 4.1), and when ensuring that acoustic indices reflect an ecologically meaningful facet of biodiversity, such indices have the potential to provide a significant contribution to ecological monitoring in complex acoustic environments.

CHAPTER 5 | LAND USE SHAPES ECOLOGICAL RESILIENCE TO TYPHOONS

THIS CHAPTER IS CURRENTLY IN PREPARATION FOR PUBLICATION.

AUTHOR CONTRIBUTION:

I designed the study with input from all coauthors, Nick Friedman sent me the audio files and I produced the acoustic index data. Kenneth Dudley conducted the geographic analyses for Ross *et al.* (2018a). I produced the automated species detection models with input from Rob McHenry and Marina Lašić. I analysed the data, produced the figures, and led the writing of the manuscript with input from Ian Donohue.

5.1 SUMMARY

Land use intensification and climate change are dominant, but independent, axes of global environmental change. Yet, the potential for land use to exacerbate the impacts of extreme weather events such as typhoons, which are projected to increase in frequency, intensity, and duration in future, is largely unknown. Here, I show that land use can shape ecological resistance to and recovery from typhoons across the landscape. Using observational data from a landscape-scale acoustic monitoring network in Okinawa, Japan, I found that more natural and less intensive land uses, particularly pre-climax scrubland, were the most resistant to typhoon impacts, yet tended to recover more slowly from them. Soundscape stability was characterised by a greater diversity of typhoon responses among open and agricultural sites relative to forested sites, which tended to respond more homogeneously across space. Bird species detections also showed species-specific increases in spatial variability following the typhoons, mirroring results from acoustic indices. My results underscore the importance of natural habitats in insuring ecosystems against disturbance, and highlight the considerable potential for land use change to amplify the effects of extreme events on ecological stability.

5.2 INTRODUCTION

Climate change is increasing the frequency, intensity, and duration of extreme weather events globally (Knutson *et al.* 2010; Kossin *et al.* 2020; Li & Chakraborty 2020). Extreme storm events such as typhoons are typified by exceptional winds and rainfall and cause structural damage to terrestrial habitats through defoliation and wind-damage (Everham & Brokaw 1996), flooding (Gardner *et al.* 1991), and salinization by sea spray (Kerr 2000). These impact, in turn, on the composition and dynamics of trees (Lin *et al.* 2020), bacterial communities (Ares *et al.* 2020), birds (Lynch 1991; Chevalier *et al.* 2019) and other animals (Donihue *et al.* 2018; Testard *et al.* 2021). Human land use—another key axis of global environmental change (Sanderson *et al.* 2002; Devictor *et al.* 2007; Newbold *et al.* 2015; Daskalova *et al.* 2020)—has the potential to moderate storm impacts (Adger *et al.* 2005). For example, anthropogenic land use intensification may exacerbate the negative impact of storms or fire on wildlife (Uhl & Kauffman 1990; Raymond *et al.* 2020), while natural habitats can buffer ecosystems against the effects of extreme weather events (Adger *et al.* 2005; Arkema *et al.* 2013; Barbier 2015; Nimmo *et al.* 2016). Despite the potential for these two key global change drivers to interact, few studies have to date

investigated explicitly the impacts of extreme events across land use types at landscape scales.

Ecological stability is the core framework for considering the impacts of disturbances across scales from populations to ecosystems (Hillebrand *et al.* 2018; Kéfi *et al.* 2019). The concept of stability is complex and multidimensional (Donohue *et al.* 2013, 2016; Hillebrand *et al.* 2018; Arnoldi *et al.* 2019), including components such as resistance to, and recovery from, disturbance (Baert *et al.* 2016; Yang *et al.* 2019), and the variability of ecological variables in time and space (Tilman *et al.* 2006; Wang *et al.* 2017). Ecological responses to disturbance also vary across spatiotemporal scales (Zelnik *et al.* 2019; Clark *et al.* 2021; Jackson *et al.* 2021; Ross *et al.* 2021c), necessitating both high-resolution and long-term monitoring of ecosystems to holistically consider stability in observational studies. Accordingly, most empirical studies measuring ecological stability in response to disturbance are experimental (Kéfi *et al.* 2019), while observational studies of disturbance typically employ space-for-time substitutions (Damgaard 2019) or consider only single-time snapshots before and after disturbance (*e.g.*, Burivalova *et al.* 2014). In such cases, isolating the relevant pathways or mechanisms through which disturbance events impact ecosystems is extremely challenging.

Recent advances in automation hold promise for advancing understanding of ecological responses to disturbance through large-scale continuous monitoring of biodiversity (Keitt & Abelson 2021). Following developments in data acquisition, storage, and processing, passive acoustic monitoring of wildlife and soundscapes is growing in popularity (Burivalova *et al.* 2019a; Gibb *et al.* 2019). As sensor networks are established to collect acoustic data autonomously (Sethi *et al.* 2020a; Sugai 2020; Keitt & Abelson 2021), a diverse range of ecological questions become answerable by leveraging high-resolution acoustic time series (Lomolino *et al.* 2015; Rossi *et al.* 2017; Deichmann *et al.* 2018; Sueur *et al.* 2019). Studies using soundscapes—that is, all sound produced in an ecosystem (Pijanowski *et al.* 2011a, 2011b), including biophony (biotic sound), geophony (natural abiotic sound, such as rain), and anthropophony (human-related sound)—to measure disturbance impacts have emerged recently, but most commonly still consider disturbance either using space-for-time substitutions or temporal snapshots (*e.g.*, Deichmann *et al.* 2017; Gasc *et al.* 2018). However, the high-resolution time series afforded by passive acoustic monitoring allows the opportunistic measurement of soundscape responses to discrete disturbances such as extreme weather events (*e.g.*, Gottesman *et al.* 2021), as well as documenting longer-term trends under climate change (Krause & Farina 2016;

Sueur *et al.* 2019). Of the few acoustic studies of storms and extreme events, most focus on marine soundscapes (Locascio & Mann 2005; Boyd *et al.* 2021; Simmons *et al.* 2021). Recently, Gottesman *et al.* (2021) also found terrestrial forest soundscapes to be less resistant than those of coral reefs to hurricane disturbance.

Here, I use audio data from a 24-site acoustic monitoring network on the island of Okinawa, Japan (Ross *et al.* 2018a, 2021b) to measure multiple dimensions of ecological soundscape stability in response to a super-typhoon that was followed five days later by an extratropical cyclone in 2018. Using machine-learning techniques to detect individual bird species in the soundscape, I also examine how typhoon impacts on the dynamics of different bird species varied across the landscape. Uniquely, my field sites span Okinawa's full range of habitat types, allowing us to show for the first time how different land uses can shape the responses of ecosystems to extreme weather events.

5.3 METHODS

5.3.1 ACOUSTIC MONITORING AND TYPHOON IMPACT

My study uses data from the OKEON (Okinawa Environmental Observation Network) Churamori Project (OKEON 美ら森プロジェクト; www.okeon.unit.oist.jp) in Okinawa, Japan. At 24 field sites across Okinawa, a Song Meter SM4 recorder (Wildlife Acoustics Inc., Concord, MA, USA) has been recording sound since at least February 2017 (Ross *et al.* 2018a). The recorders are installed at approximately breast height (~1.3m) and are programmed to record at default gain settings (+16 dB) via two omnidirectional microphones on a schedule of 10-minutes recording, 20-minutes standby, with recording starting on every hour and half hour. Data are saved to an SD card in stereo WAVE format at a sampling rate of 48-kHz. All audio data collected as part of the OKEON Churamori Project are archived with the Okinawa Institute of Science and Technology's high-performance computing centre.

I selected audio data from all 24 OKEON field sites over the periods that two large typhoons passed closest to Okinawa (Trami: 29 September, Kong-Rey: 4 October; Japan Meteorological Agency [JMA] 2020), as well as a 30-day period before (*pre-disturbance* period: 30 Aug – 28 Sep 2018) and after (*post-disturbance* period: 06 Oct – 04 Nov 2018) the typhoons hit. This comprised a total of 771,840 minutes of data for the period 30 August – 04 November 2018 inclusive (Fig. 5.1). Okinawa is increasingly exposed to more frequent and intense

typhoons (A. Iwasaki, unpublished data) with annual typhoon seasons bringing disturbance events of varying severity (Elliott & Nino 1960). Typhoon Trami was the largest typhoon to hit Okinawa since OKEON acoustic recording began, with windspeeds reaching 183 km h^{-1} on 29 September (JMA 2020). Trami was followed shortly after by Kong-Rey, which was less severe, striking Okinawa as an extratropical cyclone (JMA 2020). This period thus includes a well-characterised pre-disturbance state (Ross *et al.* 2018a, 2021b), followed by an extreme weather event and a post-disturbance period during which soundscapes had the potential to recover to their pre-disturbance states.

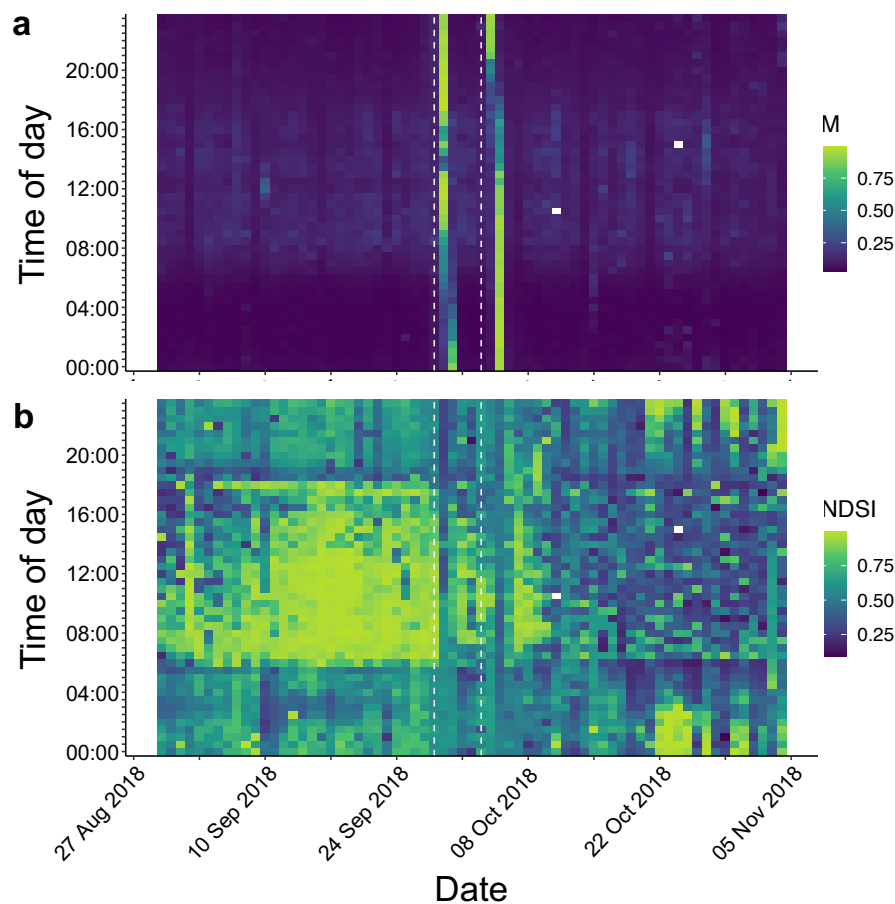


Figure 5.1 | Example of my acoustic time series. Representative example from the OKEON Chatan field site over the focal sampling period. I calculated acoustic indices based on 10-minute samples collected every half-hour (Y-axis) spanning the dates 30 Aug – 04 Nov 2018. This includes typhoons Trami (29 Sep) and Kong-Rey (04 Oct) (preceded by white dashed lines). This figure shows two acoustic indices: **a** the median of the amplitude envelope (M), where lighter colours represent greater total acoustic energy (that is, louder sound), and **b** the Normalised Difference Soundscape Index (NDSI), where lighter colours represent a dominance of biotic, rather than anthropogenic, sound. Note the clear acoustic signal of the typhoons in **a** and the subsequent drop in biophony in **b**.

For each 10-minute audio file, I calculated several commonly used acoustic indices in *R* (version 4.0.2; R Core Team 2020) using packages *seewave* (version 2.1.6; Sueur *et al.* 2008a) and *soundecology* (version 1.3.3; Villanueva-Rivera & Pijanowski 2018). Indices were chosen based on previous work in this system that found that certain indices better reflected species richness across a range of sonic conditions, while others were sensitive to geophony (Chapter 4; Ross *et al.* 2021b). I generated six acoustic indices following methods described in Chapter 4 (Table C.2; Ross *et al.* 2021b). The Normalised Difference Soundscape Index (NDSI) and its two component indices (that is, for biophony [NDSI_{Bio}] and anthropophony [NDSI_{Anthro}]; Kasten *et al.* 2012), acoustic diversity (ADiv; Villanueva-Rivera *et al.* 2011), and acoustic entropy (H; Sueur *et al.* 2008b) were chosen because they are relatively insensitive to geophony and generally reflect species richness across contexts in this system (Chapter 4; Ross *et al.* 2021b). I also calculated the median of the amplitude envelope (M; Depaetere *et al.* 2012), as this index is particularly sensitive to geophony (Chapter 4; Ross *et al.* 2021b), of which typhoons provide an extreme example (Fig. 5.1a). To facilitate comparison across indices and with other studies, index values were normalised to produce relative proportions by dividing each index by its maximum (Bradfer-Lawrence *et al.* 2020). Because NDSI ranges from -1 to +1, it cannot be scaled this way, so I normalised NDSI as $(\text{NDSI} + 1)/2$ (Fairbrass *et al.* 2017).

In addition to computing acoustic indices from recordings, I also measured the number of detected vocalisations of several bird species across Okinawa for the period 15 Sep – 31 Oct 2018 (that is, incorporating the 14 days before the typhoon events and 26 days afterwards, which allows consideration of longer post-typhoon responses), using supervised machine learning methods described in Ross *et al.* (2018a). I used Kaleidoscope Pro (version 5.3.0; Wildlife Acoustics Inc., Concord, MA, USA) to train software recognisers for detecting four target species: the large-billed crow (*Corvus macrorhynchos*, 嘴太鳥 in Japanese); the Japanese bush warbler (*Horornis diphone*, 鶯); the Ryukyu scops-owl (*Otus elegans*, 琉球木の葉木菟); and the light-vented bulbul (*Pycnonotus sinensis*, 白頭). I chose these species because together they exhibit a range of life-histories, habitat affinities, vocal repertoires, and conservation statuses, and include both invasive (*P. sinensis*) and endemic (*O. elegans*) species (McWhirter *et al.* 1996; Itô *et al.* 2000; Ross *et al.* 2018a; Inoue *et al.* 2019). I thus expect these species to vary in their sensitivity to both typhoons and land use. Species detection algorithms often transfer poorly across sites, usually because of site-

specific differences in background sonic conditions (Chapter 4, Ross *et al.* 2018a, 2021b). Nevertheless, I developed reliable recognisers ($\leq 15\%$ false positives on visual inspection) for my target species at a subset of sites across Okinawa for *C. macrorhynchos* (detected reliably at 12 field sites), *H. diphone* (9), *O. elegans* (2) and *P. sinensis* (1).

Kaleidoscope Pro uses a supervised clustering approach based on Hidden Markov Models. Local experts cross-checked automated clustering of separate sound sources and reclassified sound clusters where necessary to refine the species recognisers. Owing to the volume of data used in this study, I did not calculate exact false positive rates for my species detections. However, Kaleidoscope Pro provides a distance-from-cluster-centroid measure which approximates identity certainty, where greater distances represent detections that are less likely to be the target species. Filtering by distance-from-centroid then allows rapid removal of low certainty detections. For all presented analyses, I chose a naïve filter value of 0.5, though my results were qualitatively similar under more conservative filters (Fig. D.1).

5.3.2 GEOGRAPHIC ANALYSES

The geographic variation among my 24 recording sites is described by Ross *et al.* (2018a), who used reflectance estimates from Landsat 8 images to estimate proportional land use for various land use classes within a 1000 m circular buffer surrounding each site. The 1000 m buffer scale was deemed most appropriate for detecting land use effects on mobile taxa such as birds. I classified land use into the following categories: dense closed-canopy forest; scrubland/grassland (that is, pre-climax low intensity low/medium growth coastal and disturbed vegetation and managed grassland); agricultural land (primarily for sugarcane); and urban areas characterised by materials such as asphalt and concrete with limited vegetation. I calculated habitat heterogeneity as the standard deviation of Normalised Difference Vegetation Index (NDVI) values calculated for each pixel within the 1000 m buffer zone surrounding each site. NDVI was calculated as

$$\frac{(NIR - RED)}{(NIR + RED)}$$

where NIR and RED are the reflectance of near-infrared and red light, respectively (Pettorelli *et al.* 2005). NDVI thus represents the 'greenness' or productivity of an area. Finally, I estimated the distance from each site centroid to the nearest road and the closest coastline, using data from a 2008-2009 Geospatial Information Authority of Japan survey (<http://www.gsi.go.jp>).

5.3.3 DATA ANALYSES

I measured eight components of ecological stability from the time series of acoustic indices (Table 5.1; Fig. 5.2), after first detrending the data using a centred moving average (three-day window size) in the *forecast R* package (version 8.14; Hyndman & Khandakar 2008). This was done for all stability components except for spatial variability, which was calculated from daily mean values (Table 5.1). Increasing the temporal window size of the moving average function to five or seven days produced qualitatively similar results at the expense of reduced temporal extent and dampened soundscape dynamics (Fig. D.2), so I present results of the three-day window size. To monitor recovery, one must first define a baseline state to which disturbed values can be compared. Given the highly dynamic nature of natural soundscapes (Francomano *et al.* 2020), I chose the mean ± 1 standard deviation (SD) of pre-disturbance acoustic index values as a conservative baseline (though my results were qualitatively similar when defining a 95% confidence interval baseline; Fig. D.3). I then defined the point of recovery for my measurements of recovery time and resilience (Table 5.1) as the point from which acoustic index values had returned to and stayed within the baseline range (Mean ± 1 SD) for 24 consecutive hours (these results were also robust to recovery window size; Fig. D.4). When building log-difference time series models from which I calculated resilience (Fig. D.5), I fit generalized least squared (GLS) models via maximum likelihood estimation and included a lag-1 temporal autoregression function (φ). I first computed a partial autocorrelation function from the residuals of an ordinary least squares (OLS) model (using the *pacf* function in *R*), and then took the value at lag-1 as my temporal autoregression function φ for use in the GLS model (Metcalf & Cowpertwait 2009). When measuring resilience based on log-difference return rates, I fit linear and second-order polynomial GLS models and selected the polynomial model as the most parsimonious, based on the Akaike Information Criterion (AIC), only where $\Delta\text{AIC} \geq 10$ for the linear model (that is, where there was no support for the linear model).

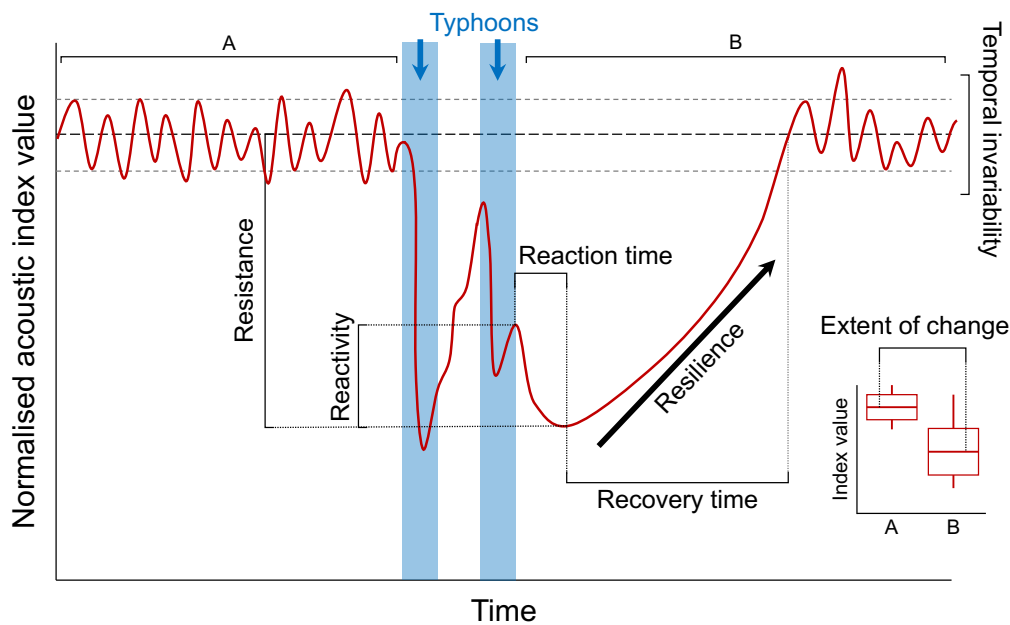


Figure 5.2 | Measuring soundscape stability from passive acoustic monitoring time series. Seven measures of ecological stability (that is, excluding spatial variability) I calculated from the time series of acoustic indices. I calculated temporal invariability over the pre-disturbance period [A], measured resistance as the difference at the point of maximum deviation and the pre-disturbance mean [dashed line], and considered a system recovered when acoustic index values returned to within the pre-disturbance range of values [within dotted lines]. Reactivity and reaction time were measured based on the difference between the point of maximum deviation and the end of the typhoon disturbance. Finally, the extent of change (a measure aimed at capturing longer-term typhoon resistance) is based on the effect size of the difference between the pre- and post-typhoon periods [A and B, respectively], and includes a p -value for the probability that the typhoon periods differ. I calculated only temporal invariability and the extent of change for the time series of individual species detections (see 5.3 *Methods*). See Table 5.1 for detailed methods.

To assess the potential for land use to moderate typhoon disturbance on acoustic indices, I built OLS models with each dimension of stability as a response variable in turn, and the seven geographic variables I calculated as additive predictor variables. Response variables were transformed as needed to meet model assumptions (see Table D.1). I tested for spatial autocorrelation of model residuals using a Moran's I test. Where model residuals were significantly autocorrelated ($p < 0.1$; Table D.1), I remodelled stability values and land use predictors using GLS models fit by maximum likelihood estimation, and included an exponential spatial correlation structure using the latitude and longitude of each site. I then calculated the relative variable importance of each predictor variable (following Burivalova *et al.* 2018; Dröge *et al.* 2021) by using the R function *dredge* (Bartoń 2020) to fit models with all combinations of predictor

variables. I sorted the resulting 128 (*i.e.*, 2^7) models by AICc (that is, after correcting for small sample sizes) and, for each predictor variable, I summed the Akaike weights of the closely competing models ($\Delta\text{AICc} \leq 2$) in which the variable appears. I did this separately based on the sign (positive versus negative) of variables in the models (Dröge *et al.* 2021). Relative variable importance thus scales from zero to one, where one indicates a land use predictor was present in all closely competing models while zero indicates that a predictor was not included in any closely competing models.

To better understand relationships between stability components and land use predictors, I then took the variable(s) with the highest relative variable importance and built OLS or GLS models (as above) using a single land use predictor. I compared the AICc of each model to a null model without any land use predictors. Where $\Delta\text{AICc} > 0$ for the null model (that is, where the land use model was the most parsimonious model based on model selection), I also used *F*-tests (likelihood ratio tests for GLS models) to test whether removing the land use predictor had a significant effect on model fit. Where predictor variables were significant at the $p < 0.1$ level, I also fitted second-order polynomial models and concluded that land use was nonlinearly related to stability in cases where $\Delta\text{AICc} \geq 2$ for the linear model.

I calculated spatial variability of mean daily acoustic index values across all sites, producing daily values of spatial stability at the landscape scale (Table 5.1). To test whether spatial variability differs with land use, I also calculated the spatial variability among sites grouped into distinct land use classes. I first identified the eight sites with the highest and lowest proportional cover of scrubland/grassland, forest, and agricultural land (chosen because these land use classes often influenced multiple stability components; see 5.4 *Results*, Table 5.2). I then calculated spatial variability across sites within each of these land use groups. Using analysis of variance (ANOVA) after ensuring data homoscedasticity (via transformation where needed, Table D.1), I tested for differences between the 30-day periods before and after the typhoons for all 24 sites, and including an interaction with categorical land use subsets (two levels: most versus least scrubland, forest, or agriculture) for 16 sites. I used Tukey HSD tests to make post-hoc comparisons among levels of significant terms.

Since bird detections were summed per day and available time series were shorter (15 Sep-31 Oct 2018) than for acoustic indices, data resolution and time series length were unsuitable for calculating several dimensions of stability. Accordingly, I calculated only the temporal invariability and extent of change of species detections (Table 5.1) for each species at each site for which I attained

reliable detection estimates (see above), and generated time series of spatial variability for the two species for which I had sufficient samples (that is, *Corvus macrorhynchos* and *Horornis diphone*). To test for differences between species in their temporal invariability and extent of change, I conducted an F -test on each component of stability separately, with species identity (*C. macrorhynchos* or *H. diphone*) as the predictor variable. Following the same statistical procedures as for acoustic indices (that is, using ANOVA and post-hoc Tukey HSD tests), I tested for typhoon effects on the spatial variability of bird detections across sites and, to determine whether species differed in their typhoon responses across space, I included an interaction between period (that is, pre- versus post-disturbance; Table 5.1) and species identity.

The Normalised Difference Soundscape Index (NDSI) correlates significantly with most of the other indices used in this study (Fig. 4.1 in Chapter 4 of this thesis) and is insensitive to a range of potentially confounding sonic conditions (Table 4.1 in Chapter 4; Ross *et al.* 2021b). As such, I focus primarily on results from stability analyses of the NDSI acoustic index for brevity, but include results from all other indices in Appendix D. All statistical analyses were conducted in *R* (version 4.0.2; R Core Team 2020), using packages *nlme* (version 3.1-152; Pinheiro *et al.* 2021), *MuMIn* (version 1.43.17; Bartoń 2020), and *DHARMA* (version 0.4.3; Hartig 2021).

Table 5.1 | Components of ecological stability measured in this study, methods of their measurement and interpretation. Stability components (see also Fig. 5.2) were calculated separately for time series of acoustic indices and bird species detections, based largely on methods adapted from Hillebrand *et al.* (2018) and White *et al.* (2020b).

Stability component	Time window of measurement	Method of measurement: acoustic indices	Method of measurement: species detections	Interpretation
Temporal invariability	30- or 14-days pre-disturbance (for, respectively, acoustic indices and species detections)	Reciprocal of the squared coefficient of variation (that is, $1/CV^2$), equivalent to the ratio of the squared mean to the temporal variance of acoustic index values across the 30-day pre-disturbance period (Wang & Loreau 2016; Wang <i>et al.</i> 2021).	Reciprocal of the squared coefficient of variation of daily summed species-specific bird vocalisations, calculated across the 14 days preceding the first typhoon.	Higher values correspond to lower variability through time (that is, higher stability).
Resistance	2 days post-disturbance	Log response ratio of the maximum absolute deviation from pre-disturbance baseline (mean) in the 48 hours following the 2 nd typhoon and the pre-disturbance mean (Hillebrand <i>et al.</i> 2018).	-	Values represent log response ratios, where zero equates to complete resistance (no change), and more extreme positive or negative values represent lower resistance through over- or underperformance, respectively (Hillebrand <i>et al.</i> 2018).
Recovery time	30 days post-disturbance	Time taken (in hours) for acoustic index values to return to baseline (that is, mean $\pm$ 1 standard deviation of pre-disturbance conditions) and stay within this range for 24 consecutive hours, starting from the point of maximum displacement (that is, the resistance point; Garnier <i>et al.</i> 2017; White <i>et al.</i> 2020b).	-	Higher values indicate slower recovery (that is, lower stability).

Resilience	From point of maximum displacement to point of recovery	Slope of regression of log difference of acoustic index values [AI] to the mean pre-disturbance baseline ($\ln[\mu_{Baseline} - AI]$) over time from the point of maximum displacement (resistance point) to the point of recovery (White <i>et al.</i> 2020b). Calculating log differences is equivalent to modelling the relative return rate, making resilience conceptually independent from resistance (Garnier <i>et al.</i> 2017; Hillebrand <i>et al.</i> 2018).	-	Values are based on log differences, so lower values represent faster rates of relative return (that is, higher stability).
Reaction time	From end of typhoon to point of maximum displacement	Time taken (in hours) between the end of the 2 nd typhoon and the point of maximum displacement (resistance point).	-	Higher values correspond to slower reaction times (that is, lower stability) while lower values represent faster-to-react systems.
Reactivity	From end of typhoon to point of maximum displacement	Absolute difference from baseline (mean) at the end of the 2 nd typhoon minus the absolute difference from baseline (mean) at the point of maximum displacement (resistance point).	-	More positive values represent higher stability (a post-disturbance buffering effect), while more extreme negative values represent lower stability (a more reactive system), and zero a non-reactive system (no difference between end of typhoon and point of maximum deviation).

Extent of change	30- or 14-day pre- and post-disturbance periods (for, respectively, acoustic indices and species detections)	z-score calculated based on a Wilcoxon signed rank test comparing daily mean acoustic index values from the 30-day pre-disturbance period to the 30-day post-disturbance period at each site.	z-scores comparing daily summed species-specific bird vocalisations from the 14 days pre-disturbance to the 26 days post-disturbance (Wilcoxon tests are robust to uneven sample sizes; Fritz <i>et al.</i> 2012).	Values represent standardised effect sizes, where more extreme positive or negative values represent lower stability (that is, a larger post-disturbance increase or decrease, respectively). Where extent of change values $\pm$ 95% C.I. do not span zero, this represents a significant ($p < 0.05$) post-disturbance change. Though conceptually similar to resistance, extent of change represents longer-term change relative to resistance—an important distinction given the need to combine instantaneous measures of stability with longer-term metrics to reveal stability responses through time (Yang <i>et al.</i> 2019).
Spatial variability	One value per day	Coefficient of variation (σ/μ) among field sites in daily mean acoustic index values on each date (Donohue <i>et al.</i> 2013).	Coefficient of variation among field sites in daily summed species-specific bird vocalisations on each date. Measured for <i>C. macrorhynchos</i> and <i>H. diphone</i> only due to sample size.	Higher values represent higher variability in space, which unlike for temporal (in)variability, is stabilising as spatial variability represents asynchronous biomass fluxes within or among species, in turn providing spatial insurance through patch dynamics (Loreau <i>et al.</i> 2003; Leibold <i>et al.</i> 2004; Wang <i>et al.</i> 2021).

5.4 RESULTS

5.4.1 ACOUSTIC INDICES

Across all acoustic indices and dimensions of stability, the set of closely competing models (that is, those with $\Delta\text{AICc} \leq 2$) often included fixed effects of land use (Fig. 5.3), including most often the proportion of forest cover (in 27 of the 42 possible model sets; Table 5.2), followed closely by the proportion of scrubland (26 cases), and agricultural and urban areas (24 cases each). Where included in the closely competing models as an explanatory variable, distance from the nearest coastline had, on average, the highest relative variable importance—that is, the highest explanatory power—followed by the proportion of scrubland, agriculture, and forest (Table 5.2). Despite occurring relatively rarely in the set of closely competing models, distance from the nearest road generally had high explanatory power where present (Table 2). Across acoustic indices, temporal invariability was explained by fixed effects with the highest relative variable importance (that is, was best explained by land use effects), followed by reaction time, reactivity, and resistance (Fig. 5.3). Resilience was least related to land use, which likely reflects greater influence of recovery time relative to resistance, since recovery time also was not often strongly related to land use (Fig. 5.3).

Table 5.2 | Summary of land use variables included in the set of closely competing models ($\Delta\text{AICc} \leq 2$) across acoustic indices and stability dimensions. For each fixed effect (see 5.3 *Methods*), frequency of inclusion is how often each land use was included in the set of closely competing models (out of 42 total across indices and stability dimensions). Mean relative variable importance is the average of all relative variable importance values (that is, regardless of directionality) where a given fixed effect was included (that is, excluding zeroes; Fig. 5.3).

Fixed effect	Frequency of inclusion in closely competing models	Mean relative variable importance
%Forest	0.64 (27)	0.49
%Scrubland	0.62 (26)	0.54
Heterogeneity	0.48 (20)	0.39
Distance: Coast	0.5 (21)	0.63
%Agriculture	0.57 (24)	0.5
%Urban	0.57 (24)	0.35
Distance: Road	0.21 (9)	0.5

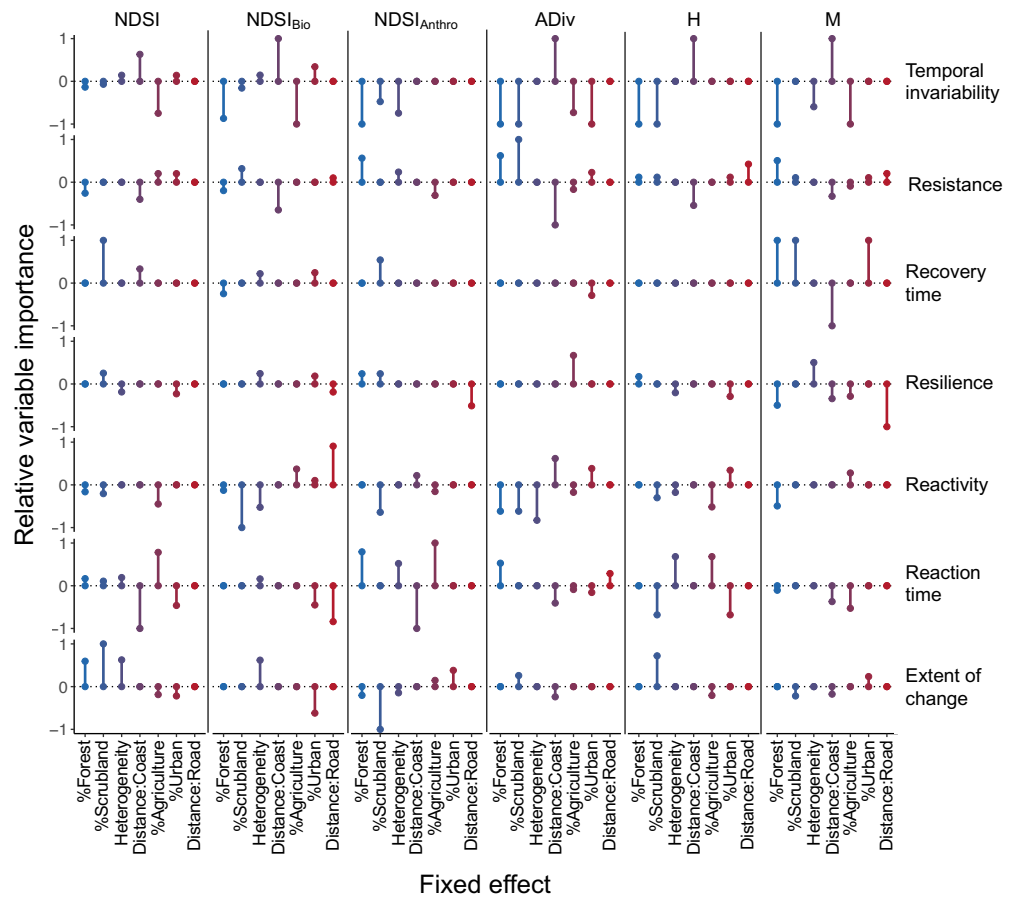


Figure 5.3 | Relative variable importance of land use predictors of soundscape stability. Predictor variables (x-axes) included the proportion of forest, scrubland, agriculture, and urban land within a 1000 m radius around each field site, habitat heterogeneity (that is, the range of vegetation density values within this area based on NDVI, see 5.3 *Methods*), and the distance from each site centroid to the nearest coastline and nearest road. Relative variable importance (y-axes) scales -1 to 1, where 0 indicates that a variable was never included in the set of closely competing models ($\Delta\text{AICc} \leq 2$), while values closer to 1 or -1 indicate, respectively, an important positive or negative contribution of a given variable. Models were constructed separately for six acoustic indices: NDSI, NDSI_{Bio}, NDSI_{Anthro}, ADiv, H, and M, and for each dimension of stability: temporal invariability, resistance, recovery time, resilience, reactivity, reaction time, extent of change. For calculation of stability components, see Table 5.1.

Across indices, scrubland/grassland was the land use type that was most frequently related to stability. Higher proportions of scrubland were associated with a lower extent of change (that is, higher longer-term resistance; Table 5.1) following the typhoons for NDSI (Null model $\Delta\text{AICc} = 3.42$; ANOVA: $F_{2,22} = 6.31$, $p = 0.002$; Fig. 5.4g), NDSI_{Anthro} ($\Delta\text{AICc} = 4.87$; $L.\text{Ratio}_{4,22} = 7.78$, $p = 0.005$; Fig. D.7g), and H ($\Delta\text{AICc} = 1.22$; $F_{2,22} = 3.83$, $p = 0.063$; Fig. D.9g) and higher short-term resistance for ADiv ($\Delta\text{AICc} = 2.58$; $F_{2,21} = 5.38$, $p = 0.031$; Fig. D.8b). Higher proportional scrubland was also related to greater reactivity for

NDSI_{Bio} ($\Delta\text{AICc} = 0.52$; $F_{2,21} = 3.12$, $p = 0.092$; Fig. D.6f), NDSI_{Anthro} ($\Delta\text{AICc} = 1.47$; $F_{2,21} = 4.14$, $p = 0.055$; Fig. D.7f), and H ($\Delta\text{AICc} = 4.67$; $F_{3,20} = 5.64$, $p = 0.001$; Fig. D.9f). Higher proportional scrubland was related to slower recovery times for both NDSI ($\Delta\text{AICc} = 9.49$; $F_{2,17} = 15.5$, $p = 0.001$; Fig. 5.4c) and NDSI_{Anthro} ($\Delta\text{AICc} = 0.33$; $F_{2,16} = 3.16$, $p = 0.094$; Fig. D.7c). The proportion of agriculture also explained acoustic index stability in some cases. Higher proportional area of agriculture was associated with slower reaction times for both NDSI (Null model $\Delta\text{AICc} = 0.51$; ANOVA: $F_{2,21} = 3.11$, $p = 0.092$; Fig. 5.4e) and NDSI_{Anthro} ($\Delta\text{AICc} = 1.8$; $F_{2,21} = 4.5$, $p = 0.046$; Fig. D.7e). Higher proportional agriculture also related negatively to the temporal invariability of NDSI ($\Delta\text{AICc} = 1.22$; $F_{2,22} = 3.83$, $p = 0.063$; Fig. 5.4a), and to ADiv resilience ($\Delta\text{AICc} = 1.4$; $F_{2,20} = 4.09$, $p = 0.057$; Fig. D.8d). Finally, forest cover was also related to stability (Fig. 5.3), but only for two acoustic indices. For NDSI_{Anthro}, higher forest cover was negatively related to temporal invariability (Null model $\Delta\text{AICc} = 8.03$; ANOVA: $F_{2,22} = 12.3$, $p = 0.002$; Fig. D.7a) but positively related to resistance ($\Delta\text{AICc} = 1.87$; $F_{2,21} = 2.76$, $p = 0.11$; Fig. D.7b). Higher proportional forest cover was also associated with higher reactivity ($\Delta\text{AICc} = 1.54$; $F_{2,20} = 4.26$, $p = 0.052$; Fig. D.10f) and slower recovery times for M ($\Delta\text{AICc} = 1.06$; $F_{2,20} = 3.73$, $p = 0.068$; Fig. D.10c).

Though proportional cover of scrubland, agriculture, and forest were included most frequently in the closely competing model sets and tended to have high relative variable importance where present (Table 5.2, Fig. 5.3), I also found significant relationships between other land use predictors and various dimensions of acoustic index stability (Figs. D.6 and D.10). Distance from coastline was related to less variable NDSI_{Bio} values (Null model $\Delta\text{AICc} = 8.66$; ANOVA: $F_{2,22} = 13.2$, $p = 0.001$; Fig. D.6a), but lower resistance of NDSI_{Bio} ($\Delta\text{AICc} = 1.31$; $F_{2,21} = 3.96$, $p = 0.06$; Fig. D.6b). Distance from the nearest road was related to slower reaction times for NDSI_{Bio} (Null model $\Delta\text{AICc} = 1.78$; ANOVA: $F_{2,21} = 4.48$, $p = 0.047$; Fig. D.6e), and to greater resilience for M ($\Delta\text{AICc} = 3.78$; $F_{2,18} = 7$, $p = 0.016$; Fig. D.10d). Finally, higher habitat heterogeneity was related to greater resilience of NDSI_{Bio} (Null model $\Delta\text{AICc} = 0.36$; $F_{2,12} = 3.6$, $p = 0.082$; Fig. D.6d). In all other cases, the null model was selected over the competing land use model(s) based on AICc, or fixed effects of land use were not significant at the $p < 0.1$ level (Figs. 5.4 and D.6-D.10).

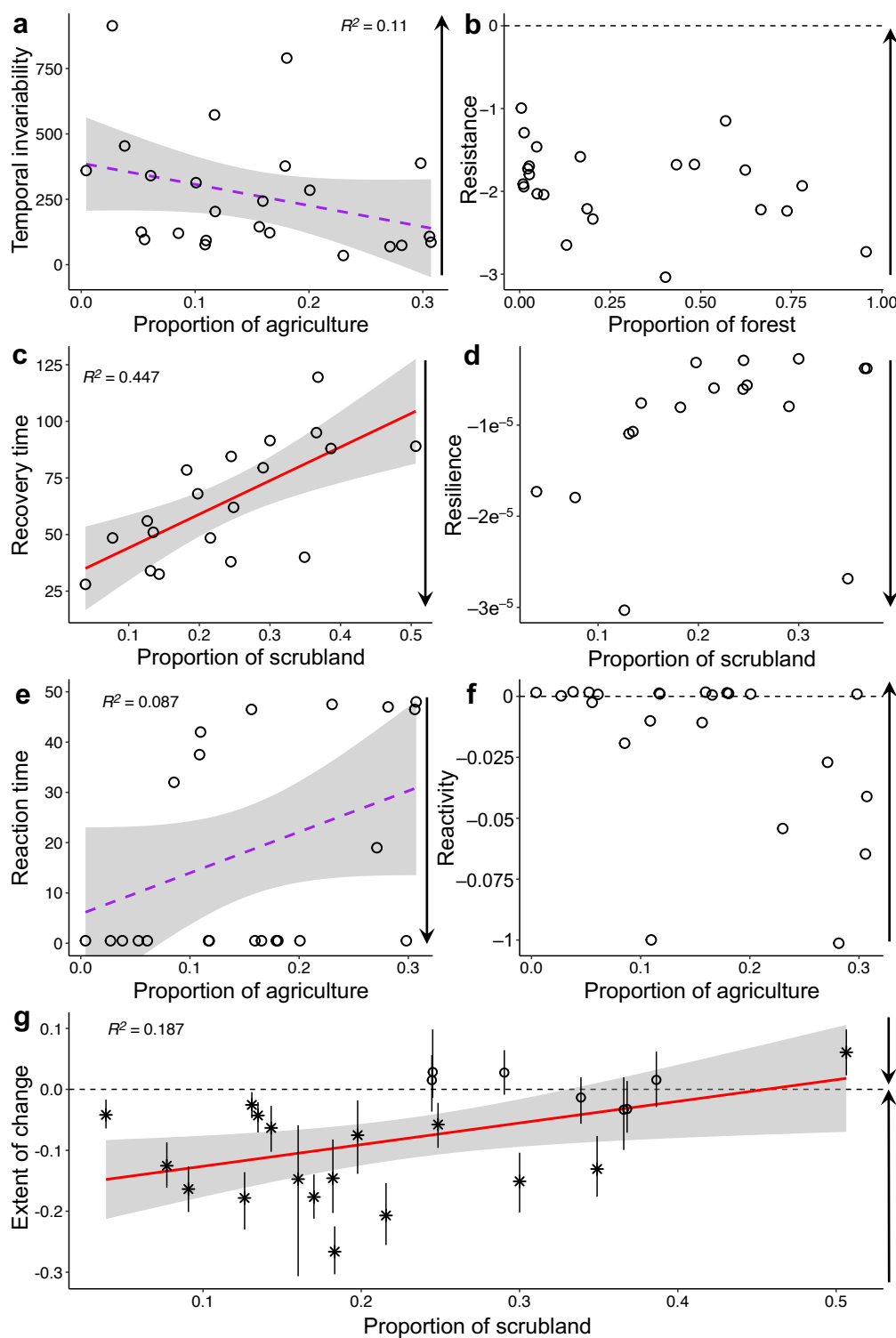


Figure 5.4 | Relationships between land use and multiple dimensions of NDSI stability. For each dimension of stability (except for spatial variability, the results for which are shown on Fig. 5.5), plots show the most important land use variable (based on model selection results, see Fig. 5.3) plotted against the stability of NDSI values. In each case, I tested the significance of the land use variable, and present significant ($p < 0.05$) stability ~ land use relationships with red model slopes, and closely competing models ($p < 0.1$) with dashed purple slopes (see 5.3 *Methods*). I tested seven dimensions of stability for NDSI values: **a** temporal invariability; **b** resistance; **c** recovery time; **d** resilience; **e** reaction time; **f** reactivity; and **g** extent of change. **g** Significant extent of change values

(based on Wilcoxon signed rank test, $p = 0.05$) are represented with asterisks (that is, when there is a significant decrease [below zero] or increase [above zero] in acoustic index values following the typhoons, where error bars show the 95% confidence interval around the difference [effect size], Table 5.1). To aid interpretation, arrows to the right of each plot point towards more stable values for each dimension of stability (see Table 5.1 for detailed interpretation). See Figs. D.6-D.10 for other acoustic indices.

I observed a post-disturbance increase in the variability of soundscapes across sites. Spatial variability increased significantly after the typhoons for NDSI (ANOVA: $F_{1,58} = 87.3$, $p < 0.001$; Fig. 5.5a), NDSI_{Bio} ($F_{1,58} = 146.2$, $p < 0.001$; Fig. D.11a), ADiv ($F_{1,58} = 33.7$, $p < 0.001$; Fig. D.13a), H ($F_{1,58} = 31.4$, $p < 0.001$; Fig. D.14a), and M ($F_{1,58} = 6.7$, $p = 0.012$; Fig. D.15a), and decreased significantly for NDSI_{Anthro} ($F_{1,58} = 8.44$, $p = 0.005$; Fig. D.12a). For NDSI, the sites with highest scrubland cover had lower spatial variability than the least scrubland sites (ANOVA: $F_{1,116} = 62.4$, $p < 0.001$; Fig. 5.5b) but this pattern was not affected by the typhoons ($F_{1,116} = 0$, $p = 0.995$). In contrast, forest land use interacted significantly with time period to shape spatial variability ($F_{1,116} = 6.54$, $p = 0.012$; Fig. 5.5c). The post-typhoon increase in spatial variability was not significant ($p < 0.05$) among the most forested sites (Tukey HSD: $p_{\text{adj}} = 0.071$), whereas among the least forested sites, it was ($p_{\text{adj}} < 0.001$; Fig. 5.5c). Conversely, agricultural sites had higher NDSI spatial variability than my least agricultural sites ($F_{1,116} = 329$, $p < 0.001$) and agriculture interacted with time period ($F_{1,116} = 12.8$, $p < 0.001$; Fig. 5.5d). The spatial variability of NDSI among agricultural sites increased following the typhoons ($p_{\text{adj}} < 0.001$), but there was no post-typhoon change for the least agricultural sites (Fig. 5.5d). Results for other indices were broadly similar, but agriculture did not explain typhoon disturbance (except for M; Fig. D.15d) and I found a significant interaction between scrubland and time period; there was a larger post-typhoon increase (a decrease for NDSI_{Anthro}) in spatial variability among least scrubland sites than among the sites with the highest proportion of scrubland (Figs. D.11b-D.15b).

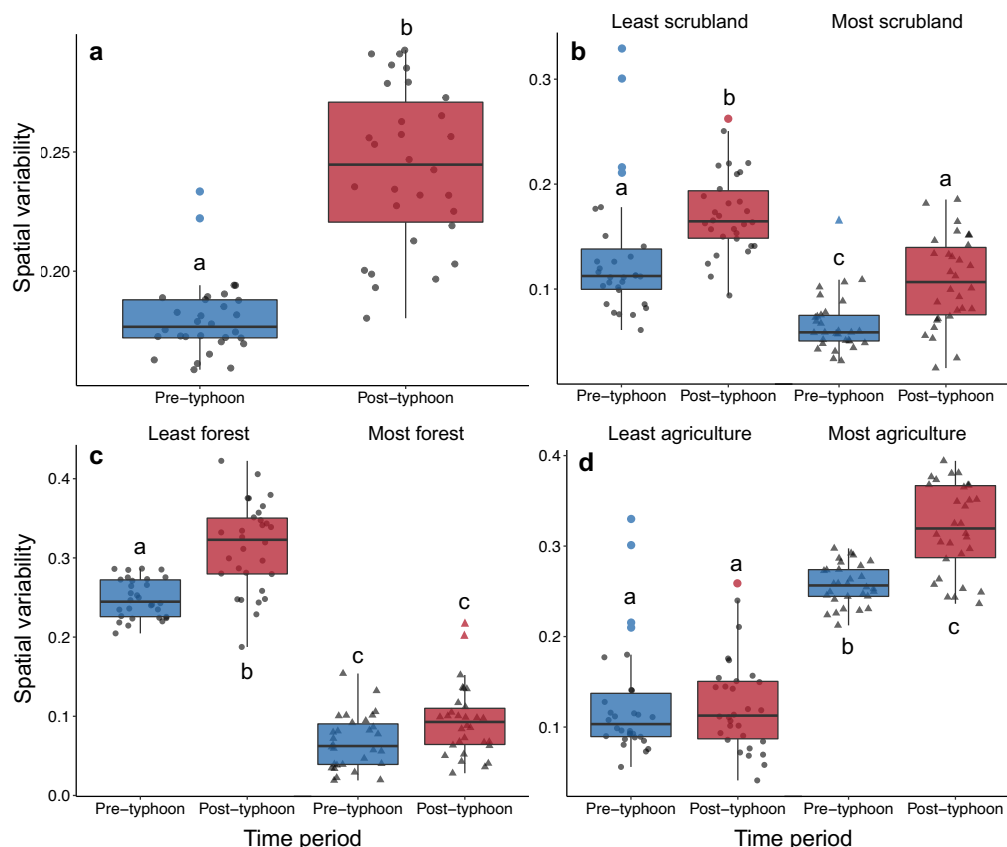


Figure 5.5 | Effects of typhoons and land use on NDSI spatial variability. Boxplots represent the range (box = median and interquartile range) of daily spatial variability values for NDSI across dates in before [blue] versus after [red] the typhoons where spatial variability is calculated as the coefficient of variation of NDSI values (Table 5.1) across **a** all sites, and for the 8 sites with least [left, circles] and most [right, triangles] proportional cover of: **b** scrubland/grassland; **c** forest; and **d** agriculture (see 5.3 *Methods*). Significant ($p < 0.05$) pairwise contrasts are denoted with superscript/subscript letters.

5.4.2 BIRD SPECIES DETECTIONS

Across the 24 cases where I measured the extent of change and temporal invariability of bird species detections, I found that, in most cases, bird species showed a significant decrease in vocalisation detections following the typhoons (Figs. D.1 and D.16a). For both *Corvus macrorhynchos* and *Horornis diphone*, typhoon impacts were not explained by any land use variables for either extent of change or temporal invariability (Null model $\Delta AIC_c = 0$ in all cases; Fig. 5.6). However, when comparing the extent of change in detections between the two species, I found that *H. diphone* was affected more negatively following the typhoons than *C. macrorhynchos* (ANOVA: $F_{1,19} = 9.64$, $p = 0.006$; Fig. 5.6e). This pattern was driven by the consistently negative extent of change in *H. diphone* detections (Fig. 5.6c) compared to a balance of positive, negative, and neutral values for *C. macrorhynchos* (Fig. 5.6a). Despite variation among species

and sites in temporal invariability of detections (Fig. D.16b), there was no difference between *C. macrorhynchos* and *H. diphone* in their temporal invariability values ($F_{1,19} = 0.8$, $p = 0.38$; Fig. 5.6f).

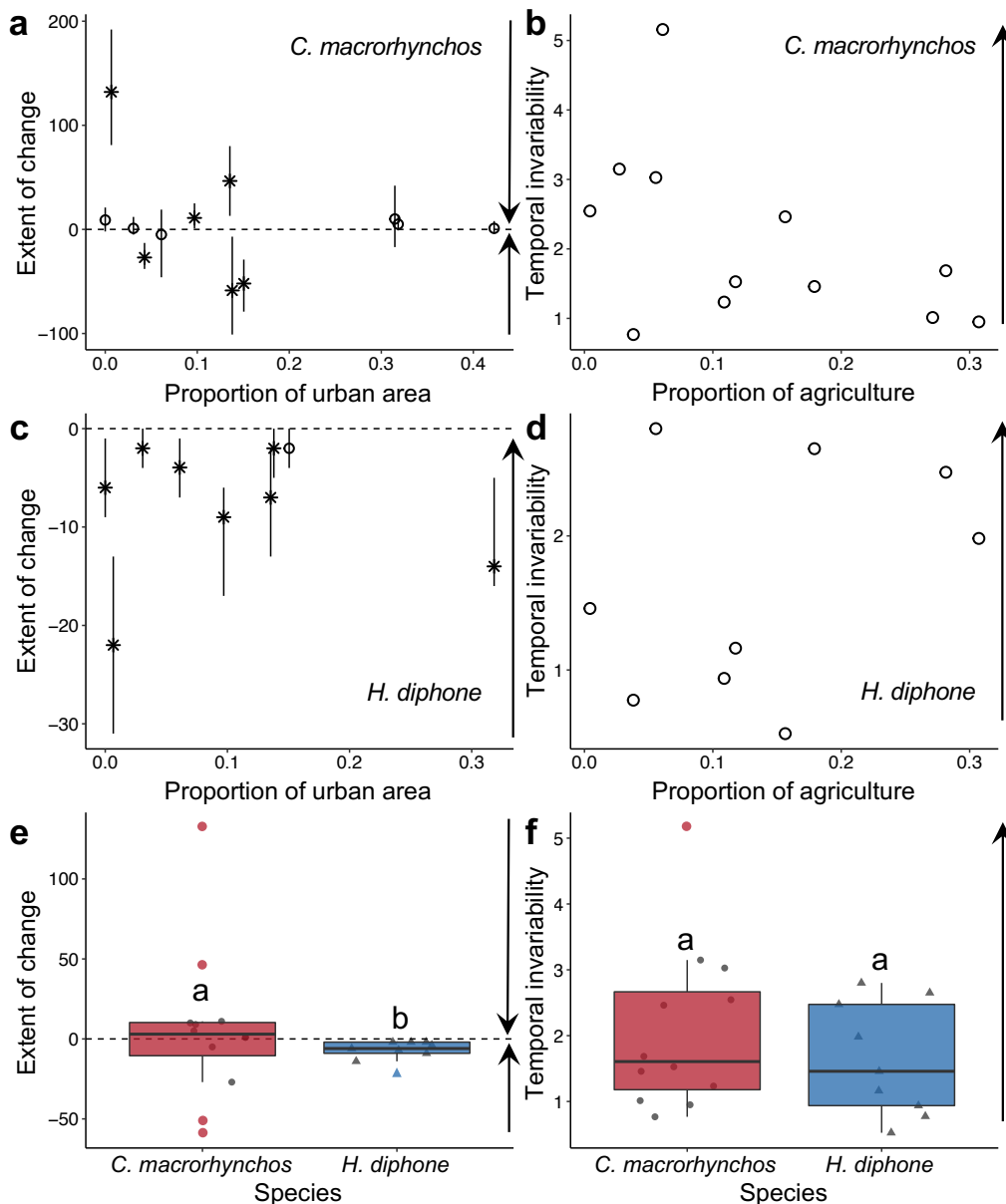


Figure 5.6 | Relationships between land use and stability of bird species detections. For two dimensions of stability (extent of change [a,c,e] and temporal invariability [b,d,f]; see Table 5.1), plots a-d show the most important land use variable (based on model selection results) plotted against the stability of daily bird detections for a-b *Corvus macrorhynchos* and c-d *Horornis diphone*. Boxplots (e-f) represent the range (box = median and interquartile range) of stability values across sites for each species (*C. macrorhynchos* [red, circles] and *H. diphone* [blue, triangles]) for each of e extent of change, and f temporal invariability. To aid interpretation, arrows to the right of each plot point towards more stable values for each dimension of stability (see Table 5.1 for detailed interpretation).

When measuring the spatial variability among sites for bird species detections, my two focal species differed in their responses to typhoons (Fig. 5.7). I found a significant interaction between time period and species identity ($F_{1,76} = 5.0$, $p = 0.028$); after the typhoons, *H. diphone* spatial variability increased relative to pre-typhoon values (Tukey HSD: $p_{\text{adj}} = 0.001$) whereas *C. macrorhynchos* variability did not increase post-typhoon (Fig. 5.7b).

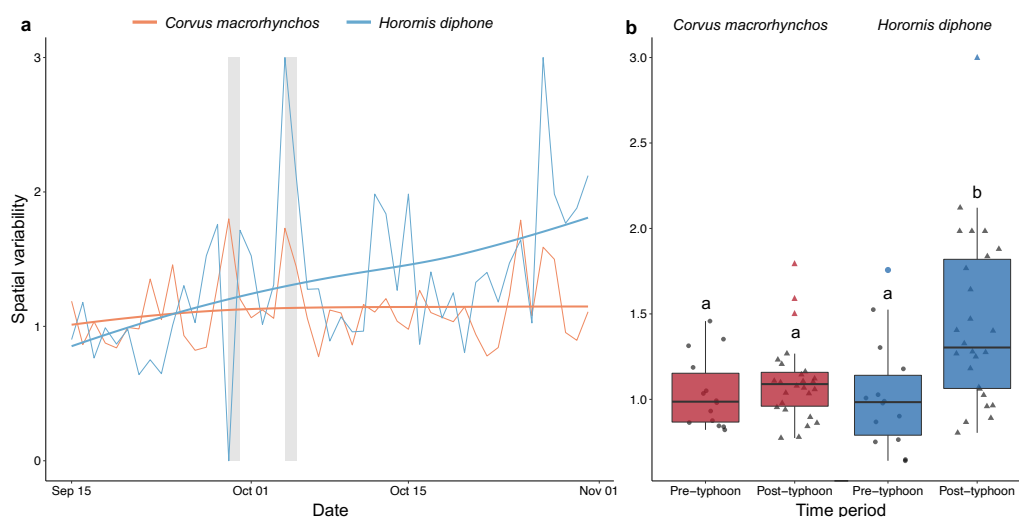


Figure 5.7 | Bird detection spatial variability through time. **a** Time series of spatial variability of bird species detections for two species (*Corvus macrorhynchos* [red] and *Horornis diphone* [blue]) across all sites for which recognisers were reliable (that is, 15 and 9 sites, respectively, see 5.3 *Methods*). Time series show changes in spatial variability resulting from typhoon impacts [grey bars]. **b** pairwise statistical tests of typhoon effects and species identity on spatial variability. Boxplots represent the range (box = median and interquartile range) of daily spatial variability values for bird detections across dates before [circles] versus after [triangles] the typhoons for each of *C. macrorhynchos* [red] and *H. diphone* [blue]. Significant ($p < 0.05$) pairwise contrasts are denoted with superscript letters.

5.5 DISCUSSION

My results indicate clearly that land use can modify the stability responses of ecosystems to extreme weather events. Every acoustic index I measured and bird species I quantified was altered in some way following the typhoons, indicating the considerable potential for extreme weather events to disrupt natural soundscapes. Moreover, the relationships between land use and stability responses were multifaceted, with stability responses to the typhoons varying across land use categories and along different dimensions of stability. Broadly, soundscapes from sites with more natural land uses, and particularly pre-climax

scrubland, were more resistant to typhoon impacts but recovered more slowly. Though I cannot derive mechanistic understanding from an observational study such as this, my results suggest that the observed associations between land use and various dimensions of soundscape stability at the site level may have been driven by heterogeneous responses among unforested sites in space (see Thompson *et al.* 2014; Wang *et al.* 2021) and differential responses between bird species (*e.g.*, Leary & Petchey 2009; Moore & Olden 2017). Taken overall, my results underscore the potential for natural habitats and their associated biodiversity to insure ecosystems against disturbance.

Generally, I found that land use explained significant variance in the stability responses of soundscapes to typhoon disturbance. Resistance is a crucial axis of ecological stability measuring short-term defence against disturbance (Donohue *et al.* 2013; Nimmo *et al.* 2015), while my measurement of the extent of change captured longer-term disturbance resistance (Yang *et al.* 2019). Across several acoustic indices, pre-climax vegetation in the form of scrublands and grasslands were generally more resistant to typhoon disturbance measured via resistance and extent of change. Forest cover was also related to higher resistance in my study (see also Nimmo *et al.* 2016), but only in the case of anthropophony ($\text{NDSI}_{\text{Anthro}}$). Along other dimensions of stability, forest cover was related negatively to stability for two indices ($\text{NDSI}_{\text{Anthro}}$ and M). $\text{NDSI}_{\text{Anthro}}$ results generally opposed NDSI_{Bio} , indicating that observed decreases in biophony following the typhoons were accompanied by an increase in low frequency anthropophony and geophony (Simmons *et al.* 2021), producing a downward shift in the relative contribution of biophony to the overall soundscape (measured via NDSI). That forest cover was related to more reactive and slower to recover soundscapes in terms of their total volume (measured via M) perhaps reflects a change to forest structure caused by physical typhoon damage or salinization (S.R.P-J.R. pers. obs.; Everham & Brokaw 1996; Kerr 2000; Zampieri *et al.* 2020). Equally, the higher resistance of biophony in open scrublands may indicate that the typhoons did not significantly alter vegetation structure, and thus habitat availability, of these open habitats as much as for closed canopy forests.

The contribution of land use to ecological stability in the face of typhoons was multifaceted, with several land use types simultaneously relating positively and negatively to stability along different dimensions. For example, while soundscapes of scrublands and natural grasslands tended to be more resistant to typhoon impacts, these same sites recovered more slowly, and were more reactive when measured with different acoustic indices. The contrasting contributions of land use to different components of stability may suggest a high dimensionality

of stability, whereby multiple metrics provide distinct but complementary information on the overall stability of the system (Donohue *et al.* 2013, 2016; Domínguez-García *et al.* 2019; Kéfi *et al.* 2019; Yang *et al.* 2019). Experimental results increasingly support the notion that drivers of stability may act divergently along multiple dimensions of stability (Chapter 3; Baert *et al.* 2016; Hillebrand & Kunze 2020; White *et al.* 2020b; Ross *et al.* 2022; see also Magurran *et al.* 2018). In keeping with my result that forest cover was related to higher resistance but slower recovery times and more variable soundscapes for two acoustic indices (NDSI_{Anthro} and M), Nimmo *et al.* (2016) found that tree cover enhanced resistance but lowered resilience of bird species incidence and richness in response to a decade-long drought in Australia.

The proportion of urban area was never related to stability for any of my measured acoustic indices (including anthropophony). This finding contrasts with results of Joo *et al.* (2011), who found that biophony was more variable in urban than rural areas. It is also surprising given the prevalence and impact of noise pollution on wildlife (Buxton *et al.* 2017; Senzaki *et al.* 2020) and Okinawa's strong rural-urban gradient (Ross *et al.* 2018a). Agriculture—Okinawa's other dominant anthropogenic land use (Fig. D.17)—was, however, consistently related to lower soundscape stability within sites, though agricultural sites had higher spatial variability than non-agricultural sites. Soundscapes in agricultural sites were more variable and had lower resilience compared to natural habitats. This suggests that agricultural intensification—a key global change driver (Tscharntke *et al.* 2005; Laurance *et al.* 2014)—may amplify the effects of extreme weather events in future as climate change increases the frequency, intensity, and inland reach of landfalling typhoons (Knutson *et al.* 2010; Kossin *et al.* 2020; Li & Chakraborty 2020). Given the potential for nonadditive effects of agricultural land use and extreme events, greater effort should be paid to managing for resilience in agroecosystems (Spears *et al.* 2015; Haughey *et al.* 2018; White *et al.* 2021). My finding of an association between stability and agricultural, but not urban, land use supports recent evidence showing declines in bird community stability with agricultural intensification but not urbanisation (Olivier *et al.* 2020). Taken together, these results suggest a contrasting potential for two key land use axes (urbanisation and agricultural intensification) to shape ecological stability.

Overall, typhoons reduced the density of bird vocalisations detected via my Hidden Markov Models. These results complement reports of bird population declines and compositional shifts following extreme events (Lynch 1991; Jiguet *et al.* 2011; Chevalier *et al.* 2019; Maxwell *et al.* 2019). Owing to the difficulty in

estimating abundance from audio recordings (*e.g.*, Pérez-Granados *et al.* 2019), I cannot attribute declines in vocalisations directly to mortality or population reductions. Nevertheless, that I generally found a decrease in vocal activity of several species across multiple sites suggests a change in either the density (*e.g.*, Lynch 1991; Wiley & Wunderle 1993) or behaviour (*e.g.*, Locascio & Mann 2005; Boyd *et al.* 2021; Testard *et al.* 2021) of sound-producing animals in response to typhoons. Post-storm mortality due to altered food and habitat availability is more common than direct mortality during storms (Wiley & Wunderle 1993; Kerr 2000). As such, habitat specialists are often replaced by generalists from the regional species pool following extreme events or disturbance (Edwards *et al.* 2013; Burivalova *et al.* 2014). The difference in habitat affinity between my focal bird species may thus explain my finding of species-specific responses to disturbance. At the landscape scale, I detected a widespread decline in vocalisations of the Japanese bush warbler (*Horornis diphone*), a habitat specialist, whereas the generalist large-billed crow (*Corvus macrorhynchos*) on average neither declined nor increased. *Horornis diphone* may thus have experienced a loss of suitable habitat following the typhoon-induced destruction of vegetation while the generalist crow did not (Wiley & Wunderle 1993). Despite differences in the extent of change of *H. diphone* versus *C. macrorhynchos* across sites, the stability of bird detections did not vary as a function of land use here. Though for *C. macrorhynchos* this pattern supports an earlier finding that detections of this species did not change along Okinawa's urbanisation gradient (Fig. D.17; Ross *et al.* 2018a), the limited sample sizes and range of species considered here prevents definitive understanding of the drivers of bird species tolerance to extreme events.

Across all acoustic indices, I found consistent post-typhoon increases in spatial variability across sites. These results suggest a typhoon-induced divergence of response trajectories, where differences in acoustic responses to the typhoons across sites resulted in higher post-typhoon spatial variability. I also detected an effect of land use on spatial variability across acoustic indices. Predominantly, sites with the highest proportion of scrubland and natural grassland underwent a less marked increase in spatial variability following the typhoons. That is, the least scrubland sites responded more heterogeneously in space than did scrubland sites. This result supports my finding that scrublands were more resistant to typhoons, and hence acoustic indices did not diverge considerably across scrubland sites following disturbance. Similarly, unforested sites showed a greater post-typhoon increase in spatial variability than among forested sites, suggesting that forests generally responded uniformly to disturbance, while unforested sites

had divergent response trajectories. Agricultural sites tended not to modify typhoon impacts but had higher among-site variability than less-agricultural sites (though the opposite was true for $\text{NDSI}_{\text{Anthro}}$ and H). For bird species detections, in support of species-specific typhoon effects on extent of change, species identity interacted with typhoons to shape spatial variability. As with their extent of change, I found no significant effect of the typhoons on *Corvus macrorhynchos*. However, following the typhoons, *Horornis diphone* spatial variability increased—a pattern supporting both a greater sensitivity of the specialist *H. diphone* than the generalist *C. macrorhynchos*, and consistent with my finding of a post-typhoon increase in spatial variability across acoustic indices. Overall, my results therefore suggest spatial variability as a key axis of stability when characterising the responses of soundscapes to typhoons at the landscape scale (see also Chapter 3; Loreau *et al.* 2003; Wang *et al.* 2021).

My study is one of the first to assess ecological responses to typhoons using high-resolution acoustic data, and to reveal the capacity for land use to shape stability responses to extreme events. It comprises a significant advance for several reasons. First, unlike most studies of discrete disturbance events (*e.g.*, Gottesman *et al.* 2021), this study was conducted in a system for which the soundscape had been previously characterised and where the performance of acoustic indices is well understood (Chapter 4; Ross *et al.* 2018a, 2021b). Second, I used high-resolution time series to measure multiple dimensions of stability; an important shift away from studies considering only temporal snapshots before versus after disturbance (Gasc *et al.* 2018; Burivalova *et al.* 2021). Third, studies rarely analyse both acoustic indices and bioacoustic species detections as I have here (see also Ross *et al.* 2018a), and using machine-learning recognisers for individual bird species provides more direct assessment of disturbance impacts on bird incidence than do acoustic index proxies (*e.g.*, spectral saturation; Burivalova *et al.* 2018; Gottesman *et al.* 2021) of bird detections alone. A joint bio- and ecoacoustic approach thus allowed us to tie typhoon responses of acoustic indices to those of individual species more directly than previous studies on extreme events in the soundscape (Locascio & Mann 2005; Gottesman *et al.* 2021). Finally, my data came from 24 field sites representing the full range of Okinawa's land use types (Fig. D.17). By combining high-resolution time series across multiple sites at the landscape scale, I revealed how ecological stability varies across the landscape in response to an extreme event.

My findings support the utility of passive acoustic monitoring for revealing disturbance impacts and monitoring recovery (Deichmann *et al.* 2018; Gasc *et al.*

2018; Burivalova *et al.* 2019a; Duarte *et al.* 2021). Where deployed as multi-site sensor arrays (Sethi *et al.* 2020a; Sugai 2020), acoustic monitoring programmes have a growing capacity to reveal near-real-time disturbance impacts at large spatial scales, and I thus support growing efforts to characterise and conserve the world's natural soundscapes (Dumyahn & Pijanowski 2011). Using data from a landscape-scale sensor network with well-characterised soundscapes (Ross *et al.* 2018a, 2021b), I revealed a novel relationship between land use and extreme weather events, as well as preliminary evidence of the spatial mechanisms that may underpin site- and species-specific disturbance responses. As Okinawa is exposed to larger and longer lasting typhoons under climate change (Elliott & Nino 1960; Ares *et al.* 2020; Li & Chakraborty 2020), my results provide an important baseline understanding of how land use can modify typhoon impacts, suggesting that natural habitat, and particularly grasslands and forests, may be key to insuring ecosystems against extreme weather events (Gibson *et al.* 2011; Nimmo *et al.* 2016; Gottesman *et al.* 2021). I also found that anthropogenic land uses provided contrasting contributions to stability; agriculture shaped stability responses in Okinawa, while urbanisation did not (see also Olivier *et al.* 2020). My work highlights the susceptibility of Okinawa's forests to extreme events, and the need for careful management and stewardship of these vulnerable and irreplaceable natural habitats in a future characterised by joint pressures from two key axes of global environmental change—land use and climate change.

CHAPTER 6 | GENERAL DISCUSSION

“Disturbances and stability are multidimensional. Our understanding of them is not.”

Donohue *et al.* (2016) *Ecology Letters*

6.1 THE STABILITY OF ECOSYSTEMS UNDER GLOBAL ENVIRONMENTAL CHANGE

The work presented in this thesis comprises an important step towards a general and mechanistic understanding of the impact of global environmental change on the overall stability of ecosystems. Using a combination of theory (Chapter 2; Ross *et al.* 2021a), a multifactorial field experiment (Chapter 3; Ross *et al.* 2022), and observational data from a high-resolution acoustic monitoring network (Chapters 4 and 5; Ross *et al.* 2021b), I measured multiple dimensions of ecological stability in response to several key elements of global environmental change. I studied the effect of species extinctions (Chapters 2 and 3), extreme events (Chapters 3 and 5), and land use (Chapter 5) on ecological stability, and revealed a general erosion of stability in response to global change, as well as reporting novel interactions between multiple global change drivers. Moreover, I demonstrated nature’s foundational role in stabilising ecosystems in variable environments or in response to pulse disturbances, including the contributions of biodiversity and natural land use to ecological stability.

Generally, across my theoretical, experimental, and observational work, I found that global environmental change erodes multiple dimensions of ecological stability. In Chapter 2, I showed that species extinctions compromise the capacity of ecological networks to provide ecosystem services, specifically through changes to *network fragility*—a simple empirically-quantifiable component of bipartite species-traits networks that relies only on the number of species, their traits, and links between the two (Ross *et al.* 2021a). In other words, through their effects on the dispersion of species and their functional traits, sequential extinctions increase the probability of catastrophic ecosystem service failure (see also Keyes *et al.* 2021). In Chapters 3 and 5, I reported destabilising effects of extreme events (pulse disturbances) on aquatic food webs and terrestrial soundscapes, respectively. I found that realistic experimental heatwaves (based on an IPCC RCP8.5 high-emissions scenario targeted to the local region in Hokkaido, Japan;

Moss *et al.* 2010) destabilised the functional and compositional variability of macroalgal communities, though to different degrees and over different time scales (Chapter 3). Similarly, successive typhoons (that is, a natural multi-pulse disturbance) impacted bird species and soundscapes at the landscape scale across the island of Okinawa, and destabilised multiple components of ecological stability (Chapter 5). That said, my results were nuanced, with context-dependencies and multifaceted responses of ecological stability when measured across multiple dimensions. For example, in Chapter 3 I found that functional and compositional responses of macroalgal communities to heatwaves were largely independent of one another, as supported by recent work simultaneously considering both functional and compositional stability (Baert *et al.* 2016; Hillebrand & Kunze 2020; Jacquet & Altermatt 2020; White *et al.* 2020b; see also Magurran *et al.* 2018). Moreover, the multiple dimensions of ecological stability measured throughout this thesis were not consistently and strongly correlated (Chapters 3 and 5), further supporting the notion that stability should be treated as a multidimensional concept to be of practical use for management (Donohue *et al.* 2013, 2016; Baert *et al.* 2016; Nimmo *et al.* 2016; Garnier *et al.* 2017; Hillebrand *et al.* 2018; Arnoldi *et al.* 2019; Radchuk *et al.* 2019; Yang *et al.* 2019; Ross *et al.* 2021c). Among the idiosyncratic impacts of global change on stability, I found that functional and compositional stability responded to heatwaves over different temporal scales (Chapter 3; Ross *et al.* 2022), highlighting the importance of scale when measuring and interpreting ecological stability (Clark *et al.* 2021; Ross *et al.* 2021c). Similarly, my results from Chapter 4 suggest that care should be taken in the interpretation of acoustic indices across sonic contexts and seasons (Ross *et al.* 2021b), with insect noise, geophony (wind, rain, *etc.*) and anthropophony all potentially obstructing the biological foundations on which acoustic indices are assumed to be built.

Some of the context-dependent effects of global change on ecological stability were a result of novel interactions among global environmental change drivers. For example, I found that trophic structure (that is, the presence or absence of a dominant predatory fish) moderated the stability of macroalgal communities to experimental heatwaves (Chapter 3; Ross *et al.* 2022). Specifically, where fish were absent, macroinvertebrate herbivores experienced predatory release, which, in turn, may have caused the observed spatial homogenisation of macroalgae by overgrazing (see also Kordas *et al.* 2017). These results highlight the importance of considering biotic multipliers of climate change (Zarnetske *et al.* 2012), where biodiversity, including community structure and biotic interactions, can regulate ecological responses to climate

change and extreme events (Kishi *et al.* 2005; Rasher *et al.* 2020). I also revealed a novel interaction between land use and typhoons when measuring the responses of soundscapes to typhoon disturbance at the landscape scale (Chapter 5). Pre-climax scrubland was particularly resistant to typhoon disturbance (though at the expense of slower recovery), while forests were resistant for one of our measured acoustic indices (see also Nimmo *et al.* 2016), but were otherwise vulnerable and destabilised by typhoons since forested sites responded more homogeneously in space. I also found that of Okinawa's two dominant anthropogenic land use gradients, agriculture worsened typhoon impacts (though agricultural sites responded heterogeneously in space) whereas urbanisation did not (see also Olivier *et al.* 2020). These results underscore the potential for natural habitats to stabilise ecosystems and soundscapes in response to climate change and extreme events (Uhl & Kauffman 1990; Arkema *et al.* 2013; Nimmo *et al.* 2016; Raymond *et al.* 2020). Taken together, the interactions discussed in Chapters 3 and 5 highlight nature's foundational role in promoting biodiversity regulation (*e.g.*, Gotelli *et al.* 2017), and in buffering ecological communities against disturbance (*e.g.*, Nimmo *et al.* 2016; Rasher *et al.* 2020).

6.2 CORE MECHANISMS DRIVING ECOLOGICAL STABILITY

6.2.1 SPATIAL INSURANCE

I found that spatial variability was a key axis of ecological stability for both multitrophic freshwater communities (Chapter 3) and soundscapes across sites (Chapter 5). These results are consistent with theory suggesting spatial processes such as asynchrony (Thompson *et al.* 2014, 2015; Wang & Loreau 2016; Wang *et al.* 2021) and patch dynamics (Leibold *et al.* 2004; Hammond *et al.* 2020; Suzuki & Economo 2021) as key determinants of community structure and stability (Loreau *et al.* 2021). I found that experimental heatwaves destabilised algal communities by homogenising them in space (Chapter 3; Ross *et al.* 2022). However, a common predator (*Cottus nozawae*) exerted trophic control of macroinvertebrate herbivores, stabilising algal composition in space despite exposure to heatwaves. These results closely match those of Kordas *et al.* (2017), who found that herbivorous limpets enabled intertidal communities to resist warming through their indirect effects on several key herbivores. Moreover, I found that soundscape and species responses to typhoons were mediated by differential responses among sites (Chapter 5), with a habitat-specific increase in spatial variability following disturbance. Unforested sites were more

heterogeneous in space following typhoon impacts, while forested sites responded relatively uniformly to typhoon disturbance. Taken together, my results add credence to the notion that spatial variability is a key mechanism underpinning multidimensional ecosystem stability (Loreau *et al.* 2003; Wang & Loreau 2014). As such, specific attention should be paid to the spatial scale at which biodiversity, functioning, and stability are measured in any study (Wang & Loreau 2014; Chase *et al.* 2018, 2019; Gonzalez *et al.* 2020; Ross *et al.* 2021c), as well as increasing efforts to develop scaling rules for ecological stability across space (Wang *et al.* 2017; Clark *et al.* 2021).

6.2.2 RESPONSE DIVERSITY

As May (1973) noted, biodiversity per se cannot explain the generally positive diversity-stability relationship. One mechanism now often proposed as among the most promising candidates for explaining the relationship between biodiversity and ecological stability is response diversity. Response diversity characterises the range of different physiological or ecological responses (*e.g.*, population growth rate), in direction and/or magnitude, to a given disturbance: ecological communities with a higher diversity of responses should better resist disturbances and, due to compensatory dynamics among species, maintain stable biomass, composition, or functioning (Yachi & Loreau 1999; Elmqvist *et al.* 2003; Nyström 2006; Gonzalez & Loreau 2009; Mori *et al.* 2013). In Chapter 5, I found that bird species responded differently to a multi-pulse disturbance in the extent of change of their vocalisation detections. This finding is consistent with the idea that species-specific differences in tolerance versus vulnerability to multiple disturbances can shape community level responses to disturbance (Vinebrooke *et al.* 2004; Winfree & Kremen 2009; Brennan & Collins 2015; Bhaskar *et al.* 2017). However, the limited sample size of my species detection algorithms (Chapter 5) precluded empirical quantification of response diversity in my study. Moreover, while the conceptual foundation for response diversity in ecology is now well established (Elmqvist *et al.* 2003; Nyström 2006; Suding *et al.* 2008; Mori *et al.* 2013), there remains a disconnect with a small but growing literature measuring response diversity empirically (*e.g.*, Leary & Petchey 2009; Brennan & Collins 2015; Bhaskar *et al.* 2017; Moore & Olden 2017; Herrando-pérez *et al.* 2019). Consequently, there is no agreed-upon framework for measuring response diversity theoretically, experimentally, or observationally, limiting the evidence that response diversity may drive ecological stability. Clearly, the concept has potential as a candidate mechanism (*e.g.*, Pennekamp *et al.* 2018; Sasaki *et al.*

2019), but robust methodologies for the empirical quantification of response diversity must be developed and applied across systems before a process-based understanding of ecological stability is achievable.

6.3 FUTURE PROSPECTS

6.3.1 ECOLOGICAL STABILITY IN THE AGE OF AUTOMATION

With advances in automated data collection and analyses (Keitt & Abelson 2021), passive acoustic monitoring now often provides valuable information on biological communities and entire soundscapes (Chapter 4; Deichmann *et al.* 2018; Linke *et al.* 2018; Bradfer-Lawrence *et al.* 2019; Burivalova *et al.* 2019a; Desjonquères *et al.* 2020; Guan *et al.* 2021; Ross *et al.* 2021b). The recent influx of acoustic data goes some way towards releasing ecology from its historic data limitation and, though methodological debates still rage (*e.g.*, Fuller *et al.* 2015; Gasc *et al.* 2015; Fairbrass *et al.* 2017), there is clear potential for acoustic approaches to reveal new insight into long-standing ecological questions or pressing global challenges (Chapter 5; Sueur *et al.* 2019; Sugai 2020; Duarte *et al.* 2021). Ecoacoustic studies are now moving away from refining methods towards establishing core hypotheses and questioning whether there are general rules in ecoacoustics (*e.g.*, Lomolino *et al.* 2015; Francomano *et al.* 2020; Lomolino & Pijanowski 2021). Such a shift provides a considerable step towards real-time monitoring of communities and soundscapes (Van Parijs *et al.* 2009; Aide *et al.* 2013; Buxton *et al.* 2018b; Ross *et al.* 2018a; Sethi *et al.* 2018, 2020a), including measuring disturbance and recovery in complex systems (Chapter 5; Gasc *et al.* 2018; Gottesman *et al.* 2018, 2021; Burivalova *et al.* 2021). Automated real-time ecological monitoring can aid conservation, for example through real-time detection of extreme events (Chapter 5) or illegal logging (Sethi *et al.* 2020b). When combined with other high resolution ecological time series (*e.g.*, Dornelas *et al.* 2018), I anticipate a shift away from reactive management in coming years, towards conservation efforts informed by mechanistic and predictive science (Mouquet *et al.* 2015).

6.3.2 QUANTIFYING THE CONTRIBUTION OF INDIVIDUAL SPECIES TO ECOLOGICAL STABILITY

As multiple disturbances unfold and interact in the Anthropocene, there is increasing potential for press disturbances to modify the impact of pulse disturbances (Harris *et al.* 2018; Jentsch & White 2019; Birk *et al.* 2020). For

example, amidst the joint biodiversity and climate crises, biotic and abiotic global change drivers increasingly interact (Chapter 3; Zarnetske *et al.* 2012; O'Connor & Donohue 2013; O'Connor *et al.* 2015; Kordas *et al.* 2017; White *et al.* 2018; Rasher *et al.* 2020; Ross *et al.* 2022). I demonstrated that biodiversity and natural vegetation can buffer the effects of extreme climatic events on ecosystems (Chapters 3 and 5; see also Kishi *et al.* 2005; Nimmo *et al.* 2016; Kordas *et al.* 2017; Rasher *et al.* 2020). This, in turn, highlights the potential to measure the contribution of individual species or functional groups to ecological stability (Chapters 2 and 3; Ross *et al.* 2021a; see also Dee *et al.* 2019; White *et al.* 2020b). Through consideration of the importance of individual species in underpinning the stability of ecosystems and their services, we can gain precise understanding of the specific elements of biodiversity that stabilise ecosystems against disturbance (Chapter 2; Ross *et al.* 2021a), enabling mechanistic insight into the insurance effect of biodiversity (Yachi & Loreau 1999; Loreau *et al.* 2021). Such insight will provide a focus for management effects, allowing targeted conservation of key contributors to ecological stability and the continued supply of ecosystem services (Chapter 2; Petchey & Gaston 2002; Worm *et al.* 2006; Palumbi *et al.* 2009; Isbell *et al.* 2015a; Lefcheck *et al.* 2015; Fanin *et al.* 2017; Maseyk *et al.* 2017; Dee *et al.* 2019; White *et al.* 2020b; Greenop *et al.* 2021; Keyes *et al.* 2021; Ross *et al.* 2021a). Beyond individual species contributions to stability, intraspecific trait variation reveals the potential for individuals to drive ecological responses to disturbance (Ross *et al.* 2017; Herrando-pérez *et al.* 2019; Des Roches *et al.* 2021), and genetic variation can drive ecosystem change (McClean *et al.* 2015; Kahiluoto *et al.* 2019; Moreno-Mateos *et al.* 2020). Increasing focus of the contribution of individuals and species to ecological stability will reveal how disturbances can propagate through ecosystems, providing important insight into the scaling of ecological stability (Wang *et al.* 2017; Clark *et al.* 2021).

6.4 CONCLUDING REMARKS

Ultimately, the results presented in this thesis emphasise the value of biodiversity and natural habitats in insuring species, communities, soundscapes, and ecosystem services against global environmental change. Accordingly, my findings support the recent emphasis of management efforts targeting not only single species or areas of conservation concern, but increasing focus on the importance of ecological complexity and species interactions (Harvey *et al.* 2017; Seibold *et*

et al. 2018; Heinen *et al.* 2020; Moreno-Mateos *et al.* 2020). My work underscores biodiversity's foundational role in stabilising ecosystems along multiple dimensions in response to disturbance (Chapters 2 and 3; Ross *et al.* 2021a; see also Pimm 1984; Yachi & Loreau 1999), and the necessity of conserving the world's dwindling natural habitats (Chapter 5; see also Gibson *et al.* 2011; Barnes *et al.* 2017; Daskalova *et al.* 2020; Olivier *et al.* 2020). Accordingly, to mitigate the potentially compounding effects of multiple global change drivers, greater effort should be made to manage ecosystems and their emergent properties for stability in fluctuating environments (Allen *et al.* 2011; McPhearson *et al.* 2015). With greater focus on managing for multifunctionality (Hector & Bagchi 2007; Fanin *et al.* 2017; Manning *et al.* 2018) and the continued delivery of ecosystem services (Chapter 2; Kremen 2005; Winfree & Kremen 2009; Keyes *et al.* 2021; Ross *et al.* 2021a), successful conservation of species and ecosystems should be achievable, since my work adds to mounting evidence that biodiversity and natural habitat promote the stable delivery of ecosystem functions and services (Zavaleta *et al.* 2010; Isbell *et al.* 2015a; Soliveres *et al.* 2016; Sasaki *et al.* 2019; Mori *et al.* 2021), and thus the sustainability of human societies (Mastrángelo *et al.* 2019). To achieve a sustainable future, promotion of biodiversity's fundamental role in shaping ecological stability will be key (*e.g.*, Mori *et al.* 2021), as will the explicit definition (Donohue *et al.* 2016), measurement (Pimm *et al.* 2019), and continued monitoring of ecological stability using near-real-time approaches (*e.g.*, Burivalova *et al.* 2019a; Keitt & Abelson 2021) to respond more reflexively to disturbance events in future. Donohue *et al.* (2016) highlighted a disconnect between the multidimensional nature of both disturbances and stability, and the limited range of angles from which these concepts are generally studied. By using complementary methods to reveal how multiple elements of global change interact to erode ecological stability, my work takes an important step towards a more holistic and multidimensional understanding of both disturbance and stability. Such a step will be essential for futureproofing ecosystems in an era characterised by intensifying disturbance regimes and unrelenting global environmental change.

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APPENDIX A | SUPPLEMENTARY MATERIAL TO CHAPTER 2

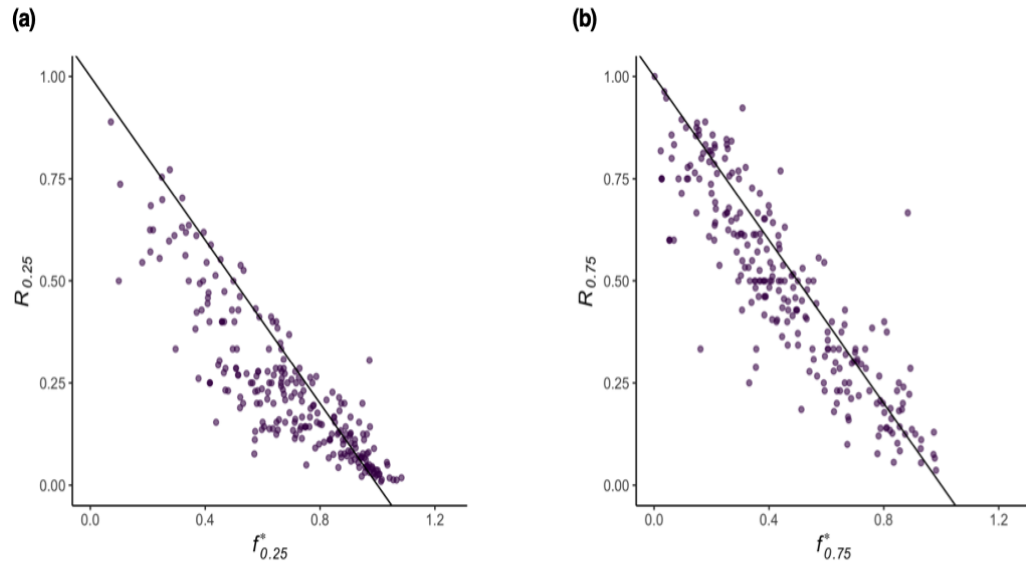


Figure A.1 | Relationships between simulated robustness of ecosystem service supply quartiles R_c and analytically-estimated network fragility f_c^* where $c =$ (a) 0.25 (for which $\lambda_{0.25} = -1.65$) and (b) 0.75 (for which $\lambda_{0.75} = -1.35$), from the analysis of 251 empirical networks as described in Fig. 2.4.

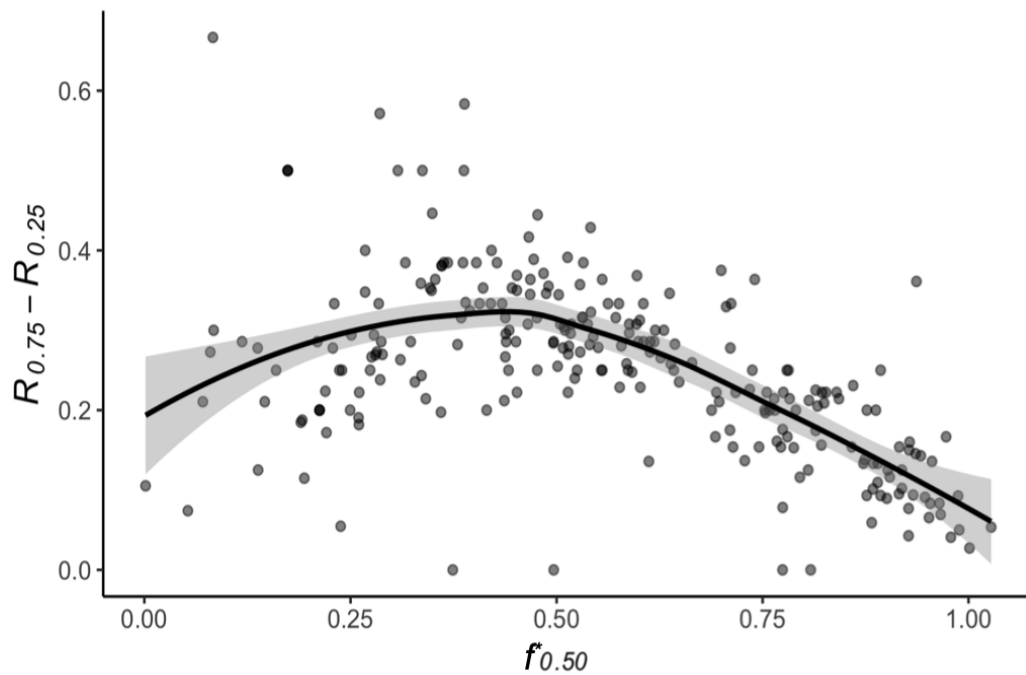


Figure A.2 | Uncertainty in robustness of ecosystem service supply calculated from 251 empirical networks is greatest at intermediate values of network fragility ($f_{0.5}^*$). I quantified uncertainty as the interquartile range $R_{0.75} - R_{0.25}$. A loess smoother (span = 0.8) with 95% confidence intervals is shown to illustrate the concave relationship.

A.1 ROBUSTNESS IN THE SIMPLIFIED MODEL

In the main text (see 2.3 *Methods*), I describe an analytically tractable model of ecosystem processes (*e.g.*, services), seen as Boolean functions of the presence/absence of S species (but one could think of populations or even individuals). I distinguish species from their N functional traits, and consider a special set of Boolean functions of the form

$$E = \text{AND} \circ \text{OR}^N: \{0,1\}^S \rightarrow \{0,1\}^N \rightarrow \{0,1\}$$

where $\text{OR}^N: \{0,1\}^S \rightarrow \{0,1\}^N$ is a mapping from species to traits configurations. It is the Cartesian product of N (partial) OR functions associated with traits (thus, a trait is present if at least one species that has this trait is present). I model the universe of OR^N as random bipartite networks with connectance p . Deriving an expression for the distribution of fraction of species extinctions that lead to a loss of service is the goal of this subsection. I start from the probability of having lost at least one trait when n species are lost. The latter reads

$$P(n_e \leq n) = 1 - (1 - q^{S-n})^N; q = 1 - p \quad (\text{A1})$$

where n_e would be the number of extinctions that led to the loss of the first trait. If I write $p(n_e)$, the probability of the loss occurring after exactly n_e extinctions

$$P(n_e \leq n) = \sum_{n_e=1}^n p(n_e) \quad (\text{A2})$$

One can understand Equation (A1) from the following argument. Consider one functional trait and write its distribution over species as a vector

$$\underbrace{[0,0,0, \dots, 0]}_{S-n}, \underbrace{[1, \dots, 1]}_n$$

Extinctions proceed from the right, removing entries until only the $S - n$ last entries remain. The trait is still represented at this stage if not all remaining entries are zero. The probability of all these entries being zero is q^{S-n} and, thus, the probability of the trait still being present is $1 - q^{S-n}$. That all traits are present then reads $(1 - q^{S-n})^N$, so that the complementary probability is the probability that at least one trait is lost after n extinctions, thus that $n_e \leq n$.

I have not yet conditioned on the fact that the process ought to be running when all species are present. The probability of a trait being present before extinctions take place is $1 - q^S$. The probability of all traits being present is therefore $(1 - q^S)^N$, which gives us that $p(0) = 1 - (1 - q^S)^N$. From Bayes' theorem it holds that

$$P(n_e \leq n) = p(n_e \leq n | n_e = 0)p(0) + P(n_e \leq n | n_e > 0)(1 - p(0))$$

By definition, $P(n_e \leq n | n_e = 0) = 1$. I deduce that the conditional probability

$$P(n_e \leq n | n_e > 0) = \frac{P(n_e \leq n) - p(0)}{1 - p(0)}$$

This is the cumulative probability of number of extinctions leading to the loss of at least one trait. From this expression it is straightforward to deduce any percentile of the actual probability distribution $P(n_e)$. For instance, its median $n_{0.5}$ is such that, by definition:

$$P(n_e \leq n_{0.5} | n_e > 0) = 0.5$$

More generally, the c^{th} percentile of $P(n_e)$ is the number n_c such that

$$P(n_e \leq n_c | n_e > 0) = c$$

which I can invert to get that

$$n_c = S - \frac{\log(1 - (1 - q^S)\bar{c}^{1/N})}{\log q} \quad \bar{c} = 1 - c$$

I define robustness $R(E)$, along a specific extinction scenario, as the fraction n_e/S . I thus have that the c^{th} percentile of the distribution of robustness reads

$$R_c(E) = 1 - f_c; \quad f_c = \frac{\log(1 - (1 - q^S)\bar{c}^{1/N})}{S \log q}$$

where I defined a family of network fragility measures $(f_c)_{0 < c < 1}$.

A.2 TIME TO SERVICE FAILURE

If I assume a constant rate λ of species extinction, I can deduce from the derivations in Appendix A.1 the median time to functional extinction, as follows. Let p_t be the probability that a given species, present at time 0, went extinct by time t . This probability is simply

$$p_t = 1 - e^{-\lambda t}$$

On the other hand, consider the median time $t_{0.5}$ needed for $SR_{0.5}$ extinctions to occur, which, is the median number of extinctions needed to lose the function. I have that

$$Sp_{t_{0.5}} \approx SR_{0.5} \Leftrightarrow p_{t_{0.5}} = R \Leftrightarrow \lambda t_{0.5} = -\log(1 - R_{0.5}) = -\log(f_{0.5})$$

Note that this formula cannot be true at very high values of R (or low values of network fragility), where I know that an explicit logarithmic dependence in S should manifest (indeed $t_{0.5} \sim \log S$ if $R = 1$), a behaviour that takes over the simple heuristic formula (which diverges at $R = 1$).

A.3 RANDOM BOOLEAN MODEL

A.3.1 REDUNDANCY OF RANDOM BOOLEAN FUNCTIONS

A Boolean function E^* has output 0 or 1 depending on the configuration of N bits:

$$E^*: x \in \{0,1\}^N \rightarrow \{0,1\}$$

There are 2^N bit configurations, and to each a function associates 0 or 1. Consider the case $N = 3$. The configuration space is

$$\{0,1\}^3 = \{(000), (100), (010), (110), (001), (101), (011), (111)\}$$

A function assigns a 0 or a 1 to these configurations, for instance:

$$E_0^* = [00000000]$$

assigns 0 to all configurations. It is the 0th function. In fact, to each function I associate a number which is its output list in base 2. For instance:

$$E_{69}^* = [10100010] = 1 + 0 + 2^2 + 0 + 0 + 0 + 2^6 + 0 = 69$$

is the 69th function. The last function is

$$E_{255}^* = [11111111] = 1 + 2 + 2^2 + 2^3 + 2^4 + 2^5 + 2^6 + 2^7 = 255$$

so that there are $1 + 255 = 2^8$ functions. More generally, for any N there are 2^{2^N} functions. I can uniformly sample the space of functions by assigning at random—and with equal probability—the output 0 or 1 to each configuration. This procedure is equivalent to sampling numbers between, say, 0 and 10,000 by picking each of 4 digits from a uniform distribution over 0,1,2,...,9.

I will consider functions that have output 1 when all bits are 1, and 0 when all bits are 0.

$$E^*(1,1, \dots, 1) = 1; E^*(0,0, \dots, 0) = 0$$

Starting from the configuration where all bits are 1, I am interested in the redundancy of functions. That is, the number of single bit flips required (a bit is flipped at most once) to change the function output from 1 to 0. The least redundant function is the logical AND, since one bit flip is enough (redundancy = 1), the most redundant function is the logical OR, since all bits must be flipped (redundancy = N). From my sampling procedure I deduce that, for a random function, the probability that its output changes after n flips is 2^{-n} , and the probability that it takes all bits to be flipped is $2 \times 2^{-(2^N-1)}$ (and not $2^{-(2^N-1)}$ since the output must be 0 if all bits are zero; I can check that, with this constraint, the probability sums to one over the $2^N - 1$ bit flips). I deduce that, for a typical function, redundancy is exponentially distributed with an average of two. Over a uniform sampling of functions their mean redundancy will distribute around two, with the distribution becoming increasingly peaked as N grows (Fig. A.3).

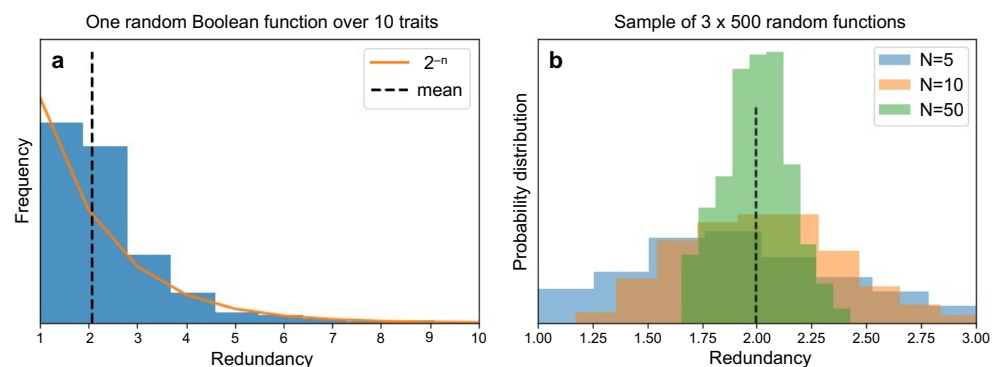


Figure A.3 | a) redundancy of a random Boolean function over $\{0, 1\}^N$, with $N = 10$. Starting from the configuration $(1, 1, \dots, 1)$ the number of bitflips needed to change the function's output is exponentially distributed, with mean 2. b) for $N = 5, 10, 50$, I sample 500 functions and plot their mean redundancy. I see that, as N grows, the distribution becomes increasingly peaked around 2. Thus, for large N , a typical function requires approximately two bitflips to change its output.

A.3.2 SIMULATION OF THE RANDOM MODEL

From A.3.1, I expect that choosing $E^* = \text{AND}$ (the least redundant function) over trait configurations is representative of a random choice, taken uniformly over the space of Boolean functions. Here, I demonstrate this using simulations. I generate random S -species to N -traits networks and informally sample a Boolean function E^* in $\text{bool}(N)$, the space of Boolean functions over $\{0, 1\}^N$. I compare the results for robustness to the case where $E^* = \text{AND}$. As expected, the random choice

systematically gives a larger robustness yet without qualitatively affecting the universal relationship between network fragility and robustness (Fig. A.4).

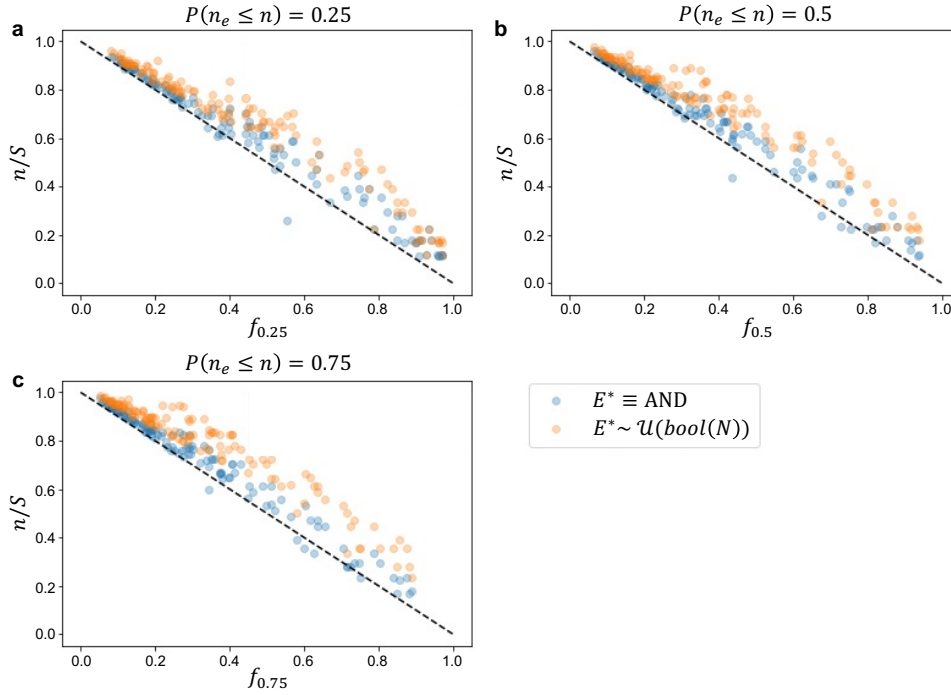


Figure A.4 | The logical AND for the auxiliary function E^* on trait configurations vs a uniform random choice over the whole space of Boolean functions $\text{bool}(N)$. I compare the first quantile **a**, the median **b**, and the third quantile **c** of the distribution n_e/S as a function of the corresponding fragility measure ($f_{0.25}$, $f_{0.5}$, and $f_{0.75}$, respectively). As expected, the random choice shifts the distribution to slightly larger values of robustness but without qualitatively affecting its relationship with network fragility.

APPENDIX B | SUPPLEMENTARY MATERIAL TO CHAPTER 3

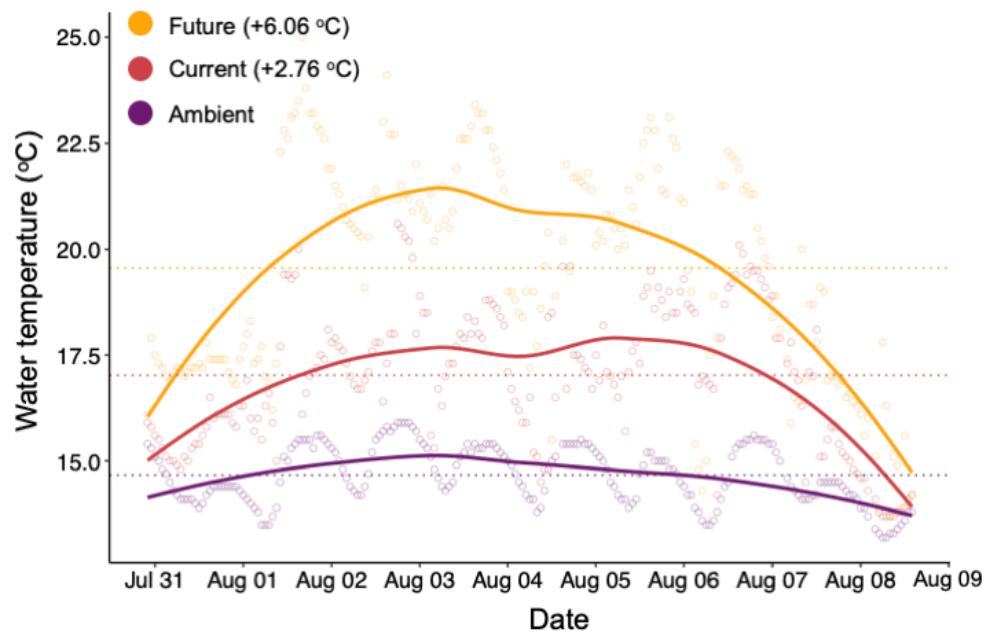


Figure B.1 | Water temperatures during heatwaves in my experimental mesocosms. Hourly water temperatures measured from the three header tanks next to the outflow during the heatwave period (*i.e.*, days 21-30 of the experiment). Temperature differences among treatments were achieved by mixing heated and ambient stream water. The resulting heatwaves fell within the range of observed (*i.e.*, current heatwave treatment) or projected (*i.e.*, future heatwave treatment) heatwaves based on local weather station and dynamical downscaling modelled data, respectively (see Table B.1). I included a realistic (that is, based on values from Table B.1) two-day heatwave onset duration (days 21-22), followed by a five-day heatwave peak (days 23-27), and a three-day heatwave decline (days 28-30), before returning to ambient. Points represent hourly recorded temperature values, and lines loess smoothers (span = 0.85) for the ambient (unheated) treatment (purple), the current (lower-intensity) heatwave treatment (red), and the future (higher-intensity) heatwave treatment (orange). Dotted lines represent the overall treatment-specific mean water temperatures, highlighting above-ambient temperature differences of +2.76 °C and +6.06 °C for the current and future heatwave treatments, respectively.

Table B.1 | Experimentally-induced heatwave properties and range of observed current (1995-2017, $n = 10$) and projected future (2076-2096, $n = 12$) heatwaves for the summer period matching my experiment duration (10 June to 11 September). Bold numbers represent the conditions produced by my experimentally induced heatwaves. Mean heatwave intensity and temperature variation represent, respectively, the average temperature and coefficient of variation above ambient conditions over the heatwave peak duration period (that is, excluding onset and decline: last column). Onset and decline rates represent, respectively, the speed of the raising and receding limbs of the heatwave prior to reaching full heatwave intensity. See Fig. B1 for the temperature time series reproduced for each heatwave during the heating period.

	Current Heatwave ($n = 10$)	Future Heatwave ($n = 12$)
Mean Heatwave Intensity (°C)	2.76 (2.71-5.44)	6.06 (5.85-7.73)
Heatwave Temperature Variation (°C)	0.39 (0.43-1.98)	0.27 (0.69-3.19)
Heatwave Onset rate (°C/day)	0.73 (0.22-3.73)	1.49 (0.36-6.02)
Heatwave Decline rate (°C/day)	0.68 (0.36-2.14)	1.15 (0.58-3.45)
Onset duration	2 (N/A)	2 (N/A)
Decline duration	3 (N/A)	3 (N/A)
Heatwave peak duration	5 (5-12)	5 (5-19)

Table B.2 | List of variables analysed in this study. Data transformation represents the transformation conducted in order to homogenise variances of a given variable making it suitable for statistical model assumptions.

Community component	Variable	Variable	Data transformation
Macroinvertebrates	Richness	-	-
	Total abundance	-	-
	Composition	-	-
Ecosystem processing	Leaf shredding	Macroinvertebrate	-
		Microbial	Log ₁₀
Macroalgae	Biomass (Total Chlorophyll <i>a</i>)	-	-
		Temporal Variability	Log ₁₀
		Spatial Variability	-
	Composition	-	-
		Temporal Variability	Log ₁₀
		Spatial Variability	Log ₁₀

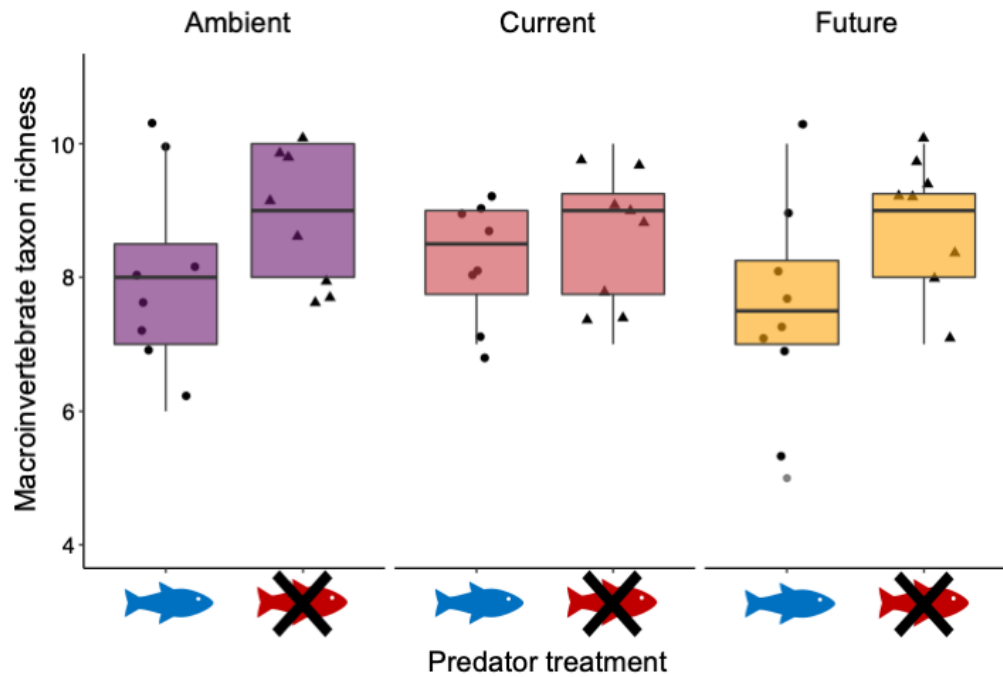


Figure B.2 | Predator extinctions increase macroinvertebrate taxon richness. Total macroinvertebrate taxon richness per mesocosm at the end of the experiment (Day 50). Boxplots represent the range (box = median and interquartile range) of values across eight mesocosms within each treatment in the presence or absence of predatory fish (X-axis) under the ambient temperature (left), current heatwave, and future heatwave (right) treatments.

Table B.3 | Model outputs for ANOVA and PERMANOVA tests of treatment effects on all response variables measured during heatwaves and at the end of the recovery period following the heatwaves. Model outputs show effects of heatwave treatment (control/current/future), predator (present/absent), and their interaction. Significant results ($p < 0.05$) are shown in bold and significance level marked ($^{\wedge} = p < 0.1$, $^* = p < 0.05$, $^{**} = p < 0.01$, $^{***} = p < 0.001$).

Response variable	Period	Heatwave	Predator	Heatwave x Predator
Benthic algae	Heatwave			
Total biomass		$F_{2,42} = 0.62, p = 0.53$	$F_{1,42} = 0.97, p = 0.33$	$F_{2,42} = 0.46, p = 0.63$
Functional temporal variability		$F_{2,42} = 0.43, p = 0.65$	$F_{1,42} = 0.80, p = 0.38$	$F_{2,42} = 0.14, p = 0.87$
Functional spatial variability		$F_{2,40} = 0.59, p = 0.56$	$F_{1,40} = 1.14, p = 0.29$	$F_{2,40} = 1.74, p = 0.19$
Composition		$F_{2,42} = 0.19, p = 0.90$	$F_{1,42} = 9.67, p < 0.001^{***}$	$F_{2,42} = 2.26, p = 0.09^{\wedge}$
Compositional temporal variability		$F_{2,42} = 0.41, p = 0.67$	$F_{1,42} = 0.96, p = 0.33$	$F_{2,42} = 3.33, p = 0.05^*$
Compositional spatial variability		$F_{2,24} = 1.08, p = 0.36$	$F_{1,24} < 0.01, p = 0.99$	$F_{2,24} = 6.65, p = 0.005^{**}$
Benthic algae	Recovery			
Total biomass		$F_{2,42} = 13.2, p < 0.001^{***}$	$F_{1,42} = 22.1, p < 0.001^{***}$	$F_{2,42} = 0.41, p = 0.67$
Functional temporal variability		$F_{2,42} = 9.46, p < 0.001^{***}$	$F_{1,42} = 6.06, p = 0.02^*$	$F_{2,42} = 0.31, p = 0.74$
Functional spatial variability		$F_{2,40} = 0.81, p = 0.45$	$F_{1,40} = 0.15, p = 0.70$	$F_{2,40} = 1.16, p = 0.32$
Composition		$F_{2,42} = 5.74, p = 0.001^{**}$	$F_{1,42} = 1.10, p = 0.37$	$F_{2,42} = 1.37, p = 0.29$
Compositional temporal variability		$F_{2,42} = 2.73, p = 0.08^{\wedge}$	$F_{1,42} = 0.38, p = 0.54$	$F_{2,42} = 1.89, p = 0.16$
Compositional spatial variability		$F_{2,114} = 1.78, p = 0.17$	$F_{1,114} < 0.001, p = 0.98$	$F_{2,114} = 5.88, p = 0.004^{**}$
Macroinvertebrate	Recovery			
Composition		$F_{2,42} = 2.19, p = 0.03^*$	$F_{1,42} = 7.25, p < 0.001^{***}$	$F_{2,42} = 1.26, p = 0.25$
Richness		$F_{2,42} = 0.31, p = 0.73$	$F_{1,42} = 5.96, p = 0.02^*$	$F_{2,42} = 0.46, p = 0.63$
Density		$F_{2,42} = 1.37, p = 0.27$	$F_{1,42} = 31.4, p < 0.001^{***}$	$F_{2,42} = 0.12, p = 0.88$
Leaf decomposition	Recovery			
Macroinvertebrate shredding		$F_{2,42} = 0.15, p = 0.86$	$F_{1,42} = 13.5, p < 0.001^{***}$	$F_{2,42} < 0.01, p = 0.99$
Microbial degradation		$F_{2,42} = 0.13, p = 0.88$	$F_{1,42} = 0.10, p = 0.75$	$F_{2,42} = 0.18, p = 0.83$

Table B.4 | Contribution of the three algal functional groups to the Bray-Curtis dissimilarity between predator treatments (presence/absence) on the last day of peak heating based on similarity percentages (Simper) analysis. p -values are from 1000 permutations of a permutational multivariate analysis of variance (PERMANOVA), where significant values ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$) represent cases where between group differences are an important component of a functional group's contribution to dissimilarities.

Predator present vs absent					
Functional group	% contribution to group dissimilarity	Mean chlorophyll a (predator present)	Mean chlorophyll a (predator absent)	PERMANOVA, p value	Significance
<i>Cyanobacteria</i>	49.4	0.46	0.42	<0.001	***
<i>Diatoms</i>	26.2	0.88	0.9	<0.001	***
<i>Green algae</i>	24.4	0.010	0.013	1.0	

Table B.5 | Contribution of the three algal functional groups to the Bray-Curtis dissimilarity between ambient temperatures and (a) a current and (b) future heatwave treatments at the end of the 20-day recovery period based on similarity percentages (Simper) analysis. *p*-values are from 1000 permutations of a permutational multivariate analysis of variance (PERMANOVA), where significant values ($\wedge = p < 0.1$, $p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$) represent cases where between group differences are an important component of a functional group's contribution to dissimilarities.

a) Ambient vs current heatwave

Functional group	% contribution to group dissimilarity	Mean chlorophyll <i>a</i> (Ambient)	Mean chlorophyll <i>a</i> (Current heatwave)	PERMANOVA, <i>p</i> value	Significance
<i>Cyanobacteria</i>	48.9	0.44	0.38	0.17	
<i>Green algae</i>	29.2	0.017	0.025	0.36	
<i>Diatoms</i>	21.9	0.9	0.92	0.058	$\wedge$

b) Ambient vs future heatwave

Functional group	% contribution to group dissimilarity	Mean chlorophyll <i>a</i> (Ambient)	Mean chlorophyll <i>a</i> (Future heatwave)	PERMANOVA, <i>p</i> value	Significance
<i>Cyanobacteria</i>	54.0	0.44	0.39	0.006	**
<i>Diatoms</i>	24.0	0.9	0.92	0.004	**
<i>Green algae</i>	22.0	0.017	0.012	0.77	

Table B.6 | Macroinvertebrate taxa contributing most to the Bray-Curtis dissimilarity between (a) ambient temperature and future heatwave treatments, and (b) predator present and predator absent treatments at the end of the 20-day recovery period based on Similarity percentages (Simper) analysis. *p*-values are from 1000 permutations of a permutational multivariate analysis of variance (PERMANOVA), where significant values ($p < 0.05 = *$, $p < 0.01 = **$, $p < 0.001 = ***$) represent cases where between group differences are an important component of a taxon's contribution to dissimilarities.

a) Ambient vs future heatwave

Species/morphotype	% contribution to group dissimilarity	Mean abundance (Ambient)	Mean abundance (Future heatwave)	PERMANOVA, <i>p</i> value	Significance
<i>Chironomidae</i> sp. A	23.2	0.16	0.26	0.01	*
<i>Perlodidae</i> sp.	17.4	0.37	0.30	0.24	
<i>Orthocladiinae</i> sp.	17.1	0.23	0.17	0.47	
<i>Baetis thermicus</i>	12.4	0.084	0.054	0.09	
<i>Sternomoera yezoensis</i>	9.7	0.061	0.1	0.31	
<i>Biwadriliidae</i> sp.	3.7	0.011	0.035	< 0.001	***
<i>Brachycentrus americanus</i>	3.5	0.007	0.023	0.14	

*Cumulative % contribution to group dissimilarity = 87.0%

b) Predator present vs absent

Species/morphotype	% contribution to group dissimilarity	Mean abundance (predator present)	Mean abundance (predator absent)	PERMANOVA, <i>p</i> value	Significance
<i>Chironomidae</i> sp. A	21.3	0.176	0.244	0.17	
<i>Orthocladiinae</i> sp.	21.3	0.282	0.138	< 0.001	***
<i>Perlodidae</i> sp.	17.4	0.361	0.325	0.59	
<i>Baetis thermicus</i>	11.7	0.021	0.1	0.002	**
<i>Sternomoera yezoensis</i>	10.7	0.051	0.112	< 0.001	***
<i>Neophylax japonicus</i>	3.0	0.02	0.018	0.96	

*Cumulative % contribution to group dissimilarity = 85.4%

APPENDIX C | SUPPLEMENTARY MATERIAL TO CHAPTER 4

Table C.1 | Sonic conditions under which the performance of my focal acoustic indices was examined. Structure indicates the data structure of the variable with levels explained.

Predictor variable	Structure	Details
<i>Anthropophony</i>	Binary (0 = no anthropophony, 1 = audible anthropophony)	Human sound occurs in the low frequency range, affecting the performance of some acoustic indices (Kasten <i>et al.</i> 2012; Fairbrass <i>et al.</i> 2017).
<i>Geophony</i>	Binary (0 = no geophony, 1 = audible geophony)	Wind and rain have the potential to confound acoustic indices by producing broadband sound (Bradfer-Lawrence <i>et al.</i> , 2019; Sánchez-Giraldo <i>et al.</i> , 2020).
<i>Insects</i>	Binary (0 = no insects, 1 = audible insect stridulations)	Cicada choruses and repetitive orthopteran sounds have been found to influence the results of several acoustic indices (Fuller <i>et al.</i> 2015; Buxton <i>et al.</i> 2018a).

Table C.2 | The acoustic indices used in this study, their calculation method and interpretation and corresponding R functions, and previous studies relating these indices to either point-count data, or data collected via an aural inventory approach. All acoustic indices were calculated using the *R* packages *seewave* (Sueur *et al.* 2008a) and *soundecology* (Villanueva-Rivera & Pijanowski 2018). Note that the ndsi function sums amplitude values across all 1-kHz frequency bands, which does not correspond to the original suggestion to use only the largest frequency band (Kasten *et al.* 2012). The use of each method should be dependent on the specific question being asked, with $NDSI_{max}$ providing a clearer balance of anthropophony to biophony, thereby giving anthropophony a stronger influence on NDSI values when using this method (Stuart Gage, pers. comm). References to previous studies are as follows: 1 = Jorge *et al.* (2018), 2 = Mammides *et al.* (2017), 3 = Bradfer-Lawrence *et al.* (2020), 4 = Machado *et al.* (2017), 5 = Buxton *et al.* (2018a), 6 = Fairbrass *et al.* (2017), 7 = Fuller *et al.* (2015), 8 = Eldridge *et al.* (2018), 9 = Depraetere *et al.* (2012), 10 = Roca & Proulx (2016), 11 = Sueur *et al.* (2008b).

Acoustic Index	R function	R package	Calculation method and interpretation	Related to point-count data?	Related to aural inventory?
Acoustic Complexity Index (ACI) (Pieretti <i>et al.</i> 2011)	acoustic_complexity	soundecology	Estimates the complexity of the short-time discrete Fourier transform matrix, by computing average absolute amplitude difference between pairwise combinations of adjacent cells. ACI therefore gives greater weight to sounds that are modulated in amplitude, i.e. reducing the importance of sounds with constant amplitude. ACI should finally be standardised per recording minute.	1-3	5-8

Higher values represent greater change in amplitude, thought to capture the irregularity of biophony. Low values represent little change in amplitude, meaning that sound intensity does not vary over time.

Acoustic Diversity Index (ADiv) (Villanueva-Rivera <i>et al.</i> 2011)	acoustic_diversity	soundecology	Computes the short-time discrete Fourier transform and cuts the resulting value into a predetermined number of frequency bands (1 band = 1 kHz by default). Then selects only the relative amplitude of each band above a specified dB threshold and calculates the Shannon entropy on only those bands. ADiv is bounded between 0 and log number of frequency bands. Values closer to 0 represent pure tones, i.e. all acoustic energy in a single frequency band, whereas values closer to the maximum value indicate an even spread of acoustic energy across frequency bands, representing either an evenly noisy soundscape or a silent one.	1-3	4-8
Acoustic Evenness Index (AEve) (Villanueva-Rivera <i>et al.</i> 2011)	acoustic_evenness	soundecology	Computes the short-time discrete Fourier transform and cuts the resulting value into a predetermined number of frequency bands (1 band = 1 kHz by default). Then calculates the Gini coefficient to measure of acoustic power distribution inequality. Bounded 0-1, higher values represent greater unevenness in the distribution of acoustic power, i.e. most sound intensity occurs in restricted range of frequencies. Values closer to 0 represent low variation in intensity among frequency bands.	1-3	5,7

Acoustic Richness Index (ARic) (Depraetere <i>et al.</i> 2012)	AR	seewave	Calculated based on the ranks of temporal entropy (H_t, see below) and amplitude of the signal (M, see below). M and H_t are calculated and ranked in ascending order. ARic is then calculated as the position of each recording in these ranks relative to the sample size. As ARic is a ranked index it scaled 0-1, where values closer to 0 indicate a higher rank along the amplitude-by-evenness (M-by-H_t) axis, i.e. a more consistently loud soundscape. Values closer to 1 indicate a lower rank along the M-by-H_t axis, i.e. a soundscape with lower average amplitude, lower evenness, or likely both.	2	5,9
Bioacoustic Index (BioA) (Boelman <i>et al.</i> 2007)	bioacoustic_index	soundecology	Computes the dB mean spectrum and takes BioA as the area under the curve between two frequency limits (2 kHz-11 kHz). The value is a function of both the number of occupied frequency bands and their amplitude. BioA is relative to the quietest frequency band, meaning that low values represent even acoustic activity across frequency bands, and high values represent greater disparity between the quietest and loudest frequency bands.	1-3	6-8

Acoustic Entropy (H) (Sueur <i>et al.</i> 2008b)	H	seewave	Calculated based on the Shannon index, by multiplying the relative amplitude across time (H_t , see below) by the relative amplitude across frequency bands (H_f). H is bounded 0-1 and increases with greater amplitude evenness across frequency bands, such that 1 = an even signal (either noisy across all frequency bands or entirely silent), and 0 = a pure tone (all amplitude energy in a single frequency band).	1-3	5,7,10,11
Temporal Entropy Index (H_t) (Sueur <i>et al.</i> 2008b)	H_t	seewave	Calculates the Shannon evenness of the Hilbert amplitude envelope. The amplitude envelope is scaled by its sum, making it equivalent to transforming it into a probability mass function. Note that even time units with low probability mass function (equivalent to rare species in the classical use of the metric) can influence the value of H_t . Higher values represent a more even amplitude envelope through time, <i>i.e.</i> , lower temporal variability in acoustic power, corresponding to a soundscape producing constant invariable sound.	-	8
Median of the Amplitude Envelope (M) (Depraetere <i>et al.</i> 2012)	M	seewave	Computes the median of the Hilbert amplitude envelope scaled by the digitisation depth of each recording. M has bounds 0-1, where higher values (closer to 1) indicate soundscapes that are louder on average.	3	5

Normalised Difference Soundscape Index (NDSI) (Kasten <i>et al.</i> 2012)	ndsi	soundecology	Splits the spectrogram across frequency bands into anthropophony and biophony (see below). NDSI is then the ratio between the two components, with bounds of -1 to +1 (scaled here to 0-1 for models). Higher values indicate a greater proportion of biophony relative to anthropophony, such that +1 = no anthropophony in the soundscape.	1-3	4-8
Anthropophony (NDSI _{Anthro}) (Kasten <i>et al.</i> 2012)	ndsi	soundecology	Splits the spectrogram across frequency bands, leaving anthropophony as the sum of the amplitude within the 1-2 kHz frequency band(s) per recording. Higher values indicate more acoustic activity occurring in the lowest frequencies of the soundscape, corresponding more commonly to anthropophony than biophony.	3	-
Biophony (NDSI _{Bio}) (Kasten <i>et al.</i> 2012)	ndsi	soundecology	Splits the spectrogram across frequency bands, leaving biophony as the sum of the amplitude within the 2-11 kHz frequency band(s) per recording. Higher values indicate more acoustic activity occurring in the mid-high frequency bands of the soundscape, corresponding more commonly to biophony than anthropophony.	3	-

Table C.3 | Model selection results for acoustic index ~ measured richness relationship. Full models were GLMMs including measured richness, season, and their interaction as predictors with time-of-day and site as random effects (4.3.4 Statistical Analyses). Best fitting models are shown, likelihood ratio tests (LRT) represent a comparison to the best model with the model term removed (including the δ AIC of model term removal), thereby indicating significance of model terms: represented with * ($P < 0.05$), ** ($P < 0.01$) and *** ($P < 0.005$).

Acoustic Index	Model term	δ AIC	LRT	Significance
Acoustic Complexity Index (ACI)	Measured Richness	0	0.993	N.S.
	Season	64.6	70.6	***
	Richness * Season	53.8	59.8	***
Acoustic Diversity Index (ADiv)	Measured Richness	0	0.278	N.S.
	Season	1344	1350	***
	Richness * Season	8.72	14.7	***
Acoustic Evenness Index (AEve)	Measured Richness	0	0.043	N.S.
	Season	1313	1319	***
	Richness * Season	12.2	18.2	***
Bioacoustic Index (BioA)	Measured Richness	0	0.054	N.S.
	Season	1248	1254	***
	Richness * Season	10.8	16.8	***
Acoustic Entropy (H)	Measured Richness	0	0.523	N.S.
	Season	1596	1602	***
	Richness * Season	26.6	32.6	***

<i>Median of the amplitude envelope (M)</i>	Measured Richness	0	0.156	N.S.
	Season	197	203	***
	Richness * Season	28.2	34.2	***
<i>Normalised difference soundscape index (NDSI)</i>	Measured Richness	0	0.25	N.S.
	Season	1589	1595	***
	Richness * Season	23.8	29.8	***
<i>Acoustic Richness Index (ARic)</i>	Measured Richness	1.46	3.46	0.06282
	Season	161	167	***
	Richness * Season	10.4	16.4	***
<i>Temporal entropy index (Ht)</i>	Measured Richness	1.9	3.9	*
	Season	53.4	59.4	***
	Richness * Season	32.8	38.8	***
<i>Biophony (NDSI_{Bio})</i>	Measured Richness	0	0.055	N.S.
	Season	469	475	***
	Richness * Season	49.1	55.1	***
<i>Anthropophony (NDSI_{Anthro})</i>	Measured Richness	0	0.491	N.S.
	Season	1443	1449	***
	Richness * Season	21.4	27.4	***

C.1 SEASONAL EFFECTS ON ACOUSTIC INDEX PERFORMANCE AND SENSITIVITY

C.1.1 PERFORMANCE

Generalised linear mixed models (GLMMs) relating measured richness to acoustic index values always included an interaction term between richness and season in the best performing model (Table C.2). This reflected differences in the relationship between richness and acoustic indices in different seasons as discussed in text (4.4. *Results*, Fig. 4.1B). Figure C.1 presents all acoustic index ~ richness relationships and the effects of season as median raw acoustic index values plotted against mean site-level richness.

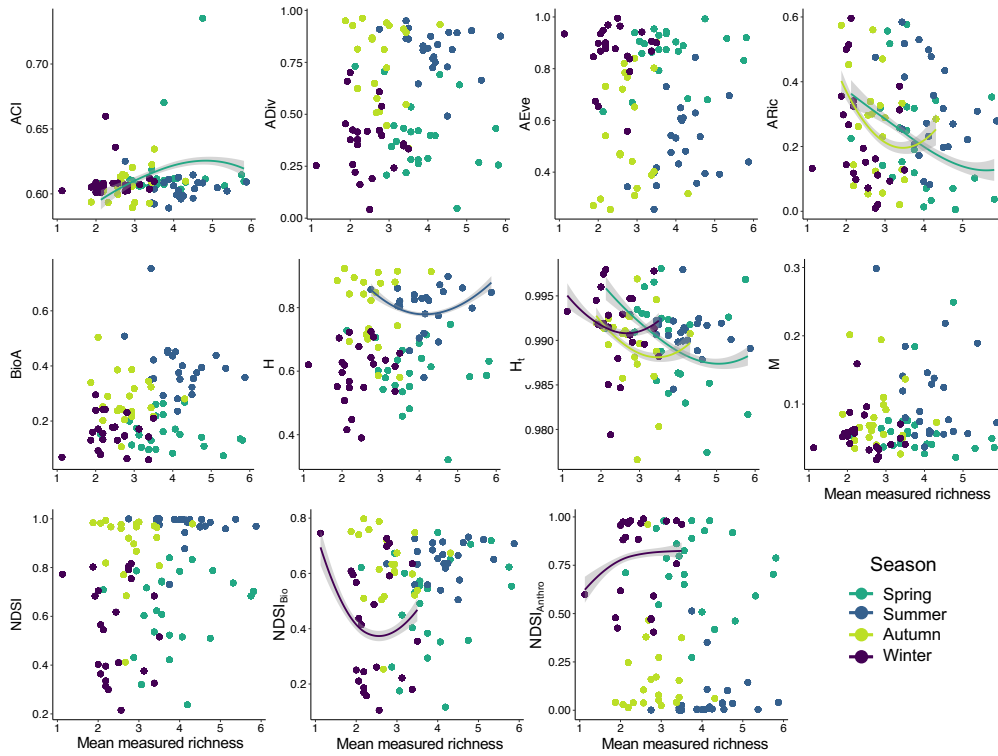


Figure C.1 | Visualisation of best performing models of acoustic index ~ richness relationships. Figure panels represent the effect of mean site-level measured richness on normalised acoustic index values, with median acoustic index data as points, and lines representing GLMM models for only those cases where model slopes differ significantly from zero. Results are split by season since in all cases, a season * richness interaction was included in the best forming models (Table C.2). NB: raw data are skewed and so model fits may not closely match median acoustic data.

C.1.2 SENSITIVITY

When including season as a fixed effect, season had a significant modifying effect on the sonic condition-by-richness interaction in all models (model selection

results not shown). When considering seasonal differences in acoustic index sensitivity, I found that ACI remained a model with low sensitivity to sonic conditions across indices (Figs. C.2-C.4), but that in several cases, the rank order of index sensitivity differed when accounting for seasonal differences. For example, when excluding seasonal differences, M was the most sensitive index on average (Fig. 4.3), but when considering season differences, this index was one of the least sensitive indices to geophony (Fig. C.3; but see Sánchez-Giraldo *et al.*, 2020). The conditions to which indices were most sensitive also varied seasonally. The majority of indices were most sensitive to insect noise during the summer or autumn (Fig. C.4), and geophony caused higher sensitivity values during autumn or winter (Fig. C.3). Both NDSI_{Bio} and $\text{NDSI}_{\text{Anthro}}$ were significantly related to richness despite the presence of anthropophony during winter but were not related to richness where anthropophony was present during other seasons.

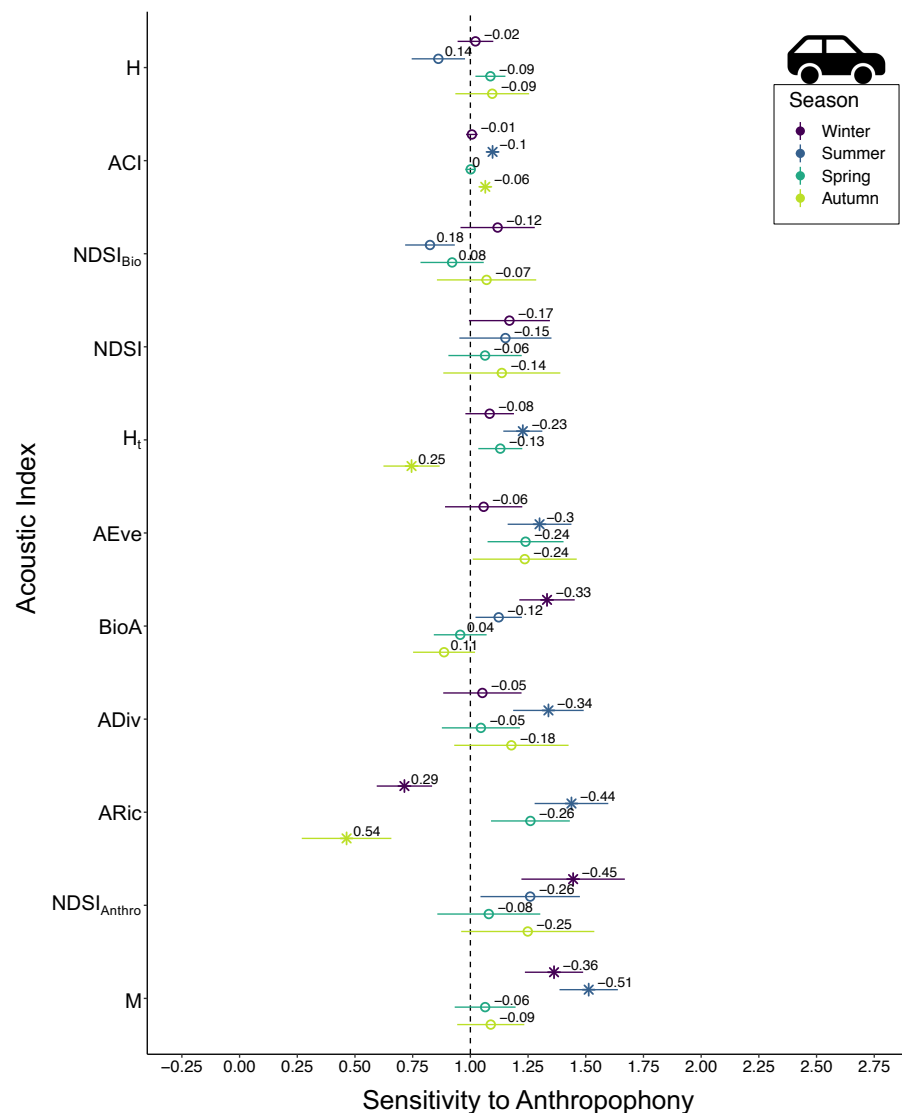


Figure C.2 | Seasonal sensitivity of acoustic indices to anthropophony. Sensitivity is the inverse of the absolute difference in model slope (i.e. change in performance) of the

acoustic index ~ mean site-level measured richness relationship between models where anthropophony is absent (baseline) versus present. Sensitivity values below 1 indicate an increase in the strength of the model slope (negative slope decreasing or positive slope increasing), while values above 1 indicate a decrease in model slope (negative slope increasing or positive slope decreasing) where anthropophony is present. Numbers represent the absolute difference in model slopes (inverse of sensitivity). Asterisks represent significant differences between model slopes in the presence versus absence of each sonic condition (two-sided test, $P = 0.05$) based on t -statistics. Indices are ordered top-bottom by sensitivity values.

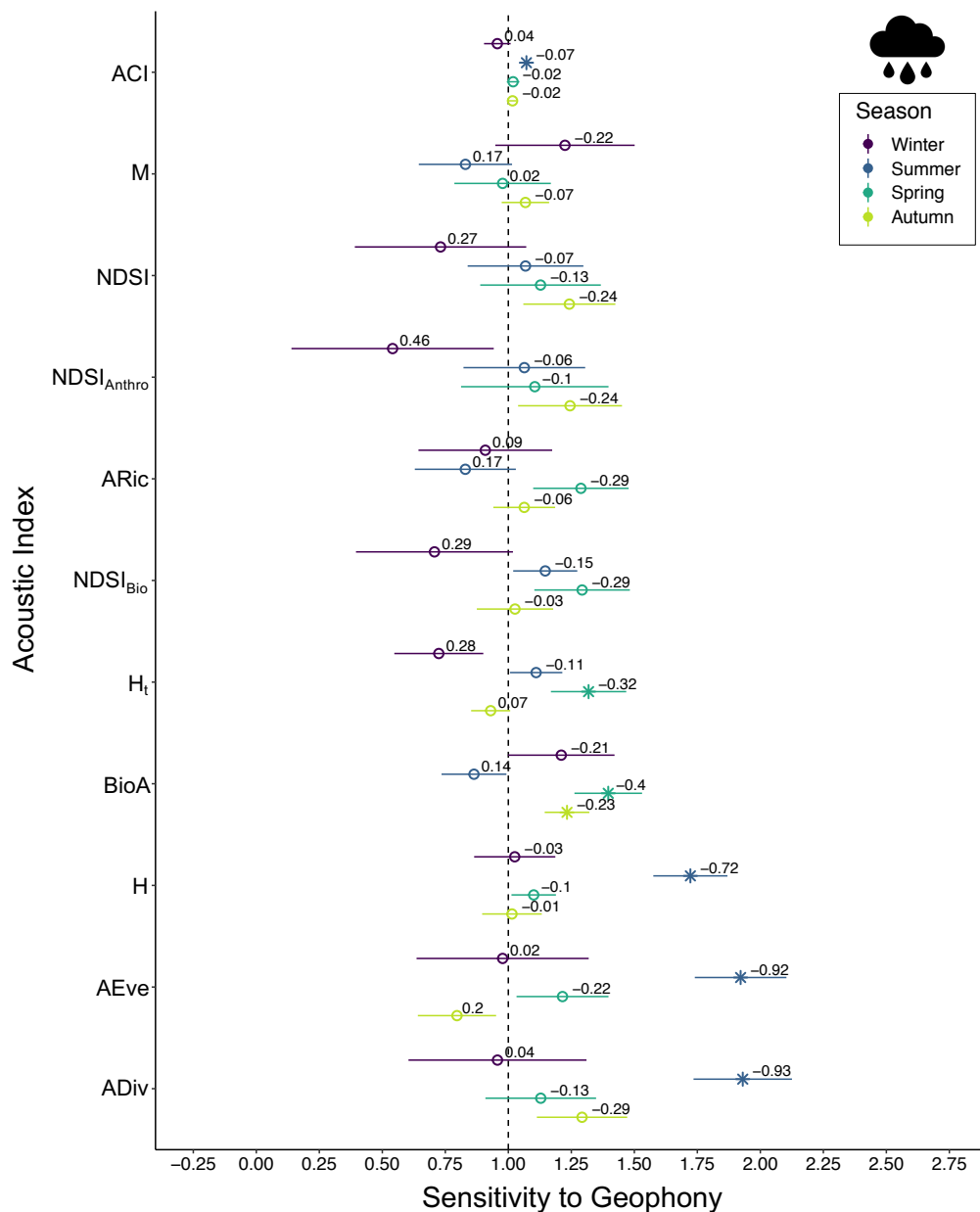


Figure C.3 | Seasonal sensitivity of acoustic indices to geophony. Figure format follows Fig. C.2 considering geophony as my confounding condition instead of anthropophony.

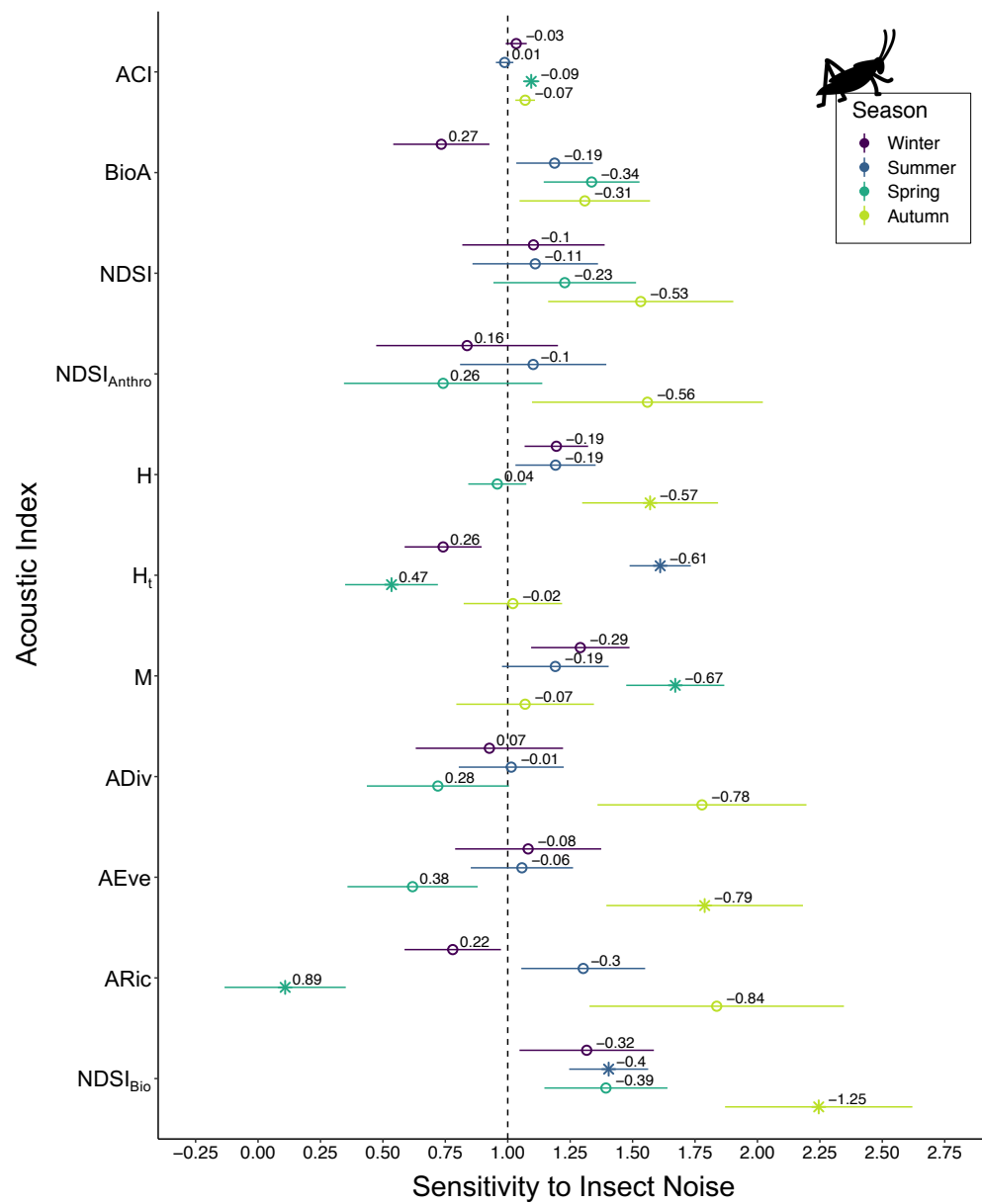


Fig. C.4 | Seasonal sensitivity of acoustic indices to insect noise. Figure format follows Fig. C.2 considering Insect Noise as my confounding condition instead of anthropophony.

APPENDIX D | SUPPLEMENTARY MATERIAL TO CHAPTER 5

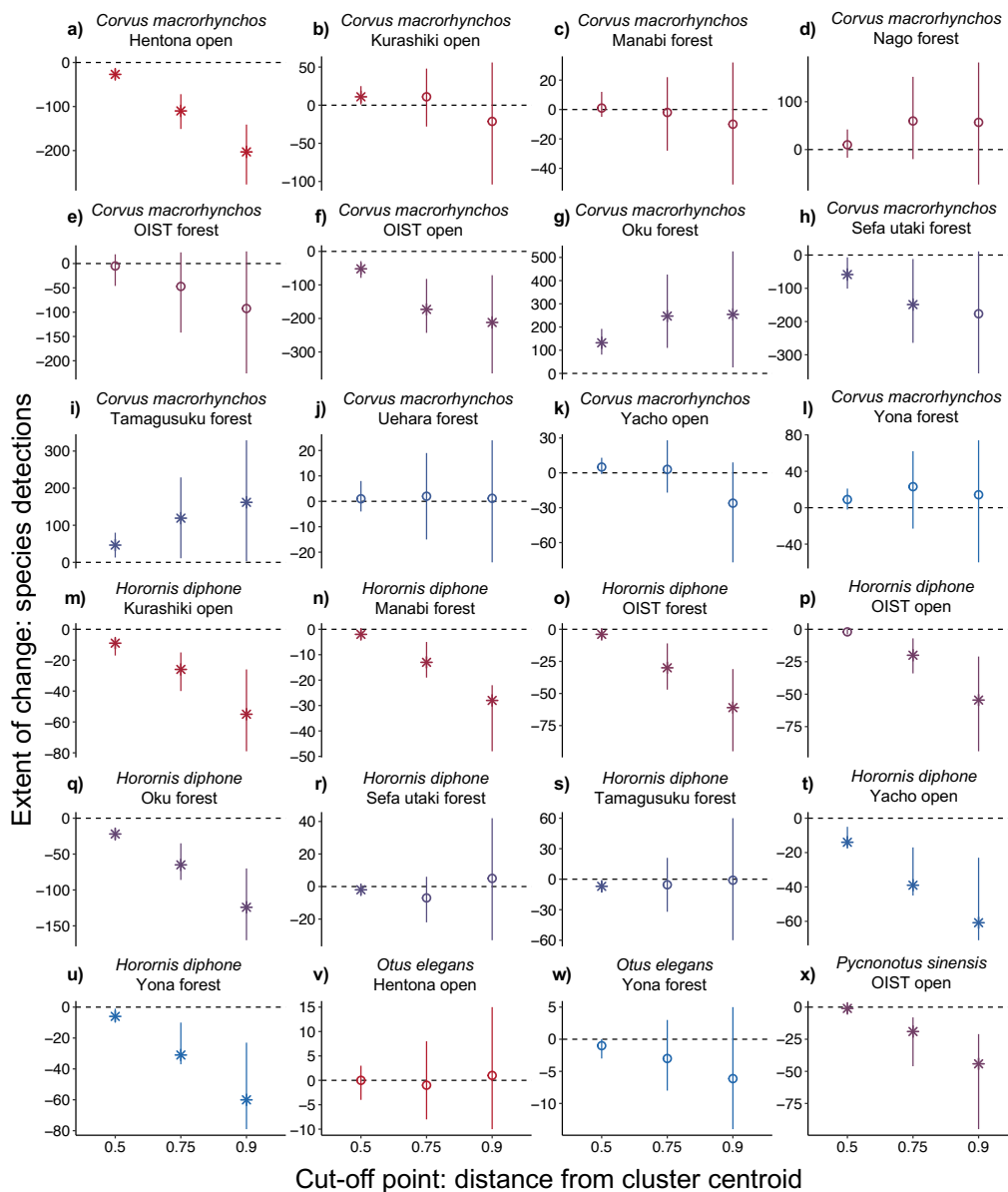


Figure D.1 | Extent of change for bird species detections with different error tolerances. Larger distances from the cluster centroid [x-axis] include signals with lower certainty (that is, more likely to not be the sound type of interest; an error). Generally, increasing distance from cluster centroid produces more extreme extent of change values (due to larger sample sizes). Extent of change values are for all sites at which I have data for each species: **a-l)** *Corvus macrorhynchos*, **m-u)** *Horornis diphone*, **v-w)** *Otus elegans*, and **x)** *Pycnonotus sinensis*.

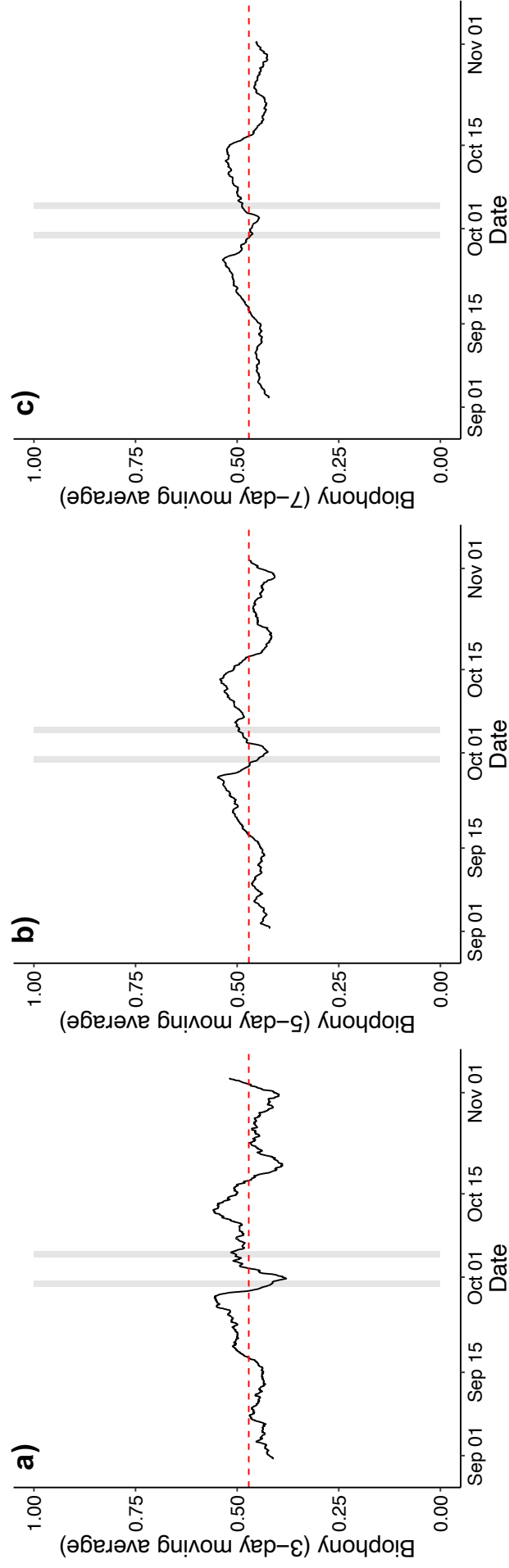


Figure D.2 | Comparison of Biophony ($NDSI_{Bio}$) time series at the Manabi forest (Manabi no mori) field site after detrending using moving average window sizes of **a)** 3 days, **b)** 5 days, and **c)** 7 days. Red dashed lines represent the pre-disturbance baseline value (mean). Grey windows indicate the periods of typhoons Trami (29-30 Sep 2018) and Kong-Rey (04-05 Oct 2018).

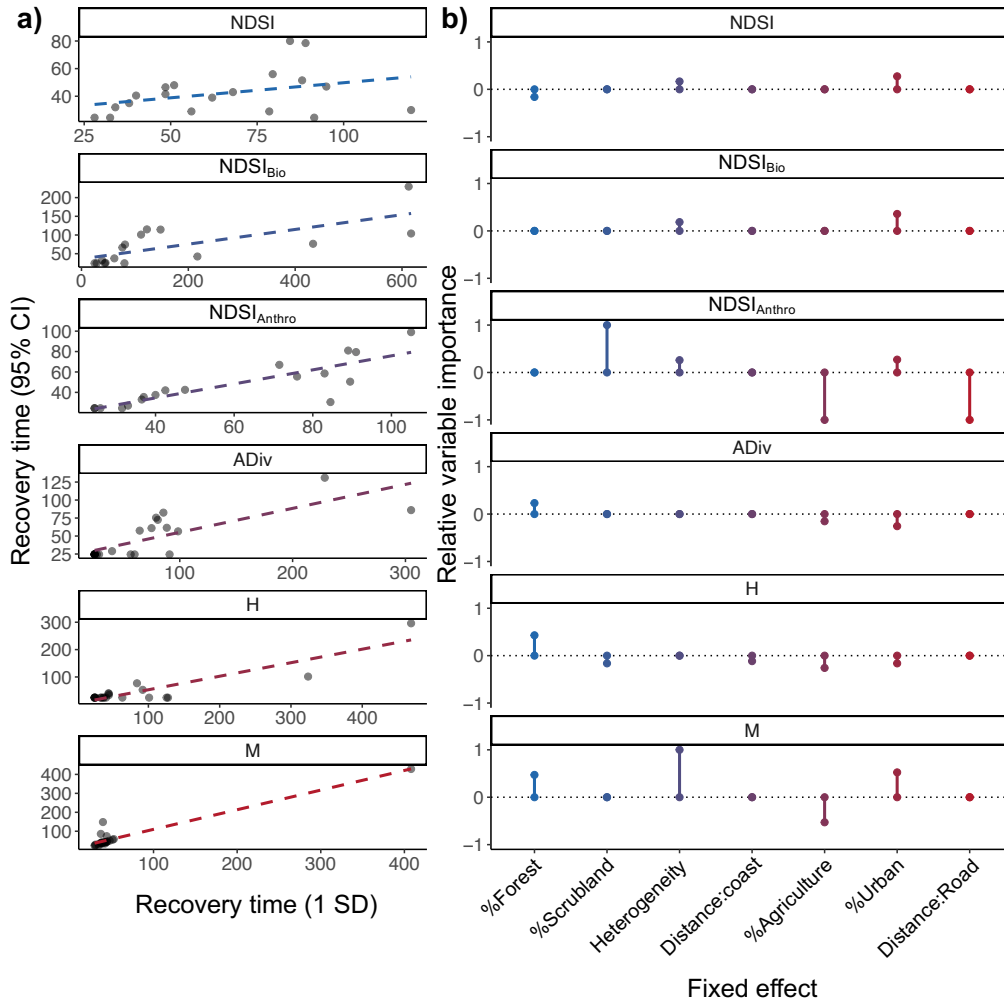


Figure D.3 | Comparison of recovery time values based on baseline period of mean $\pm$ 1 standard deviation or $\pm$ 95% confidence interval. **a)** Linear regression showing relationship between the two methods of calculating recovery time for each acoustic index. **b)** Relative variable importance (following Fig. 5.3) for recovery time values for each acoustic index calculated using baseline mean $\pm$ 95% confidence interval. See Fig. 5.3 for recovery time results based on a baseline period of mean $\pm$ 1 standard deviation.

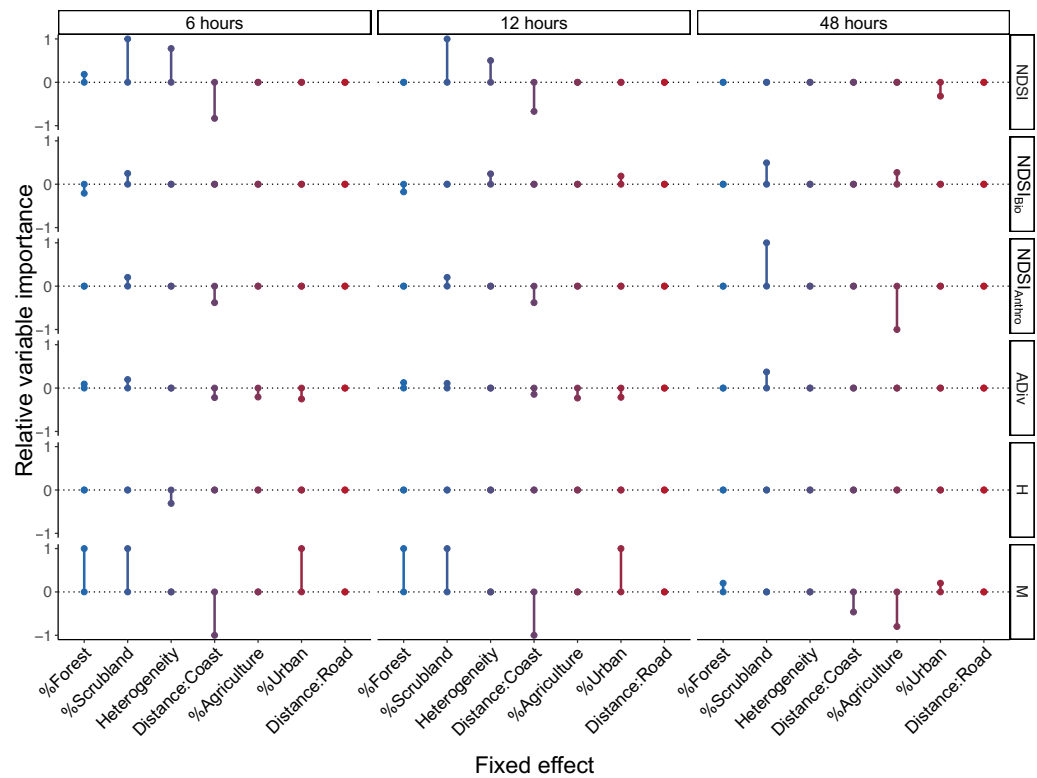


Figure D.4 | Comparison of recovery time model results between recovery window sizes. Relative variable importance (following Fig. 5.3) for recovery time values for each acoustic index calculated using recovery window sizes of 6 hours (left), 12 hours, and 48 hours (right). See Fig. 5.3 for recovery time results based on a window size of 24 hours.

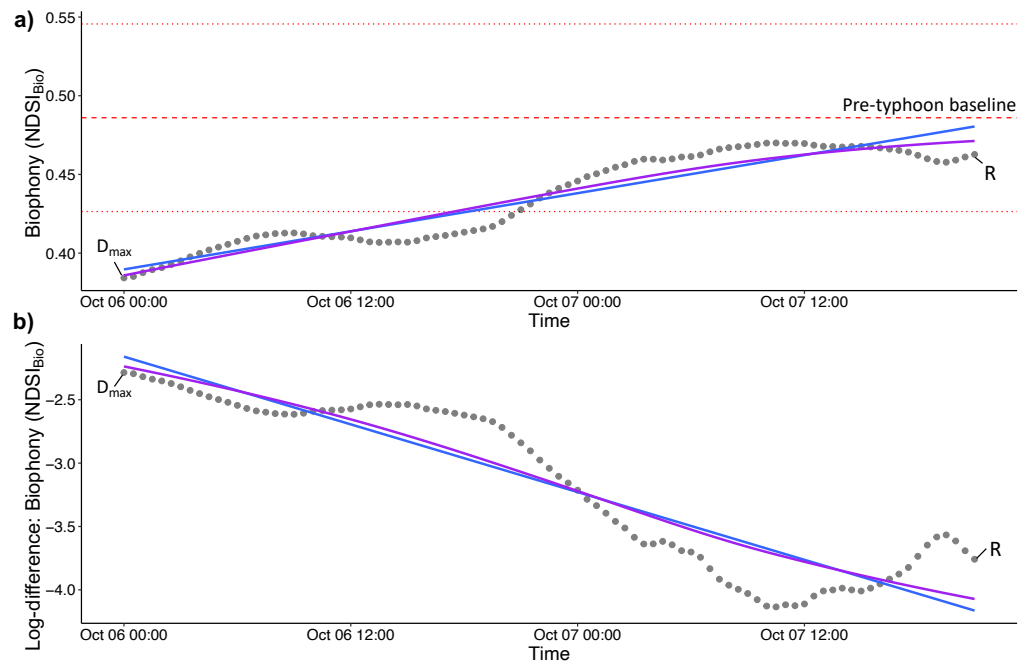


Figure D.5 | Illustrative example of resilience time series. Time series of **a)** biophony (NDSI_{Bio}) and **b)** log-difference biophony values for the Chatan field site based on a 3-day moving average detrend and a 24-hr recovery window size. Resilience is calculated as

the model slope of the log-difference time series between the point of maximum deviation ($D_{\max}$) and the point of recovery (R). Model slopes are illustrated with a linear model (blue line) and a second order polynomial (purple line). In cases, such as this one where there is no difference in model performance (determined statistically via AICc), the linear model coefficient is taken as the resilience value to avoid overfitting.

Table D.1 | List of variables analysed in this study. For each combination of **a)** acoustic index or **b)** bird species and stability component (see 5.3 *Methods*), data transformation represents the transformation conducted to homogenise variances of a given variable making it suitable for statistical model assumptions. Moran's I and associated *p*-values are results from Moran's test of spatial autocorrelation on model residuals. In cases where *p*-values < 0.1 (*, **bold**), I remodelled data using models accounting for spatial error. NB: spatial variability was calculated across sites, so does not have an associated Moran's test.

a) Acoustic indices

Acoustic Index	Stability component	Data transformation	Moran's I	Moran's <i>p</i> -value
NDSI	Invariability	Log	-0.092	0.560
	Resistance	-	-0.078	0.715
	Recovery time	-	-0.021	0.656
	Resilience	+ Constant, Cube root	-0.123	0.485
	Reaction time	Square root	-0.151	0.231
	Reactivity	Inverse, Cube root	-0.159	0.189
	Extent of change	-	-0.153	0.188
	Spatial variability	-	-	-
NDSI _{Bio}	Invariability	Log ₁₀	-0.030	0.872
	Resistance	-	-0.166	0.171
	Recovery time	Log	-0.096	0.826
	Resilience	-	-0.176	0.545
	Reaction time	Square root	-0.053	0.933
	Reactivity	-	-0.089	0.624
	Extent of change	-	-0.028	0.855
	Spatial variability	-	-	-
NDSI _{Anthro}	Invariability	Log ₁₀	-0.068	0.768
	Resistance	-	-0.119	0.402
	Recovery time	-	-0.176	0.177
	Resilience	-	-0.117	0.649
	Reaction time	Square root	-0.161	0.189
	Reactivity	-	-0.177	0.135
	Extent of change	-	-0.213	0.040*
	Spatial variability	-	-	-
ADiv	Invariability	Log ₁₀	-0.079	0.673
	Resistance	-	-0.006	0.649
	Recovery time	Log ₁₀	-0.197	0.099*
	Resilience	-	-0.186	0.131
	Reaction time	Log	-0.113	0.443
	Reactivity	-	-0.078	0.709
	Extent of change	-	-0.181	0.098*
	Spatial variability	-	-	-
H	Invariability	Log ₁₀	-0.098	0.507

	Resistance	-	0.012	0.513
	Recovery time	Inverse	-0.098	0.609
	Resilience	-	-0.249	0.032*
	Reaction time	Log	-0.243	0.026*
	Reactivity	-	-0.152	0.230
	Extent of change	-	-0.067	0.776
	Spatial variability	-	-	-
M	Invariability	-	-0.186	0.089*
	Resistance	-	-0.214	0.058*
	Recovery time	-	-0.177	0.159
	Resilience	-	-0.023	0.767
	Reaction time	Log	-0.096	0.556
	Reactivity	-	-0.042	0.948
	Extent of change	-	-0.097	0.513
	Spatial variability	Cube root	-	-

b) Bird species detections

Bird species	Stability component	Data transformation	Moran's I	Moran's <i>p</i> -value
<i>C. macrorhynchos</i>	Invariability	-	0.056	0.298
	Extent of change	Inverse	0.070	0.235
<i>H. diphone</i>	Invariability	-	-0.211	0.710
	Extent of change	Inverse	-0.296	0.467
Bird detections	Spatial variability	Log	-	-

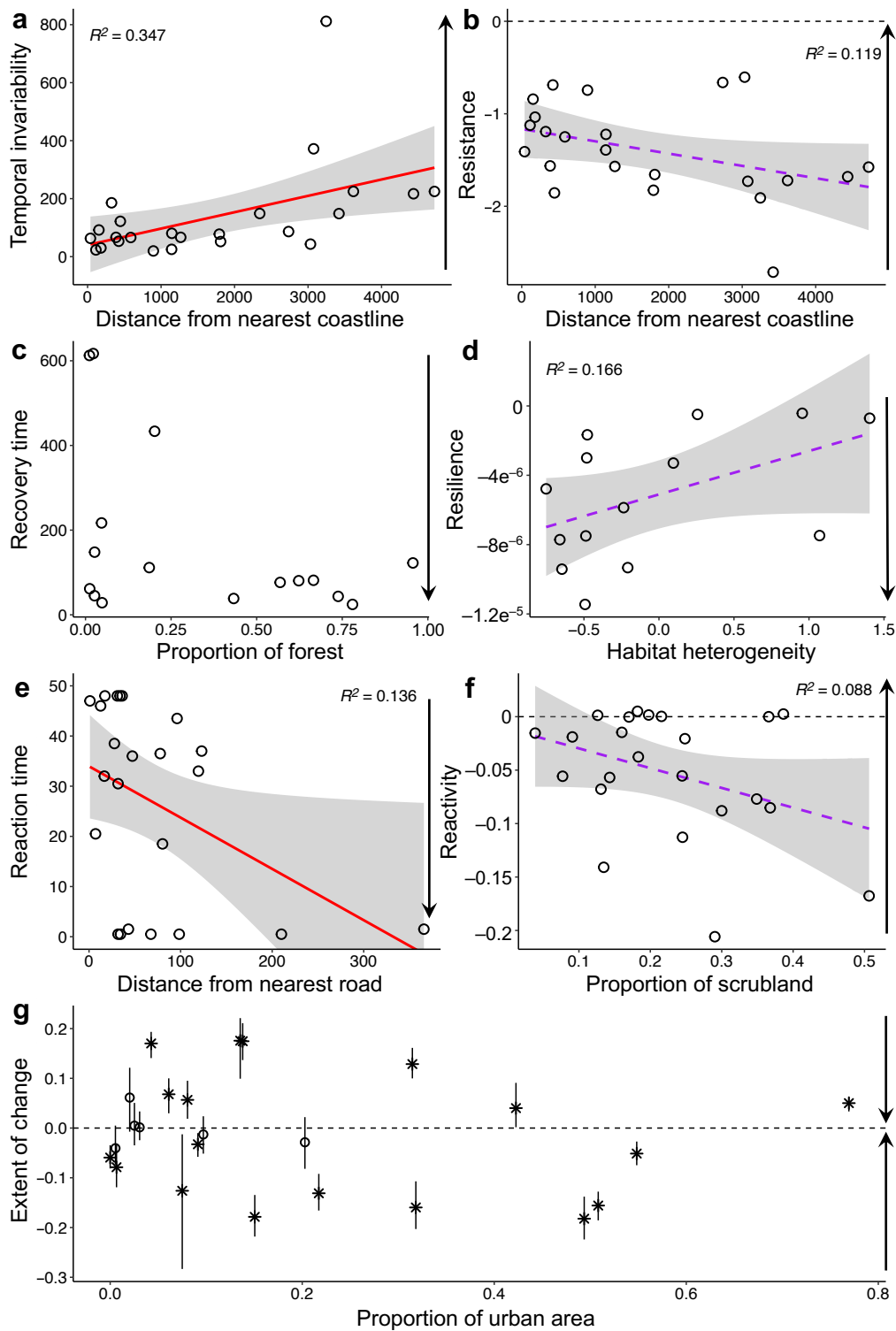


Figure D.6 | Effects of land use on multiple dimensions of NDSI_{Bio} stability. For each dimension of stability, plots show the most important land use variable (based on model selection results, see Fig. 5.3) plotted against the stability of NDSI_{Bio} values. Figure legend follows Fig. 5.4.

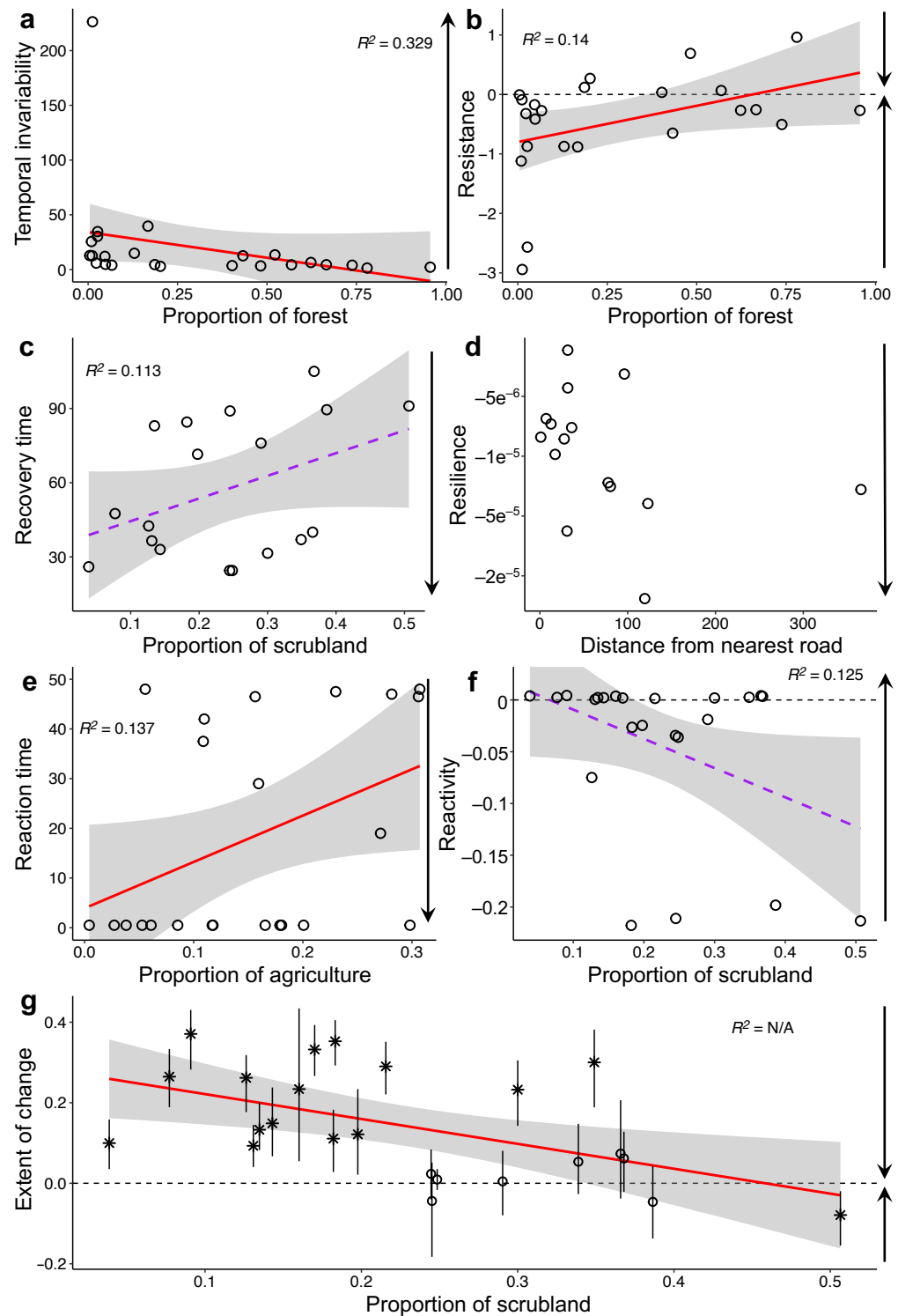


Figure D.7 | Effects of land use on multiple dimensions of NDSI_{Anthro} stability. For each dimension of stability, plots show the most important land use variable (based on model selection results, see Fig. 5.3) plotted against the stability of NDSI_{Anthro} values. Figure legend follows Fig. 5.4.

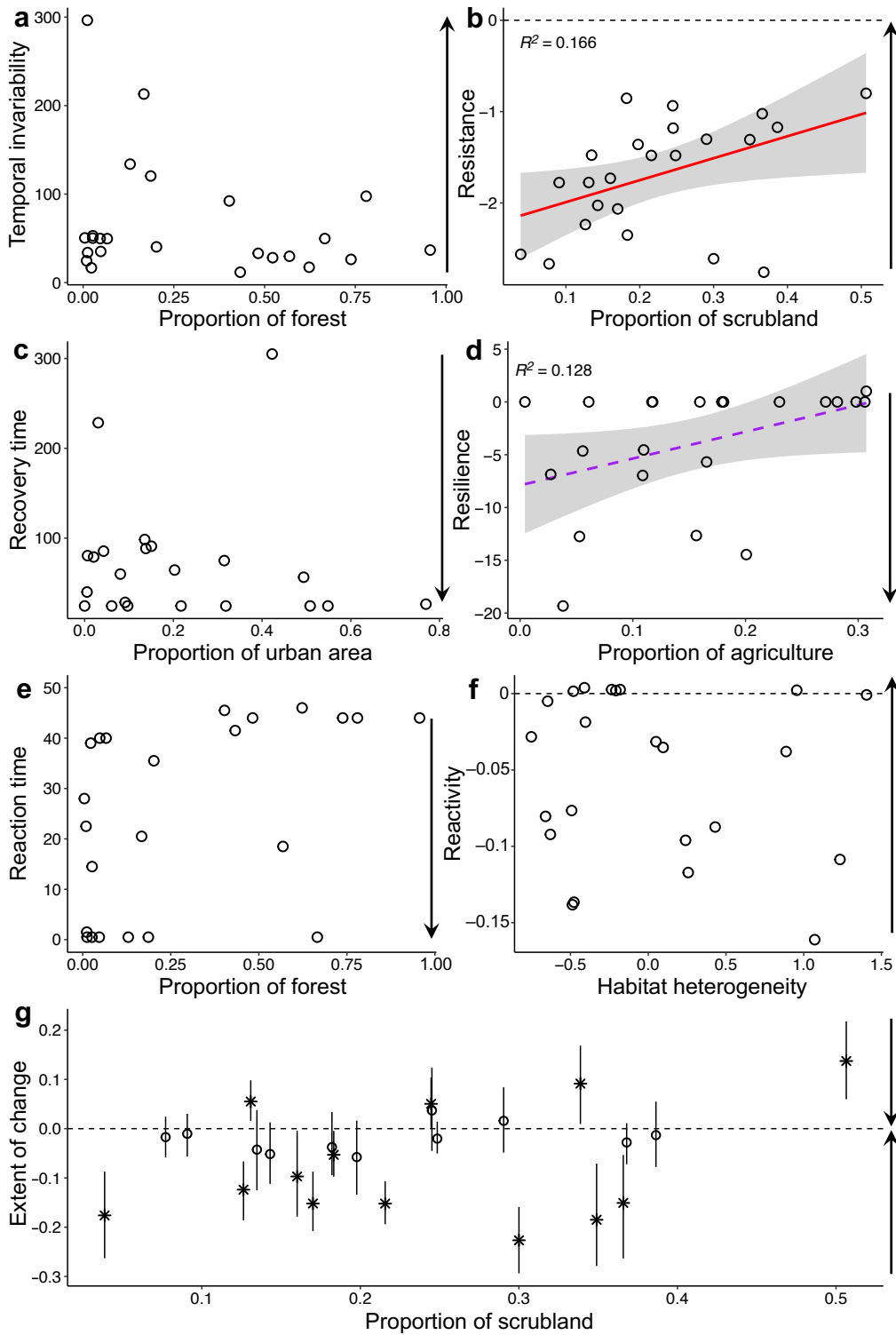


Figure D.8 | Effects of land use on multiple dimensions of ADiv stability. For each dimension of stability, plots show the most important land use variable (based on model selection results, see Fig. 5.3) plotted against the stability of ADiv values. Figure legend follows Fig. 5.4.

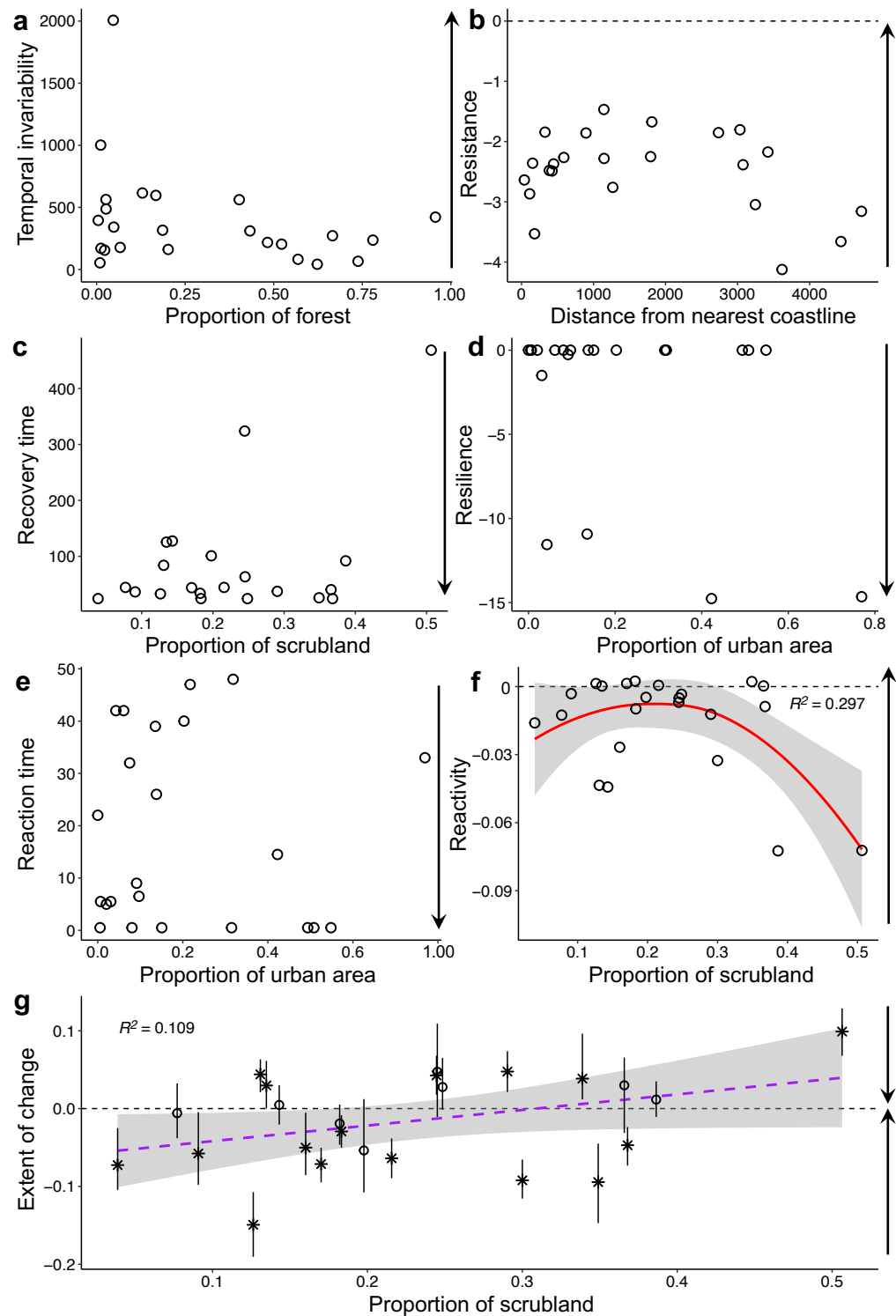


Figure D.9 | Effects of land use on multiple dimensions of H stability. For each dimension of stability, plots show the most important land use variable (based on model selection results, see Fig. 5.3) plotted against the stability of H values. Figure legend follows Fig. 5.4. In panel f, model curve represents a loess smoother (span = 2) selected via model selection (see 5.3 Methods).

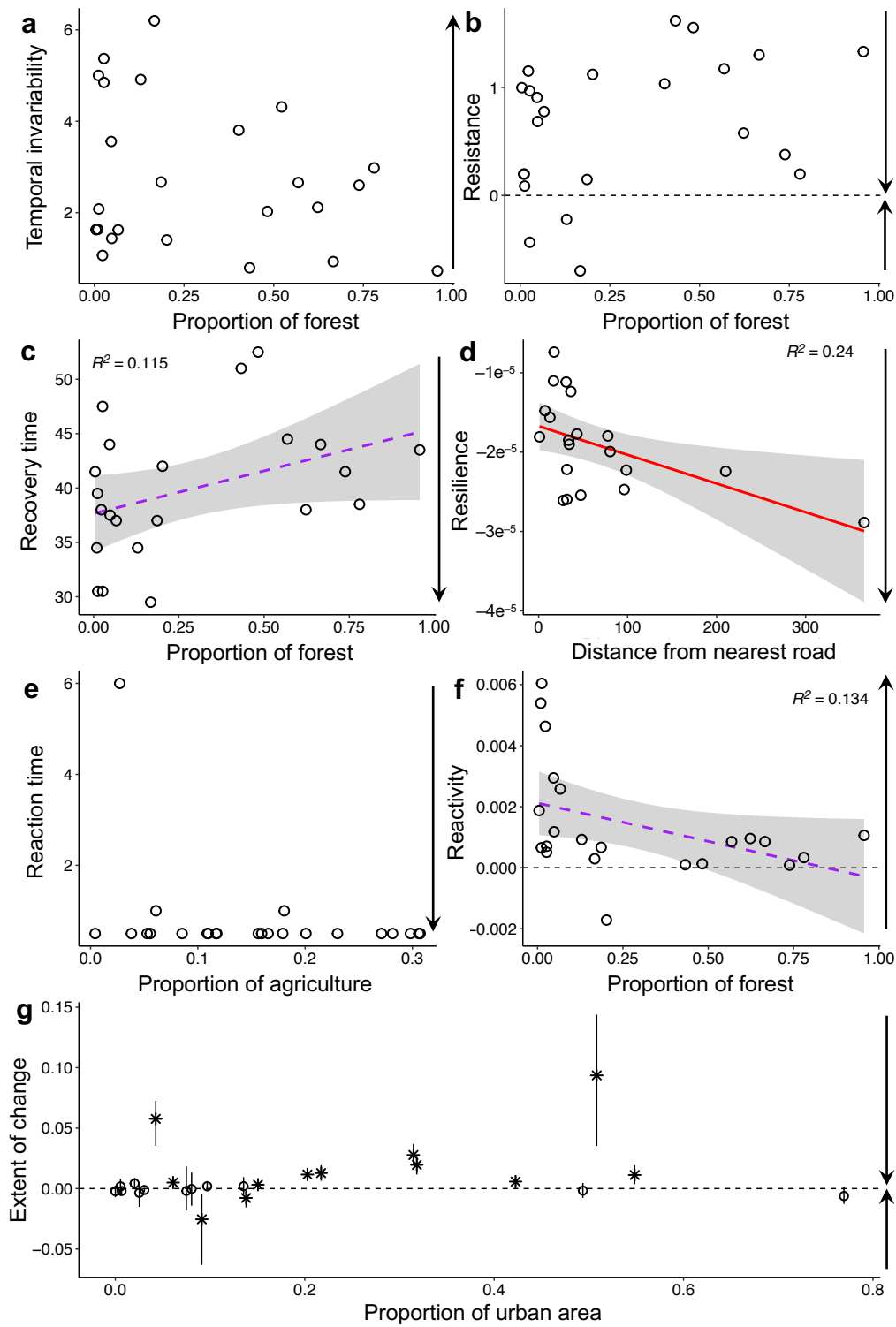


Figure D.10 | Effects of land use on multiple dimensions of M stability. For each dimension of stability, plots show the most important land use variable (based on model selection results, see Fig. 5.3) plotted against the stability of M values. Figure legend follows Fig. 5.4.

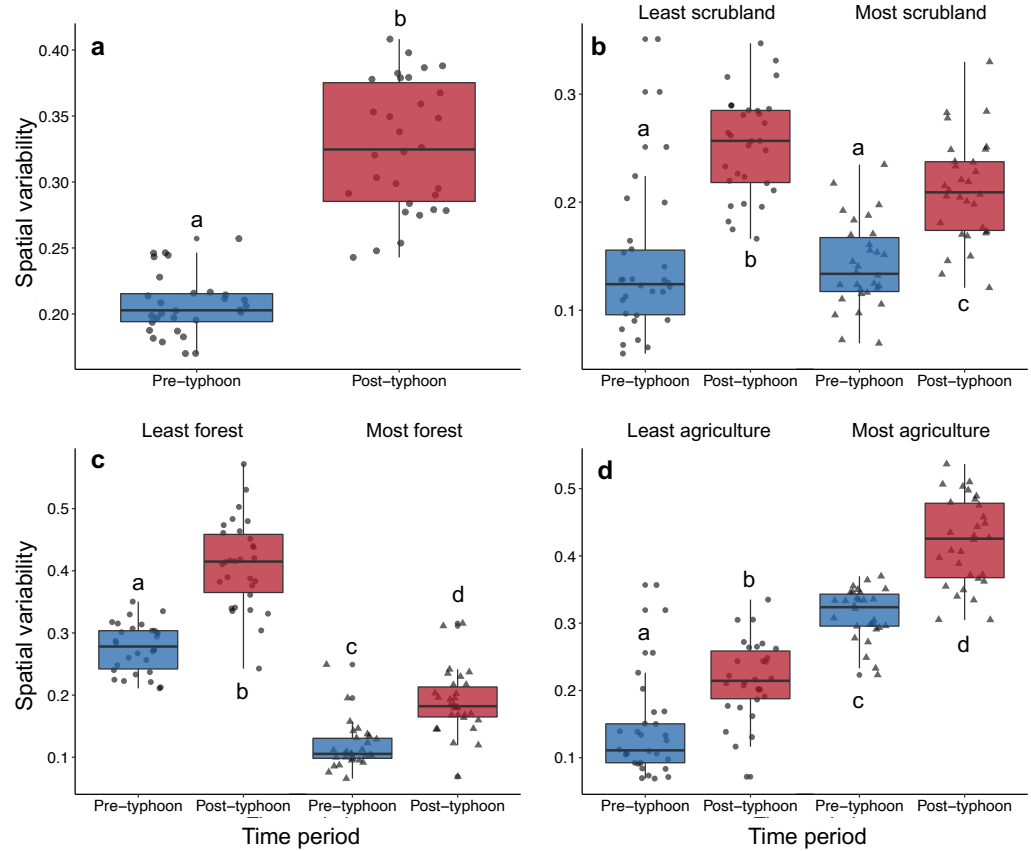


Figure D.11 | Effects of typhoons and land cover on NDSI_{Bio} spatial variability. Figure legend follows Fig. 5.5 but for the NDSI_{Bio} index.

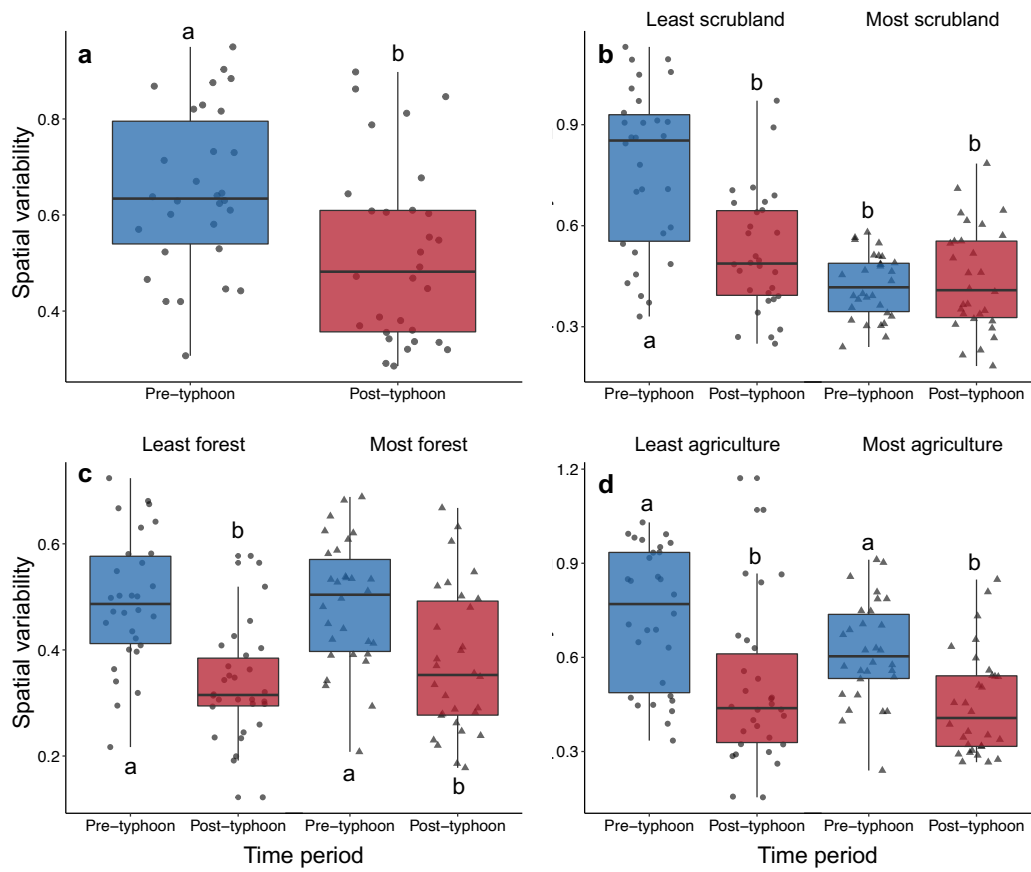


Figure D.12 | Effects of typhoons and land cover on $NDSI_{Anthro}$ spatial variability. Figure legend follows Fig. 5.5 but for the $NDSI_{Anthro}$ index.

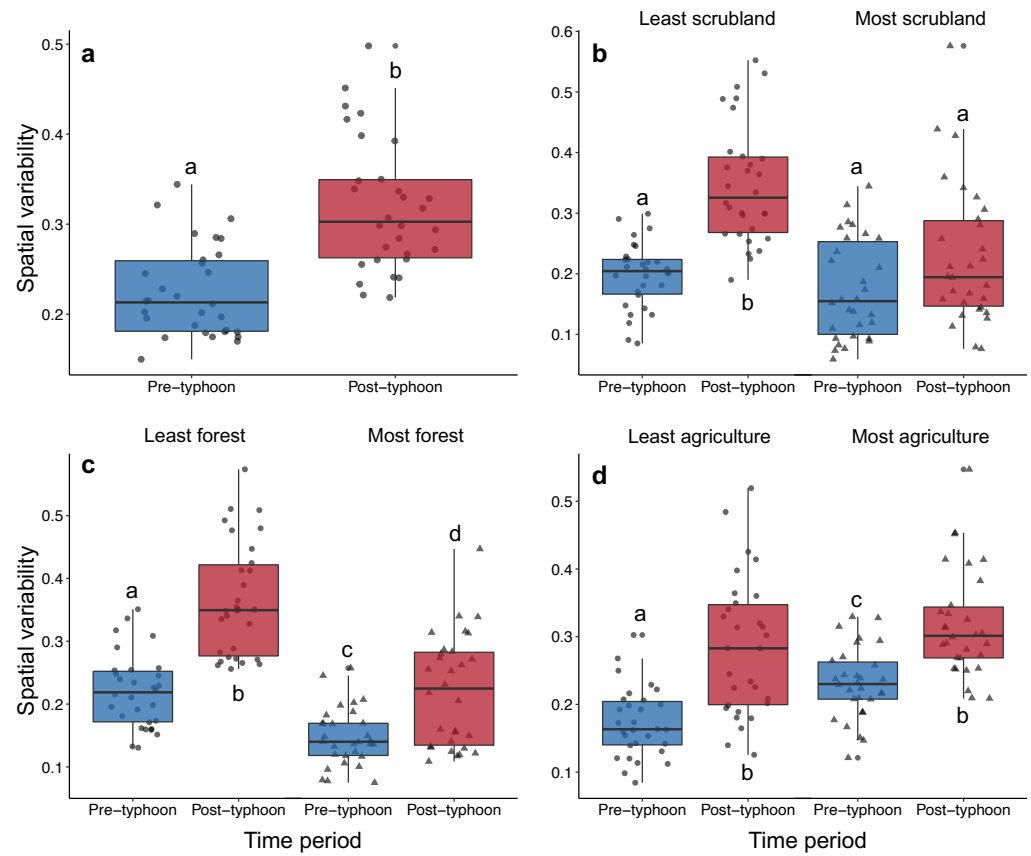


Figure D.13 | Effects of typhoons and land cover on ADiv spatial variability. Figure legend follows Fig. 5.5 but for the ADiv index.

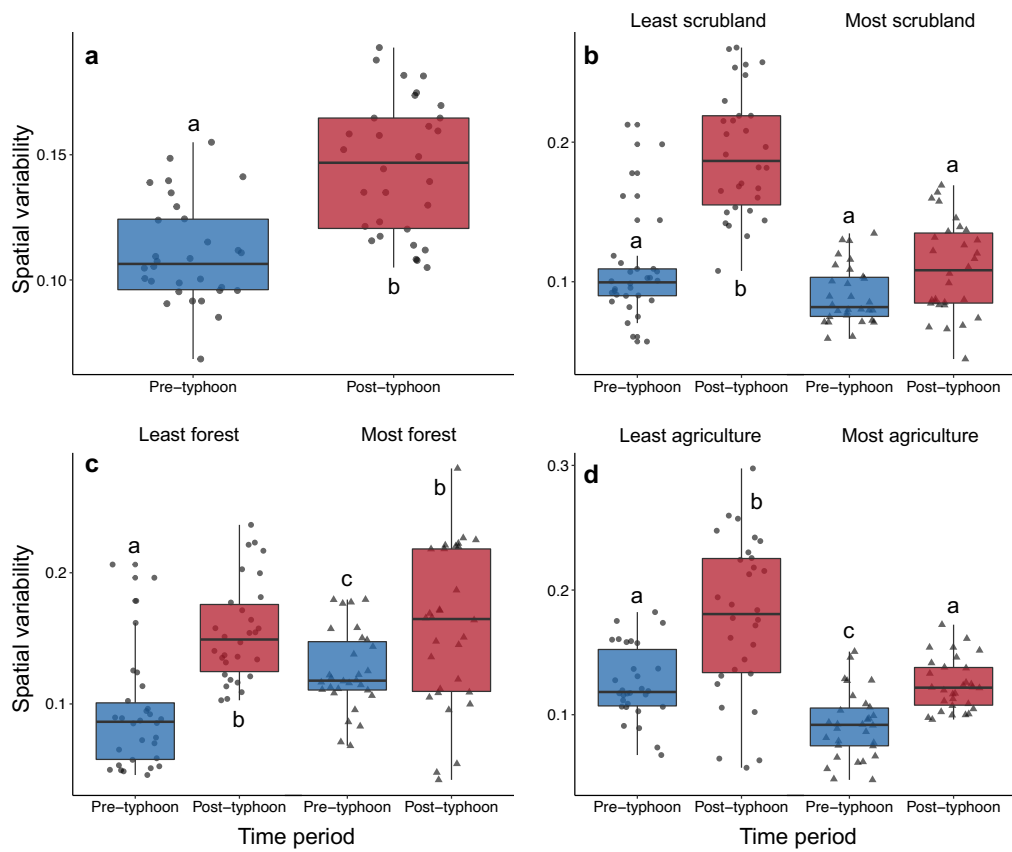


Figure D.14 | Effects of typhoons and land cover on H spatial variability. Figure legend follows Fig. 5.5 but for the H index.

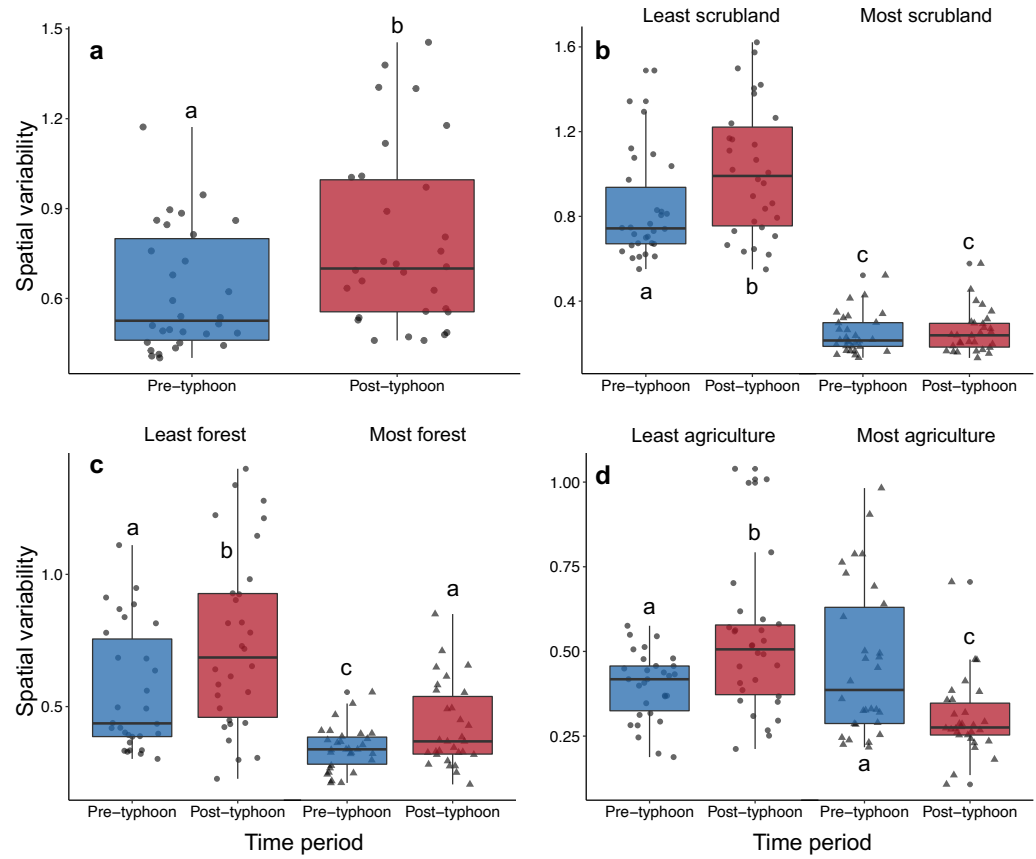


Figure D.15 | Effects of typhoons and land cover on M spatial variability. Figure legend follows Fig. 5.5 but for the M index.

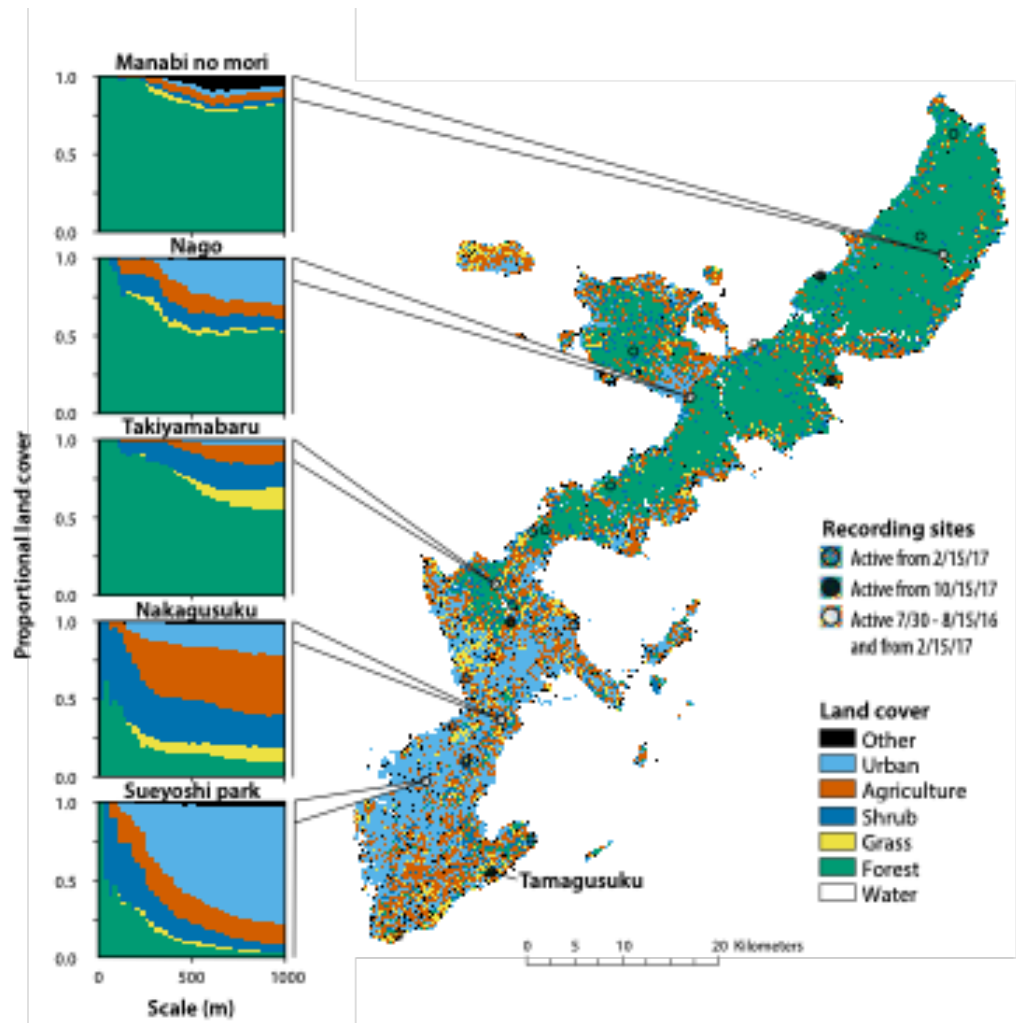


Figure D.17 | Land cover features and locations of study sites. Land cover map of Okinawa with five focal sites from a preliminary study (Ross *et al.* 2018a). Left panels represent the proportional land cover at different scales for circular buffers around each field site from 25 to 1000 m (1 km). Note that land cover is grouped into six categories (that is, different from the grouping used in Chapter 5): forest, grasses, shrubs, agriculture, urban and other (see Ross *et al.* 2018a). The map displays land cover using the same colour scale. Recording sites are marked according to their active dates. Reproduced from Ross *et al.* (2018a), with permission.