THE ROLE OF PLANT DIVERSITY IN THE FUNCTIONING OF ECOSYSTEMS: FROM MECHANISMS TO REAL-WORLD APPLICATIONS

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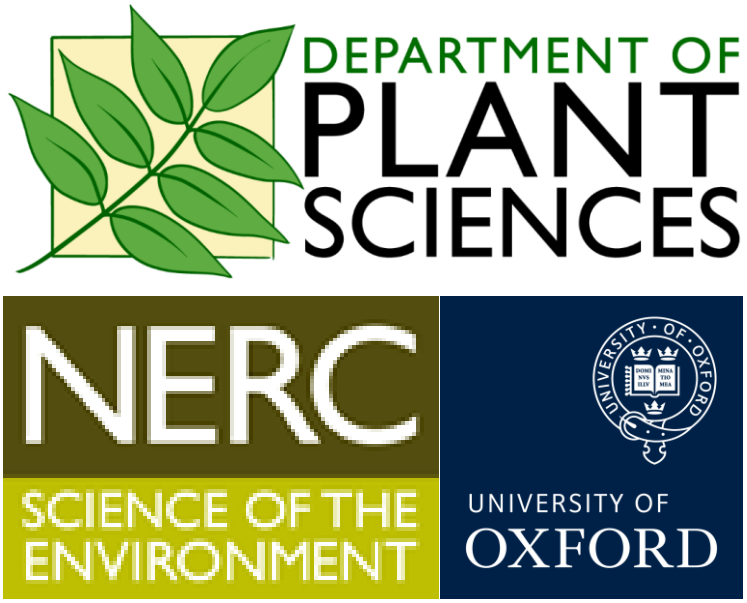

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For Gill Tuck, Kevin Tuck, and Helen Smith

I have been privileged to meet and collaborate with many people. Most of all, it has been a pleasure to know and work alongside my supervisors, Andy Hector and Lindsay Turnbull. This thesis is the product of the fun and discovery we have shared throughout the last three and a half years.

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Supplementary material for each thesis chapter can be found in the accompanying CD.

Abstract

Loss of biodiversity can impair the functioning of ecosystems. That is the broad consensus after 20 years of research, encompassing the diversity of plants and other taxa in a range of ecosystems. Thus, current global threats to plant diversity may also threaten the functioning of ecosystems and the ecosystem services that they provide to human societies. But, a recent consensus paper concluded that we need to better understand biodiversity-function relationships in the context of real-world change. A research frontier was laid out with two main areas of focus: the mechanisms for biodiversity-function relationships, and the real-world applications of biodiversity-functioning for ecosystem management. I present four studies that span this frontier.

Firstly, I show that existing methods underestimate the impact of diversity loss on the remaining plant community. I tested the accuracy of a method for measuring the strength of competition in natural communities. Competition is one of the ecological processes that structure plant communities, so is key to understanding the causes and consequences of diversity loss. I found that this method consistently underestimates the strength of competition, which undermines our ability to infer how strongly plant communities are structured by competition. Methods need to be improved to progress our ability to predict the impacts of diversity loss.

Secondly, I show how better retention of resources can lead more diverse communities to function as well as, or better than depauperate communities. I developed a mechanistic model of competition for a single resource that is lost over time, to explain how diverse communities could increase ecosystem functioning more than less diverse communities. I found that transgressive overyielding, where species mixtures outperform the best monoculture, was possible but rare. Mixtures commonly performed as well as the best monoculture. This model offers explanations for results found in long-term experiments.

Thirdly, I show how using higher levels of tree diversity could improve the effectiveness of re-afforestation schemes restoring tropical forest structure and functioning. I analysed the survival and growth of seedlings during the first decade of a field-scale long-term experiment in selectively logged tropical forest. I found that species varied independently in their survival, growth and responses to environmental variation. The number of surviving trees, and their stem area, might be less variable throughout this complex landscape if more diverse mixtures of species are planted. This could improve the effectiveness of restoration of these degraded forest ecosystems.

Finally, I show that organic agriculture supports higher levels of biodiversity with the potential for associated ecological benefits. I assessed how organic and conventional farms relatively impact biodiversity. Agriculture is the largest global land use and therefore greatly impacts biodiversity, which may undermine ecosystem functioning and even the provisioning services that farming depends upon. Thus, there is great need to understand realistic impacts of agriculture on biodiversity, to understand its consequences for real-world ecosystems and potential implications for food security. I found that biodiversity is reduced by a third overall on conventional farms relative to organic farms. Plant diversity is reduced by almost three quarters. There is a clear local ecological benefit to organic farming. Future work should ascertain how this realistic level of diversity loss will impact the functioning of ecosystems.

I conclude by discussing this research in the context of the mechanisms and applications of plant biodiversity effects on ecosystem functioning. Finally, I describe some emerging topics and methods that will aid future progress in this field.

Chapter 1
General Introduction

The functional importance of plant biodiversity

Plants are fundamental to life on Earth. Their ability to transform the sun's energy into living matter, called photosynthesis, is a process that sustains many lives other than their own, including the lives of humans. Their use of photosynthesis to produce organic compounds from carbon dioxide and water, known as primary production, is the basis of almost every food chain. This makes green plants the building blocks of most ecosystems across Earth's land and ocean—the most vital producers of the world. Plants are the ultimate modifiers of their environment, most notably by regulating the climate and producing the very air we need to breathe. They also provide the food, medicines, materials, and fuels we need to go about our everyday lives (RGB Kew 2016).

It should be a concern, therefore, that the diversity of plants on Earth is under threat. Human activity is placing great strain upon global biodiversity—the variation of genes, species, and ecosystems that make up the diversity of life—one of the descriptions of a safe planetary operating space for humanity (Rockström *et al.* 2009; Mace *et al.* 2014). Many plant species are threatened with extinction due to decreased population sizes, and at least 139 known species are already extinct (IUCN 2015). Current extinction rates for animals and plants are estimated to be 100–1000 times greater than what we historically see in the fossil record (Pimm *et al.* 2014; Ceballos *et al.* 2015), and these estimates may be overly conservative (Régnier *et al.* 2015). The most recent reports estimate that one in five plant species are threatened with

extinction, perhaps even more (Brummitt *et al.* 2015; Pimm & Joppa 2015).

There are many costs to biodiversity loss. The extinction of any species means irreversibly losing a unique lineage of evolutionary history, compounded by the fact that extinction is often focused within related groups of species (Purvis & Hector 2000). Another consequence of losing plant diversity is that it undermines the vital functional role plants play within ecosystems (Cardinale *et al.* 2012; Hooper *et al.* 2012; Naeem *et al.* 2012). This fact may not seem surprising, given that as a functional group they are vital to ecosystem processes. But it was only recently discovered that having a diversity of plant species helps sustain the functioning of ecosystems, and hence there is an ecosystem-level cost to losing plant diversity (Cardinale *et al.* 2012).

Biodiversity and ecosystem functioning

Over the past two decades, hundreds of studies have shown that losing biodiversity on average reduces the functioning and stability of ecosystem processes (Cardinale *et al.* 2012; Tilman *et al.* 2014). At a conference in 1992, researchers presented hypotheses that more diverse communities of species are more productive, use resources more efficiently, and show greater stability in these ecosystem processes (Schulze & Mooney 1993). Early experiments supported these hypotheses, finding that increased species diversity produced communities with higher primary productivity (Naeem *et al.* 1994, 1995) and that this productivity was more resistant to environmental change (Tilman & Downing 1994). This field of study became known as biodiversity-ecosystem functioning research (also known as biodiversity-functioning or BEF).

The first generation of experiments followed, conducted mainly in grassland plant communities, focusing on primary productivity and its relationship with species composition and richness (Tilman *et al.* 1996; Hector *et al.* 1999), although functional group descriptions of biodiversity were also studied (Hooper & Vitousek 1997; Tilman *et al.* 1997a). These experiments found that nutrient use, total plant abundance, and productivity all depended upon what species (and functional types) were present, but also increased on average as the community included more species. Increases in species richness typically showed diminishing returns, approaching an asymptotic productivity in the most diverse treatments.

The first explanation for this pattern was that species differ in their resource requirements, due to niche differentiation, such that they show complementary resource use and as a result collectively use more (Tilman *et al.* 1997b). This harks back to Darwin's principle of divergence, whereby natural selection causes species to diverge into complementary niches that lower interspecific competition (Darwin 1859; McNaughton 1993; Hector & Hooper 2002). Darwin focused on explaining what causes biological diversity, but he also hypothesised what consequences biodiversity would have for the functioning of ecosystems. In doing so, he suggested that the mechanisms for maintaining biodiversity are the same as those that create a functional role for biodiversity within ecosystems. Since then, a rich body of theory has emerged on the maintenance of biodiversity via the stable coexistence of competing species (Tilman 1982; Chesson 2000; Adler *et al.* 2007). And this theory was used to explain how diverse mixtures of species could be more productive by partitioning resources (Tilman *et al.* 1997b; Loreau 1998a, 2004; Yachi & Loreau 1999; Mouquet *et al.* 2002).

But a second explanation argued that niche differentiation was not the cause for increased and more stable ecosystem functioning, leading to contentious debate (Aarssen 1997; Grime 1997; Huston 1997; Tilman *et al.* 1997b, 1998; Wardle *et al.* 1997; Doak *et al.* 1998; Loreau 1998b; Hector 2000; Huston *et al.* 2000). The alternative explanation was that having more species is not important in itself; it only increases ecosystem functioning because there is a greater likelihood of the best performing species being present. By this logic, only species identity is important and there is no intrinsic functional value to species diversity. Methods were devised to tease apart the two explanations for biodiversity effects (Loreau & Hector 2001), and subsequent work has shown that they are not mutually exclusive (see below and chapter 3 for more).

A consensus emerged on the effects of biodiversity on ecosystem functioning after a first generation of synthesis (Hooper *et al.* 2005; Balvanera *et al.* 2006; Cardinale *et al.* 2006, 2007; Worm *et al.* 2006; Stachowicz *et al.* 2007; Cadotte *et al.* 2008): diverse communities could more effectively capture limiting resources and convert those resources into biomass. The same general result was found across terrestrial, marine, and freshwater ecosystems; within many organism groups spanning different trophic levels; and using genotypic, species, and functional expressions of biodiversity. Following a continued explosion of experiments there was another round of synthesis (Cardinale *et al.* 2011, 2012; Hooper *et al.* 2012; Naeem *et al.* 2012), and a consensus emerged that species identity and richness are both important aspects of biodiversity for ecosystem functioning. It is still not clear how prevalent niche differentiation is as a mechanism for biodiversity-functioning effects, nor is it clear what biological processes would be involved in such niche differentiation.

Box 1.1. Glossary

Term	Definition
Biodiversity	The variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems (CBD 2010).
Community	A group of species populations co-occurring in the same place and time, comprising a subset of the species that could co-occur. The potential species pool is determined by speciation and dispersal. The realised group of species co-occurring is influenced by species interactions, drift, and ongoing dispersal (see Vellend 2010).
Ecosystem	A complex of species communities and their non-living environment interacting as a functional unit (CBD 2010).
Ecosystem function	Properties of ecosystems that are determined by ecological processes. They are usually driven by species communities using their abiotic environment. Examples include primary productivity, nutrient retention, and litter decomposition.
Biodiversity-ecosystem functioning, also biodiversity-functioning or BEF	Mainly experimental study of how ecosystem functions depend on the diversity of species communities.
Niche	The set of environmental conditions that allow a species to satisfy its minimum requirements, so that the birth rate of a local population is equal to or greater than its death rate, plus the set of *per capita* effects the species has on these environmental conditions (Chase & Leibold 2003).
Niche differentiation, also niche partitioning	The process by which competing species use their environment differently in such a way that favours their stable coexistence. This lowers competition between species, relative to competition within species.
Stable coexistence	The maintenance of diversity of competing species, due to stabilising niche differences strong enough to overcome relative fitness differences. The demographic signature of coexistence is that species limit their own population growth more than they limit their competitors.
Complementarity	Positive complementarity between species in a community occurs when the performance of those species in mixture are on average higher than expected, given the weighted averages of their performances in monocultures. For example, species mixtures might yield more than expected based on monoculture yields—also known as overyielding.

The future of biodiversity-functioning research

In the most recent consensus paper, Cardinale *et al.* (2012) described the current state of knowledge and then listed emerging challenges for the next generation of experiments. They suggested that, for biodiversity-functioning research to better inform policy and manage the consequences of biodiversity loss, future work should focus on increasing its "realism, relevance and predictive ability" (Figure 1.1). Doing so would strengthen our understanding of how biodiversity loss might impact the provisioning and regulating services that ecosystems provide to humanity. To meet these challenges, they suggested three key areas for development.

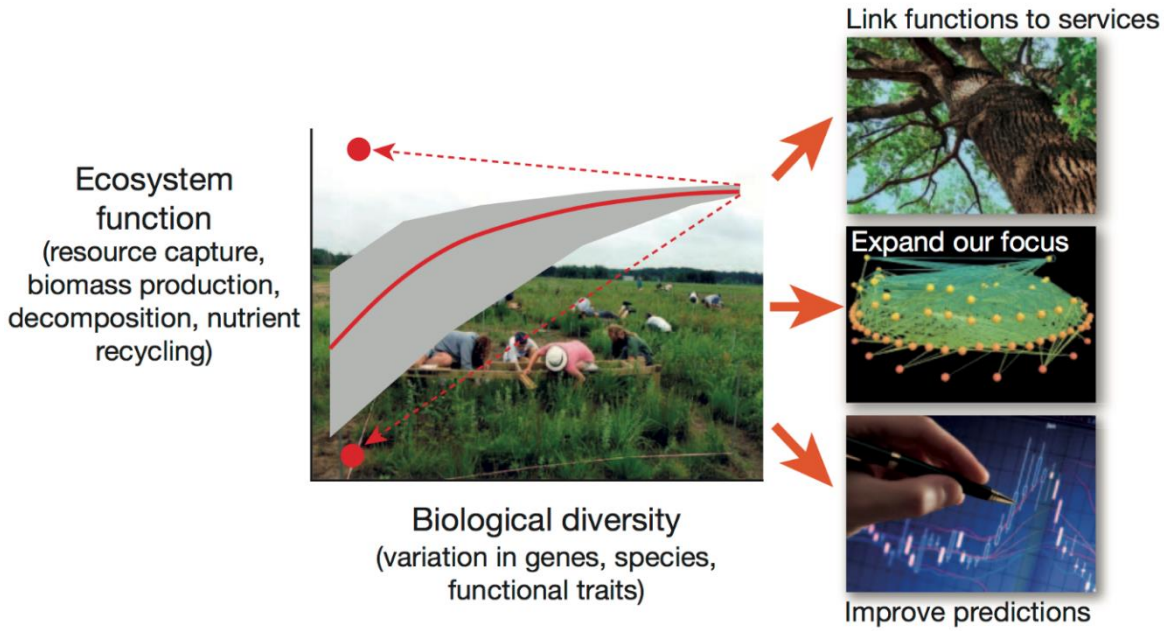

Figure 1.1. Consensus and the future. *Left*: The consensus on the form of biodiversity-functioning relationships. *Right*: Research can progress by improving our predictive and mechanistic knowledge, expanding our focus of experiments, and linking functions to services in real-world ecosystems. From Cardinale *et al.* (2012).

Firstly, to improve our ability to predict the impacts of diversity loss, we need mathematical modelling that will develop our mechanistic understanding of biodiversity-functioning effects. Such modelling would also help us scale experimental results up to insights for whole landscapes. Secondly, as well as scaling up the

modelling we should scale up our experimental focus, in terms of the temporal and spatial scale of experiments and also the types of ecosystems that experiments encompass. These landscape-level experiments would provide insights at the scale most relevant to management and better reflect the nature of real-world ecosystems. Thirdly, we should use these experiments to link realistic scenarios of diversity loss with the provisioning and regulating services that ecosystem functions support.

So far the effects of plant diversity on ecosystem functioning have been extensively demonstrated in controlled experiments, and in ecosystems that are amenable to controlled study. Most experiments have been short-term and small-scale. The early evidence is that some effects of diversity only become apparent at larger temporal and spatial scales, and so most experiments may have underestimated the impacts of diversity loss (Dimitrakopoulos & Schmid 2004; Tilman *et al.* 2006; Cardinale *et al.* 2007; Duffy 2009; Venail *et al.* 2010; Reich *et al.* 2012). Theory was first developed to explain the early experiments (Tilman *et al.* 1997b). Theoretical frameworks that can unify biodiversity-function research by scaling in time, space, and biological organisation are in development (Loreau 2010b). But we still lack the mechanistic understanding of how interactions between species influence the way diverse communities perform (Turnbull *et al.* 2013). Continued interplay between theory and experiments will be needed to further develop our basic ecological understanding of how plant communities are structured, from interactions between individuals up to the population, community, and ecosystem levels of organisation (Loreau 2010a).

One of the criticisms of biodiversity-functioning research has been that such

controlled experiments are not relevant to real-world ecosystems and therefore this research is of limited relevance to understanding the impacts of global biodiversity change (Srivastava & Vellend 2005; Duffy 2009; Wardle & Jonsson 2010). Such criticisms focused on the abstracted nature and small spatial scale of past experiments, which may not reflect the scope and scale of biodiversity change in real-world ecosystems—although the spatial scale of biodiversity change is in itself a hotly debated topic (Vellend *et al.* 2013; Dornelas *et al.* 2014; Newbold *et al.* 2015; Gonzalez *et al.* 2016). As Cardinale *et al.* (2012) noted, the connection between biodiversity-function research and the realistic impacts of diversity loss on ecosystem functions and services needs to be verified further. This can be achieved by understanding the scale of actual biodiversity loss in real-world ecosystems, and placing biodiversity-functioning experiments more closely within this real context. As part of this effort, we should look at the most important drivers of global biodiversity change and ensure that research includes all ecosystems that are functionally important for global ecosystem services.

This new generation of research will largely take place in complex landscapes, which have been altered by humans and are naturally variable in their environment. The biology of the systems may also be structurally complex and include long life-histories. Experiments will have to be more large-scale and long-term to capture these complex spatial and temporal dynamics (Scherer-Lorenzen 2014). Carrying out these new experiments will determine the utility of biodiversity-functioning for the management of real-world ecosystems, from ecological restoration to the provision of ecosystem services like carbon storage (Mori *et al.* 2016).

From mechanisms to applications

The outlook for future research put forward by Cardinale *et al.* (2012), and others, can be summarised as one with two frontiers: the mechanisms and the applications. We need the mechanisms to understand the causes of biodiversity effects on ecosystem functioning. And we need the applications to understand the relevance of this work in a world of global change. Here, I will present four specific studies which follow the broad scope that has been laid out.

I will begin in chapter 2 by studying interactions between plant species, the main deterministic force that structures plant communities (Rees *et al.* 2001). The strength of interactions within and between species determines the types and number of species that stably coexist in diverse communities, and also the relative abundances of each species. Species interactions drive effects of diversity on ecosystem functioning by altering the *per capita* performance of species within the community (Loreau & Hector 2001). So, to develop a predictive understanding of how plant diversity influences the functioning of real-world ecosystems, we need a predictive understanding of species interactions in natural plant communities. In chapter 2, I will test the predictive accuracy of the foremost method for predicting the effect of species interactions in natural communities (Mack & Harper 1977; Pacala & Silander 1990; Rees *et al.* 1996; Martorell & Freckleton 2014). The method has predominantly been used to study competitive interactions, but it can be applied to other types of interactions as well. Observational data are collected for co-occurring species, which are then used to predict how each species would respond to the removal of interacting species (see chapter 2). The test I will present is the first of its kind, whereby I apply

this observational method to experimental species mixtures (i.e. polycultures). Monocultures of each species, where they are grown in isolation, provide an independent test of the method's prediction. The experimental community is composed of sand-dune annual species, which are simple to observe and provide multiple generations. These species communities are known to be structured by competition, which is mediated by seed size (Rees 1995; Turnbull *et al.* 1999, 2004). This prior knowledge will help verify whether the method has realistically captured dynamics between these species. I will then compare the method's predictions with our test to understand whether this method can be used to infer how natural plant communities are structured.

In chapter 3, I will mathematically model the growth of species which interact in diverse communities, in order to understand what mechanisms can drive positive effects of plant diversity on productivity. The biological processes that underlie diversity effects are still not fully understood (Cardinale *et al.* 2012). Modelling can help to formalise trait-based mechanisms into testable hypotheses, which can then be tested using experimental data. We need these mechanistic models to understand whether diversity effects can be explained by resource partitioning among species, positive interactions, different natural enemies, or any other cause (Turnbull *et al.* 2013). I will focus on identifying what mechanisms can generate the most definitive evidence of positive diversity effects: when mixtures of species are more productive than any one species could achieve in isolation, a phenomenon known as transgressive overyielding. I will begin with a model published by Turnbull *et al.* (2013), whereby species grow throughout a season by competing for one shared limiting resource. Species differ in their resource consumption as defined by a trait-based functional

trade-off, between their ability to capture resources quickly and their ability to access a large pool of resources. This trade-off can allow species to stably coexist and also generate a complementarity effect of diversity (see chapter 3). But it is not sufficient for transgressive overyielding to occur. I will propose a mechanism for transgressive overyielding, by assuming that a fixed proportion of the remaining resources not yet locked up in plant tissue is lost over time via environmental leaching. I hypothesise that species mixtures will achieve a greater envelope of resource capture throughout the season and as a result capture more and leach fewer resources than the best component monoculture.

In chapter 4, I will begin looking at the applications of biodiversity-function research. I will propose a mechanism by which species diversity could stabilise ecosystem functioning in selectively logged tropical forests, and show whether this could improve the ecological restoration of these forest ecosystems. Large areas of South East Asian tropical forest have been selectively logged, which has depleted populations of the dominant dipterocarp trees and threatened the ecosystem's plant diversity more widely (Sodhi *et al.* 2010; Maycock *et al.* 2012). These tropical forest ecosystems are important for a range of globally and locally valuable ecosystem services, such as carbon storage (Saner *et al.* 2012). Efforts to restore dipterocarp populations, and the complex canopy structures they produce, have involved replanting the logged species back into the degraded forest (Kettle 2010). But replanting has only been implemented using low diversity stands, and the effectiveness of this restoration method has gone untested. These three factors—the diversity loss that has occurred, the functional importance of these ecosystems, and the opportunity for restoration—make the tropical forests of South East Asia a useful setting for taking

biodiversity-function experiments into real-world ecosystems. Furthermore, the complexity of these ecosystems has so far inhibited biodiversity-function study in the region. Extending research into this ecosystem will improve our understanding of the generality of biodiversity-function relationships. It will also inform how biodiversity change in these human-altered ecosystems impacts the ecosystem services they provide. In chapter 4, I present the initial results from the first large-scale long-term biodiversity experiment in these tropical forests: the Sabah Biodiversity Experiment (Hector *et al.* 2011b). In this experiment, dipterocarps have been replanted into the selectively logged forest at varying levels of species diversity. We can then ask how species diversity of the replanted species impacts the effectiveness of this restoration technique. I analyse the first decade of the survival and growth of these replanted species to understand: (i) how the species differ in functionally important traits, (ii) how species differ in their responses to the heterogeneous environment across this complex landscape, and finally (iii) how these factors might create a spatial insurance effect of diversity, whereby diverse mixtures show less variable performance and ensure successful restoration throughout the complex landscape.

In chapter 5, I investigate the scale of diversity loss within real-world ecosystems, focusing on agricultural landscapes by comparing the biodiversity impacts of organic and conventional farming. In order to place biodiversity-function experiments within the context of realistic diversity loss, and to understand the ecosystem-level consequences of that loss, we need to first understand how biodiversity is changing in real-world ecosystems. In an age when virtually nowhere is untouched by human impacts, this means understanding how human activity drives biodiversity loss. Agriculture has the greatest impact of all human activities, as it

already covers more than a third of Earth's ice-free land (Ellis & Ramankutty 2008). Not only could agriculture be impacting biodiversity across vast areas of the planet, but there could be knock-on effects for ecosystem functioning worldwide. Furthermore, agricultural systems themselves depend on many services provided by the ecosystems in which they are situated. These ecosystem services could include provision of pollination, natural pest control, and enhanced soil nutrient cycling. Before we can study the ecosystem-level consequences of different farming strategies we should know how they impact farmland biodiversity. In chapter 5, I will conduct a global meta-analysis of published biodiversity studies that compared organic and conventional farms. There is an ongoing debate on the relative merits of these two farming strategies for biodiversity conservation in the context of increasing global food demands (Tilman *et al.* 2011). I will use these studies to estimate the relative effects of organic and conventional practices across a broad range of taxa, environments and geographical regions. I will also investigate the importance of landscape-scale context, by regressing these estimated relative effects against metrics of land-use intensity. This work will inform environmental management policies and help devise strategies for agricultural development that minimise biodiversity loss. It will also lay the groundwork for future biodiversity-function studies that can link farmland biodiversity to ecosystem services across entire agricultural landscapes.

Finally, I will conclude by synthesising the results from these four studies. I will discuss each study's contribution to the next generation of biodiversity-function research. I will then describe some of the future work that would help progress our understanding of the mechanisms and applications of biodiversity-functioning, including some emerging techniques that will facilitate this progress.

Chapter 2
Observational Methods Underestimate The Strength Of Competition Among Plant Species

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SLT, LAT and MR designed the analyses and drafted the paper. SLT performed the analyses. LAT designed the experiment. JP collected data.

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Context

In order to understand the biological causes of plant diversity and predict the functional consequences of losing plant diversity, we need to accurately measure the ecological processes that underpin our understanding. Species interactions like competition are the main deterministic forces that structure plant communities. The strength of interactions within and between species determines the types and number of species that stably coexist in diverse communities, and also the relative abundances of each species. Species interactions also drive the effects of diversity on ecosystem functioning by altering the *per capita* performance of species within the community. The community-level properties that determine ecosystem functions are the product of which species are present in the community and the interaction between those species. Therefore, in order to develop a predictive understanding of how plant diversity influences the functioning of real-world ecosystems, we need a predictive understanding of species interactions in natural plant communities. And in order to have a predictive understanding of species interactions, we need tried and tested methods for measuring species interactions, which consistently and accurately predict how plant communities respond when diversity is lost. Here, I show that existing methods underestimate the impact of diversity loss on the remaining plant community.

Chapter Summary

Competition among neighbouring plants for shared resources is one of the key ecological forces that shapes plant communities. But measuring competition has always been a challenge, leaving controversy over the relative role of competition between species. Observational methods for measuring plant competition have

become popular. This approach assumes that we can infer competitive effects from natural variation in the densities of co-occurring species. The effect of competition between species is quantified by predicting how the population size of each species would respond to competitor removal. However, this approach remains untested. We tested the predictive accuracy of this method by combining observational and experimental approaches. We grew four sand-dune annual species in monoculture and mixture. Their local compositions were left to naturally develop, making our data relevant to natural communities. We performed an observational analysis on the mixtures and predicted how each species would perform in the absence of competitors. We compared these predictions with our independent test: the monocultures, where each species was grown in isolation. We predicted that competitive ability increased with seed size, a well-known aspect of competition between these species. We occasionally predicted strong responses to competitor removal. Even so, we consistently underpredicted the effect of interspecific competition, for most species by at least half that observed. The method failed our test so we should infer competition from natural communities with care. We suggest that the method underpredicted the effect of competitor removal because the data lack information on fundamental niches. Species are observed after they have been confined to realised niches by competition, so we lack the information to predict how they will respond to competitive release.

Introduction

Competition for shared limiting resources is the fundamental assumption that underpins community ecology (Darwin 1859; Tansley 1917; Clements *et al.* 1929; Gause 1934; Macarthur & Levins 1967; Harper 1977; Grime 1979; Tilman 1982, 1988; HilleRisLambers *et al.* 2004, 2012; Adler *et al.* 2010; Craine & Dybzinski 2013). By understanding the nature of competition between species we can understand how they coexist (Chesson 2000), as coexistence requires that species limit themselves more than they limit others (Adler *et al.* 2007). This is the basis of the ecological niche concept, in which species are expected to evolve in a direction that will minimise interspecific competition, otherwise competitive exclusion is the inevitable outcome (Roughgarden 1976; Rees *et al.* 2001; Chase & Leibold 2003; Le Gac *et al.* 2012; Rabosky 2013). Yet, despite this clear theoretical expectation, the nature of competition in real plant communities has always been controversial (Grime 1963, 1973; Connell 1983; Tilman 1987; Goldberg *et al.* 1999; Connolly *et al.* 2001; Silvertown 2004; Craine 2005; Levine & HilleRisLambers 2009; Rajaniemi *et al.* 2009; Rees 2013; Trinder *et al.* 2013).

While any farmer or gardener can confirm that competition depresses plant performance, it is less clear how best to measure the extent and nature of this competitive suppression in natural communities. One obvious way is to add or remove plants and measure the response of their neighbours (de Wit 1960; Clatworthy & Harper 1962; Silander & Antonovics 1982). While seemingly straightforward, removal experiments have been heavily criticised because, among other things, species respond over different timescales (Putwain & Harper 1970; Allen & Forman 1976). Hence, the

immediate response to the removal of a particular species might differ greatly from a longer term outcome.

Another common method is to experimentally grow focal plants surrounded by different numbers and types of neighbours. Such experiments often reveal that interspecific competition is strong and asymmetric (Goldberg & Barton 1992; Gurevitch *et al.* 1992; but see Law & Watkinson 1989). But it is not clear how to translate these measurements into the field, where densities and conditions could be very different. In short, all direct manipulative methods for measuring the strength of competition among plant species have been criticised, as either methodologically flawed or because they take place under unrealistic ecological conditions (Connell 1983; Connolly 1986; Wilson 1995; Freckleton & Watkinson 1997).

Partly in response to these criticisms, plant ecologists have turned instead to observational approaches (Rees *et al.* 1996; Law *et al.* 1997; Freckleton & Watkinson 1999, 2000). Rather than manipulating the system, observational methods exploit natural variation in density and species composition found within real plant communities and can be used to estimate individual-level competitive effects. For example, in neighbourhood modelling, detailed spatial maps of all plants allow focal plant size or fecundity to be modelled as a function of the number and identity of close neighbours. Using this method, estimates of individual-level competition coefficients have been obtained in both artificial and natural settings (Mack & Harper 1977; Coomes *et al.* 2002; Turnbull *et al.* 2004; Stoll & Newbery 2005). Alternatively, counting the numbers of plants in permanent quadrats allow researchers to track changes in population sizes from year to year at small spatial scales. Changes in

population size between years can then be modelled as a function of the number of neighbours, again allowing competition coefficients to be estimated (Pacala & Silander 1990; Rees *et al.* 1996).

The pattern of interspecific interactions estimated from such observational analyses is mixed (Law *et al.* 1997; Freckleton *et al.* 2000; Stoll & Newbery 2005; Martorell & Freckleton 2014). But many studies have found that interactions between competing species in the field are extremely weak (Rees *et al.* 1996; Turnbull *et al.* 2004; Mutshinda *et al.* 2009; Comita *et al.* 2010; Martorell & Freckleton 2014). However, this result throws up a problem. If competition between species is really so weak as to be negligible, then species would show little or no response to the removal of others. This was best illustrated by Martorell & Freckleton (2014) who parameterised a population model for each species in their community separately and then quantified the effect of removing the remaining species. Their results showed that very little response was expected overall—though some species showed positive or negative responses, and rarer species seemed most suppressed by competitors. But this overall result, in turn, suggests that plant communities are not fundamentally competitive, a result clearly at odds with most experimental work. So are the weak interspecific interactions estimated using observational data simply some artefact of the method, or are plant communities in nature truly non-competitive?

To resolve this paradox it is essential to combine observational methods for estimating competition coefficients with an independent test of model predictions within the same system. Here we present results from an experiment conducted under semi-natural conditions in which a community of annual plants was established and

allowed to grow and reproduce for several years. The communities were subdivided into small cells to which we could fit models of population growth using observed cell counts taken from the last two years of the experiment. After fitting models and estimating competition coefficients, we predicted how each species would respond to the removal of the others, and similar to Martorell & Freckleton (2014), we predicted very little response to removal. However, we could then compare these predicted population sizes with those of monocultures of each species established at the same time. These comparisons revealed that the effect of interspecific competition had been grossly underestimated. Our work therefore reveals that when observational methods uncover weak interspecific interaction coefficients within natural communities, individual species might still suffer from strong interspecific suppression.

Methods

Overall approach

Our overall approach is summarised in Figure 2.1. To test the accuracy of predictions made using observational approaches, we first needed a suitable dataset with which to fit appropriate models. In this case, we had established semi-natural communities consisting of seven species of sand-dune annuals subdivided into small cells (see *Experiment*). Population sizes of all species were recorded in two consecutive years. For each of the five common species, we then fitted a population model in which changes in local population size from one year to the next are assumed to be a function of both its own density and the densities of other species. Depending on the details of model structure (see *Models*) interactions between species can be positive as well as negative.

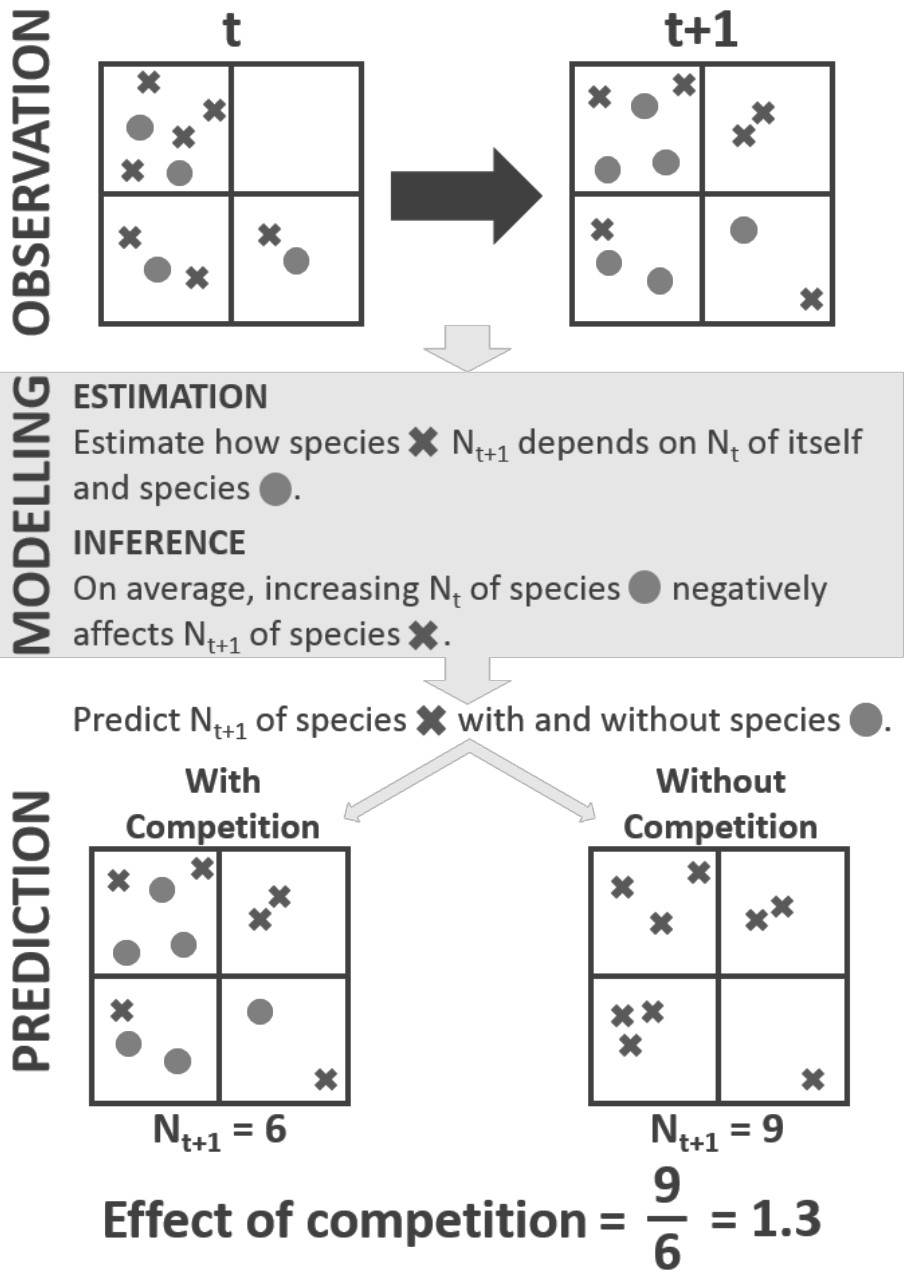

Figure 2.1. The method for estimating the effect of interspecific competition. Observational data on the population sizes of each species in a community is collected over multiple years. For each species, the change in population size from one year to the next is modelled as a function of its own density and the densities of other species. Once models are parameterised, they can be used to predict the population size of each species when: (i) interacting species are present at their observed abundances, and (ii) interacting species are removed. These two predictions are compared with one another to quantify the effect of competition.

Once the models are fitted, we can predict the effect of competitors on the focal species by setting population sizes of competitor species to zero and re-calculating the predicted population size of each focal species (Martorell & Freckleton 2014). But to

test whether these predictions are indeed accurate, we require additional data. In this case, our experiment included monoculture plots, which had been established at the same time. We therefore compared our predictions about the expected effect of the removal of competitors with observations of population sizes from monoculture plots (see *Test*).

Experiment

Seven species of sand-dune annuals were grown for four years (2010–13) in a common garden experiment in Zürich, Switzerland. The study species and their seed sizes were: *Saxifraga tridactylites* L. (0.006 mg), *Arabidopsis thaliana* [L.] Heynh. (0.025 mg), *Cerastium diffusum* Pers. (0.045 mg), *Arenaria serpyllifolia* L. (0.088 mg), *Veronica arvensis* L. (0.112 mg), *Myosotis discolor* Pers. (0.213 mg), and *Valerianella locusta* [L.] Laterr. (0.851 mg). They germinate in autumn and flower in spring. We analysed data for only five of these species, because *Veronica* and *Valerianella* were too rare.

The experiment consisted of 80 (1 x 1 m) plots. A concrete lattice was inserted so that each plot consisted of 56 (7 x 7 cm) individual cells filled with a low-nutrient mixture of sand and compost (Figure 2.2). The lattice walls were sufficiently thick (2.5 cm) that plants in adjacent cells never overlapped aboveground. Thus, we assumed that plants within cells competed for resources, while plants in adjacent cells did not. Plants dispersed seeds freely within plots, but barriers to dispersal prevented seed movement between plots. Subdividing the plots into cells provided the fine-grained information necessary for parameterising our models. We grew eight monocultures of each species and 24 mixtures containing all seven species.



Figure 2.2. Example of an experimental plot, divided into 56 cells by a concrete grid. This is a mixture plot photographed immediately after seven cells were harvested in 2011.

In order to create variation in density, a gradient of disturbance was applied across plots. This facilitated the fitting of nonlinear population models, which is often hampered by a lack of information at low density (Law & Watkinson 1987; Rees *et al.* 1996). Plots were disturbed by removing all plants from a fixed proportion of cells at the end of every growing season, just before the plants set seed. In mixture plots we applied five levels of disturbance: 12.5%, 25%, 50%, 75%, and 87.5%. In the monocultures there were only eight plots per species, so we imposed only three disturbance levels: 12.5%, 50%, and 87.5%. We selected which cells to destroy in a stratified random way, destroying a fixed number of cells from each row in a plot grid. In 2012 and 2013 there was a highly significant negative relationship between disturbance and average density per cell, indicating that the disturbance treatment was successful in creating a density gradient (Supplementary Material SA1).

The experiment was established from seed in 2010 using a constant total density of 1000 seeds per plot. The number of individuals in all cells was recorded at the end of the growing season for three years (2011–13), although only occupancy was recorded from the mixture plots in 2011. The transition 2012–13 is therefore the most completely sampled and was used for the model fitting. The end-season biomass of each species was estimated by destructively harvesting and weighing seven cells from each plot during application of the disturbance treatment.

Models

To ensure that our conclusions were not dependent on model choices, we fitted three models with varying assumptions about the nature of species interactions and the nature of dispersal within plots. We either assumed that: (i) all seeds remain in their natal cells, or (ii) some fraction of seeds (m) remain in the natal cell while the rest ($1 - m$) join a global seed rain.

The general form of model 1 (eqn 2.1) is:

$$N_{t+1,i,c} = mr_i F_c + (1-m)\langle r_i F_k \rangle_k \qquad N_{t,i,c} > 0, \quad (2.1)$$

where $N_{t+1,i,c}$ is the population size in year t+1 of focal species i in cell c. The population growth rate of species i in the absence of competition, r_i, is modified by density-dependent interactions in the following way:

$$F_c = \left[\frac{N_{t,i,c}}{1+\sum_{j=1}^{5} \alpha_{ij} N_{t,j,c}}\right], \quad (2.2)$$

where α_{ij} is the *per capita* effect of species *j* on species *i*. Thus, the first term in eqn 2.1 describes the expected number of individuals of species *i* in year *t*+1 that originated in the natal cell. Similarly, the average value of F_c among the cells within a plot can be calculated using:

$$\langle F_k \rangle_k = \left[\frac{1}{p} \sum_{k=1}^{p} \frac{N_{t,i,k}}{1+\sum_{j=1}^{5} \alpha_{ij} N_{t,j,k}} \right], \quad (2.3)$$

where *p* is the total number of cells within a plot. Thus, the second term in eqn 2.1 describes the expected number of immigrants arriving from other cells within the plot.

Model 2 (eqn 2.4) contains only the first, within-cell-growth term from eqn 2.1, and thus assumes that no seeds disperse outside their natal cells:

$$N_{t+1,i,c} = \left[\frac{r_i N_{t,i,c}}{1+\sum_{j=1}^{5} \alpha_{ij} N_{t,j,c}} \right] = r_i F_c \qquad N_{t,i,c} > 0, \quad (2.4)$$

Model 3 (eqn 2.5) has a different structure. In this case we assume that within cells population growth is density-dependent, but is only sensitive to the density of conspecifics:

$$N_{t+1,i,c} = \left[\frac{r_i N_{t,i,c}}{1+\alpha_{ii} N_{t,i,c}} \right] q_{t+1,i,c} \qquad N_{t,i,c} > 0, \quad (2.5)$$

where *q* is an index of cell quality. Other species affect the focal species by modifying the quality of cells:

$$q_{t+1,i,c} = \frac{e^{(\beta_0 + \sum_{j \neq i}^{5} \beta_j N_{t+1,j,c})}}{1 + e^{(\beta_0 + \sum_{j \neq i}^{5} \beta_j N_{t+1,j,c})}}, \quad (2.6)$$

This cell quality index is a logistic function of the densities of other species in year t+1 and their *per capita* effects on the focal species, β_j. For each focal species we estimate a basal cell quality, β_0, and the quality of each cell can deviate above or below this value depending upon the density of other species present in the same year. Model 3 allows species interactions to be positive as well as negative (eqn 2.6)—in contrast to models 1 and 2 where they are constrained to be negative. Positive interaction coefficients might indicate facilitation. But they might simply indicate that the seedling densities of both the neighbour and focal species tend to be positively correlated, perhaps because they share a preference for the same types of cells.

All models were fitted using *rjags v3-14* (Plummer 2014) in *R v3.1.2* (R Core Team 2014). Each model assumed that N_{t+1} was Poisson distributed. To estimate the competition coefficients we specified non-informative priors, assuming they had a normal distribution ($\mu = 0$, $\sigma^2 = 1000$). Competition coefficients were constrained to be positive—i.e. competitive—by applying an exponential transformation. A common concern when parameterising these models is that the competition coefficients and the population growth rates in the absence of competition (r_i) can be correlated, because they trade off against each other (Rees *et al.* 1996). This can produce an unstable estimation process, whereby both parameters increase or decrease together and yet give an equally good model fit. To avoid this instability we informed the estimation process on meaningful values of r_i by specifying an informative prior for each species that used the best information we had on their maximum capacity for growth. We

specified these informative priors by assuming a gamma distribution with an expected value equal to the average 2012–13 population growth observed in high-disturbance monocultures (gamma: *shape* = mean 2012–13 growth; *rate* = 1; E[X] = *shape*/*rate*). When fitting model 3 to *Myosotis*, we fixed β_0 at zero (basal cell quality = 0.5) to stabilise the estimation process, because there were significant trade-offs between r_i and β_0.

We ran all models with three sampling chains. We ensured each model had sufficiently converged on the target distribution by running an adaptation period of 40000 samples (plus 10000 burn-in). Following adaptation we monitored 10000 samples from the chains, thinning to every 10th sample to reduce autocorrelation—giving us 1000 samples from each posterior distribution. We checked that the chains had converged by plotting the sampling chains, posterior densities and chain autocorrelation. We used Gelman plots to check that chains had converged on the same target distribution (Brooks & Gelman 1998). We also checked models by: (i) testing that they can recover known parameters from simulated data, (ii) examining residual diagnostic plots, (iii) plotting the model fit, and (iv) comparing simulated and observed data to look for systematic differences between models and observations (Gelman & Hill 2007). Predicted data qualitatively resembled the observed data, although the observed data often showed a longer tail of right skewness. Finally, we compared model performance using DIC (Plummer 2002). To facilitate comparisons among models, all models were fitted only to cells where N_t was positive.

Analysis

We examined interaction matrices from the parameterised models to look for patterns in competitive effects. We then used the parameterised models to quantify the

effect of competition at the population level, by predicting population sizes in the presence and then in the absence of all other species (by setting populations sizes of other species to zero). We constructed intervals on the predicted population sizes without competitors from posterior samples within each cell. We averaged across these cell-level predictions to get the median predicted population size without competitors and its 95th percentile range. These median and interval values were then expressed relative to the average predicted population size when competitors are present. The *predicted effect of competitor removal* is thus the ratio between the focal population sizes with and without competitors (N_{t+1} *without* / N_{t+1} *with*).

We assessed the observed extent of competitive release by regressing the population sizes in 2013 on the population sizes in 2012 for both mixtures and monocultures. The slope of the regression line through the origin is therefore the population growth rate. We tested whether there was a significant effect of mixture vs monoculture on the growth rate of each species. If the regression slope in monoculture is, on average, steeper than in mixture, then there is a clear positive effect of removing competitors on population growth. In 2012 the range of population sizes in mixtures and monocultures was similar, so it was easy to compare treatments. The *observed effect of competitor removal* is thus the ratio between monoculture and mixture slopes (*monoculture* / *mixture*).

Test

Finally, to test whether our predictions matched our independent observations, we compared the *predicted effect* of competitor removal with the *observed effect*. We described each model's predictive accuracy by expressing the predicted effect as a

percentage of the observed effect. We showed the credible range in each model's predictive accuracy by using the interval for its predicted effect, which captures uncertainty in the estimation process.

Results

Models

Model 1 was the preferred model for three species—although for two species all models performed equally well (Supplementary Material SA1)—hence we focus on results from model 1. The competitive effects estimated by model 1 were asymmetric and structured by seed size (Figure 2.3). If a species had large seeds then it usually had a strong competitive effect on those with smaller seeds. In addition, for most species the strength of intraspecific competition was greater than the strength of competitive suppression by smaller seeded species, but weaker than competitive suppression by larger seeded species (Figure 2.3). Within the context of this seed-size pattern, *Myosotis* is anomalous. The model estimates that it is strongly affected by several of the smaller seeded species.

This seed-size pattern was even more pronounced when the model did not include dispersal (model 2, see Supplementary Material SA1). When we allowed for positive interactions, however, the pattern disappeared: instead all interactions were scattered around zero, as many positive as there were negative (model 3). Broadly speaking, all models estimated the effects of interactions with high precision.

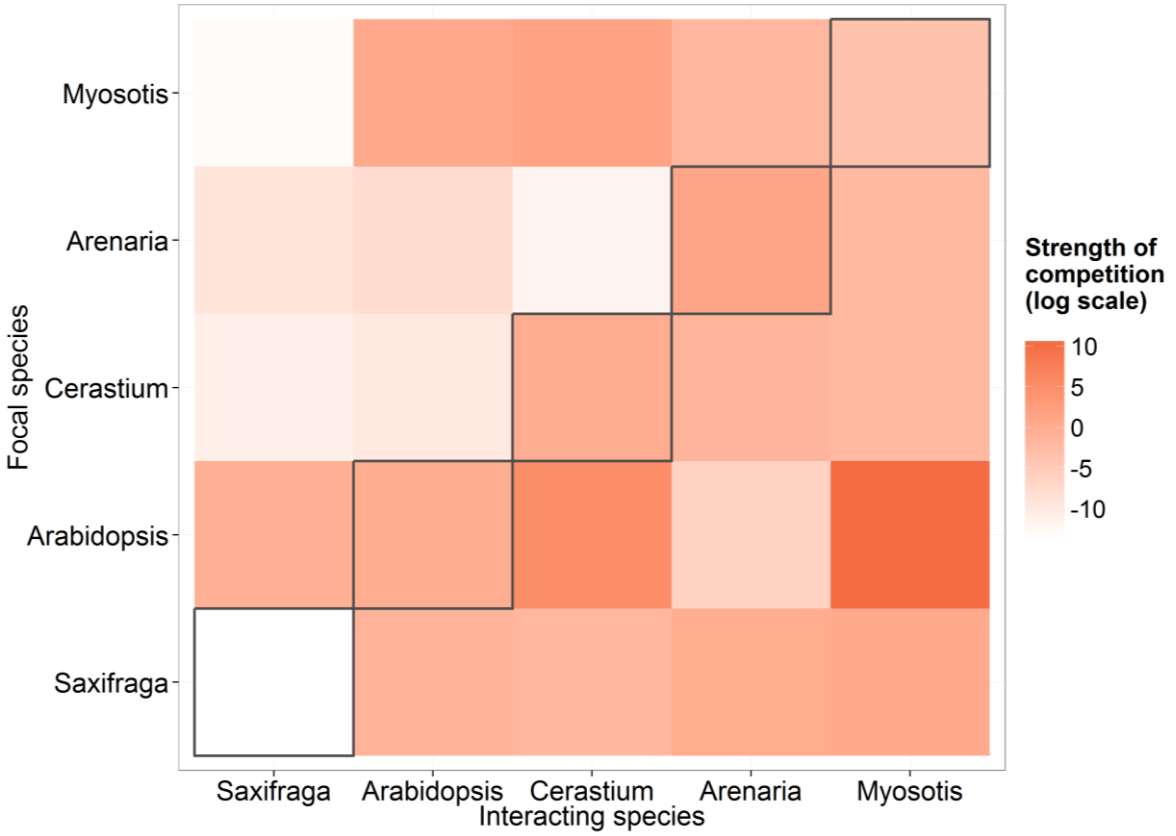

Figure 2.3. Competition is asymmetric and related to seed size. The competitive effects of interacting species (columns) on the population size of each focal species (rows). The highlighted diagonal are intraspecific competitive effects. Weak competitive effects are pale and stronger effects are darker (effects are log-scaled, so negative values describe more neutral effects). Species are ordered left to right and bottom to top by increasing seed size. Broadly speaking, competitive effects are linked to seed size, with large-seeded species exerting stronger effects. Model 2 shows even stronger seed-size structure (Supplementary Material SA1).

Analysis

Using these parameterised models we calculated the *predicted effect of competitor removal* within each cell (Figure 2.4). The seed-size structure of *per capita* interactions in Figure 2.3 is also clear in the population-level effects (Figure 2.4). For *Saxifraga* and *Arabidopsis*, model 1 predicted at least a doubling in population size in 50% of cells and they are predicted to increase by five-fold or more in 10% of cells. In contrast, larger seeded species are predicted to show a weaker response to competitor removal in most cells (75% of the time their ratio response is close to 1, i.e. no change). *Myosotis* is predicted to respond more strongly on average than *Arenaria* or *Cerastium*,

reflecting the relatively strong competitive effects of other species on *Myosotis* (Figure 2.3). Model 2 predicts smaller population-level responses of *Myosotis*, better conforming to the trend that large-seeded species respond less strongly to the removal of small-seeded competitors (Supplementary Material SA1).

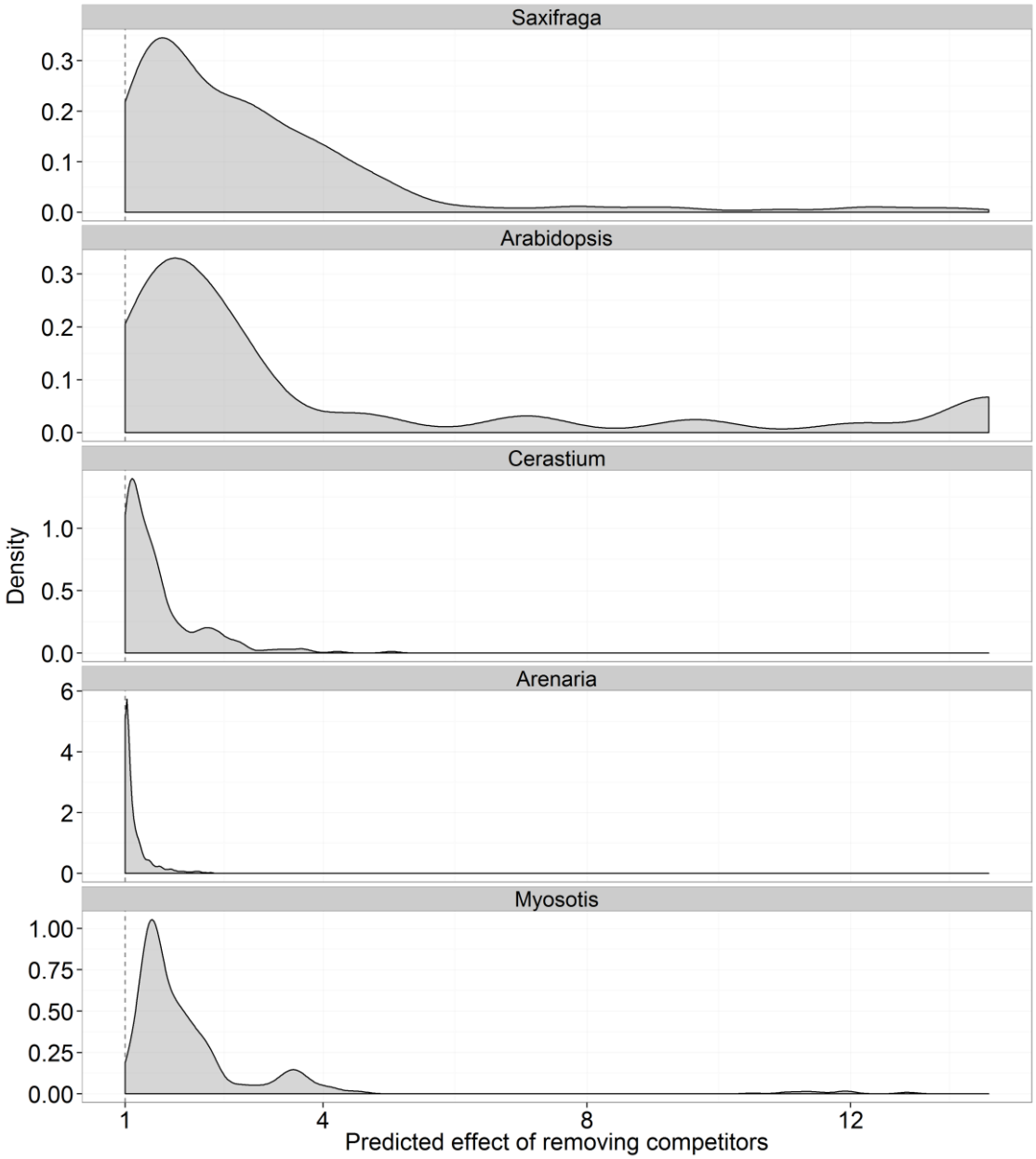

Figure 2.4. Population-level effects of removing competitors. Distributions of the predicted effect of competitor removal at the cell level. An effect size of 2 means that the population size is predicted to double in response to competitor removal. In most cells the predicted effect is small but in some it is large. The x-axis has been truncated for clarity (removing <1% of cases). Species differences reflect the strength of competition shown in Figure 2.3. Predictions from model 2 show an even stronger seed-size structure (Supplementary Material SA1).

For the *observed effects of competitor removal*, there was a significant three-way interaction between species, diversity level and density ($F_{4,140}$ = 3.4, p = 0.01). Inspection of the slopes revealed that in four out of five cases, the slope in the monoculture is much steeper than that in mixture: for most species, population growth at least doubled when grown in monoculture (Figure 2.5). The only exception was *Myosotis*, whose population growth was higher in the mixture; although when we used biomass data rather than population sizes, the population growth in monoculture and mixture was the same (Supplementary Material SA1). *Myosotis* may have responded differently to interspecific competition because it was competitively dominant in mixtures. The hierarchy for average cell biomass in mixture was *Myosotis* > *Arenaria* > *Cerastium* > *Saxifraga* > *Arabidopsis*—broadly in decreasing order of seed size. It is clear that species densities are reduced by interspecific competition, especially if they have smaller seeds.

Test

Comparison of the *predicted* (Figure 2.4) and *observed effects* (Figure 2.5) revealed that the models made poor predictions about the population-level response to the removal of competitors (Figure 2.6). Models consistently underpredicted the effect of interspecific competition in four cases, but overpredicted in the case of *Myosotis* (Figure 2.6). The three different models had similar predictive accuracies, despite differences in the way they describe species interactions (Figure 2.6).

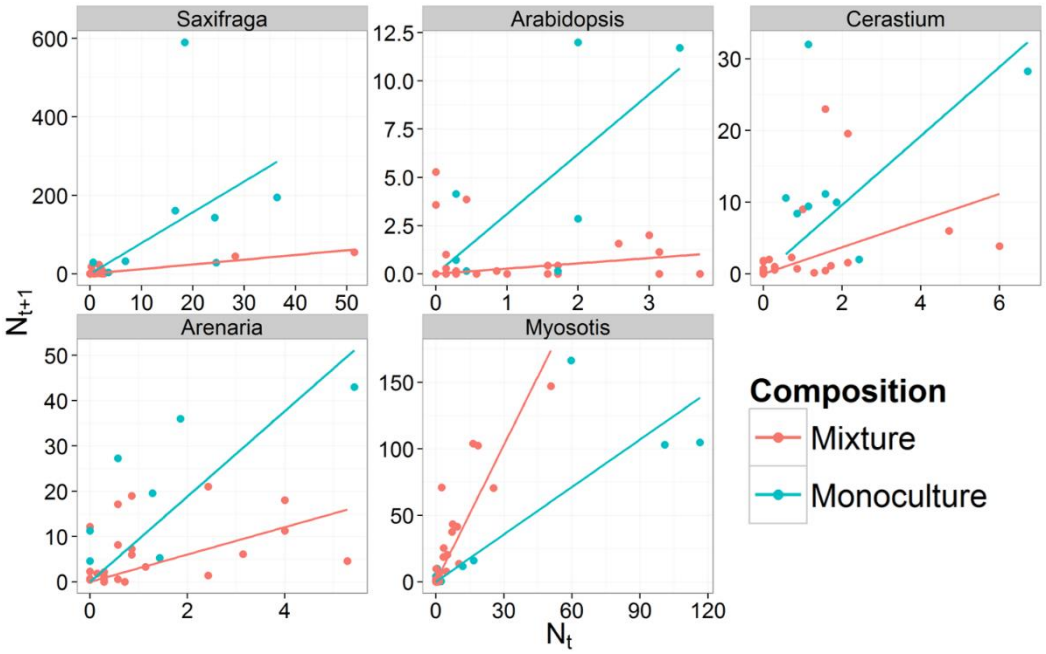

Figure 2.5. Population growth rate is higher in monocultures than in mixtures. The plot-level average cell population sizes in 2013 (N_{t+1}) versus 2012 (N_t) for each species. Blue dots show monocultures, red dots show mixtures. The regression lines, fitted through the origin, show the average population growth rate. Species are ordered by increasing seed size. Population growth rates were higher in monocultures than mixtures for four species. The exception was *Myosotis*, which was competitively dominant. In terms of population size *Myosotis* performed much better in the mixtures, but biomass data show no difference between diversity treatments for this species (Supplementary Material SA1).

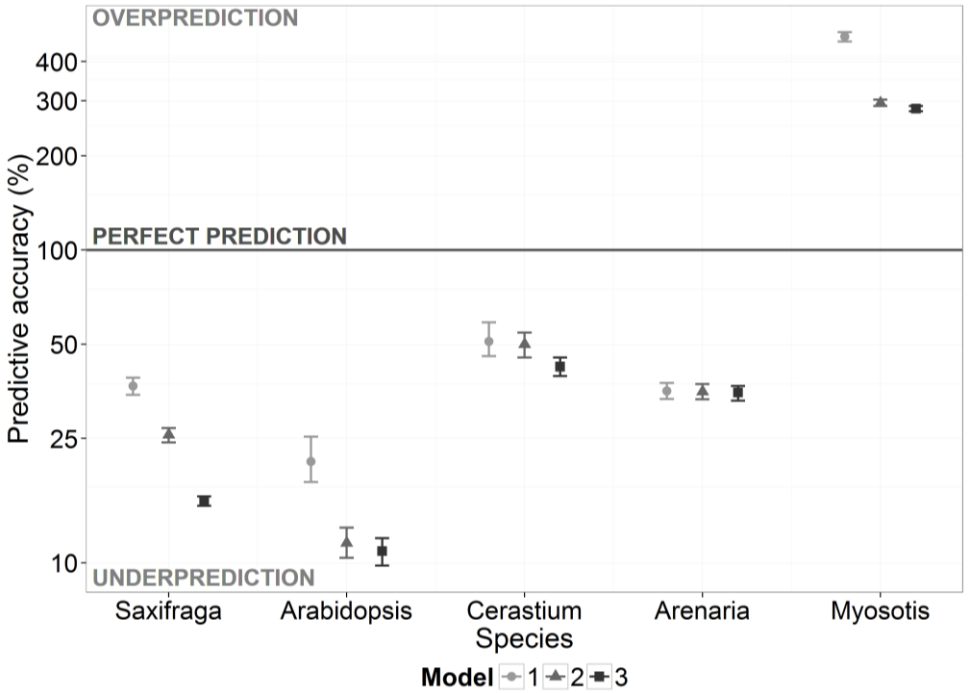

Figure 2.6. The effect of competition is consistently underpredicted. We assessed how accurate our predictions were by comparing the *predicted effects* shown in Figure 2.4 with the *observed effects* shown in Figure 2.5. Predictive accuracy is the predicted effect shown as a percentage of the observed effect (log-scaled). All three models behaved similarly.

Discussion

We used tried and tested techniques to fit community models to observational-style data garnered in an experimental context. The models appeared to capture the relative competitive abilities of species, as the interaction matrices obtained are consistent with previous work (Rees 1995; Turnbull *et al.* 1999, 2004). This result, and other diagnostic tests, encourage us to believe that we fitted sensible models to the data. We then used the models to predict what would happen to each species once competitors were removed. Uniquely, we were able to provide an independent test of the model predictions, as the experiment included monoculture plots in which each species was free from interspecific competition. The models made poor predictions about the expected extent of competitive release. For most species the extent of competitive release was severely underpredicted, suggesting that we had underestimated the strength of interspecific interactions in multi-species communities.

Why did we underestimate the strength of interspecific competition?

The first possibility is that we fitted poor models, but this seems unlikely. The competition coefficients were well-estimated with small standard errors, from independent sampling chains that converged on the same posteriors. Model uncertainty was very low, reflected by the narrow intervals in Figure 2.6. The models were a good fit to the observed data. Distributions of cell population sizes in data simulated from the models closely resembled that of the observed data, further indicating that there was no systematic bias. The three models we fitted described species interactions differently and yet all poorly predicted the effect of interactions in

the same way. Our test was fair, as it expressed the same effect as our predictions—the mean change in population size in response to competitor removal—and did so over the same range of data. The wide variation in observed data meant that we avoided potential underestimation due to observing species only at high densities (Law & Watkinson 1989). These reasons lead us to believe that our analysis was not at fault for underestimating the strength of interspecific competition, but instead the underlying problem is more profound.

The second possibility is that models which estimate the strength of competition in natural communities simply cannot be used to predict the effects of species loss. This might happen because species in natural communities are already confined by competition to realised niches. The fundamental niche represents all conditions in which a species can exist, whilst the realised niche is those conditions in which the species actually exists in the presence of interacting species (Chase & Leibold 2003). If species are confined to parts of the habitat where they tend to compete best, then the strength of interspecific competition, as assessed by these methods, will be weak. In contrast, once competitor species are removed the remaining species may be able to expand their niche—assuming that their fundamental niche is wider than their realised niche. But without information on fundamental niches we cannot know the extent that species will respond to competitor removal. Therefore, to predict species responses from natural communities is to predict beyond the range of available information. This explanation for weakly interacting natural communities has previously been called the ghost of competition past (Connell 1980; Law & Watkinson 1989). It may explain why interspecific competition measured in natural communities is often weaker (Turnbull *et al.* 2004; Stoll & Newbery 2005; Comita *et al.* 2010) than

that measured in experiments (Gurevitch *et al.* 1992). Our results suggest this is a general problem that is likely to be present in any analysis using similar principles. Further simulation modelling is required to confirm this idea.

What are the implications?

Ecologists have argued long and hard about the best way to measure competition; in particular, because the results of experimental work conflict with direct measurements of competitive interactions in natural communities. Our study potentially provides a resolution to this debate. In experiments plants are forced to compete, whereas in natural communities plants often display strong spatial aggregation that increases the chance of meeting conspecific neighbours.

Species may aggregate in natural communities due to local dispersal. Freckleton & Watkinson (2000) recommended that the scale of sampling should reflect the dispersal abilities—and resulting clumping—of the species being monitored, to ensure that multiple species are observed within sampling units. But the larger the scale at which data are sampled, the more the effect of local interactions becomes blurred. There are ways to incorporate dispersal into the modelling (Pacala & Silander 1990), as we have done.

Aggregation can also be caused by species-specific requirements for particular ecological conditions (Law *et al.* 1997). This has been suggested before as an explanation for the weak nature of estimated interspecific effects (Rees *et al.* 1996; Freckleton & Watkinson 2000), but the magnitude of this problem has never been quantified. These methods have assumed a homogeneous environment. We believe this assumption was problematic even in our experimental setting—it was also

considered by Mack & Harper (1977). Perhaps this problem could be addressed by measuring environmental variation, although it is not clear which variables are important to describe species preferences. But ultimately, if species rarely interact due to spatial aggregation then the effect of their interactions will be limited.

If species weakly interact in natural communities because they have been confined to realised niches, then we should be wary of interpreting models parameterised using observational data to conclude whether such communities are strongly structured by interactions (Martorell & Freckleton 2014). If much of the competition goes unseen we cannot claim whether or not communities are fundamentally competitive from such analyses. In particular, these models may give no information about how the community is likely to respond to the loss or removal of species, which is essential in a world where species are likely to be lost, for example, through new diseases (e.g. Thomas 2016).

Future directions

To understand more deeply why observational data are lacking, we need to combine experimental and observational approaches. Freckleton *et al.* (2000) used similar analytical techniques on a long-term dataset where densities were perturbed halfway through the sampling programme. However, they and others have criticised experimental approaches to estimate competition (Freckleton & Watkinson 2000, 2001). Removal experiments are still practised (e.g. Olsen *et al.* 2016), albeit more rarely and with acknowledgement of their caveats. Perhaps experimental manipulations are more in need than recent studies would suggest. There is no method to measure competition that is not flawed. Much progress has been made in critiquing

previous methods and developing new ones. We have shown that current observational methods also need refinement.

If it is possible to devise a method that accurately predicts the impact of species losses from diverse communities, what extra information would be required? Trait-based approaches may be useful in predicting which species will respond most to the loss of another species. This approach would be most effective if we are able to identify which traits best explain how remaining species will expand their niche in response to competitor removal. This could be combined with experimental approaches that remove one species at a time and measure the response of the remaining community. Experimental communities may also be useful for observing how species become confined to their realised niche if we can measure how species are affected by the gradual shift from homogenised to semi-natural conditions. Alternatively, we might need more detailed data on how species are affected by competition during specific life-history stages, rather than the more common observation of adult–adult transitions. Current observational data and methods are valuable tools, but we will need a greater combination of approaches to fully understand the role of competition between species in natural plant communities.

Supplementary Material

Supporting information may be found on the accompanying CD:
Appendix SA1. Supplementary analysis document.

Chapter 3
How Do More Diverse Plant Communities Increase Ecosystem Functions: A Mechanistic Model

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Author Contributions

SLT, AH and LAT designed the analysis. SLT performed the analysis. SLT, AH and LAT drafted the paper.

Article Status

This article in preparation to submit.

Context

In chapter 2, I tested an existing method for measuring the effect of competition in natural plant communities—a vital step in developing a predictive understanding of how real-world ecosystems respond to diversity loss. Another step towards this predictive understanding is to ascertain which biological mechanisms are most important for allowing stable coexistence between species in diverse communities, and how these mechanisms influence the role that plant diversity plays in the functioning of ecosystems. To do this, we need models that describe potential mechanisms and can be related back to data from biodiversity experiments. Not only might these models improve our ability to predict the impacts of diversity loss at the ecosystem level, but such models may also help us scale up experimental results to give landscape-level insight. Also, to predict for new contexts, such as future events or unprecedented environmental conditions, we need a causal understanding of biodiversity effects on ecosystem functioning. Without understanding what processes drive the patterns that we observe, we cannot confidently predict what patterns will be observed in new contexts. Here, I present one potential mechanism that may drive the biodiversity effects that have been observed in experiments thus far.

Chapter Summary

After much synthesis and meta-analysis, it is clear that more diverse plant communities are on average more productive. Both species composition and richness drive this positive effect of diversity. But it is still not clear what biological processes underlie the benefit of having more species. The mechanism first proposed was that species partitioned resources, thereby capturing more in total. This is one of the

processes that can create complementarity effects, those effects that cannot be explained purely by species identity. But complementarity effects can be driven by other mechanisms, such as positive interactions or differing natural enemies. The most definitive evidence of complementarity is when a species mixture is more productive than every monoculture of its component species. But this definitive evidence is rarely found, as it most often emerges during long-term experiments. Experiments have begun testing how mixtures can yield more than the best monoculture yield. But we need mechanistic models to formalise hypotheses and test their ability to explain experimental results. Here, we extend the modelling work published by Turnbull *et al.* (2013), who modelled the seasonal growth of species that competed for one shared limiting resource. In their model, there was a trade-off between the ability to capture resources quickly and the ability to access a large resource pool. Complementarity was possible in their model, but it was impossible for mixtures to yield more than the best component monoculture. We extended this model to find what conditions might enable mixtures to outperform the best monocultures, by allowing resource availability to change over time as a result of environmental leaching. We hypothesised that when the availability of resources also depends on the speed with which you can capture them, niche differences will allow mixtures to achieve a greater envelope of resource capture throughout the season. We tested whether more diverse mixtures captured more and leached fewer resources by the end of the growing season. We found that species with fast rates of resource capture could minimise leaching early on in the season, by locking up more resources in plant tissue, but they would not prevent leaching later on once they had reached their asymptotic yield. Whereas the species with access to large resource pools could capture resources later on in the season, but not prevent severe leaching earlier. We found that species mixtures could combine the strengths of these

two strategies, creating a greater total envelope of resource capture throughout the season. As a result, mixtures commonly reached the same yield as the best component monoculture when resources leached from the soil. Some mixtures even reached a higher yield than the best monoculture, albeit rarely. It was also occasionally possible for mixtures to leach fewer resources than the most leaching-resistant monoculture. Consequently, the presence of resource leaching strengthens the effect of diversity on yield and provides a mechanistic explanation for some patterns observed in long-term biodiversity experiments.

Introduction

Plant communities with more species achieve higher and more stable productivity on average, seemingly because they use resources more effectively (Balvanera *et al.* 2006; Tilman *et al.* 2014). This is the consensus that emerged from 20 years of results concerning how current rates of biodiversity loss may harm the functioning of ecosystems (Duffy 2009; Cardinale *et al.* 2012; Hooper *et al.* 2012; Naeem *et al.* 2012). Ecosystem functioning typically increases rapidly at first and then saturates at higher species richness (Cardinale *et al.* 2011), though the form of this relationship can shift (Figure 3.1; Tilman *et al.* 2001). But the processes that cause this positive effect of diversity on functioning are less well understood.

Theory on species coexistence and resource competition was used to explain why species mixtures were more productive than monocultures (Tilman *et al.* 1997b; Loreau 1998a; Mouquet *et al.* 2002). Niche differences allow species to partition resources and therefore capture more resources in total (Gross *et al.* 2007; Cardinale *et al.* 2011). Niche differences can also allow competing species to stably coexist, by causing species to limit themselves more than they limit others (Chesson 2000; Adler *et al.* 2007). Thus, the niche differences that make coexistence possible might create positive diversity effects that persist through time. Indeed, Loreau (2004) showed that in a Lotka-Volterra framework stably coexisting species inevitably show positive diversity effects. As this effect of diversity focuses on complementary resource use it was called the complementarity effect, but is also known as overyielding (Trenbath 1974).

But a second explanation argued that niche differentiation was not the cause of

enhanced productivity in mixtures (Aarssen 1997; Huston 1997; Tilman *et al.* 1997b; Loreau 1998b). Instead, if the most productive species in monoculture was competitively dominant, then any mixture dominated by this species would become more similar to the most productive monoculture. As the mixture becomes more diverse the chances of including the most productive species increases, and so the average productivity of more diverse mixtures increases. Here, resource competition between species is a zero-sum game: dominance of one species comes at a direct cost to weaker competitors—whereas if niche differences were involved, the community would capture more resources than expected from a zero-sum combination of its constituent monocultures, hence the name overyielding. As this second explanation of positive diversity effects depends only on selecting the most productive species, it was called the selection effect.

To test these hypotheses, Loreau & Hector (2001) developed the additive partition of biodiversity effects. The additive partition calculates a net biodiversity effect by comparing the yield of a mixture with its expected yield based on monocultures of its constituents. There is no net biodiversity effect if a mixture containing n equally abundant species achieves a yield equal to the sum of $1/n$th of each monoculture. The net biodiversity effect is the sum of selection and complementarity effects. A positive selection effect occurs when species with above average monoculture yield have the highest relative yields in mixture. This occurs when the most productive species is competitively dominant. Negative selection effects are caused by species with below average monoculture yields becoming dominant in mixture. If only selection effects occur, the relative yield total in mixture will be 1, because gains by one species come at a corresponding cost to others. A

complementarity effect, or overyielding, therefore occurs when the relative yield total is greater than 1.

Complementarity effects have often been found in biodiversity experiments, but the exact mechanism underlying these effects is unclear (Spehn *et al.* 2005; Weis *et al.* 2007; van Ruijven & Berendse 2009; Cardinale *et al.* 2011; Eisenhauer 2012; Roscher *et al.* 2012) because there is no direct correspondence between niche differences and complementarity effects (Carroll *et al.* 2011, 2012; Turnbull *et al.* 2013). Turnbull *et al.* (2013) showed that if we observe complementarity we cannot assume that the mixture is stable, therefore observed diversity effects might be transient. Niche differences are a necessary but insufficient condition for coexistence and complementarity, because relative fitness differences can overcome their stabilising effect and dilute their overyielding effect. This raises questions about the utility of *post hoc* statistics like the additive partition. To progress, we need a more mechanistic understanding of how niche differences contribute to diversity effects (Hooper *et al.* 2005; Cardinale *et al.* 2011; Turnbull *et al.* 2013).

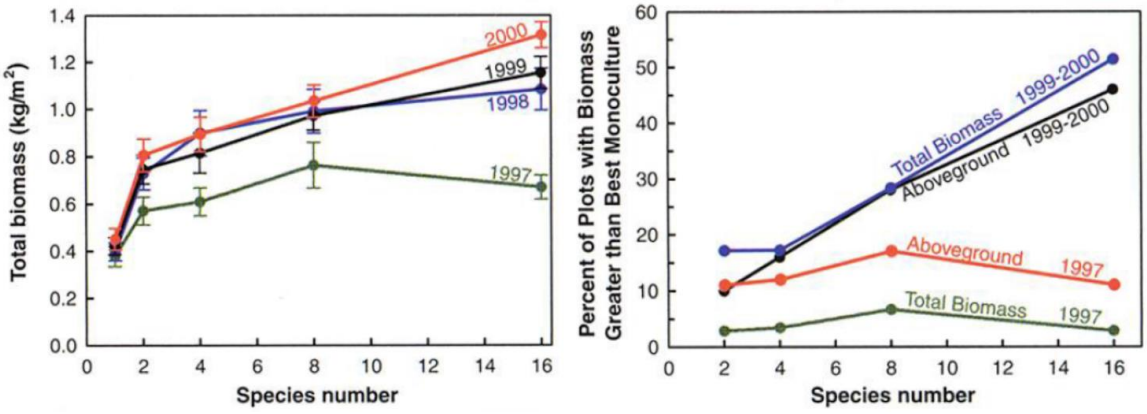

Figure 3.1. Biodiversity effects and transgressive overyielding at Cedar Creek. *Left*: Biodiversity effects saturated at higher levels of biomass over time. *Right*: Transgressive overyielding became increasingly common and dependent on species richness. Modified from Tilman *et al.* (2001).

Another concern is that our observations do not fully match with theoretical expectation. In theory we might expect a mixture of species to yield more than even the most productive monoculture of its component species, a phenomenon known as transgressive overyielding (Tilman *et al.* 1997b). But in reality, transgressive overyielding is rarely found (Cardinale *et al.* 2011). Transgressive overyielding cannot be explained by the selection effects described above and therefore shows definitive evidence of complementarity. Here, we explore how transgressive overyielding can be generated and how often we should expect to see it.

Long-term biodiversity experiments are an interesting case to look for transgressive overyielding. Pacala & Tilman (2002) showed that overyielding may grow over time as complementarity accumulates, and so transgressive overyielding may emerge as experiments continue. This is exactly what was found in perhaps the best-known long-term experiment to date, the Cedar Creek Biodiversity Experiment (Tilman *et al.* 2001; Fargione *et al.* 2007; Reich *et al.* 2012). The species mixtures at Cedar Creek have seen low extinction—so they are stable—and have become more likely to reach a higher yield than the best monoculture (Figure 3.1). Reich *et al.* (2012) suggested that species became less functionally redundant after roughly 10 years, as the community was structured by competition and became more differentiated in resource acquisition traits. It appears that the mixtures capture and retain available resources more efficiently (Fargione *et al.* 2007). But under what conditions can this more complete resource capture occur? And can we always expect that this should lead to transgressive overyielding? We need models of growth and resource dynamics throughout a season to ask what is required for a mixture to outperform all of its monocultures.

Turnbull *et al.* (2013) developed a discrete-time model of plant growth over a growing season and analysed the season-end yield of different communities. In the model plants compete for a shared pool of one limiting resource. Species within the community are defined by two resource-use traits: their rate of resource capture and the volume of soil they can access. The model was an included-niche model, because species have access to a nested subset of the resources available to all other species. If there was a trade-off between the rate of resource capture and the volume of accessible resources then stable coexistence was possible. Application of the additive partition to model results demonstrated that this also produced a complementarity effect; however, transgressive overyielding was impossible because mixtures could never access more resources than the best monoculture. When there was a trade-off between the rate of resource capture and the volume of accessible resources, yield increased with diversity in a manner typical of experimental results: approaching but never exceeding the best monoculture yield (Cardinale *et al.* 2011). We will build from Turnbull *et al.'s* (2013) model, by changing its assumptions to try to generate transgressive overyielding and replicate patterns from long-term experiments.

Here, we build from Turnbull *et al.* (2013) by including dynamic resource availability throughout a season. Turnbull *et al.* assumed a fixed resource pool size that is only diminished as plants capture resources. We have included environmental leaching that reduces the total resource pool size over time. We assumed that a fixed proportion of the remaining resources not yet locked up in plant tissues would be leached at each time step. We expected that transgressive overyielding would emerge, because mixtures could prevent leaching of resources in a way that no monoculture could (explained in detail below). Briefly, this arises because of the trade-off in

resource capture traits: species that access more resources in total are prone to lose resources early on, because of their initially slow growth rates, while species that grow quickly are prone to lose resources later in the season, as the total resource pool that they can access is small. In contrast, a mixture can potentially combine the strengths of both, creating a greater envelope of resource capture than any monoculture.

Methods

We simulated a community of 16 species. We further assumed that there was a trade-off between the ability to capture resources quickly and the ability to access a large resource pool (Figure 3.2, see *Model*). The trade-off, which represents different rooting depth strategies (Berendse 1979), is necessary for stable coexistence. In several leaching scenarios, we assessed: (i) monoculture performance; and (ii) performance in mixtures of varying diversity (see *Analysis*). We also assessed whether the species coexisted and that therefore mixtures would be stable over time.

Model

The model describes daily increments in the growth of individual plants over a growing season:

$$M_{i,t} = M_{i,t-1} + I_{i,t} \tag{3.1}$$

where $M_{i,t}$ is the mass of a single individual of species i on day t and $I_{i,t}$ is the growth increment of a single individual. The growth increment is described by a logistic function:

$$I_{i,t} = \begin{cases} \theta_i M_{i,t-1} N_0 \left[\frac{N_0 V_i - P_{t-1} - L_{i,t-1}}{N_0 V_i}\right] & I_{i,t} > 0, \\ 0 & I_{i,t} < 0, \end{cases} \quad (3.2)$$

where θ_i is the resource uptake rate of species i, N_0 is the initial concentration of resources in the soil, and V_i is the volume of soil that species i can access. Therefore, $N_0 V_i$ defines the total pool of resources available to species i. P_{t-1} is the total resources locked up by plant growth in all preceding time intervals and $L_{i,t-1}$ is the total resources leached from the soil volume accessible to the ith species during all preceding time intervals. Growth of any plant removes resources from the system, regardless of species. Hence the resources locked up by plant growth in all preceding time intervals is:

$$P_{t-1} = \sum_{i=1}^{k} n_i M_{i,t-1} \quad (3.3)$$

where the number of individuals of each species (n_i) within a growing season is fixed and k is the total number of species in the community.

Resources are also lost to leaching ($L_{i,t-1}$). Leached resources cannot be recovered, nor can plant biomass be lost or transferred between species within a growing season. The growth increment decreases over time as the resource pool is depleted through a combination of plant uptake and leaching. Because some species have access to a larger resource pool than others, negative growth increments are possible. Hence, if the combined resources lost through uptake and leaching exceeds the total pool available to species i, the growth increment in all subsequent time

intervals is set to zero. Notice this assumes that resources are drawn preferentially from shared pools.

To determine how leaching affects the resources available to species *i*, we first need to consider loss of resources from the system as a whole. We assumed that a fixed proportion (λ) of the resources not yet taken up by plants (P_t) or previously lost to leaching (L_{t-1}) is leached from the system in each time interval (in each time interval plants grow first and then leaching occurs, hence P_t and not P_{t-1}). Thus the total resources lost to leaching by time *t* is given by:

$$L_t = L_{t-1} + \lambda[N_0(V_{max} - V_{min}) - P_t - L_{t-1}] \quad (3.4)$$

We assumed that only some fraction of the total resources available were susceptible to leaching. Hence, V_{max} is the maximum possible soil volume that can be exploited by any species and $N_0(V_{max} - V_{min})$ defines the total soil resources that can potentially be lost to leaching. Finally, we assumed that the leached resources were lost equally across the soil profile. Hence, the total resources lost from the soil available to the ith species ($L_{i,t-1}$; see eqn 3.2) is given by:

$$L_{i,t-1} = \frac{L_{t-1}V_i}{V_{max}} \quad (3.5)$$

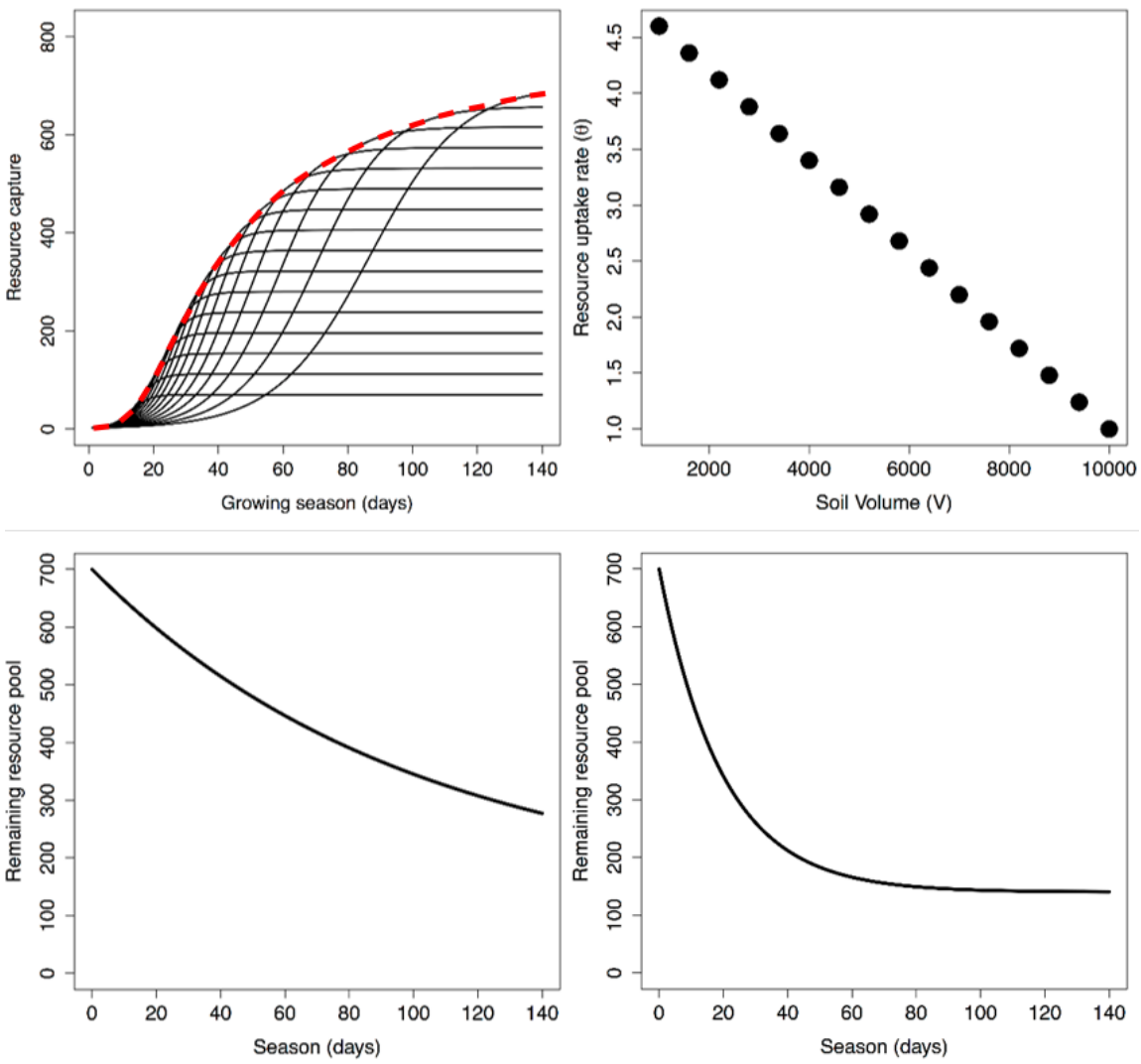

Figure 3.2. Resource leaching as a mechanism for biodiversity effects. *Above*: Species fall along a trade-off that mediates their growth. Species growth throughout a season (*top left*) is determined by the volume of soil it can access (V_i) and the rate at which it can capture soil resources (θ_i). As V_i increases, θ_i decreases following a linear trade-off (*top right*). In the top left, the red dashed line shows the expected envelope of resource capture that only mixtures can achieve. *Below*: Curves show rates at which leaching depletes resources without plant growth (*bottom left*: λ = 1% of remaining pool per day; *bottom right*: λ = 5% of remaining pool per day).

Model exploration

Following Turnbull *et al.* (2013) the model was run for a growing season of 140 days. The initial resource concentration, N_0, was fixed at 0.07. The mass of each individual on day 1 was 0.002 grams. Total plant density was set to 1024 individuals, a simplifying assumption based on the fact that biodiversity experiments are sown at constant density. In mixtures at the beginning of season 1, these individuals are equally

distributed among species, again reflecting the commonest design in biodiversity experiments. The relative abundances of species in mixtures were allowed to change from one season to the next. The expected fraction of individuals belonging to species *i* next season was determined by the fraction of the total biomass that species *i* had accumulated at the end of the current season. Random variation in the relative abundances of species was introduced by using these expected fractions as a vector of probabilities in a multinomial distribution (Chasalow 2012). From one season to the next we assumed that the biomass of all individuals is removed and they re-grow from an initial size of 0.002 grams once more. The resource pool is also restored to its original levels at the beginning of the season. We present results from simulations using a single value of V_{min} ($1/5^{th}$ V_{max}) but we also explored models in which the entire resource pool was allowed to leach away and the qualitative results were unchanged. When $\lambda = 0$, the model is equivalent to that in Turnbull *et al.* (2013). Varying λ changes the rate of leaching (Figure 3.2). We ran simulations with λ = 0, 0.5%, 1% and 5% per day. The precise rate of leaching did not affect results, so here we compare outputs from models: (i) without leaching; and (ii) with a rate of leaching of 1% per day.

The 16 species in our community were defined by their rates of resource capture (θ_i) and by the volume of soil resources that they can potentially access (V_i). The accessible soil volume (V_i) for each species was drawn equidistantly from a range of 1000 to 10000, so that the species broadly covered the parameter space. This tenfold range in soil volume, which determines season-end yield, reflects the tenfold range of biomass often found among monocultures in grassland biodiversity experiments (e.g. Naeem *et al.* 1995; Hector *et al.* 1999, 2011a). We assumed a linear trade-off between the soil volume and the rate of resource capture, such that the rate of resource capture

varied between 1 and 4.6 (θ_i = 5 – 0.0004*V_i; Figure 3.2). This variation in resource capture rate reflects the maximum range of growth rates measured for plants with similar life-histories (Turnbull *et al.* 2012). The lowest resource capture rates were large enough for all monocultures to reach a season-end yield close to their asymptotic yield (Figure 3.2).

The mechanism

We expected that, in the presence of resource leaching, we might see transgressive overyielding, which is impossible without leaching. In the absence of leaching, the yield of each species (i.e. their season-end biomass) is determined solely by the volume of soil that each species can access (V_i). Therefore the species with access to the largest volume of soil achieves the highest monoculture yield. If the same species is combined in mixture with other species that have access to a smaller resource pool, but grow faster, then the total yield of the mixture will in fact be lower than the best monoculture, because of a dilution effect caused by competition. Over time, the relative abundance of the species with access to the largest volume of soil may increase in mixture, hence the total mixture yield may approach, but never exceed the yield of the best monoculture.

However, if resource leaching occurs throughout a growing season then we now expect total yield to also depend on the envelope of resource capture throughout the season (Figure 3.2). Resources that are lost early in the season through leaching will simply not be available later. Hence, the combined biomass in mixture might be higher when a fast-growing species is present to prevent the leaching of those resources. Even so, the presence of species with access to a larger volume of soil is still required to

achieve a high yield by the end of the season, because those species with access to a smaller resource pool will reach their asymptotic yield quickly and leaching will ensue later in the season. Therefore, species with high resource capture rates and species with access to large soil volumes are expected to be different and complementary. By combining these species in mixture, we expected that they would create a greater total envelope of resource capture, which includes rapid early growth and high season-end yield (see the red dashed line in Figure 3.2 top left panel). In doing so, we predict that the mixtures will capture more and leach fewer resources than the best component monoculture. Our analysis will assess whether this expectation was valid, and whether this new complementarity is enough to overcome the negative effects of dilution and competition in mixtures.

Analysis

The effect of biodiversity on biomass is log-linear (Hector *et al.* 1999), so we simulated growth in communities with 1, 2, 4, 8 and 16 species richness. We used all possible species compositions within each richness level to analyse patterns of growth and season-end yield over multiple seasons. To see whether our model might reflect common results from biodiversity experiments we analysed how yield was dependent on species richness in our community of 16 species. We analysed the relationship between yield and species richness after the first and tenth growing season, to see how changes in the relative abundance of each species affected the shape and strength of the diversity effect. As well as analysing yield, we analysed whether species richness affected resource loss throughout the season.

To understand how mixtures differ from monocultures in a simpler case, we

looked in detail at mixtures of two species. We compared mixtures with their two component monocultures, and analysed the amount of resource that was captured, leached, or left unused by each composition throughout the season. We did this for 120 two-species mixtures but focused on one mixture where the two species (i) were shown to coexist, (ii) were relatively dissimilar in their traits, and (iii) produced results that were either indicative of all mixtures or demonstrative of important results.

We tested for coexistence between species pairs by simulating the growth of each 2-species mixture over 200 seasons. This was enough time for all species interactions to stabilise at their equilibrium abundances (Supplementary Material SA1). Without leaching, the mean time to extinction for non-coexisting pairs was 31.4 seasons (range: 6–197). We analysed which combinations of species coexisted under different leaching scenarios. We also examined the coexistence of species in the full 16-species mixture, to see which species became dominant and how many could coexist.

Finally, to understand how leaching affects species coexistence and diversity effects, we analysed how resource-use traits affected species responses to leaching. We assessed which traits made species the most productive, most leaching-resistant, and most efficient at utilising the resources that they can access.

Results

Full species mixture

The model with no leaching produced the diversity effects that we expected. Average yield increased with species richness but saturated at the highest richness levels (Figure 3.3). No mixtures were more productive than the most productive

monoculture. In fact, almost no mixtures approached the yield of the best monoculture (defined as producing a yield greater than or equal to 95% of the best monoculture yield). Furthermore, although the average yield increased with diversity, the maximum yield observed at each diversity level actually decreased (maximum yields after one season for each richness level: *1* = 685; *2* = 668; *4* = 649; *8* = 612; *16* = 560). As the relative abundances of species in mixtures changed over ten seasons, the maximum yields of mixtures relative to monocultures was enhanced, but only slightly (maximum yields: *1* = 685; *2* = 673; *4* = 654; *8* = 624; *16* = 558).

When resources leached at a rate of 1% per day, the best mixture compositions reached a yield that matched or exceeded that of the best component monoculture, producing the more flat-topped relationship seen in Figure 3.3 (maximum yields after one season for each richness level: *1* = 395; *2* = 403; *4* = 405; *8* = 395; *16* = 367). Thus, it was common for mixtures at all levels of diversity to reach effectively the same yield as the best monoculture (roughly a quarter of all mixture yields were greater than or equal to 95% of the best monoculture yield). This also produced a slight steepening of the relationship between average yield and diversity. Occasionally, we also observed transgressive overyielding, although this was rare and found in less than 1% of cases. After ten seasons, the incidence of transgressive overyielding was reduced further. Transgressive overyielding was only found in mixtures with two or four species; higher diversity mixtures never showed transgressive overyielding. Even when transgressive overyielding was found, the increase in maximum resource capture was never qualitatively large.

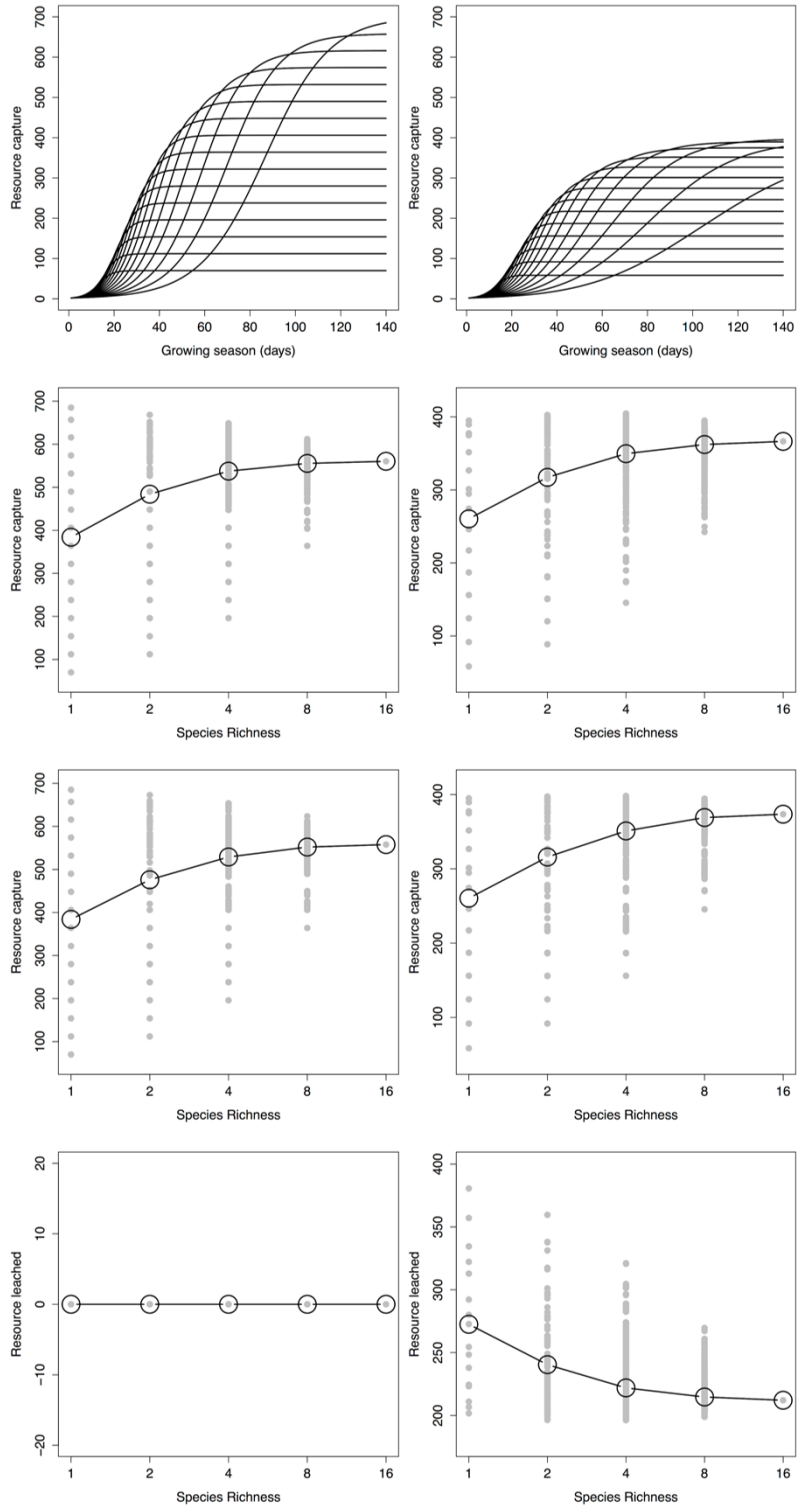

Figure 3.3. Leaching strengthens the biodiversity effect and can create transgressive overyielding. The resource capture and leaching dynamics of a 16-species community when no leaching occurs (*left*) and when 1% of resources are leached per day (*right*). From *top* to *bottom*: (i) monoculture growth curves; (ii) resource capture vs. species richness after the first season; (iii) resource capture vs. species richness after the tenth season; (iv) resources leached vs. species richness after the first season. Grey dots show individual species compositions, whilst the black lines and dots show the average trends.

Leaching impeded the growth of species that had access to a large resource pool but had low uptake rates (see the growth curves in Figure 3.3). Although this impeded growth reduced the absolute yield at every level of species richness, leaching enhanced the yield of mixtures relative to the monocultures. This strengthened biodiversity effect was robust to changes in the relative abundances of species over ten growing seasons (Figure 3.3). The flat-topped relationship between diversity and yield when resources were leached cannot be solely due to increased dominance of the most productive species (which would cause mixtures to approach the best monoculture yield), because the same relationship was found after one season when species were equally abundant.

More diverse mixtures also leached fewer resources on average (Figure 3.3). A small number of mixtures leached fewer resources than the most leaching-resistant monoculture (minimum level of leaching after one season, for each richness level: *1* = 202; *2* = 196; *4* = 196; *8* = 199; *16* = 212). A lower level of leaching than the most leaching-resistant monoculture was found in mixtures with two, four or eight species, but never in the full mixture with sixteen species. The effect of diversity on both the average and minimum leaching was unchanged after ten seasons of growth (minimum level of leaching after ten seasons, for each richness level: 1 = 202; 2 = 197; 4 = 197; 8 = 197; 16 = 201). Those mixtures that reached a yield greater than the best monoculture yield were not necessarily the same mixtures that leached fewer resources than the most leaching-resistant monoculture (because it was also possible for resources that were not leached to remain unused at the end of the season).

Two species mixture

Figure 3.4 illustrates more clearly how a mixture with two species can yield as much as, or even more than, the best component monoculture. The two species differ greatly in the total resource pool that they can potentially access, and the highest yield in monoculture comes from the species with access to the largest resource pool. With no leaching, the mixture has a better yield than the average of the two monoculture yields, but yields less than the best monoculture (Figure 3.4).

With 1% leaching per day, the mixture yielded more and leached fewer resources than the highest-yielding monoculture. This occurred for the reasons outlined above: the species with access to the large resource pool does not capture resources quickly, and is therefore prone to high losses from leaching early in the season (Figure 3.4). The species with access to a smaller resource pool has a higher rate of resource capture and therefore loses fewer resources early on when losses are at their highest. The losses due to leaching mean that the monoculture yields of the two species are actually very similar, although the faster-growing species has reduced losses from leaching. The mixture captures resources at an intermediate rate early on and the species with access to a larger resource pool continues growth within the mixture later on. Thus, by the end of the season, the mixture yields slightly more than either monoculture and leaches an intermediate amount (Figure 3.4).

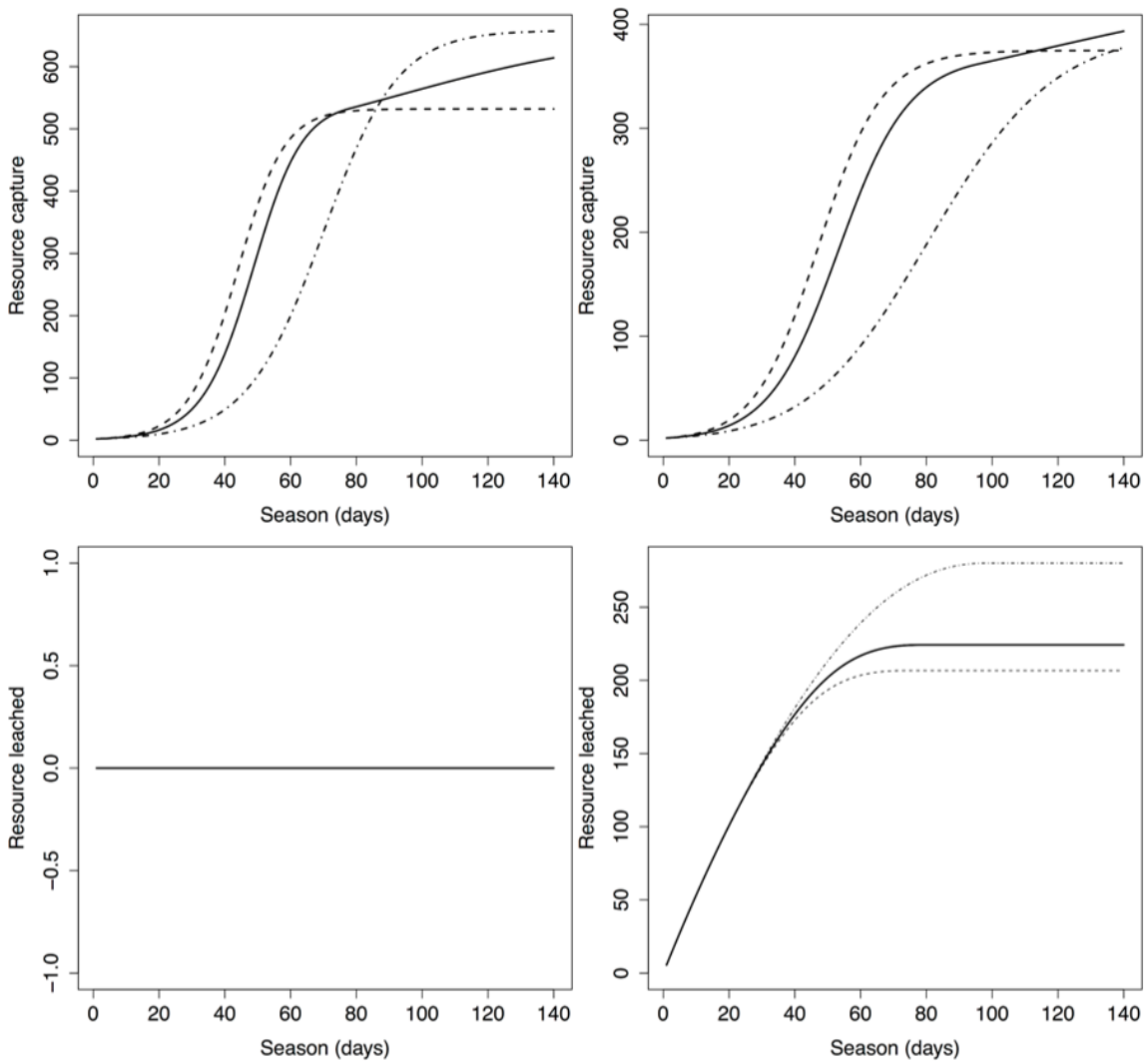

Figure 3.4. Transgressive overyielding in a two-species mixture. Two species (V_1 = 7600, dashed lines; V_2 = 9400, dot-dashed lines) were grown in monocultures and together in mixture (solid lines). These species were grown without leaching (*left*) and with 1% leaching per day (*right*), to show trends in resource capture (*top*) and resource leaching (*bottom*) for each composition. With leaching, the mixture yields slightly more the best monoculture, because species 2 (V_2 = 9400) cannot capture as many resources before they are leached.

Coexistence

With no leaching, 63% of species pairs coexisted. With 1% leaching per day, 58% of pairs coexisted. Coexistence occurred across a broad intermediate range of trait space, where species pairs tended to either share access to medium-sized resource pools or show extreme differences in their access to resources (Figure 3.5). Pairs on the edges of the trait space, where species shared either extremely low or high resource access, resulted in competitive exclusion. Exclusion happened more quickly on average

when resources leached (No leaching = 31.4 seasons; 1% leaching per day = 22.6 seasons). The range of trait space where coexistence was possible remained mostly unchanged by increased rates of leaching (Figure 3.5). However, on the fringes of this trait space, leaching made exclusion more likely when species had access to large resource pools and less likely when species had smaller sized pools.

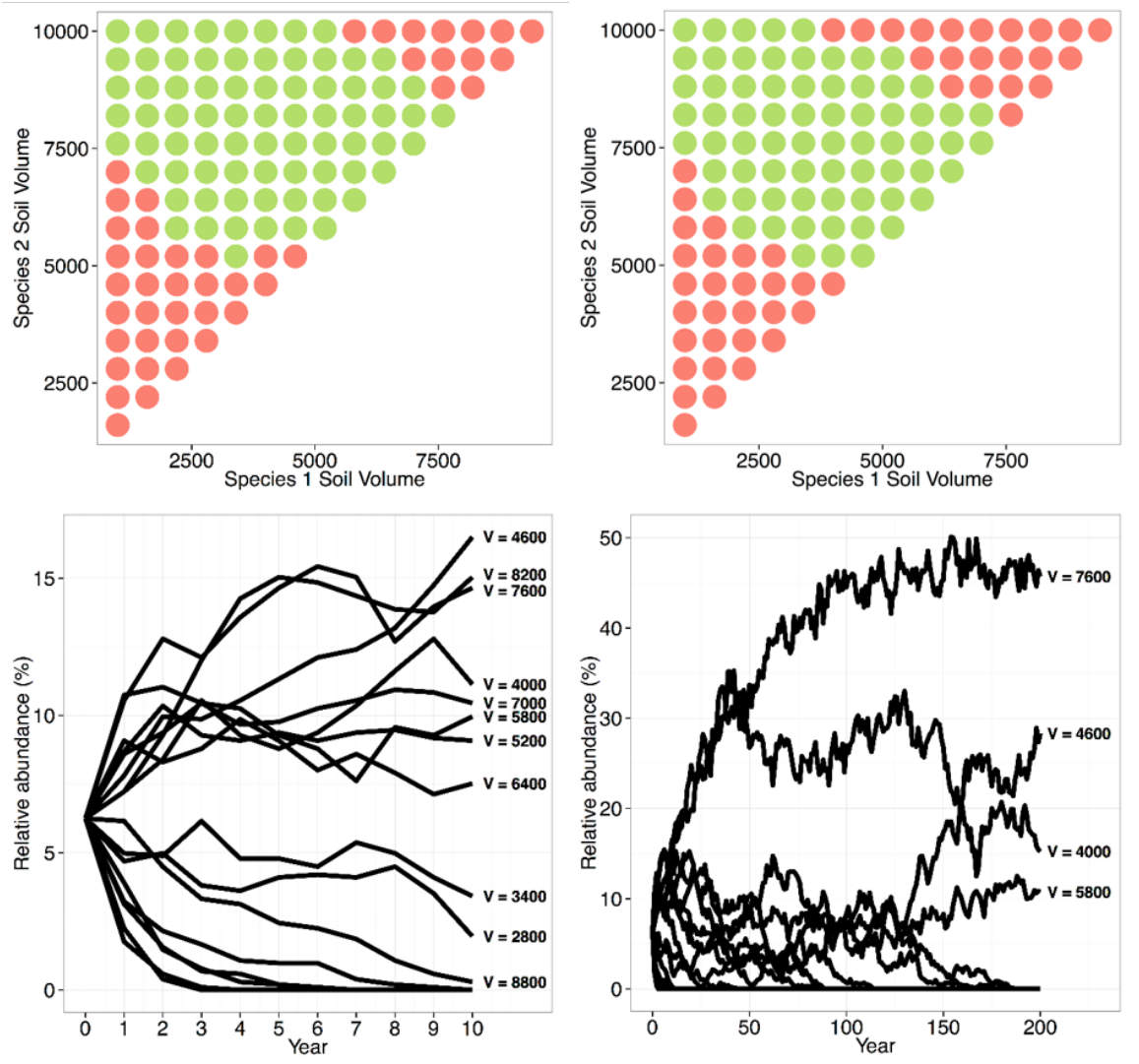

Figure 3.5. Leaching has little effect on coexistence. *Top row*: Pairwise interactions show which pairs result in exclusion or coexistence (red = exclusion, green = coexistence). Species coexisted if both were present after 200 years. The soil volume (V) parameter space that permits coexistence includes pairs of species that differ greatly, plus pairs that are more similar as long as they share resource pools of intermediate size. Species that share similarly extreme levels of resource access result in exclusion. This result is not affected by leaching (*top left* = no leaching; *top right* = 1% leaching per day). *Bottom row*: Eleven species from the 16-species mixture coexist after 10 years, and four stably coexist after 200 years (both plots shown are with 1% leaching per day—results without leaching are similar, see Supplementary Material SA1).

Eleven species from the full 16-species mixture were still present after ten seasons, both with and without leaching (Figure 3.5). After 200 seasons, five species from the full mixture stably coexisted without leaching. With 1% leaching per day, four species from the full mixture stably coexisted (Figure 3.5). With 1% leaching, the maximum relative abundance of any species from the full mixture, after 200 seasons, was 45% of the fixed community density (each species began with $1/16^{th}$, i.e. 6.25%).

Trait performance

When species were growing in monoculture and there was no leaching, every species was able to capture almost all resources available to them (defined by N_0V_i, see the solid line in Figure 3.6). Because species were able to almost realise their full resource capture potential, they had a resource "efficiency" close to 1. However, when leaching was included no species could capture all resources available to them in monoculture before part of their resource pool was leached (Figure 3.6). As species could no longer realise their full resource capture potential, their resource efficiencies were lower (Figure 3.6).

With 1% leaching, the species that could potentially access a resource pool size of 8800 captured the most resources in monoculture; species with access to larger resource pools could not capture resources quickly enough to achieve the same yield. The most resource efficient species were those with the fastest rates of resource capture (Figure 3.6). However, because the most efficient species could not prevent global leaching from a large portion of the soil profile, these monocultures leached the most resources in absolute terms. Total resource leaching was minimised by the species with access to a resource pool of size 7000 (Figure 3.6).

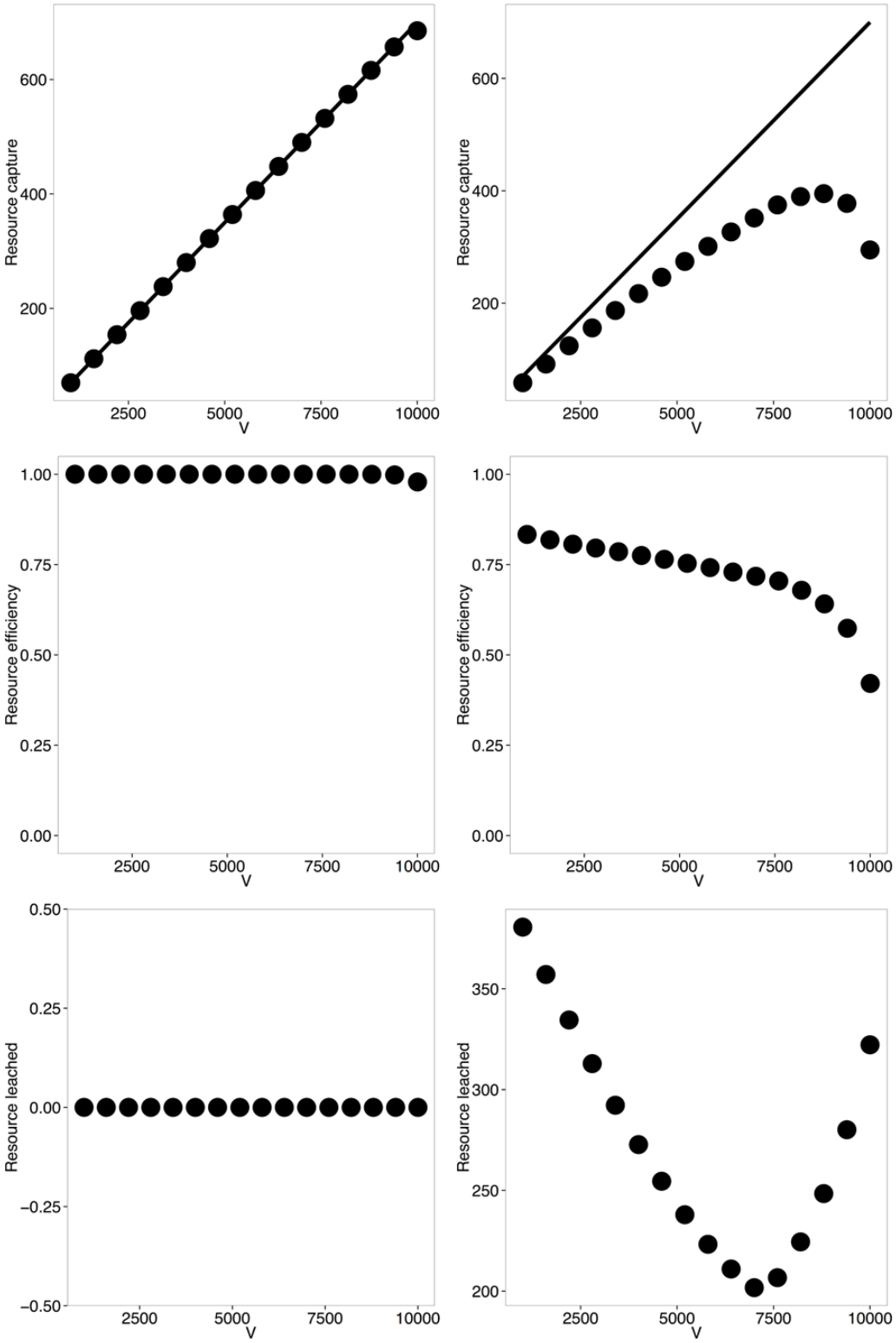

Figure 3.6. Species with medium- to large-sized resource pools minimise leaching but species with fast uptake more efficiently capture resources. Performance of each species in monoculture without leaching (*left*) and with 1% per day leaching (*right*). *Top*: Resources captured (points = realised resource capture; solid line = maximum possible capture). *Middle*: Efficiency of resource capture (realised capture / maximum capture). *Bottom*: Resources leached. Species that capture resources more quickly are able to capture a larger proportion of the resource pool they can access. But species with medium- to large-sized resource pools can minimise the leaching and maximise the capture of resources from the global pool.

Discussion

We used a model that described the growth of plants as they competed for a shared resource pool, to examine previously unexplored ways in which a mixture of species might capture more resources than any of its component monocultures, a phenomenon known as transgressive overyielding. We began with a model where transgressive overyielding was impossible (Turnbull *et al.* 2013), and changed its assumptions to search for a mechanism for transgressive overyielding that could explain results from long-term biodiversity experiments (Tilman *et al.* 2001; Fargione *et al.* 2007; Reich *et al.* 2012). We introduced leaching of the resource pool into the model, varied its severity, and assessed how the plant community's ability to retain and capture resources depended on the number of species that were present. We included a trade-off between the rate of resource capture and the total pool of resources that the species could access. We expected mixtures to outperform the best component monoculture by collectively capturing and retaining more resources than any monoculture could achieve (see *Methods*). As we expected, we found that mixtures could yield more than the best monoculture yield when resources leached from the soil. This suggests that even niche differentiation on a single resource may be a viable mechanism for transgressive overyielding, given a species functional trade-off and temporal dynamics such as resource leaching.

Transgressive overyielding has been demonstrated in other models where plants compete for two or more resources—or niche axes generally—in a heterogeneous habitat (Tilman *et al.* 1997b). The model presented here is an unusual case to look for transgressive overyielding, because species competed for only one

available resource which did not vary spatially. When leaching occurred, species were differentiated temporally rather than spatially and we expected that this would provide sufficient axes for niche differentiation to create transgressive overyielding. There have been many models of species coexistence via temporal mechanisms (e.g. Chesson 1994; Chesson & Huntly 1997; Purves & Pacala 2005; Angert *et al.* 2009). However, how these mechanisms may contribute to transgressive overyielding has not been explored (but see Loreau (2000) for discussion of temporal niche differentiation and insurance effects)—the model presented here provides such a demonstration.

Our model with one resource was a particularly interesting model to match with biodiversity experiments, because these experiments begin with homogeneous environments where there are few niche axes to exploit (Cardinale *et al.* 2011). As experiments progress, variation in resources and conditions will inevitably emerge and it appears that these changes can elucidate otherwise hidden effects of diversity (Reich *et al.* 2012). In a similar way, we expected temporal variation in resource availability via leaching to create diversity effects that strengthened as mixtures retained and captured more resources than any monocultures. Whilst the full 16-species mixture in our model did yield increasingly better over time, relative to the average monoculture yield, the effect was not strong enough to suggest an accumulation of biodiversity effects. Any change in the yield of a mixture in our model will be due to changes in the relative abundances of its component species, as there was no explicit mechanism for biodiversity effects such as reduced leaching to accumulate over multiple seasons.

We expected that species with rapid resource uptake would capture resources

before they were leached whilst species with access to a large resource pool would continue to capture any remaining resources later in the season. No monoculture would be able to capture resources as completely as a mixture, because they would either capture resources too slowly to prevent heavy leaching or would access too small a resource pool to achieve a high yield. We found transgressive overyielding in a small number of the mixture compositions, primarily because the species with access to large resource pools—previously the best monocultures—could no longer capture as many resources before they were lost (Figure 3.3). This slight reduction in the relative fitness of species with access to large resource pools can be seen in our exploration of how leaching influences the traits allowing coexistence (Figure 3.5).

An interesting pattern in our results is the flat-topped relationship between yield and diversity (Figure 3.3). A similar pattern was shown by Tilman *et al.* (1997b), using a model of competition for a single resource, but their model could not make transgressive overyielding possible. This flat-topped pattern is only present in our model when resources are leached, and is not caused simply by dominance of the best monoculture. The fact that mixtures can commonly yield as much as the best monoculture is a strong demonstration of biodiversity effects in itself, regardless of whether mixtures yield more than the best monoculture. In order to yield as much as the best monoculture, positive complementarity effects must overcome the negative effects of the diluted relative abundance of the most productive species. This dilution effect explains why mixtures do not yield as much as the best monoculture without leaching, despite the fact that positive complementarity effects still exist (Turnbull *et al.* 2013).

The fact that transgressive overyielding was possible, but rare, when leaching was included was an interesting phenomenon, because it matches the evidence from experiments thus far (Cardinale *et al.* 2007, 2011; Cadotte *et al.* 2008). In our model, we found transgressive overyielding in a very small proportion of mixtures (0.5%). In a meta-analysis of plant biodiversity experiments, Cardinale *et al.* (2011) found that transgressive overyielding occurred in around 37% of plant polycultures. It is perhaps unsurprising that experiments have found transgressive overyielding more often than we found here, because our model presents just one mechanism for biodiversity effects and many are likely to operate simultaneously in nature.

There are other model assumptions that we could make, which would be worth exploring. For example, our model assumed that all species grew throughout the entire season. This seems reasonable as late phenology species often still emerge around the same time as their competitors. The fact that species in our model have nested access to resources and reach peak yield at different times makes our model relevant to experiments at Cedar Creek, where rooting depth and phenology are major sources of niche differentiation (Fargione & Tilman 2005; Mueller *et al.* 2013). But the strength of the diversity effect and the prevalence of transgressive overyielding may change if species grew at different or only partially overlapping times in the season, as they may temporally partition resources more completely (Loreau 2004). We could also explore how biodiversity effects might accumulate over time by assuming that leaching depletes the resource pool that will be available next season, potentially creating a long-term benefit of reduced leaching.

Our results demonstrate why ideas should be tested by formulating them into

mechanistic models. After formalising our hypothesis as a model and scrutinising it, we conclude that resource leaching as modelled here is a potential biological mechanism to explain how mixtures in long-term biodiversity experiments become more productive than the most productive monoculture. Model-based explanations of biodiversity effects on ecosystem functioning will provide more detailed descriptions of how diversity loss may impact the functioning of real-world ecosystems (Loreau 2004; Cardinale *et al.* 2011, 2012; Loreau *et al.* 2012). They will also help separate the ideas that are truly useful from the ones that may mislead us (Turnbull *et al.* 2013). Further mechanistic modelling is required to build and generalise from experimental evidence of transgressive overyielding in order to understand how this effect is most likely generated and how often we can expect to observe it.

Supplementary Material

Supporting information may be found on the accompanying CD:
Appendix SA1. Supplementary analysis document.

Chapter 4
Insurance Effects Of Tree Diversity In Tropical Forest Restoration: Survival And Growth During The First Decade Of The Sabah Biodiversity Experiment

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SBE conceived and designed by CG, AH and GR; Overall coordination by AH and GR with field coordination by MO, CP, PS and JS with advice and support from EG, RN, RO, HT, JT, MS, WS, YSW and JS; Data protocols, collection and processing by DD, AH, MO, CP, JS, PS, BS, ST, PU, MW; Data analysed by ST, MT and AH with input from MO and CP; Paper writing led by ST and AH with MO, CP and MT and input from all authors.

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Context

In chapters 2 and 3, I dealt with the biological mechanisms that may explain the effects of plant diversity on ecosystem functioning observed thus far. But the experiments and modelling in the previous chapters are still at a level of abstraction that makes them difficult to relate directly to real-world ecosystems. Field-scale experiments will help to elucidate which mechanisms may operate at the landscape level. Efforts to capture greater realism in biodiversity-function research should aim to capture the biological and environmental complexity that characterises most ecosystems in nature. Such complexity makes study more challenging, but it may also provide the conditions necessary to describe the functional role of biodiversity in real-world ecosystems. Here, I present results from a field-scale experiment that studies the mechanisms and applications of biodiversity-functioning in selectively logged tropical forests. I propose a mechanism by which plant diversity might enhance ecosystem functioning throughout this complex landscape. I also show how this mechanism can inform the management and restoration of these human-altered forest ecosystems.

Chapter Summary

Swathes of tropical forest were degraded by selective logging before we could understand how they would be affected and whether they can recover. In SE Asia, enrichment planting with dipterocarp tree seedlings may help restore the forest's structure and functioning if enough survive to aid canopy closure. The role of tree diversity in tropical forest restoration is poorly known but planting more species-rich mixtures of dipterocarps into the forest may help ensure the seedlings avoid recruitment failure on one hand and potentially wasteful self-thinning on the other. We

analyse seedling mortality and growth over the first decade of the Sabah Biodiversity Experiment, to understand whether planting more diverse mixtures may provide such an insurance effect. Mortality was high overall but varied widely among species; their differences in survival were consistent over time. Those with high survival had slow growth and vice versa. Slow-growing species with high survival had more dense wood. Mortality and growth varied spatially across our 500 ha experiment but species responded to changing conditions in independent ways, a key ingredient for an insurance effect. As expected, given the wide spacing between seedlings, species performance did not differ between monocultures and mixtures. But their independent preferences for site conditions may provide an insurance effect of diversity: sites planted as monocultures of poorly surviving species may fail to restore stem basal area and canopy closure—planting mixtures may ensure there is always a species that can perform. Long-term monitoring is needed to determine whether mixing species with different vital rates can insure against this recruitment failure while avoiding potentially wasteful self-thinning in the best performing monocultures.

Introduction

After twenty years of debate there is now broad consensus that biodiversity has a positive effect on the functioning and stability of ecosystems (Cardinale *et al.* 2012; Tilman *et al.* 2014). However, this consensus is founded on a first generation of research from grasslands and other easily manipulated systems, which are often short-term, small-scale and highly controlled experiments. We need a next generation of experiments to quantify how biodiversity affects ecosystem functioning in more natural and applied situations, including habitat restoration (e.g. Bruelheide *et al.* 2014). Study of the relationship between biodiversity and the functioning of tropical systems has begun (Ewel & Bigelow 1996; Haggar & Ewel 1997; Lovelock & Ewel 2005; Potvin & Gotelli 2008), but the rich diversity of these systems plus their provision of important ecosystem services means further study is required. To help fill this knowledge gap for SE Asian forests we established the Sabah Biodiversity Experiment in Malaysian Borneo (Hector *et al.* 2011b). The project—a collaboration between ecologists, tropical foresters and a carbon offsetting scheme—tests the effects of tree diversity on the restoration of selectively logged forests which were enrichment planted with once-harvested species to return fully functioning ecosystems.

There are over 400 million hectares of logging estates in the tropics, and at least 20% of existing tropical forests were selectively logged between 2000 and 2005 (Edwards *et al.* 2014). These recently logged forests now cover larger areas of land than primary forest in most regions (Edwards *et al.* 2014; Laurance *et al.* 2014). In SE Asia primary forest exists in inaccessible uplands but little remains in lowlands due to unprecedented rates of deforestation (Sodhi *et al.* 2010; Gaveau *et al.* 2014). In Sabah

Malaysia, conversion to oil palm agriculture has driven forest extent from 86% in 1953 to below 50% (McMorrow & Talip 2001). Premature harvesting of previously logged areas has also been common (Reynolds *et al.* 2011). This forest loss and degradation is threatening many SE Asian plants (Sodhi *et al.* 2010), including members of the Dipterocarpaceae who dominate these forests and are a valuable timber source (Maycock *et al.* 2012). But a growing body of evidence is showing that selectively logged forest harbours greater ecosystem value than agricultural land, and even fragmented primary forest within an agricultural landscape, so long as they are not too degraded (Berry *et al.* 2010; Putz *et al.* 2012; Edwards *et al.* 2014). Some are calling to protect these vast areas from further land conversion, and maximise their conservation value by replanting with dipterocarps (Kettle 2010).

Enrichment planting is the practice of replanting seedlings into residual stands of selectively logged forest that are poorly stocked with the harvested species. The primary aims are to restock target species, either permanently or for future harvests, while rehabilitating the degraded ecosystem. Tropical tree species are often naturally found at low density so replanting logged species may help to supplement natural regeneration and overcome recruitment limitation. This might be particularly necessary for dipterocarps whose reproductive biology (irregular masting reproduction, low dispersal, no seedbank, and vulnerable seedling banks) may jeopardise regeneration. Enrichment planting aims to overcome dispersal and recruitment limitation, speeding the return to tall, complex canopies. However, evidence for the effectiveness of enrichment planting is incomplete despite its widespread implementation since the 1960s (Chan *et al.* 2008). Success will depend on how many natural seedlings remain and whether enough planted seedlings survive to

recreate the pre-logging canopy structure. Improvements in enrichment planting techniques have helped to boost success, but progress is far from complete (Chan *et al.* 2008).

The effectiveness of enrichment planting can only be assessed once key evidence gaps have been filled. One key issue is whether effectiveness is hampered by planting at low diversity; single species, or mixtures of a few species, are typically enrichment planted over large areas. The vital rates (survival and growth) of commonly planted species and their environmental preferences are not well known, limiting the ability to match species with favourable planting sites. Whether species-site matching is at all feasible is unclear since survival may vary over such fine spatial scales that its implementation is unrealistic. The role of tree diversity and how species combine in mixed-species plantings has received even less study. The dipterocarp forests of SE Asia therefore provide a unique situation where enrichment planting schemes can be used to investigate the role of tree diversity for forest functioning and restoration.

The Sabah Biodiversity Experiment, part of a network of tree diversity experiments (Verheyen *et al.* 2015), addresses these questions by manipulating the identity, composition and diversity of enrichment-planted dipterocarps to assess how effectively this practice can restore the functioning and stability of these selectively logged lowland rainforests (Hector *et al.* 2011b). Because of the wide spacing of planted seedlings (3 seedlings per 10 m of planting line) and the background vegetation left after logging, we did not expect to see biodiversity effects based on complementary species interactions this early in the experiment. Even so, enrichment

planting does provide the potential for an insurance effect based on intrinsic differences in seedling mortality and growth. The usual practice in enrichment planting schemes is to stock large areas with low-diversity mixtures, often monocultures of seedlings available from nurseries. Monocultures run the risk of recruitment failure if the planted species turns out to be a poor survivor under the given circumstances; tree density may become so depleted that the planting does nothing to supplement natural regeneration (Hector *et al.* 2011b; Saner *et al.* 2012). Planting more diverse mixtures might provide a simple insurance against such recruitment failure. Diverse mixtures might also provide a more efficient use of seedlings by avoiding wasteful levels of self-thinning of species with high survival rates.

Here, we present the mortality and growth of the first cohort of seedlings during the first decade of the project. We propose and test a potential insurance effect of tree diversity in replanting schemes, in which mixtures avoid the potential two-fold cost of monoculture planting: recruitment failure of the worst surviving species and wasteful self-thinning of the best.

Methods

Data collection

The Sabah Biodiversity Experiment (Hector *et al.* 2011b) covers 500 ha in the Malua Forest Reserve, a region of selectively logged forest bordering primary forest at Danum Valley Conservation Area located in the Malaysian state of Sabah, Borneo. Malua Forest Reserve, part of the Yayasan Sabah Forest Management Area forest concession, was logged in the late 1980s. Malua was first logged between 1984 and 1986 and, except our experiment site, again in 2007. The anticipated harvest cycle is

50–60 years, the estimated time needed to achieve a species composition similar to unlogged forest (Yamada *et al.* 2013). The Yayasan Sabah (Sabah Foundation) concession also includes the 30,000 ha Innoprise-FACE Foundation Rainforest Rehabilitation Project (INFAPRO). The Sabah Biodiversity Experiment replicates INFAPRO's enrichment-planting techniques where possible to maximise the potential for practical recommendations.

The experiment contains 124 four-hectare (200 x 200 m) plots, split between two blocks that are north and south of a logging road (see figure 1 in Hector *et al.* 2011b or Supplementary Material SA1). There are 60 plots in the north block and 64 in the south block. Seedlings were planted 3 m apart along parallel planting lines in a stratified randomised design. Each plot contains 20 planting lines spaced 10 m apart. Ninety-six of these plots comprise a diversity gradient treatment. The remainder are comprised of 12 unplanted controls, and another 16 sixteen-species mixtures that were given enhanced climber cutting (explained below). Only the 96 diversity gradient plots are analysed here.

The diversity gradient manipulates species richness using a factorial design, including replicated species compositions within species richness levels (1, 4 and 16 species). Species compositions within the four-species mixtures provide a gradient of generic richness and are designed to produce a range of canopy structures once the planted seedlings mature. Each species richness level has 32 plots. In the enhanced climber-cutting treatment, climbers are cut throughout the whole plot, not just along the lines as in standard enrichment line planting—this is said to improve recovery time during restoration.

As with standard enrichment-planting practice, following early mortality, the initial planting cohort of seedlings (cohort 1 planted 2002–2003) were supplemented with a second replanting cohort (cohort 2 planted 2009–2011). Across both cohorts, a total of 96,369 seedlings have been surveyed. Due to the scale of the experiment each full survey took two years to conduct (see Supplementary Material for histograms of seedling age). Although, to complement this large-scale but time-consuming monitoring, a subset of plots have been more intensively sampled—six extra surveys to date (Philipson *et al.* 2014). Therefore in 12 years there have been two full surveys of all seedlings. The first survey (Nov 2003–May 2005) included only the first cohort of seedlings whilst the second survey included both cohorts (Nov 2011–Sep 2013).

Here we analyse survival and growth of the first cohort using both full surveys (survival of the second cohort can only be assessed after the next survey). We recorded survival and size for every seedling each time they were visited. We measured basal diameter (2 cm) and, when they were tall enough, diameter at breast height (1.3 m). During early surveys we took ancillary measurements, such as descriptions of each seedling's local environment.

Study species

The 267 species of dipterocarp known to occur in Malaysian Borneo belong to nine diverse genera—and roughly half of these species belong to one genus, *Shorea* (Ashton 2004). The sixteen species we planted are *Dipterocarpus conformis* Slooten, *Dryobalanops lanceolata* Burck, *Hopea ferruginea* Parij, *Hopea sangal* Korth., *Parashorea malaanonan* (Blanco) Merr., *Parashorea tomentella* (Blanco) Merr., *Shorea argentifolia* Sym., *Shorea beccariana* Bruck, *Shorea faguetiana* Heim., *Shorea gibbosa*

Brandis., *Shorea johorensis* Foxw., *Shorea leprosula* Miq., *Shorea macrophylla* Ashton, *Shorea macroptera* King, *Shorea ovalis* Korth., and *Shorea parvifolia* Dyer (Supplementary Material ST1).

All species except *D. conformis* are members of the Shoreae tribe—though *Dipterocarpus* is sister to Shoreae and there is mixed support for the monophyly of Shoreae within this clade (Kajita *et al.* 1998). *Shorea, Parashorea* and *Hopea* form a polyphyletic group. Several sections within *Shorea*, covering multiple commercial timber types, are represented within our species (Ashton 1982). Our species were selected because they (i) represented those found in the surrounding forest, (ii) cover a range of traits and ecological strategies, and (iii) were sufficiently available as seedlings when we planted. The seedlings initially planted were sourced from INFAPRO; a dedicated project nursery was later set up to cultivate newly collected seedlings for the second cohort. Other species that were too scarce for the main experiment have been studied in smaller associated experiments manipulating light and water (Saner *et al.* 2010; Paine *et al.* 2012; Philipson *et al.* 2012; O'Brien *et al.* 2013, 2014, 2015), producing data on a total of 28 species.

SE Asian dipterocarps are emergent, shade-tolerant trees concentrated in aseasonally wet evergreen lowland forest on well-drained soils. They are mostly found below 800 m altitude, and their abundance and diversity declines above 400 m. They produce seeds during mast fruiting events. If these seeds do not germinate quickly they die due to heavy browsing (Hautier *et al.* 2010) or recalcitrance (O'Brien *et al.* 2013). Surviving seeds produce a seedling bank. Although dipterocarps are one late-successional functional group there is evidence for a trade-off, particularly at the

juvenile stage, between growth and survival (Philipson *et al.* 2014). Dipterocarps reach peak biomass, density and species richness on yellow or red lowland soils, where they comprise >50% aboveground tree biomass and >70% of emergent individuals (Ashton 2004). It is the dipterocarps that give these forests their exceptionally high biomass (Banin *et al.* 2014). In the 1980s, dipterocarps provided 25% of tropical hardwood supply worldwide, and 80% of this share came just from *Shorea* (Ashton 1982). Juveniles are easily disturbed during logging, undermining their regeneration; they may not return for centuries in heavily degraded soils (Ashton 2004). Palaeoecological work has shown that SE Asian tropical forests often take centuries to fully recover from disturbance—longer than any other tropical region (Cole *et al.* 2014).

Data analysis

Every seedling had its survival and size recorded in each survey (1 = alive, 0 = dead). For cohort 1 there are two surveys of all seedlings, with median age of 752 days at survey 1 and 3691 days at survey 2. Growth and survival of seedling cohort 2 cannot be analysed here as they require a second measurement, which we will have once we conduct a third full census (one of the programme's next priorities). We could not analyse growth and survival at the seedling level because there was spatial correlation within 200 m that would undermine our inference. We aggregated data to the species-within-plot level to remove within-plot spatial correlation (see Supplementary Material SA2). On average, these species-within-plot aggregations were based on 80 survival observations. This left us with 1336 plot-level observations and a minimum of three replicates for any species within a species composition.

Survival and growth were modelled by fitting two linear mixed-effects models.

Survival was assessed as the proportion of planted seedlings remaining in a plot in a given survey. Growth was assessed as change in average log-transformed basal diameter of those surviving seedlings. We kept explanatory variables as consistent as possible to help compare survival and growth: species-within-plot was fitted as a random effect (one variance for a factor with 672 levels), and the fixed effects were a three-way interaction between species identity (16 levels), species composition (33 levels), plus a representation of survey time that differed between models (as species do not occur in every composition, there are 96 species-within-composition levels). For survival, survey time was a factor with two levels, giving the average proportional survival since planting for each survey (survey 1: 0–2 years since planting; survey 2: 0–10 years since planting). For growth, instead of treating surveys as a factor, survey time was continuous (number of days since planting). The slopes of change in log size between the two surveys gave our estimated growth. Growth was therefore analysed using a subset of the survival data, using only seedlings alive at both surveys (1122 plot-level observations). Both models estimated 193 parameters: one additional variance component and 192 fixed effects. For each of the 96 species-within-composition levels, the survival model estimated two intercepts, whereas the growth estimated one intercept and one slope. These models were fitted using *lme4 v1.1-7* (Bates *et al.* 2014) in *R v3.2.1* (R Core Team 2014). Their model formulas were,

```
meanSurvival ~ species*spComposition*surveyNumber +
     (1|plot:species)
meanLogBasalDiameter ~ species*spComposition*meanSeedlingAge
     + (1|plot:species)
```

To quantify the overall performance of each species, among species compositions, we took the average of their population-level predicted values. These

species-level estimates of growth and survival in each survey were used to assess how strongly species differ, whether their ranking in survival remains consistent over time, and whether they trade off survival against growth. We correlated survival and growth with wood density and specific leaf area, which were estimated from previous experiments within our site using the same seedling cohort (Philipson 2009; Philipson *et al.* 2012; O'Brien *et al.* 2013, 2014).

Spatial variation in species survival was quantified using predictions from the random effect—plot-level deviations from the overall survival for each species. By tracking the relative effect of every 16-species mixture plot upon each species we could show whether species were responding differently to the same conditions. We tested whether species were truly responding differently to plot conditions by fitting two non-nested models: one allowing species-specific responses to plot conditions and another assuming species respond equally (species-specific responses, `(1|plot:species)`, were compared with `(1|plot)`). We compared these models by seeing how much AIC improved when species-specific responses were allowed (Pinheiro & Bates 2000).

Finally, we summarised overall plot-level performance, averaging across species, as the density of surviving seedlings; this was plotted against species richness, and then broken down into specific compositions, to assess whether a spatial insurance effect might confer an advantage to planting more diverse tree mixtures.

Results

Seedling survival and growth varied widely among species, after two and ten

years since they were planted (Figure 4.1 top panel; for estimates see Supplementary Material SA2). The proportion of first-cohort seedlings that survived overall was low (0.36 after two years and 0.12 after ten years). Species ranking in survival was consistent over the two surveys (Figure 4.1 bottom panel; Pearson's r = 0.79). After ten years the seedlings had grown to an average apex height of 1.25 m (max. = 12 m) and average basal diameter of 1.6 cm (max. = 28 cm). There was a trade-off between survival and growth among species—though this fades over time as mortality mounts and proportional survival shrinks (0–2 years, r = -0.63; 2–10 years, r = -0.43).

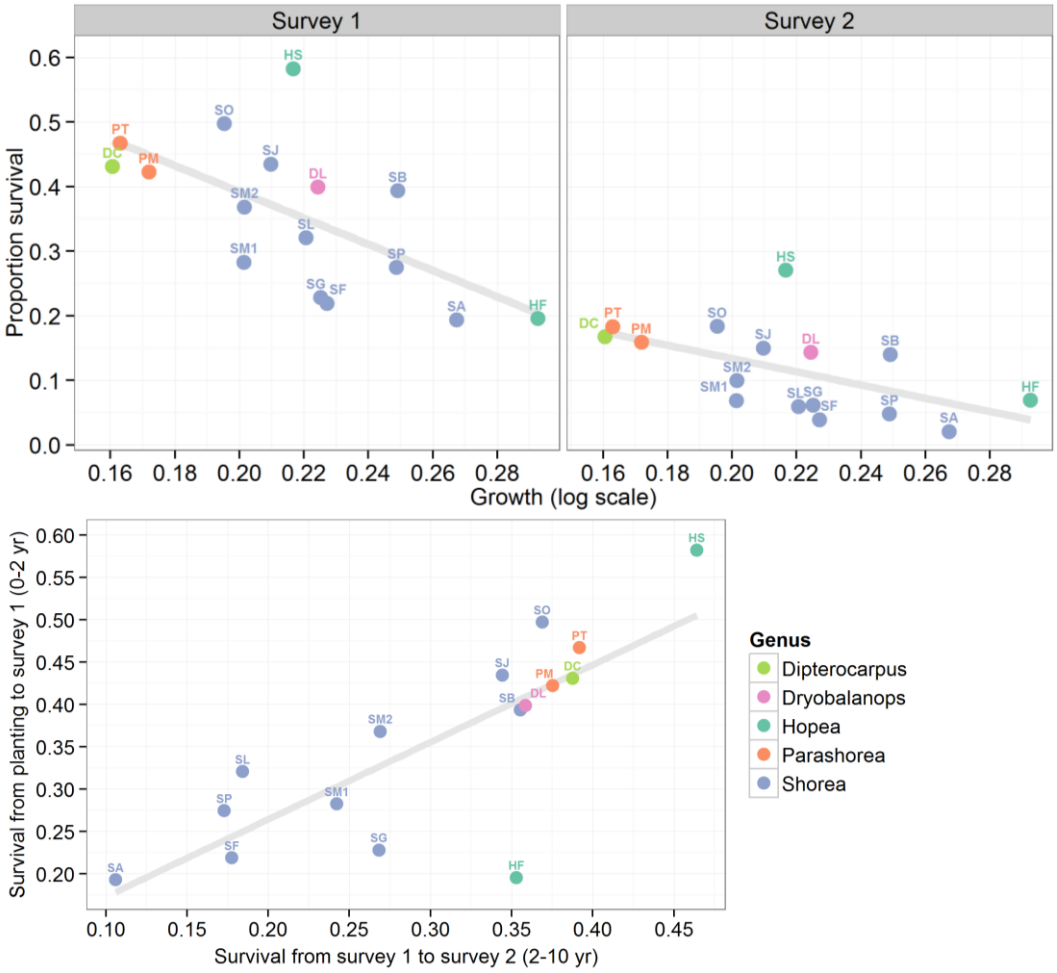

Figure 4.1. Growth trades off with survival. Growth and survival during the two survey intervals (2002–3; 2008–11). *Above*: Proportional survival (at 2 and 10 years since planting) versus growth rate (change in log basal diameter between survey 1 and 2) for the 16 species, showing a negative trade-off. *Below*: The proportion of seedlings that survived 0–2 years versus 2–10 years since planting are positively correlated, showing consistent ranking in survival over time. Species codes are shown in Supplementary Material ST1. Grey regression lines show overall trends.

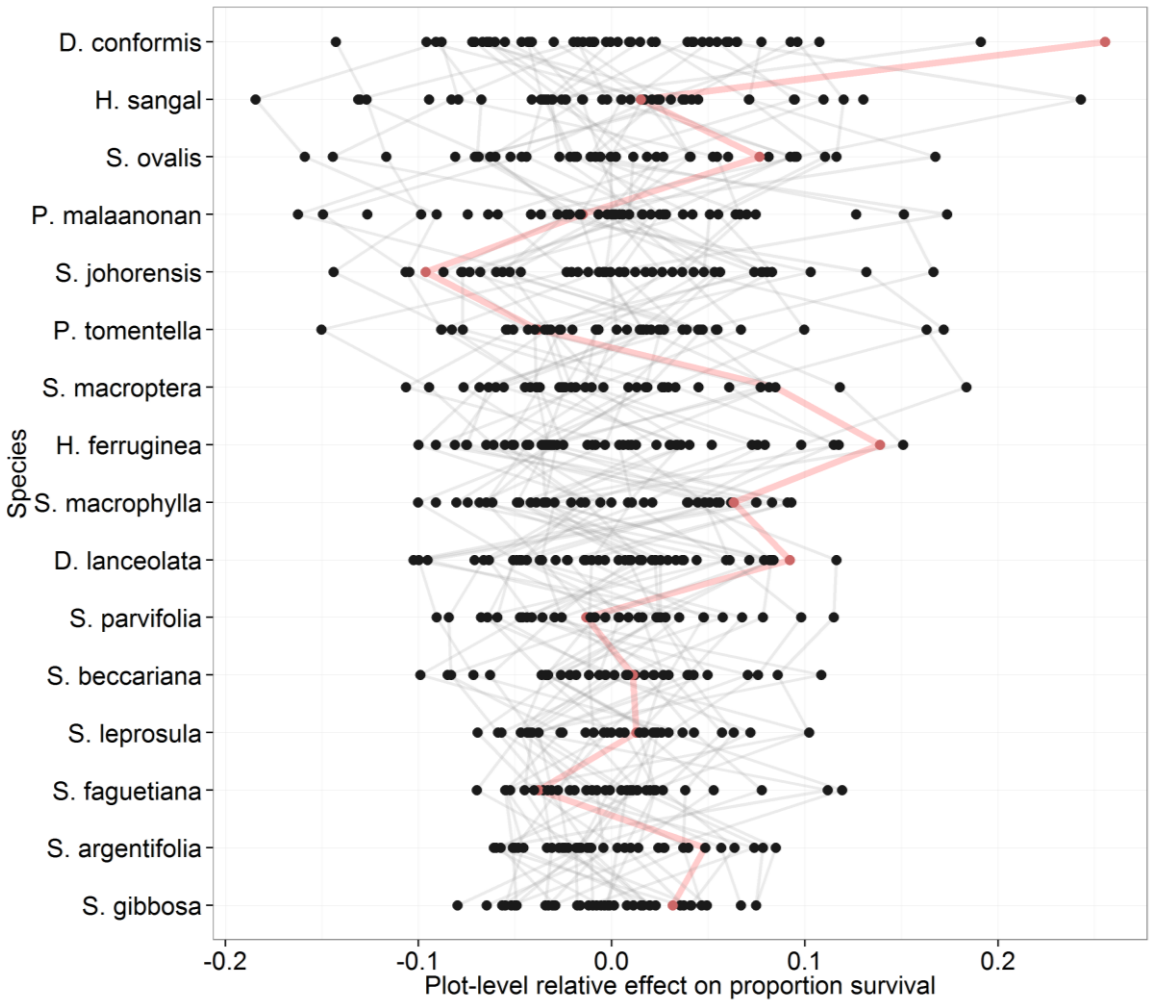

Figure 4.2. Survival spatially varies and species respond to environmental variation in different ways. The species identity by environment interaction for seedling survival in the 16-species mixtures. Points represent the average survival of a species in a plot relative to the average of that species over the whole experiment (taken from the `plot:species` random factor)—so positive values show plots with better-than-average survival. Grey lines join particular plots, illustrating the varying performance of different species in the same conditions. The red line gives one example: while this plot shows above-average survival for some species (e.g. *D. conformis* shows its highest survival) other species experience below-average survival.

We correlated survival and growth after ten years with traits that may link to ecological strategies or insights for planting practice. Wood densities for all species (excluding *H. ferruginea* whose high mortality prevented trait estimation) positively correlated with survival after ten years (r = 0.78) and negatively correlated with growth (r = -0.50). Specific leaf area weakly correlated with survival (r = 0.06) and growth (r = -0.14).

A buffering effect of increased tree diversity may occur if species show varied responses to spatial variation and respond independently or asynchronously to one another. All species showed substantial spatial variation in survival and growth across the 500 ha experiment, though some more than others (Figure 4.2). The species that showed the most variable survival across the experiment were not necessarily those that showed the most variable growth (see Supplementary Material SA2 to compare growth with the survival in Figure 4.2). Species survival also responded to plot-level conditions in different ways, so the most favourable location for one species could be one of the least favourable for another (follow the red line in Figure 4.2). When species-specific responses to plot conditions were allowed, AIC and BIC both reduced by ~19, suggesting species truly respond differently to plot conditions.

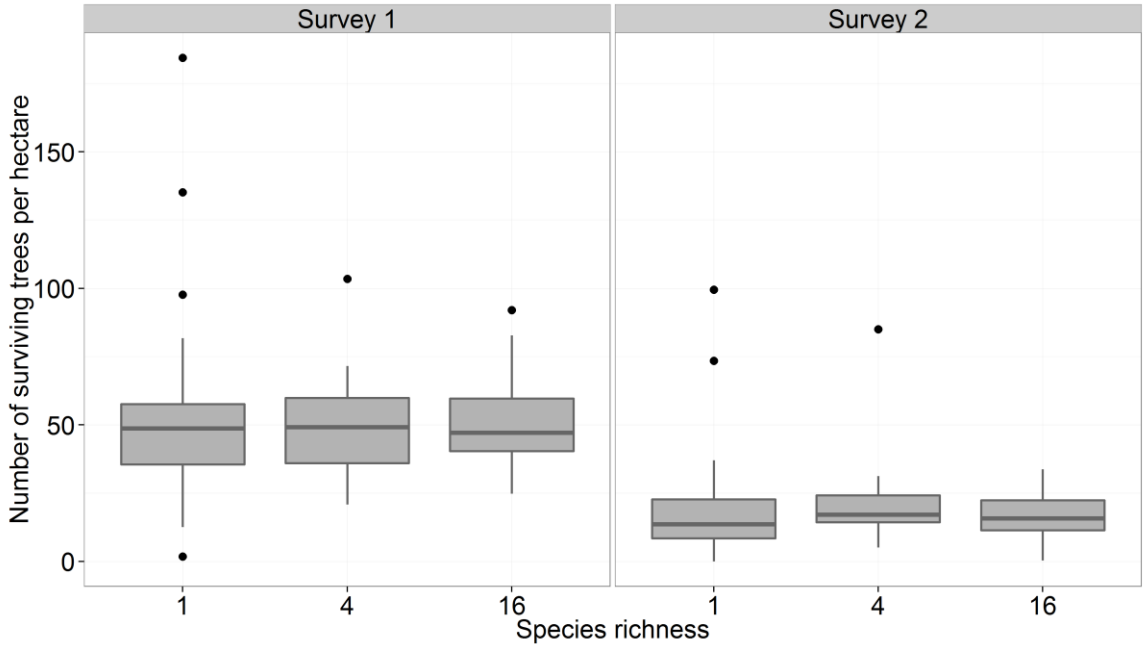

Figure 4.3. Seedling density is less variable in more diverse mixtures. Density of surviving first-cohort seedlings as a function of plot species richness. The data, showing the number of seedlings per ha within each plot, are summarised with box and whiskers: boxes show the 25th, 50th and 75th percentile density, and whiskers extend to the most extreme density values within 1.5 times the inter-quartile range. While the median density remains constant, variation among plots decreases as species richness increases, particularly after two years (survey 1).

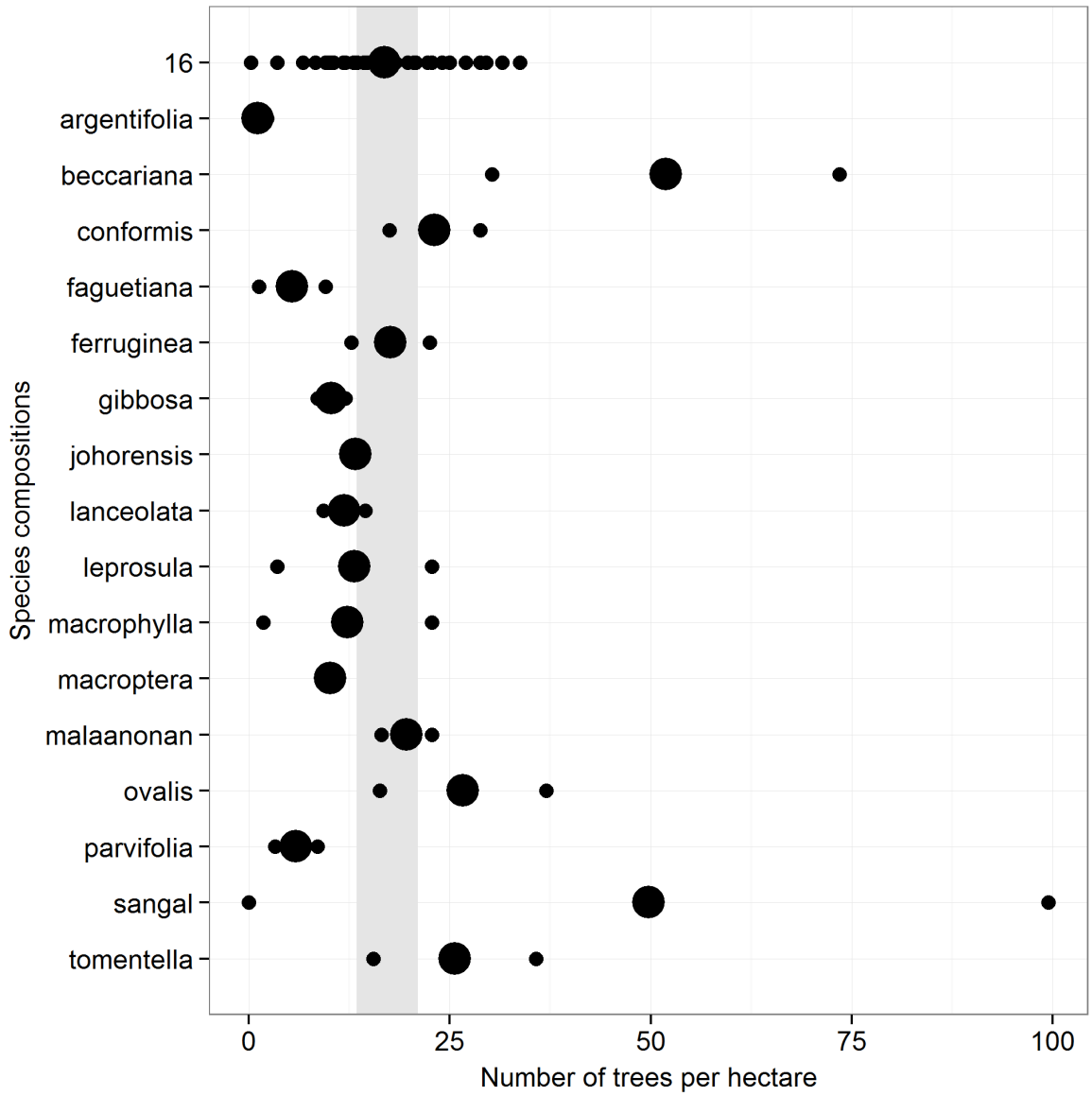

Figure 4.4. Mixtures avoid detrimentally low and wastefully high densities. Density of surviving first-cohort seedlings after ten years, in 16-species mixtures and monocultures. Small points show densities in each plot and large points are the means. The grey band shows the 95% confidence interval of the 16-species mixture mean. The confidence interval for the probability of survival, p, was obtained using the Wilson method (Held & Sabanés Bové 2014), then expressed as the number of surviving trees per ha, $(p \cdot n)/4$. Many monocultures show extreme densities compared to mixture mean.

We cannot assess this insurance effect conclusively due to the early stage of the experiment and the lack of data for the second seedling cohort. However, at the first survey the highest and lowest densities of surviving seedlings were seen in monocultures (Figure 4.3 and Figure 4.4). The species mixtures are no different from the monocultures on average, just as we expected, because interactions between

seedlings are not yet strong. The variability in density, however, does decrease as species richness increases, particularly after two years (Figure 4.3). And the replicated monocultures of a given species were often more variable than what we saw among the 16-species mixtures (Figure 4.4). Planting more diverse mixtures did initially buffer the density of surviving seedlings after two years, but mortality continued over the following eight years and average density decreased within all species richness treatments. Whether there is a long-term insurance effect of diversity on forest restoration will depend on the immediate and long-term survival of both seedling cohorts.

Discussion

Despite the early stage of the Sabah Biodiversity Experiment, several clear results emerge from our analysis of survival and growth during its initial decade. Firstly, we found a clear life-history trade-off between survival versus growth and consistent differences amongst our sixteen dipterocarps in their positions along this trade-off (Figure 4.1). Secondly, not only did species differ on average but they also responded differently to spatial variation, suggesting they specialise on different conditions (Figure 4.2). Thirdly, as expected given the wide spacing of the planted seedlings, there is no evidence of complementary species interactions in mixtures yet (Figure 4.3). Finally, the most extreme high and low seedling densities are found in particular monocultures (Figure 4.4). We discuss each of these points in turn before considering their relevance for enrichment planting schemes and the potential insurance effect of tree diversity in forest restoration.

The trade-off between survival and growth

The results of our more general analysis here support the conclusions of an earlier, more detailed analysis that identified a trade-off between growth and survival (Philipson *et al.* 2014). Our earlier work showed that these dipterocarps trade off survival against growth generally, irrespective of the light conditions they are exposed to: all species were affected by light, but their ability to grow or survive relative to others remained unchanged. This follows work in other tree communities showing that the growth-survival trade-off is a major axis of life-history variation (e.g. Grubb 1977; Pacala *et al.* 1996; Wright *et al.* 2010).

While species differences in survival rates were consistent over time in our study, species estimates of survival are not completely consistent with other studies. When comparing our survival estimates with those at the nearby INFAPRO enrichment-planting sites, the same species observed over a similar timescale experienced unrelated levels of mortality (Godoong *et al.*, unpublished data). Among the species found in both our experiment and the INFAPRO site, those that have shown the best survival so far in our experiment have not been the best survivors at INFAPRO. For example, *D. lanceolata* was clearly the best survivor at INFAPRO after 13 years, with approximately 30% survival—twice the survival rate shown by any other species at the time. However in our experiment, *S. ovalis*, also planted at INFAPRO, attained higher survival than *D. lanceolata*. These differences between our experiment and INFAPRO could be due to numerous factors, including age of seedlings and site-specific conditions (see below).

Trait-mediated trade-offs

Various authors have hypothesized links between demographic rates and plant traits, in particular wood density and specific leaf area (King *et al.* 2006; Sterck *et al.* 2006; Kraft *et al.* 2010), although some are more cautious (Anten & Schieving 2010; Larjavaara & Muller-Landau 2010; Paine *et al.* 2015). Both the results of this analysis and of our earlier work support the link of the survival versus growth trade-off with wood density, such that species with denser wood have higher survival but lower growth rates. On the other hand, both our current analysis and earlier work found no association with specific leaf area. We did find that average survival of species were positively correlated with both total biomass and root mass ratio of the initial sample of harvested seedlings, as is often found (Chan *et al.* 2008). Related experiments at the same site (with 8 dipterocarps including 7 of the species used here) have shown that individuals and species with higher levels of non-structural (soluble) carbohydrates survive longer under extreme drought—a major cause of tropical tree mortality that may be exacerbated by climate change (O'Brien *et al.* 2014, 2015). Extending this work on non-structural carbohydrates and drought survival to the Sabah Biodiversity Experiment is a next priority for the project.

Spatial heterogeneity and species-by-environment interactions

One strategy to improve enrichment planting survival rates may be to plant species in sites that will optimise their growth and survival based on their known ecology (Kettle 2010). If species respond to large-scale differences amongst sites in differing ways then there may be potential. However, if site conditions are fine-grained they may be at too small a scale to make species-site matching practical. Spatial variation in mortality over the 500 ha Sabah Biodiversity Experiment site was

substantial. Elevation is generally highest in the most northerly and southerly areas, decreasing towards the road separating the north and south blocks. There were no discernible effects of the road, nor the river (Supplementary Material SA2). Within distances of 200 m or less (within plots), percentage survival commonly varied ±10% from average and more extreme fluctuations were twice this in magnitude. Within plots, seedlings were planted with 3-m spacing along parallel lines 10 m apart. Survival tends to be more similar within lines than among them as would be expected given the shared conditions along lines (e.g. conditions when the line was planted; damage by elephants that use lines to move through the forest; canopy openness and light levels). So, while our results do show that species respond to site conditions differently, the most relevant conditions may vary at too fine a scale for species-site matching to be practical. This is supported by studies relating seedling survival to micro-topography and associated differences in soil moisture (Born *et al.* 2015).

Lack of interactions between species in mixtures

As we expected, we found no evidence for an effect of plot species richness (or composition) on growth or survival. This is because there is limited scope for interactions between trees during the early stages of the experiment given their size relative to the planting density (pre-mortality) of 3 x 10 m. However, while the average seedling height to apical meristem in 2013 was only about 1 m (including the younger second seedling cohort, see Supplementary Material SA2) some of the larger survivors from the first cohort were already approaching sizes (12 m) where they may interact with neighbours, especially along planting lines. Regular measurement of survival and growth will allow us to detect when enrichment-planted seedlings start to strongly interact.

Enrichment planting

We found high mortality for the first seedling cohort, with only 35% remaining after two years and 12% after a decade. Rapid mortality is typical for enrichment planting—hence the replanting—but levels in our experiment are higher than some rates reported elsewhere (Chan *et al.* 2008) and for the nearby INFAPRO (~50% at 3 years; MS and SWY) and INIKEA projects (~30-60% at 10 years). Intensive maintenance after planting improves survival rates (Ådjers *et al.* 1995) so it is possible that some enrichment planting schemes may achieve better survival through this route. The state of the planted seedling stock also impacts survival and growth, so it will be interesting to compare the mortality reported here with the second cohort, which came from different stock. A new survey that includes measurement of the second cohort is therefore a priority for the project. One caveat when comparing our results with the wider literature is that our seedling densities are based strictly on the enrichment-planted seedlings, whereas other projects may inadvertently or deliberately also include naturally-occurring seedlings.

Potential insurance effect of tree diversity in forest restoration

Due to the small seedling size relative to the planting density we knew there would be limited scope for interactions between species in mixtures during the initial stage of the experiment. However, we did anticipate that species differences in survival rates could provide the basis for an insurance effect of tree diversity, in which species mixtures avoid the potential recruitment failure of monocultures with low survival and the potentially wasteful self-thinning in stands of species with the highest survival. Our results show how the survival rates of these species are variable and susceptible to spatial variation, which could generate such an insurance effect. However, it is too early

to predict the eventual densities of different monocultures and mixtures, or what levels of self-thinning and recruitment failure will result. In comparison, the INFAPRO project's original goal was to reach a density of 15–30 mature harvestable (>60 cm dbh) dipterocarps per ha to replace the trees that logging operations removed (the INFAPRO area has since been protected from commercial logging). The trade-off between survival and growth means that these two contributions to stem area tend to cancel out, producing some plots with a higher density of smaller trees and others with a lower density of larger trees. However, in the long term we expect fast-growing species (lower survival and wood density) to be replaced by slow-growing species (higher survival and denser wood). Regular long-term monitoring will be essential to identify the role of tree diversity in the functioning of these ecosystems and its underlying biological mechanisms.

Supplementary Material

Supporting information may be found on the accompanying CD:
Appendix SA1. Thematic map of Sabah Biodiversity Experiment.
Appendix SA2. Supplementary analysis document.
Table ST1. Species descriptions.

Chapter 5
Land-Use Intensity And The Effects Of Organic Farming On Biodiversity: A Hierarchical Meta-Analysis

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Author Contributions

SLT, JB and LAT designed the analyses and drafted the paper. SLT performed the analyses. JA, CW and FM collected the data. The original idea for the study emerged from discussions between JB, LAT, JA, FM and CW.

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Context

In previous chapters, I have studied the mechanisms of biodiversity effects on ecosystem functioning, and shown how these mechanisms can inform the management of real-world ecosystems. Another step towards greater realism in biodiversity-functioning research is to understand what levels of diversity loss we can realistically expect to see. Biodiversity is changing at alarming rates, and biodiversity-functioning experiments have shown that this may have knock-on effects at the ecosystem level. But in order to predict the ecosystem-level impacts of diversity loss in real-world ecosystems, we need to understand how diversity impacts ecosystem functions and know what realistic levels of diversity loss to expect. Agriculture is one of the greatest global threats to biodiversity, and therefore may impair the functioning of ecosystems in which agricultural systems are situated. Furthermore, any effects on ecosystem functioning may also undermine the ecosystem services that agriculture benefits from, such as pollination and nutrient cycling. As agriculture is the largest global land use, it is imperative that we understand (i) how agriculture impacts biodiversity, (ii) how different agricultural strategies compare in their biodiversity impacts, and (iii) the consequences of these biodiversity impacts for real-world ecosystems. Here, I provide the consensus view on how different farming strategies compare in their impacts on farmland biodiversity. This provides vital basic information for the management of ecosystems and biodiversity across the globe.

Chapter Summary

The benefits of organic farming to biodiversity in agricultural landscapes continue to be hotly debated, emphasising the importance of precisely quantifying the

effect of organic versus conventional farming. We conducted an updated hierarchical meta-analysis of studies that compared biodiversity under organic and conventional farming methods, measured as species richness. We calculated effect sizes for 184 observations garnered from 94 studies, and for each study we obtained three standardised measures reflecting land-use intensity. We investigated the stability of effect sizes through time, publication bias due to the file-drawer problem, and considered whether the current literature is representative of global organic farming patterns. On average, organic farming increased species richness by about 30%. This result has been robust over the last 30 years of published studies and shows no sign of diminishing. Organic farming had a greater effect on biodiversity as the percentage of the landscape consisting of arable fields increased; i.e. it is higher in intensively farmed regions. The average effect size and the response to agricultural intensification depend on taxonomic group, functional group, and crop type. There is some evidence for publication bias in the literature; however, our results are robust to its impact. Current studies are heavily biased towards Northern and Western Europe and North America, while other regions with large areas of organic farming remain poorly investigated. Our analysis affirms that organic farming has large positive effects on biodiversity compared with conventional farming, but that the effect size varies with the organism group and crop studied, and is greater in landscapes with higher land-use intensity. Decisions about where to site organic farms to maximise biodiversity will, however, depend on the costs as well as the potential benefits. Current studies have been heavily biased towards agricultural systems in the developed world. We recommend that future studies pay greater attention to other regions, in particular, areas with tropical, subtropical and Mediterranean climates, in which very few studies have been conducted.

Introduction

Organic farming, in which insecticides, herbicides and inorganic fertilisers are entirely or largely avoided, is generally thought to be more environmentally benign than its conventional farming cousin. However, the overall benefits of organic farming for biodiversity, the environment in general, human health and food security have been intensely debated in recent years (Bengtsson *et al.* 2005; Hole *et al.* 2005; Badgley *et al.* 2007; Mondelaers *et al.* 2009; Dobermann 2012; Reganold 2012; Tuomisto *et al.* 2012; Winqvist *et al.* 2012; Gabriel *et al.* 2013). The debate turns on whether or not the decreased yields from organic farms negate any local benefits, for example to biodiversity, that such methods deliver (Seufert *et al.* 2012; but see Badgley *et al.* 2007). The logic of this argument runs as follows: lower yields push up food prices, and as a consequence more wild or marginal land is brought into agricultural production. This wild land is likely to have supported even higher biodiversity than the organic farm; hence begging the question, is there an overall cost of organic farming to biodiversity?

Organic farming provides shared benefits to both humans and wildlife while conventional farming, at least in the short term, maximises yields—thus potentially sparing wild lands elsewhere—therefore this argument is often naively framed as 'land sharing' versus 'land sparing' (Green *et al.* 2005; Vandermeer & Perfecto 2007; Fischer *et al.* 2008; Phalan *et al.* 2011; Tscharntke *et al.* 2012; Gabriel *et al.* 2013) although recently the debate has moved away from such overly simplistic dichotomies. For example, it has been argued that decisions about land sparing versus sharing are contingent on the landscape and potential yields (Hodgson *et al.* 2010; Tscharntke *et*

al. 2012; Gabriel *et al.* 2013). It is also clear that some organisms are necessary on the farm to support essential ecosystem services, such as pollination and pest control, which contribute to yield. Therefore species in farmland cannot be entirely sacrificed in order to preserve biodiversity elsewhere. In addition, some species, particularly in Europe where farming has been an integral part of the landscape for thousands of years, thrive in extensively managed farmland and are clearly threatened by agricultural intensification (Chamberlain *et al.* 2000). These species are an integral part of the European cultural landscape, and their loss has provoked both public and political outcry, leading the British Government, for example, to pledge to reverse such declines by 2020. Thus, organic farming, which generally increases both crop and landscape heterogeneity, may be one component of a land sharing strategy, delivering wider ecosystem services including amenity and conservation of culturally important species (Vandermeer & Perfecto 2007; Gabriel *et al.* 2013). In this light, quantifying the precise benefits delivered by organic farming is essential.

While there is a general consensus that organic farming increases biodiversity when compared to conventional agriculture, the magnitude of this effect seems to vary greatly, particularly among organism groups and across landscapes (Bengtsson *et al.* 2005; Batáry *et al.* 2011; Winqvist *et al.* 2012). Bengtsson *et al.* (2005) suggested that the effects of organic farming on biodiversity were likely to be greatest in intensively managed agricultural landscapes while Tscharntke *et al.* (2005) argued that agri-environment schemes would have larger effects in simple than in complex landscapes. Some of these predictions have been borne out by individual studies (Rundlöf & Smith 2006; Rundlöf *et al.* 2008a; Brittain *et al.* 2010; Diekötter *et al.* 2010; Batáry *et al.* 2011; Fischer *et al.* 2011; Flohre *et al.* 2011; Winqvist *et al.* 2012) and by meta-analysis in

which landscapes were classified as either simple or complex (Batáry *et al.* 2011). However, different studies have defined simple and complex in different ways, whereas it would be preferable to have some more objective, continuous measurement of land-use intensity with which to test these ideas more fully.

While there have been previous meta-analyses comparing conventional versus organic farming and their biodiversity and environmental impacts (Bengtsson *et al.* 2005; Batáry *et al.* 2011; Seufert *et al.* 2012; Tuomisto *et al.* 2012), we believe that a new analysis is still timely. First, previous meta-analyses have not taken account of the hierarchical structure of the data; second, a large number of new studies have been published in recent years; and third, we include here three objective and standardised measures of land-use intensity and landscape complexity measured on a continuous scale, newly obtained for each of the studies. Using an extended dataset compared to Bengtsson *et al.* (2005) we can therefore ask the following questions: (i) By how much does organic farming increase biodiversity compared to conventional agriculture? (ii) Do the effects of organic farming depend on the organism or functional group, land-use intensity and structure, and crop type? (iii) Has the reported effect size of organic farming on biodiversity decreased or remained stable over time? (iv) Is there evidence for publication bias in the literature, either because studies with negligible or negative effects of organic farming remain unpublished, or because the present studies of organic farming, which are often performed in Europe or the US (Batáry *et al.* 2011; Winqvist *et al.* 2012), are unrepresentative of the crops and regions in which organic farming is conducted globally?

Methods

Data Collection

We started with the species richness dataset published in 2005 by Bengtsson *et al.*, which included 27 studies published before December 2002. We expanded this dataset to include an additional 68 studies published between 2003 and 2011. Some of the additional data (2003–2009) were gathered for an unpublished Master's thesis (Mota 2010). Further studies from 2010–2011 were added by co-authors Ahnström and Winqvist, finishing the literature search by the end of 2011. The full dataset consists of 94 publications (see Supplementary Material SA1). When updating the dataset of Bengtsson *et al.* (2005), we used the same keywords in ISI web of knowledge: biodiversity, biological diversity, conventional farming (agriculture), and organic farming (agriculture). We searched for additional studies by scanning the bibliographies in publications identified from our search. We followed the relevant literature and discussed with colleagues throughout. Our dataset contains results from technical reports as well as peer-reviewed journals. Although it is unlikely that the data we present are complete, we believe these studies are an extensive and representative sample.

For a publication to be included in the analysis it had to provide species richness data ($n > 1$) in both organic and conventional systems. This could be in the form of raw data or the mean species richness, standard deviation and sample size in both farming systems. In some cases we used other richness data provided in the publications, for example Shannon H' (Mäder *et al.* 2002; Martínez-Sánchez 2008) or richness of taxa higher than species level (Galván *et al.* 2009; Crowder *et al.* 2010). Unfortunately, many

of the published studies do not meet these criteria and therefore did not provide sufficient data to be useful in a meta-analysis (see Supplementary Material SA2, ST3).

Organic agriculture is normally defined as any farming system where the use of pesticides, herbicides and synthetic fertilisers is prohibited or strictly limited. Organic farms often have other differences, for example they tend to use more complex crop rotations as a weed and pest control strategy, and use animal manure, green manure or compost in place of synthetic fertilisers. Conventional systems, however, use pesticides and inorganic fertilisers to various degrees, and often use simplified crop rotations and fewer crops. Due to the broad range of farming systems that can be grouped within organic and conventional definitions, the two farming systems are likely to differ between and within studies. However, despite these potential differences, we did not further subdivide farming systems to avoid using more than two treatments in the meta-analysis.

For each effect size, we extracted taxonomic and functional data on the study organism(s). We also recorded: (i) the sampling unit of the species richness data (e.g. numbers per trap or transect); (ii) the sampling scale (plot, field or farm), and; (iii) the crop type. Data on species richness was extracted from the text, tables, or figures in publications using the program *GetData Graph Digitizer v2.25* (Fedorov 2013) when necessary. Other measures of variation presented in publications were converted to standard deviations.

The information on taxonomic groups was used to create categorical covariates for different higher taxonomic units and ecological functions. For taxonomic groups we classified species as: arthropods, birds, microbes, and plants. Data on earthworms,

mammals, nematodes and protozoa were excluded from this analysis due to small sample sizes ($n < 5$). For functional groups we classified species as: producers (plants), herbivores, pollinators (as adults), predators, soil-living decomposers and others (including omnivores, and organisms with variable or unknown functional characteristics). The functional classification is based on the idea that different organism groups may contribute to different ecosystem services. We acknowledge that considerable uncertainty about ecological function exists for several groups: carabid beetles, for example, are often considered to provide pest control (Östman *et al.* 2001, 2003) but many species are known to be at least partly herbivorous seed eaters (Jonason *et al.* 2013).

We also separated the data according to crop type. Given the data we were able to identify the following crop types: cereals, grassland (usually permanent or semi-permanent leys or pastures), mixed crops (comparison made across several different crops), orchards, vegetable crops, and miscellaneous (i.e. not specified precisely in the original study). Many studies include multiple records for different organism groups or crop types on the same farm. These were treated as distinct within-study observations and used to calculate separate effect sizes for subgroups. As a result, our dataset of 94 studies was subdivided into 184 observations (see *Statistical analysis*).

Land-use intensity metrics

Three metrics of land-use intensity were collected using Google Earth (2013). We conducted new landscape analyses for all included studies in order to provide continuous standardised measures of land-use intensity and complexity. We distinguished between different land use types: field (annual and perennial crops, ley,

and grazed ley), pasture (perennial grassland used for grazing), forest (including clear-cuts), wetland, water, rural, urban, and permanent line elements (e.g. ditches, hedge rows, roads etc.). Using these land cover classifications, we calculated: (i) % arable fields—the proportion of the landscape covered by arable fields; (ii) number of habitats—the number of distinguishable habitats found in the landscape, and; (iii) average field size—the average size of arable fields in the landscape. The percentage of arable fields is a measure of land-use intensity, while the number of habitats represents landscape complexity. However, an intensively farmed region is likely to include fewer habitats than a more extensively farmed area. The average field size may reflect the overall extent of farming on the landscape but, depending on local farming practices, not necessarily farming intensity.

To calculate the three metrics we first identified a standardised sampling space at each location based on descriptions in the original publications. Where coordinates were not provided, we identified an area that we were confident included the study area based on descriptions in the text. We then identified a central measuring point, making sure it was placed in a landscape with agricultural fields, and the radius (in metres) defining the appropriate area for sampling around this point. If no information about the area of the study region was available, we visually examined the Google map image and set the radius so that the included landscape was representative of its complexity (and similar to the landscape closest to the central point). We then randomly placed five 1-km transects within this study region. The positions of the five transects were defined by sets of three randomly generated numbers. The first number, randomly selected between 0 (central measuring point) and the radius of the study region, denoted how many metres from the central point the starting point of

each transect would be situated. The second number specified the angle (degrees), defining the direction relative to the central point for which the start point of the transect should be placed. Combined, these two random numbers created a bearing, from the centre of the study region, that defined the transect location. The final number would randomly select between 0, 45, 90, or 180 degrees to specify the angle at which the transect should be drawn, 500m to each side of the start point. Transects were not allowed to cross. Our measures of landscape complexity and land-use intensity were calculated for each transect, extracted directly from Google Earth and input to our database, and averaged to give mean values of each metric for each study or sub-study region. The transects sampled were line transects with no surrounding buffer.

In some cases several studies had been conducted in the same area, in which case the same landscape data were used. When publications that garnered multiple observations had been conducted in multiple regions, and data specified per region, we collected landscape data per region. If the study region was not specified at all—but only the country—we used the mean values of all other studies in that country. The google maps analysed were always the most recent images available. This represents one caveat in our landscape analysis: for older studies there is a time lag between the date the study was conducted and the date our landscape data was collected. Many of the early studies were conducted in Europe, a region that we would expect to show the least landscape change (in agricultural areas) over the relevant timespan.

Statistical analysis

Our effect size is the log response ratio, which quantifies the proportional difference between mean species richness in conventional and organic farming

(Hedges *et al.* 1999). On the log scale, an effect size of 0 means no difference and a positive value means that the organic farm has higher species richness than the conventional farm. The log response ratio displays bias at small sample sizes, when the normal approximation to the distribution of the effect size deviates from the exact distribution. To assess the appropriateness of this approximation, $\sqrt{n \cdot \mu / \sigma}$ for both mean values within each effect size should be generally >3 (Hedges *et al.* 1999). In our dataset, only 10% of effect sizes fall below 3 while ~71% of scores exceed 6, hence the log response ratio is appropriate.

Our analysis was carried out using *R v3.0.1* (R Core Team 2013) with the R package *metahdep v1.18.0* (Stevens & Taylor 2009). The models were fitted to the data using the function *metahdep.HBLM*. We analysed 184 separate observations for subgroups within studies—i.e. different taxonomic groups or crop types. A random effect was used to account for differences across studies, for example among farming systems included within organic and conventional groups. A grand mean effect size, across subgroups, was calculated using an intercept model (Borenstein *et al.* 2009). Variables of interest, selected *a priori*, were included in a meta-regression to see if they explained any differences in biodiversity on organic versus conventional farms. These variables were: functional groups, taxonomic groups, the three landscape measures (see *Land-use intensity metrics*), crop types and scale of sampling (plot, field, or farm). Uncertainty in the regression coefficients was quantified using 95% credible intervals. Credible intervals were calculated by multiplying the posterior standard error of the coefficients by the 95% point of a *t*-distribution with $N - p$ degrees of freedom. We estimated heterogeneity between effect sizes, τ^2. This estimates the proportion of between-studies variance that is true variance, as opposed to within-study sampling

error. This heterogeneity measure was used to estimate I^2, the proportion of total variance that is due to true heterogeneity among effect sizes (Higgins & Thompson 2002).

There is hierarchical dependence between multiple observations within studies. Having several effect sizes obtained from the same publication violates the assumption that effect sizes are independent. A publication-level random effect allowed us to account for the dependency of multiple within-study observations. The non-independence among effect sizes gathered from the same publication was defined by specifying a covariance structure in the study-specific random deviations, as parameterised by τ^2 (Stevens & Taylor 2009). Defining dependence groups meant that a large group of within-study effect sizes with extreme effect sizes were down-weighted, preventing them from having a dominant effect on the overall result. By incorporating this hierarchical variance structure, we could disentangle important differences between organisms and crop types without assuming independence of observations.

The potential for bias in published results in the literature to skew synthesised results is seen as a common limitation for meta-analyses (Borenstein *et al.* 2009; Gillman & Wright 2010). There are two ways that bias could be introduced: (i) a tendency for only 'significantly positive' results to be published—the file-drawer problem, or (ii) studies are not representative of the population—i.e. there are evidence gaps in the literature, where the question has not been investigated in certain contexts. A simple ecological example would be a lack of studies representing a system relative to its global importance; this is bias produced by consensus in the literature

that is not founded on a representative sample of reality. Meta-analysis can provide a general quantitative synthesis. It should also describe bias in the literature, and indicate where that bias may lie. We investigated bias in both the forms described above.

To investigate bias in the file-drawer context, we characterised funnel plot asymmetry in the data. The funnel plot is based on the assumption that studies with smaller sample sizes (and hence higher sampling variance) are more likely to be skewed, because they have lower statistical power; hence negative and low-effect results from small-sample studies are missing from the literature. To produce a funnel plot from our hierarchical model, we plotted the residuals against precision (inverse sampling standard error) (Nakagawa & Santos 2012). In combination with this funnel plot, we conducted a trim-and-fill assessment, whereby it is assumed that skew is due to publication bias and compensates for this by filling in new effect sizes until the skew in the residuals is corrected for. To investigate this further, we conducted a cumulative meta-analysis—in which studies are progressively added to the dataset in order of increasing sampling variance—which qualitatively shows how quickly the overall mean stabilises and whether the final estimate is strongly affected by the less reliable studies. We also estimated the slope of the relationship between sampling variance and effect size. Combining these diagnostics allowed us to explore asymmetry in the data, and then, under the assumption that this is due to publication bias, assess its impact on our result. The cumulative meta-analysis approach was used to assess change in the overall effect size over time by progressively adding studies in order of publication year, and again by estimating the slope of the relationship between publication year and effect size. To investigate evidence-gap bias, we compared our dataset with global

data on the area of organic farming across the globe and for different crop types, collected from the FAO website (FAOSTAT 2013). We used this comparison to discuss how representative the current literature is of global organic farming trends.

Results

The overall mean log response ratio was 0.296 (95% CI: 0.231–0.361); this indicates that species richness on organic farms is on average 34% (95% CI: 26–43) higher than conventional. The estimated standard deviation of the true effect sizes, τ, was 0.304 (variance for $\tau = 0.0004$). This true variance among effect sizes comprised an overwhelming proportion of total variance ($I^2 = 97.4\%$). These results reveal substantial heterogeneity among effect sizes, although many studies showed a large positive effect of organic farming on biodiversity relative to conventional farming. The estimate for hierarchical dependence was positive, meaning that the covariance among within-publication effect sizes will down-weight large groups of effect sizes that would otherwise have an excessive effect on the overall result.

We found large differences in the effect of organic farming on different taxonomic and functional groups (Figure 5.1a,b; Supplementary Material ST2). For example, among taxonomic groups, plants benefited the most from organic farming (Figure 5.1b). Arthropods, birds and microbes also showed a substantial positive effect. Disaggregating organisms into functional groups showed a variety of responses: among functional groups, the largest effect size was found for pollinators while decomposers showed little effect (Figure 5.1a). The crop types showed varying responses, with large positive effect sizes in cereals and mixed farming, and moderate positive effect sizes for all others (Figure 5.1c).

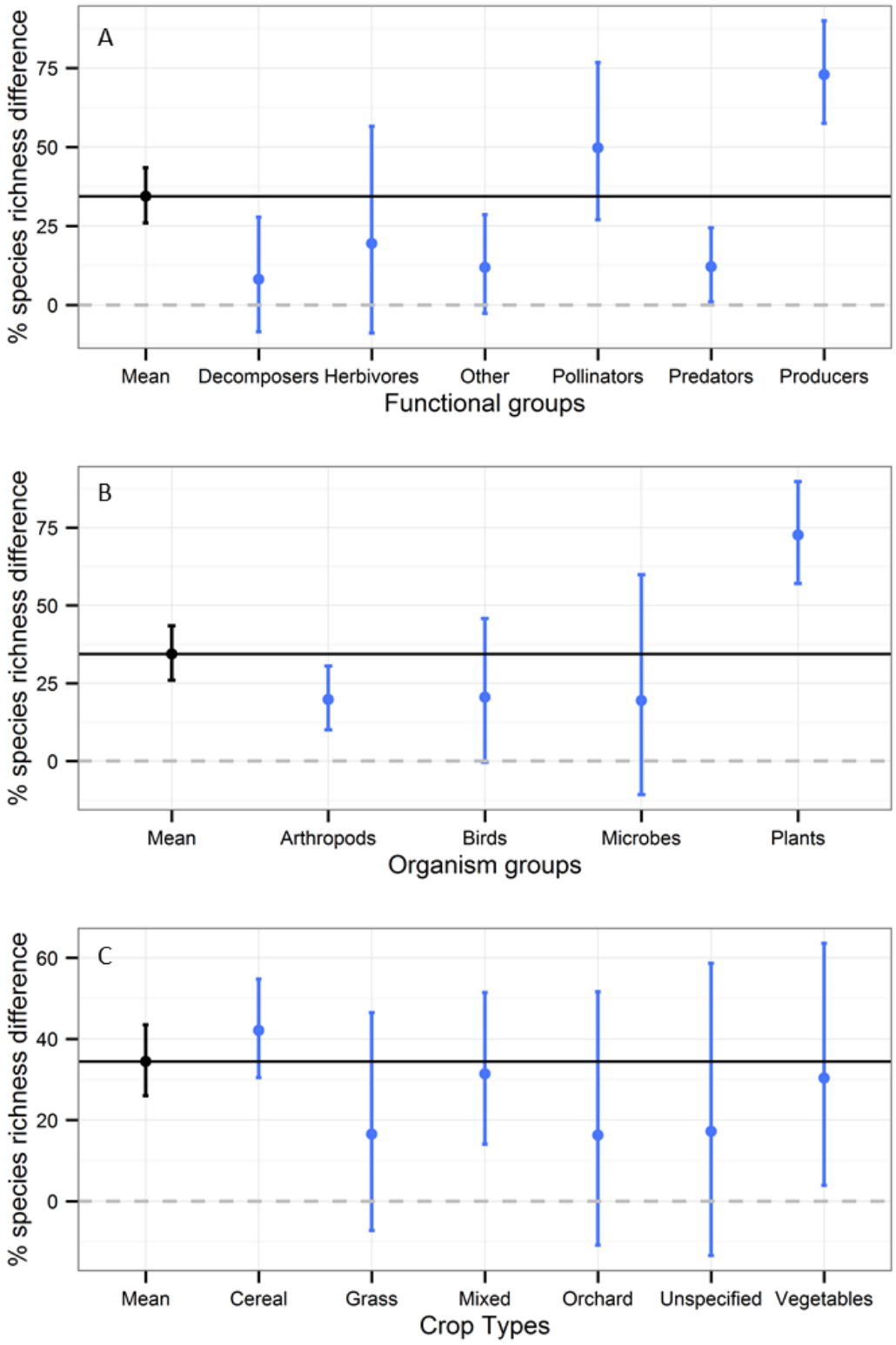

Figure 5.1. The difference in species richness (%) on organic farms, relative to conventional, classified: (A) by functional group (*n*: decomposers = 19, herbivores = 6, other = 27, pollinators = 21, predators = 49, producers = 62), (B) by organism group (*n*: arthropods = 89, birds = 17, microbes = 6, plants = 62), and (C) by crop types (*n*: cereals = 100, grasses = 13, mixed = 40, orchard = 9, unspecified = 6, vegetables = 16). The grand mean is shown in black, accompanied by the black line. Dashed lines show the zero-line. 95% credible intervals are calculated from posterior standard errors.

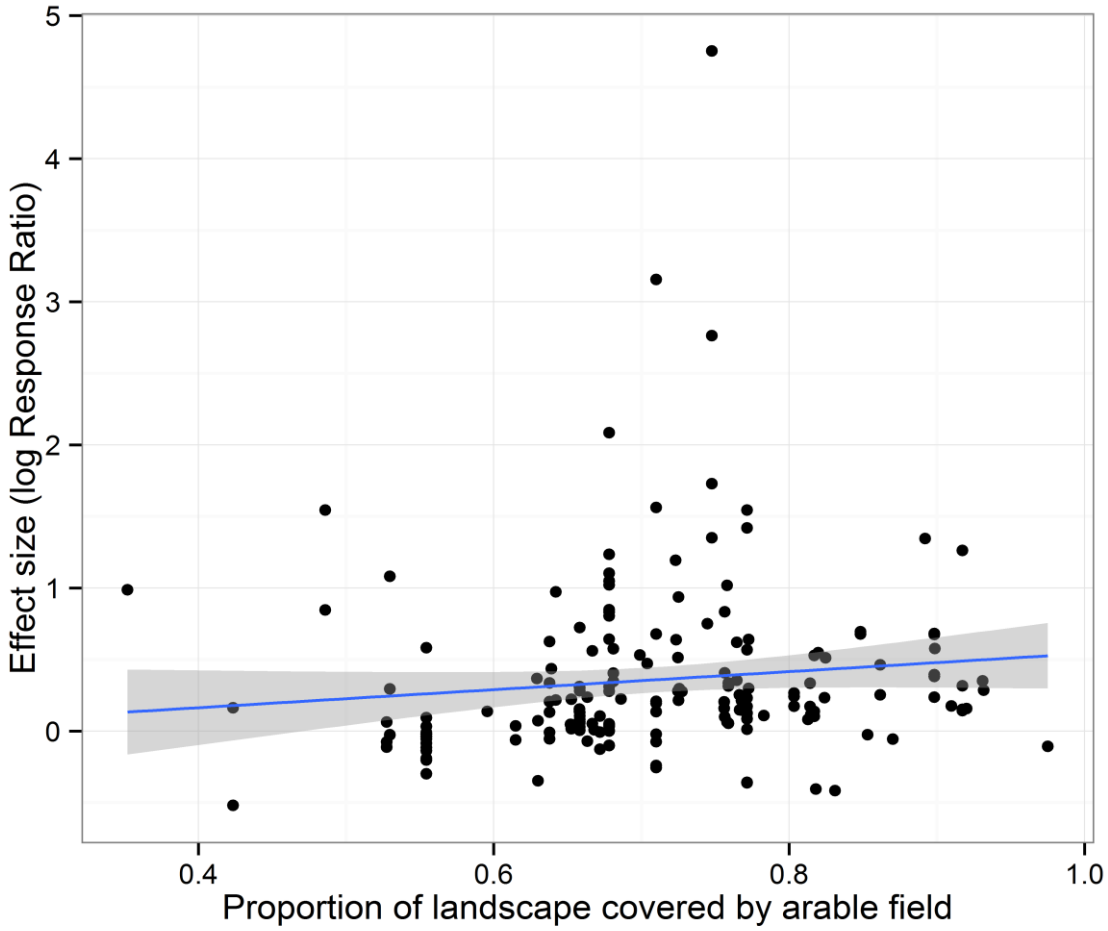

Figure 5.2. The relationship between the effect size and the proportion of the landscape covered by arable fields showing a regression slope with 95% confidence intervals.

The *percentage arable fields* had a positive effect on the magnitude of the effect size (*slope log(RR)* = 0.442, 95% CI: -0.089–0.973; Figure 5.2). To assess the sensitivity of this slope estimate to the most extreme effect sizes, we removed the four data points with *log(RR)* > 2 and re-performed the analysis; there was a small reduction in the slope estimate (0.396). Other landscape metrics had slope estimates close to zero (*number of habitats: log(RR)* = 0.006, 95% CI: -0.019–0.031; *average field size*: *log(RR)* = 0.001, 95% CI: -0.001–0.002). When the percentage of arable fields was fitted as an interaction with functional group, there was substantial heterogeneity in the resulting slopes. However, there was significant uncertainty in these estimates, possibly due to small sample sizes within some functional groups, thus we choose to report this result

qualitatively: increasing landscape intensity affected the magnitude of the effect size in the order: herbivores > other > predators > producers > decomposers > pollinators. The sampling scale of species richness observation did not appreciably change the effect size (*farm* = 0.249, 95% CI: 0.161–0.338; treatment contrasts with *farm* scale: *field* = 0.139, 95% CI: -0.002–0.279; *plot* = -0.017, 95% CI: -0.222–0.187).

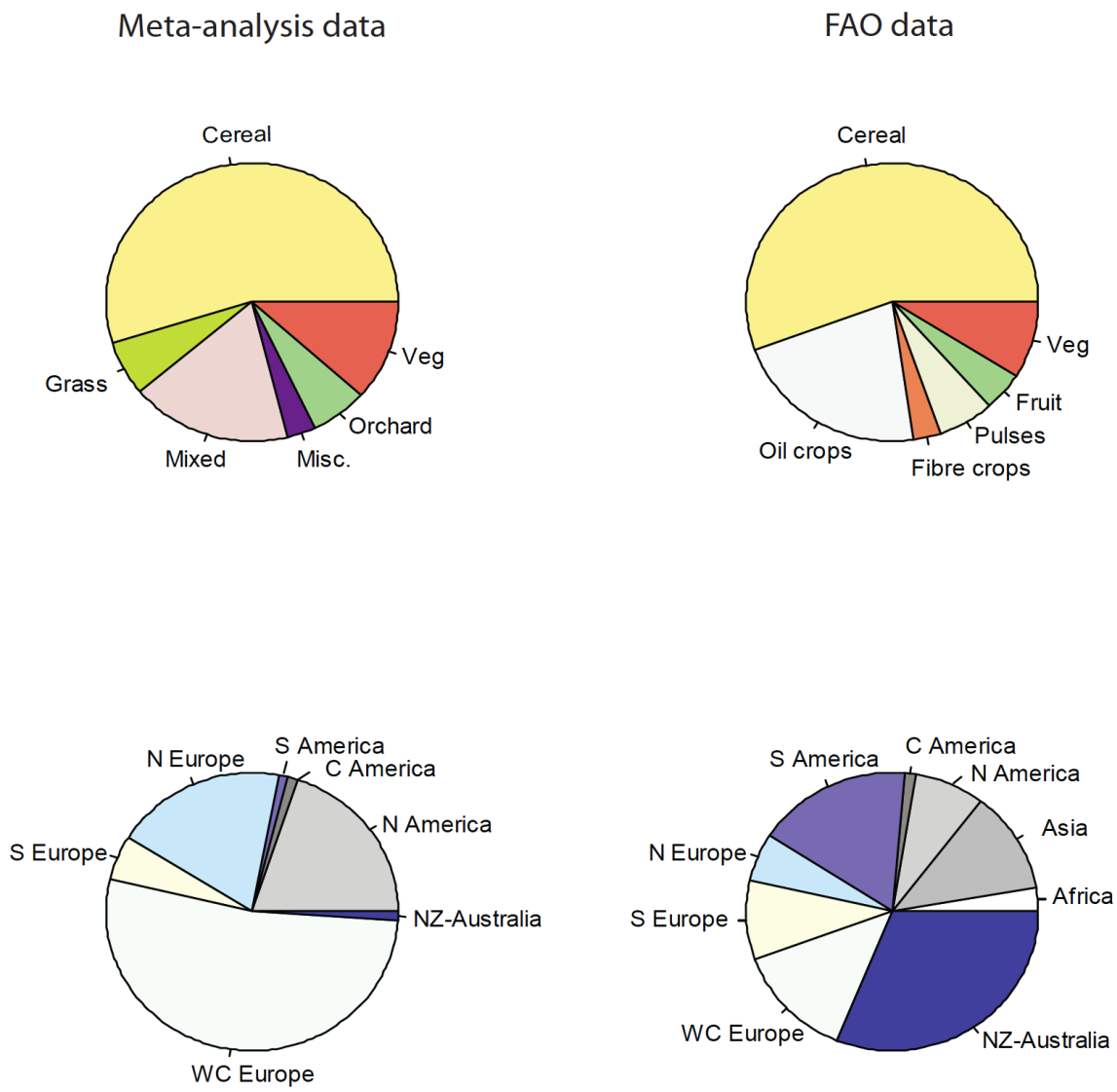

Figure 5.3. Top row: Proportions of different crop types present in the meta-analysis dataset compared with the frequency of the most commonly grown organic crops worldwide. Bottom row: Geographic origin of studies in the meta-analysis dataset compared to the area under organic production in different regions of the world. FAO data obtained from their website (FAOSTAT 2013).

The representation of different crop types in the meta-analysis was comparable to the global FAO statistics; there were similar proportions of cereals, vegetables and orchards (fruit) (Figure 5.3), although fibre and oil crops were under-represented. The geographical representation in our dataset, however, showed much less congruence (Figure 5.3): Western and Northern Europe, and to some degree North America, were highly over-represented, while studies were largely lacking from most other geographical regions, especially Asia, Africa and Australia.

The funnel plot showed some positive bias (Figure 5.4a). A trim-and-fill assessment of how publication bias could impact our inference, after correcting for positive funnel plot skew, produced a negligible reduction in the effect size (-0.0001, 3 studies added). This suggests that, if publication bias is evident, the reported effect size is robust to its impact. Investigating further, the cumulative meta-analysis of effect sizes sorted by sampling variance showed that less reliable studies caused the grand mean to increase, but not drastically so (Figure 5.4b). If we assume that this was due to publication bias then the most conservative effect size estimate is 0.190 (95% CI: 0.135–0.246), which still corresponds to a >20% increased species richness on organic farms. This was the minimum value obtained from the cumulative plot, and was reached after approximately 80 observations (out of 184) were included. This reduced effect size did not greatly alter our interpretation of the magnitude of organic farming's positive effect on biodiversity. The relationship between sampling variance and the effect size had a positive slope (0.022, 95% CI: -0.056–0.101), which confirms the positive association seen in Figure 5.4.

The cumulative meta-analysis plot for data sorted by publication date (Figure

5.4c) showed that the grand mean effect size estimated from our model was robust over time, although interestingly, many of the earliest studies reported very high effect sizes. The lack of change with time was supported by a slope estimate close to zero (0.003, 95% CI: -0.007–0.013).

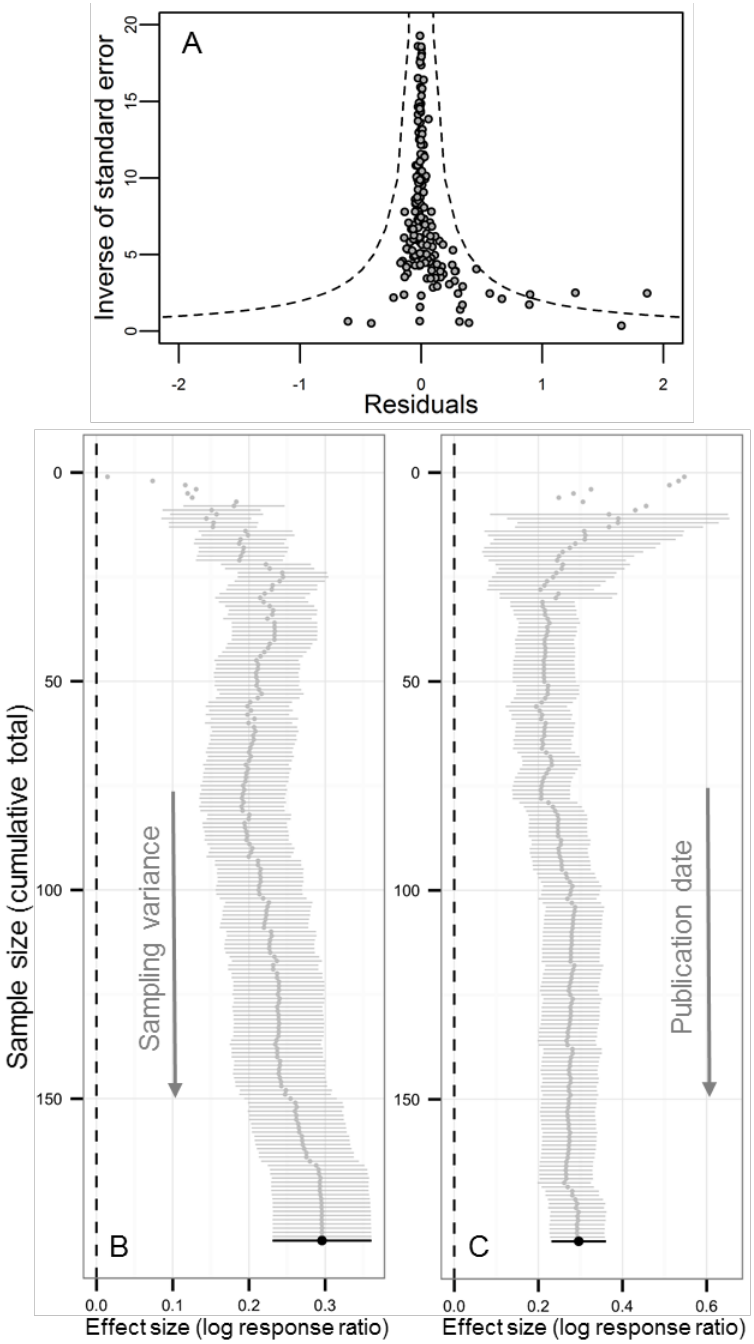

Figure 5.4. (A) Funnel plot showing asymmetry in the spread of residuals around the mean, created using the R package *meta v3.0-1* (Schwarzer 2010). The dashed line shows 95% confidence limits. (B) Cumulative meta-analysis forest plot of data sorted by increasing sampling variance. (C) Cumulative meta-analysis forest plot of data sorted by increasing publication date.

Discussion

Our updated meta-analysis shows that organic farming on average increases biodiversity (measured as species richness) by about one-third relative to conventional farming. This result has been robust over the last 30 years of published studies and shows no sign of diminishing. Organic farming is therefore a tried and tested method for increasing biodiversity on farmlands, and may help to reverse the continued declines of formerly common species in developed nations (Burns *et al.* 2013). Similar results have been previously obtained (Bengtsson *et al.* 2005; Fuller *et al.* 2005; Hole *et al.* 2005; Batáry *et al.* 2011; Garratt *et al.* 2011), but our study is the most up-to-date, deals with the hierarchical structure of multiple within-publication effect sizes, and includes standardised measures of land-use intensity and heterogeneity across all studies.

In other areas of biology and medicine, it has been noted that, with the addition of further evidence, effect sizes concerning a particular question often decrease over time (Jennions & Møller 2002). This is thought to occur because of initial publication bias against non-significant or negative results that is eventually corrected. The effect size in our new study is slightly lower than the one reported by Bengtsson *et al.* (2005); however, our analysis reveals that the grand mean effect size is robust over time (Figure 5.4c). There is therefore no sign of a dwindling effect size with the addition of further evidence. This implies that the increase in diversity with organic farming that we report here is robust, given the choice of crops and study areas included (see below for a discussion of the representativeness of our study).

Land-use intensity effects

Many authors have speculated on and investigated the importance of landscape characteristics in shaping the likely effect of organic farming on biodiversity (Bengtsson *et al.* 2005; Rundlöf & Smith 2006; Rundlöf *et al.* 2008a, b; Batáry *et al.* 2011). Here, we calculated three standardised measures of land-use intensity and heterogeneity for all studies: the proportion of arable fields, the typical field size and the number of habitats. Only the proportion of arable fields in the landscape had any significant overall effect. The difference in diversity between organic and conventional farming generally increased with increasing proportion of arable fields, although there was large variation around the estimated slope. Some of this variance may be due to different responses between functional groups (Batáry *et al.* 2011). The slope of this relationship decreased in the order: decomposers > other > predators > herbivores > producers > pollinators, suggesting that the effect of organic farming on predators is greater in intensively managed landscapes, whereas the effect of organic farming on pollinators does not increase much with land-use intensity. These differences may be due to the importance of local actions relative to regional actions and to the movement of organisms and chemicals across the landscape. For example, some pollinators are known to be sensitive to certain pesticides (Goulson 2013), leading to an EU moratorium on neonicotinoids. If an organic farmer refrains from using pesticides, then local pollinator richness might increase; however, given that these chemicals might drift substantially, and that pollinators on an organic farm will likely visit neighbouring farms, the impact of this local action might have no more effect in an intensively managed landscape compared to an extensive one.

Organism groups, crop types and spatial scale

We expected that the magnitude of the positive effect of organic farming would vary among organism groups, as this has been found repeatedly (Bengtsson *et al.* 2005; Fuller *et al.* 2005; Batáry *et al.* 2011; Garratt *et al.* 2011; Winqvist *et al.* 2011, 2012). As in previous studies, we found that plants benefited most from organic farming, probably because of restricted herbicide use (Roschewitz *et al.* 2005; Rundlöf *et al.* 2010). Arthropods, birds and microbes also benefited, with varying levels of estimated confidence. Accordingly, most functional groups—herbivores, pollinators, predators and producers—were more diverse in organic farming, with the exception of decomposers. The lack of positive effects on decomposers, which are mostly soil fauna, is surprising given that there are positive effects of organic farming on soil conditions and soil carbon (Mäder *et al.* 2002; Gattinger *et al.* 2012). This may be because variation in soil type and structure is more important for soil organisms than the farming system itself. Such interactions between factors influencing the diversity and abundance of soil organisms would repay more investigation. The strong positive effects of organic farming on herbivores and pollinators are consistent with other studies (Rundlöf & Smith 2006; Holzschuh *et al.* 2008; Rundlöf *et al.* 2008a; Garratt *et al.* 2011).

We found significant differences in the effect of organic farming among crop types. In cereal fields, which comprised >50% of the studies, organic farming had large effects, significantly higher than in vegetable crops and orchards (Figure 5.1c). This might reflect the intensive management of conventional cereal crops, with repeated applications of inorganic fertilisers and fungicides. The effect size in both vegetable crops and orchards, although positive, did not differ significantly from zero, but this could be due to small sample sizes. A lower but still significant effect was found in

grasslands (pastures and permanent or semi-permanent leys), which are generally not so intensively managed. The number of studies in grasslands, vegetables and orchards was quite low, and we recommend that these crops are given more attention in the future.

In a previous meta-analysis (Bengtsson *et al.* 2005), small-scale studies (on the plot or single field scale) showed much larger effect sizes than studies on larger spatial scales. However, we found negligible differences across scales. This suggests the general benefit of organic farming is robust across sampling scales, in contrast to recent work that suggests this benefit diminishes at larger scales (Gabriel *et al.* 2010; Crowder *et al.* 2012). The previous meta-analysis result may have been due to small sample size or publication bias, which highlights the importance of updating meta-analyses with additional evidence. We note that most of the recent studies have been conducted at the farm scale, which is the most relevant scale for evaluating both organic farming as an agri-environmental scheme for biodiversity, and for the sustainability of farming systems in general.

Publication bias

The funnel plot suggests a positively-biased spread of effect sizes (Figure 5.4a), which could be interpreted as a tendency for studies showing large positive effects of conventional farming on biodiversity to remain unpublished. However, an alternative interpretation may be that large positive effects of organic farming occur occasionally, while large positive effects of conventional farming are exceptionally unlikely. This seems reasonable given the nonlinear nature of many natural processes, such as population growth, which could occasionally fuel very large impacts of not controlling

certain groups of organisms. In any case, the positive bias is slight and has been shown to not affect our result.

Previous studies of organic farming on biodiversity have been strongly biased towards temperate Western and Northern Europe and North America (Figure 5.3), i.e. intensive farming systems in developed countries. There is extremely limited data available from other areas of the world, for example Eastern Europe, Asia, Africa, Central and Southern America—a bias that was also noted by Batáry *et al.* (2011), Martin *et al.* (2012), and Randall & James (2012). We therefore recommend that studies of organic farming practices on diversity in tropical and subtropical areas (e.g. Deb 2009; Zhang *et al.* 2013) should receive high priority. It is, for example, surprising that there are no studies on organic bananas or cacao, despite these products being widely available in European supermarkets. Mediterranean climates are also under-represented, although there are a few studies from California (Drinkwater *et al.* 1995; Letourneau & Bothwell 2008; Kremen *et al.* 2012) and South Africa (Kehinde & Samways 2012).

The organic controversy

The yields from organic farms are generally lower than conventional yields, although some controversy exists concerning the size of this effect and whether it is more prominent in developed countries (Badgley *et al.* 2007; de Ponti *et al.* 2012; Dobermann 2012; Reganold 2012; Seufert *et al.* 2012). As outlined in the introduction, this implies a potential trade-off between biodiversity and crop yields. For example, Gabriel *et al.* (2013) in a study of cereal crops in Southern England concluded that the benefits of organic farming to biodiversity were entirely bought at the cost of reduced

yield. They further suggested that the lower yields of organic farming may therefore have the unfortunate result of increasing the total area of land under agricultural production. However, there are other, often unmeasured, potential positive environmental benefits of organic farming. For example, nitrogen and phosphorus pollution caused by leaching from intensively managed fields is still a major problem in many countries, and incurs significant costs to society (Heathwaite *et al.* 2000). An overall evaluation of organic farming in relation to crop yields therefore needs to account for the effects of farming practice on a wider range of environmental factors (Mondelaers *et al.* 2009; Sandhu *et al.* 2010; Gattinger *et al.* 2012; Bommarco *et al.* 2013).

Synthesis and recommendations

This analysis affirms that organic farming usually has large positive effects on average species richness compared with conventional farming. Given the large areas of land currently under agricultural production, organic methods could undoubtedly play a major role in halting the continued loss of diversity from industrialised nations. The effect of organic farming varied with the organism group and crop studied, and with the proportion of arable land in the surrounding landscape. We found larger effects in cereals, among plants and pollinators, and in landscapes with higher land-use intensity. Despite the fact that organic farming has been suggested to have large effects on soil conditions, its effects on soil organisms were ambiguous and in general understudied. Finally, it is clear that three decades of studying the effects of organic farming on biodiversity have been heavily biased towards agricultural systems in the developed world, especially Europe and North America. We therefore recommend that other regions and agricultural systems are given much greater attention. In particular, more

studies are needed in tropical, subtropical and Mediterranean climates. Studies at any scale would be beneficial: at the farm scale because this is the economic unit of farming, and at the landscape scale because this is the scale at which many organisms respond. This would allow a more balanced and globally relevant assessment of organic farming effects on biodiversity, ecosystem services, food production and agricultural sustainability.

Data Accessibility

Meta-analysis data and R script: DRYAD entry DOI: 10.5061/dryad.609t7 (Tuck *et al.* 2014b). FAO statistics on organic farming coverage: FAOSTAT (2013).

Supplementary Material

Supporting information may be found on the accompanying CD and in the online version of this article:
Appendix SA1. List of studies included in the meta-analysis.
Appendix SA2. PRISMA flowchart showing the data collection decision process.
Table ST1. Model estimates.
Table ST2. Coefficient estimates for subgroups included in Figure 5.1.
Table ST3. List of studies rejected during data collection, with reasons for rejection.

Chapter 6
General Discussion

Overview

The effects of biodiversity on ecosystem functioning, hereafter called biodiversity-function, is a vast field of study. It connects the maintenance of diversity in species communities with the fluxes of energy and matter in ecosystems. Biodiversity-function relationships found in experiments are a major development in basic ecological science, which can bridge the gap between population, community and ecosystem scales of study. They highlighted an indirect consequence of biodiversity loss, that the functioning of entire ecosystems may be threatened, including those that provide services for humans. But to improve both our ecological understanding of the functional role of biodiversity in ecosystems and our applied understanding of how real-world ecosystems are affected by biodiversity change, we need further developments. Firstly, we need to explain what biological mechanisms drive the biodiversity-function relationships found in controlled experiments. Secondly, we need a next generation of long-term, field-scale experiments conducted in complex landscapes, which will have direct relevance to real-world ecosystems and their management. The work I have presented has an ambitious scope: beginning with the study of interactions between populations and the mechanisms for biodiversity effects, and ending with human impacts on biodiversity and how we might use this research to improve the conservation of real-world ecosystems.

In chapters 2 and 3, I tested a method for measuring plant interactions in natural communities and then analysed how those interactions might determine

properties of plant communities. These chapters firstly give a potential resolution to debate on what forces shape the diversity and composition of plant communities and then improve our understanding of the mechanisms by which diverse plant communities can enhance ecosystem functioning. I found that a major method for measuring competition in natural communities is flawed, and recommended that different approaches are required to truly measure the role of species interactions in structuring plant communities. I then used simulation modelling to connect experimental evidence with relevant theory, to assess when we might expect to find definitive evidence of positive biodiversity effects. These two chapters dealt with the mechanistic basis for biodiversity-function relationships and our technical ability to describe them—vital for interpreting past experiments and as a basis for progressing into real-world ecosystems.

In the remaining chapters, the concern was firstly to push the frontier of biodiversity-function research into complex landscapes, where this research can have more applied impact. And secondly to equip ourselves with the knowledge on biodiversity change that is required to comprehend the real-world importance of this research. I analysed results from one of the first experiments in complex landscapes, where biodiversity change has been severe and the potential cost to ecosystem functions and services is great. I found initial evidence, from a long-term experiment, that diversity could help improve the effectiveness of forest restoration. I then scaled up even further to focus on global biodiversity change, rather than its functional role in ecosystems. To know how biodiversity change will impact real-world ecosystems we must know what change is occurring. I found that intensive agriculture reduces the diversity of farmland wildlife by a third overall. We might use this information to meet

global food requirements whilst minimising its cost to wildlife. Other work that I have been involved with looked at the effects of land use more widely and found that the impacts of human land use on biodiversity are severe, but there is scope for future mitigation (see Appendix III).

Measuring interactions in plant communities

In chapter 2, I tested the predominant method for measuring the effect of competition in natural plant communities. The method is an observational approach that assumes we can infer the effects of interactions from natural variation in the densities of co-occurring species. The effect of competition between species is estimated by predicting how the population size of each species would respond to the removal of competitor species. We performed this observational analysis on experimental mixtures and compared the prediction with our test: monocultures, where species grow without competitor species. The method consistently underpredicted the effect of competitor removal, undermining any inferences that can be made using this method regarding how interactions structure plant communities.

If plant species did not interact, understanding the effects of diversity on ecosystem functioning would be simple. We would only need information on the abundances of each species in a community and their performance in monoculture. But this is clearly not the case. Even selection effects of diversity are the product of interactions. Huston (1997) described the selection probability effect—that diversity increases the probability of including any species—as an artefact of experimental design. But others showed that this probabilistic side-effect is not in itself sufficient to create any effect of diversity (Loreau & Hector 2001; Cardinale *et al.* 2004; Weis *et al.*

2007). For any species to contribute to a diversity effect, they must alter the *per capita* performance (e.g. relative yield) of other species through interactions like competition (Loreau & Hector 2001). Thus, regardless of debate on what mechanisms drive diversity effects (see *Mechanisms of diversity effects*), competition is key to understanding how species combine in diverse communities to influence ecosystem functions. The method tested in chapter 2 estimates the effect of competition by predicting the impact of species loss. Such a method is clearly relevant to the study of the impacts of biodiversity loss on the community-level properties that drive ecosystem functions.

Understanding the role of competition in structuring plant communities and consequently driving ecosystem functions requires tried and tested methods for quantifying the strength of competition. Evidence of interactions in biodiversity experiments is clear, because the biomass of multi-species communities cannot be described as just the additive combination of monoculture biomasses (Cardinale *et al.* 2011). But taking biodiversity-function research out into natural ecosystems means that we need robust methods for measuring interactions in natural communities, which can reliably predict the effects of losing species. There are many methods for measuring competition—some are experimental, some are observational—but overall they do not give the same results (Gurevitch *et al.* 1992; Rees *et al.* 1996; Martorell & Freckleton 2014). We therefore need to understand why different methods give different results, which methods accurately predict the effects they intend to quantify, and what causes any inaccuracies in these predictions. The flaws in the major experimental methods are well documented (Connell 1983; Freckleton & Watkinson 2000), but until now the observational methods had received less scrutiny.

The method tested in chapter 2 is predominantly conducted using observational data, but interestingly the approach was first taken using experimental data (Mack & Harper 1977). An experiment could control for confounding variables like soil nutrients, moisture, light and temperature. Confounding variables can obscure the effects of the density of one species on the future density of another species, because correlation in the environmental responses of two species can be misconstrued as an effect of species interactions. This is one of the potential reasons why the observational method poorly predicted the effects of competitor removal. If true, it would highlight where experiments can help in the study of plant competition. However, we underpredicted the effect of competitor removal even in our semi-controlled experiment. Our primary explanation, that it is impossible to infer the fundamental role of competition in natural communities because of the ghost of competition past, suggests the problem is more profound. This would explain why experimental and observational evidence do not generally agree, but it would not yet provide a solution. Further modelling is required to confirm this idea. Perhaps such modelling will suggest new methods, but it may potentially show that we will never be able to use observational techniques to quantify whether plant communities are fundamentally competitive. Debate on the importance of interactions will continue unless this matter is resolved.

Debate over methodologies and interpretation have made species interactions perhaps the most contentious topic in all of ecology. The role of local interactions in shaping the assembly and composition of plant communities has been a dividing line in many of the field's important developments (Lewin 1983; Connor & Simberloff 1984; Gilpin & Diamond 1984; Abrams 1986; den Boer 1986; Roughgarden 1986; Adler *et al.*

2007; Vellend 2010). Much of community ecology is based on the idea that niche partitioning and competition are key to understanding the maintenance of biodiversity (Darwin 1859; Hutchinson 1957; Macarthur & Levins 1967; Chesson 1991, 2000; Levine & HilleRisLambers 2009; HilleRisLambers *et al.* 2012). But others have claimed that large-scale forces like dispersal and drift are more important (Connor & Simberloff 1979; Ricklefs 1987; Ricklefs & Schluter 1993; Hubbell 2001).

Study of competition is important for biodiversity-function research, because much of the ecological theory invoked to explain diversity effects is based on coexistence between competitive species, often involving competition for resources (Tilman & Downing 1994; Tilman *et al.* 1997a; Loreau 1998a, 2010b). However, just as with other topics in community ecology, the role of niche partitioning caused by competition has been hotly debated in biodiversity-function research (Tilman *et al.* 1996; Aarssen 1997; Huston 1997; Tilman 1997; Loreau 1998b; Hector *et al.* 1999; Hector 2000; Huston *et al.* 2000). There is still a lack of strong evidence for niche partitioning as the major cause of diversity effects, perhaps because such specific mechanisms are rarely cited when diversity effects have been measured (Cardinale *et al.* 2011). The early debates were addressed by quantifying complementarity and selection effects (Loreau & Hector 2001), but in order to develop a mechanistic understanding of diversity effects we now need to move beyond these terms (Carroll *et al.* 2011, 2012; Loreau *et al.* 2012; Turnbull *et al.* 2013). Doing this will require further modelling, measuring, and testing of species interactions. By improving methods to infer competition from natural communities, we can better inform hypotheses about how diverse plant communities in nature can sustain ecosystem functions. For other work I have contributed to, that examined the predictability of

plant–soil interactions rather than plant–plant interactions, see Appendix II (Mehrabi & Tuck 2015).

Mechanisms of diversity effects

In chapter 3, I explored the modelling that will be required to understand what mechanisms drive biodiversity effects. I presented a model of the seasonal growth of species that competed for one shared limiting resource. Species differed according to a functional trade-off between their rate of resource capture and the volume of resource pool they can access. This trade-off enabled stable coexistence and complementarity effects. But it was not possible for diverse mixtures to reach a higher yield than the best monoculture of its component species without extra niche differentiation. We hypothesised that mixtures might yield more than the best monoculture if we included environmental resource leaching throughout the season. We assumed that resources not yet locked up in plant tissues could be leached from the soil profile. We simulated growth of communities with varying species richness and measured how much of the resources had been captured and leached by the end of the season. We expected mixtures to capture more and leach fewer resources, because species that could capture resources quickly would minimise leaching early in the season, whilst species that could access more resources in total would continue to exploit the remaining resource pool later on. As we expected, some species mixtures did capture more resources than the best monoculture in the presence of leaching—although this was only a small proportion of all mixtures. Resource leaching differentiated species in time by making some resources accessible only to those species that can capture resources quickly enough. Mixtures that combine the strengths of different species along the

trade-off could capture resources effectively throughout the entire season, thereby reaching a higher season-end yield. Whilst it was rare for mixtures to outperform the best monoculture, they frequently performed as well as the best monoculture due to the same mechanism. This mechanistic model offers a biological explanation for biodiversity effects observed in long-term experiments.

The modelling presented was intended to draw directly from long-term biodiversity experiments, where there is greatest opportunity for measuring and testing how species interact and what effect this has on ecosystem functions. The case for complementarity effects such as resource use of species in mixtures has been demonstrated in theory. Models have shown that mixtures should commonly yield more than expected from the properties of its component species, which is known as overyielding. Experiments have verified this expectation, and some biological mechanisms for overyielding have even been elucidated. A greater number of models have been used to explore when we should expect mixtures to yield more than its highest yielding monoculture, also known as transgressive overyielding. But the mechanisms that could generate this most definitive effect of diversity have been less well explored and, as transgressive overyielding has mostly been found in long-term experiments, it is not clear how often we should expect to see it.

By now much experimental evidence has shown that complementarity effects are common, even though the role of niche differentiation is still unclear (Cardinale *et al.* 2007, 2011). Multiple species usually contribute to the increased biomass in diverse mixtures (Tilman *et al.* 2001; Hector & Bagchi 2007). Positive complementarity effects often increase over time (Reich *et al.* 2012; Ravenek *et al.* 2014)—sometimes with

concomitant decreases in selection effects (van Ruijven & Berendse 2003; Fargione *et al.* 2007). These patterns suggest that the complementarity effects observed, at least in these experiments, are not a transient effect of artificial species mixtures (but see Turnbull *et al.* 2013).

Various mechanisms for complementarity have been suggested. At the Jena Experiment, some suggested mechanisms have been that species differ in rooting depth and architecture (Dimitrakopoulos & Schmid 2004), but more recently that higher diversity might reduce the effects of plant–soil feedbacks (Ravenek *et al.* 2014). Similarly at Wageningen, diverse mixtures were shown to use nitrogen more efficiently (van Ruijven & Berendse 2005) but negative density-dependent effects may also be important, for example species-specific root herbivory by nematodes (De Deyn *et al.* 2004; van Ruijven & Berendse 2009). Other experimental work in similarly agricultural contexts found that transgressive overyielding was common and linked to having a diversity of functional traits regarding resource acquisition and growth strategies (Finn *et al.* 2013). Perhaps the best evidence of transgressive overyielding has been from Cedar Creek (Tilman *et al.* 2001), where diverse communities showed increased input and retention of nitrogen due to complementary rooting and belowground resource use, primarily between legumes and C4 grasses (HilleRisLambers *et al.* 2004; Fargione & Tilman 2005; Fargione *et al.* 2007; Mueller *et al.* 2013). Thus, belowground rooting and resource capture mechanisms were a natural choice to explore transgressive overyielding in mechanistic models.

Loreau (2010a) showed what conditions are required to find transgressive overyielding using a two species Lotka-Volterra model. Stable coexistence, and hence

overyielding, requires that the inferior competitor is limited more by itself than by the competitive effect of the superior competitor. In this case, the inferior competitor would overyield but the superior competitor would not, resulting in a lower yield than the superior competitor in monoculture. Transgressive overyielding requires the additional condition that both species are limited more by themselves than by the other species.

To summarise the relationship between coexistence and overyielding: overyielding can occur even in transient mixtures and hence does not guarantee persistent diversity effects (Carroll *et al.* 2011, 2012; Loreau *et al.* 2012; Turnbull *et al.* 2013); if mixtures stably coexist, it follows that they will overyield—there is sufficient niche differentiation for a community to yield more than expected from the properties of its component species; but for a community to yield more than its highest yielding species in monoculture, i.e. show transgressive overyielding, even stronger niche differentiation is required than that necessary for stable coexistence (Loreau 2010a). Therefore, in simple Lotka-Volterra models, the conditions for coexistence and diversity effects are clear. Nevertheless, measuring competition in plant communities remains problematic (see chapter 2) and measuring the effects of niche differentiation has rarely been achieved (but see Levine & HilleRisLambers 2009). Without strong measurement it will remain difficult to know when conditions for diversity effects are fulfilled.

In more complex models of plant competition, that for example allow nonlinear *per capita* population growth rates, the relationship between coexistence and diversity effects can be less clear (Gilpin & Justice 1972; Loreau 2010a). It is still not known how

frequently populations exhibit nonlinear population growth functions. And some mechanisms for species coexistence, such as transient nonequilibrium coexistence, do not predict the same functional consequences of diversity for ecosystem functions (Loreau 2010a). So question marks remain on the generality of such a simple set of conditions to necessitate persistent effects of diversity in plant communities.

The model presented in chapter 3 helps identify the conditions under which we might expect to find transgressive overyielding. It appears that even when mechanisms for transgressive overyielding are at work, we should not expect mixtures to yield more than the best monoculture very often. This gives new light in which to consider the rarity of transgressive overyielding observed in experiments. Future work combining experiment and theory should continue to elucidate when and how mixtures outperform monocultures. Doing so will strengthen our understanding more broadly of the functional consequences of species diversity for ecosystems. Understanding theory and small-scale experiments is an important platform for scaling up to the experiments in complex landscapes that can inform management of real-world ecosystems.

Diversity effects in complex landscapes

In chapter 4, I presented initial results from one of the first long-term biodiversity-function experiments that will be conducted in complex environments, at landscape level, with real-world application. I analysed the first decade of survival and growth at the Sabah Biodiversity Experiment, which is situated in selectively logged lowland forest in South East Asia. The experiment will elucidate biodiversity-function effects in tropical forests, and will help inform the restoration of these degraded

ecosystems. The experimental seedlings were planted into the background forest in a way that replicated the restoration practice. By analysing the survival and growth of these seedlings, we could estimate how many replanted trees remain and at what stem density. We found that species differed in survival and growth, following a survival-growth trade-off. Species also responded differently to the wide range of conditions throughout the landscape. These differing responses could create a spatial insurance effect of diversity, thereby ensuring successful restoration throughout the complex landscape.

The effect of plant diversity on ecosystem functioning has been extensively studied in small-scale, controlled conditions that usually strive to minimise environmental heterogeneity (Cardinale *et al.* 2011). In previous chapters I explored the methodological and theoretical developments required to refine our understanding of the mechanisms underlying the biodiversity effects already observed. These developments provide a platform for another frontier in biodiversity-function research: taking experiments out into natural plant communities, with a more complex range of life histories, in complex landscapes, that directly relate to real-world conservation management (Duffy 2009; Hillebrand & Matthiessen 2009; Brose & Hillebrand 2016). The experiment in chapter 4 is one example of this growing effort.

Tropical forests are important for, amongst other things, their rich diversity, the locally and globally valuable ecosystem services they provide, and economically valuable products such as timber (Sodhi *et al.* 2010; Maycock *et al.* 2012; Edwards *et al.* 2014). Changes in land use, particularly due to agriculture and logging, have drastically changed tropical forests and will continue to do so (Newbold *et al.* 2015, see

Appendix III). Much biodiversity is threatened or has already been lost. In addition to the direct costs of this biodiversity change, there may also be knock-on effects at the ecosystem level, on the functioning of tropical forest ecosystems and the services these functions provide us. But the functional consequences of biodiversity change for tropical forest ecosystems is not clear because very few experiments have explored these regions (but see Potvin & Gotelli 2008; Yang *et al.* 2013). Because changes in tropical forest are current and due to human activity, they also present a useful setting to explore the real-world applications of biodiversity-function research. In South East Asia, vast areas have been selectively logged and already restocked by enrichment planting programmes. The enrichment planting was partially intended to aid forest restoration by helping reproduce the emergent canopy of old growth forest. But the effectiveness of this technique has not been fully tested, despite its widespread application. The history of land use, enrichment planting, and the natural variation in environmental conditions that is inherent to the systems is complex, producing a landscape that is fragmented and patchy at varying spatial scales.

In chapter 4, I showed that enrichment planting with diverse mixtures of trees may spread the risk of failed restoration in complex landscapes, by utilising species-specific responses to variable environmental conditions. The average restorative effect of enrichment planting would be maintained throughout the whole landscape. Whereas monocultures might, in unfavourable areas, fail to achieve any restorative effects (or retain overly dense stands of trees, potentially leading to wasteful self-thinning that would undermine efficient enrichment planting across large areas). The results in chapter 4 show the potential improvements in enrichment planting, as informed by biodiversity-function research. Improving this practice may help sustain

the functioning and conservation value of these forests. How much of this potential is realised will only become clear as this long-term experiment continues. Further monitoring needs to observe future survival and growth until the planted trees mature and reproduce. It will then be interesting to see how interactions between mature trees affect mixture performance relative to monocultures, and whether planting boosts recruitment of future dipterocarp generations. The restorative effect of this practice on the background degraded forest, which seedlings were planted into, is not yet clear. This is an important step for quantifying how replanting more diverse plant communities can boost functioning of the wider forest ecosystem over time.

It has been shown that effects of biodiversity on ecosystem functioning not only increase over time, but also with increasing spatial scale (Dimitrakopoulos & Schmid 2004; Venail *et al.* 2010; Cardinale *et al.* 2011), and increasing environmental heterogeneity (Finke & Snyder 2008; Tylianakis *et al.* 2008). This suggests that small-scale controlled biodiversity experiments may have underestimated the impact of biodiversity loss on ecosystems, and that study in large-scale, complex environments will be needed to estimate the full effects (Cardinale *et al.* 2012). Such heterogeneous environments, with multiple sources of variability and more opportunities for niche differentiation, will be ideal settings to study the effects of biodiversity on multiple ecosystem processes at the same time (Duffy 2009; but see Wardle & Jonsson 2010).

There are many challenges for biodiversity-function research in complex landscapes. It will be harder to control external factors, reducing our power for inference. Many factors affect ecosystem processes and there is mixed evidence on their relative importance as drivers of ecosystem change (Grace *et al.* 2007; Hooper *et*

al. 2012; Tilman *et al.* 2012). One solution could be to analyse biodiversity-function relationships within a constrained set of conditions. The constraining effect of productivity on biodiversity has been measured correlatively at large scales (Mittelbach *et al.* 2001; Adler *et al.* 2011; Fridley *et al.* 2012; Grace *et al.* 2012, 2016; Pan *et al.* 2012). Though this correlative work fundamentally differs from experimental work, it might aid research in complex landscapes. If external factors cannot be controlled it would help to know how they interact with the biodiversity-function relationship. Then they may be controlled *post hoc* and the biodiversity-function relationship can be examined, constrained within the conditions found in the landscape (Loreau 2010a). Globally distributed experiments are a more controlled way to find general patterns in forest ecosystems (Borer *et al.* 2014). Our experiment is part of such a network (Verheyen *et al.* 2015). There are also emerging methods and topics that will help extend biodiversity-function study into complex landscapes (see *What is the future?*).

The scale of the problem

In chapter 5, I quantified the effects of different farming strategies on farmland biodiversity, including plants and many other taxa. I did this by meta-analysing 30 years of published studies that compared the farmland biodiversity found on intensive conventional farms and extensive organic farms. I found that 34% of overall farmland wildlife is lost on conventional farms relative to organic farms—for plants alone, 73% of species are lost. The biodiversity experiments in grasslands, often rooted in landscapes with agricultural history, show large effects of plant species loss on ecosystem functioning (Tilman *et al.* 2001; van Ruijven & Berendse 2003; Roscher *et*

al. 2005). There is still debate on the relative merits of extensive and intensive farming for global biodiversity (Foley *et al.* 2011; Phalan *et al.* 2011; Tilman *et al.* 2011), but evidence suggests that intensive farming is especially damaging for the functioning of the ecosystems in which the farms are situated. This research was successfully communicated to European policymakers (see Appendix IV).

To understand the real-world relevance of biodiversity-function research, we need to know how biodiversity in real-world ecosystems is changing. Global biodiversity is undeniably changing and the predominant cause is human activity (Pereira *et al.* 2010; Barnosky *et al.* 2011; Pimm *et al.* 2014; Ceballos *et al.* 2015). The problem is so serious that rates of biodiversity loss might exceed the boundaries of a planetary "safe operating space for humanity" even more dramatically than climate change (Rockström *et al.* 2009; Mace *et al.* 2014). Thus, we should measure how human activity drives biodiversity change and then understand the knock-on effects of this change for natural ecosystems—I have provided such measurements of biodiversity change within agricultural systems.

To understand the functional consequences of global biodiversity for ecosystems, we need to solve problems about describing biodiversity and measuring its change. Species diversity is changing in a multitude of ways: the composition and structure of species communities, the dominance of species groups, species invasions and biotic homogenisation, and species being driven to rarity and ultimately extinction (Butchart *et al.* 2010; Magurran 2016). Extinction is irreversible—and the effects of species loss is the domain of biodiversity-function research—so it is crucial we understand how much extinction is going on. Out of the 5–10 million species that might

exist on Earth, 1.9 million have been described (Mora *et al.* 2011)—though misidentification and synonymies present great uncertainty in our knowledge (Goodwin *et al.* 2015). According to IUCN (2015), 903 known species have gone extinct since 1600. Whilst this may comprise a small fraction of global biodiversity, it represents a rate of extinction 1000 times greater than that documented in the fossil record (Pimm *et al.* 2014). But lacking information on the most diverse taxa means this extinction rate could be grossly underestimated (Régnier *et al.* 2015). Uncertainty remains on the scale of global biodiversity and how it is changing, and what types of biodiversity change most impact ecosystem functioning. But wherever truth lies within that uncertainty it seems the scale of the global biodiversity crisis is severe.

Within this global context, there is a current debate on how local species diversity has responded to recent pressures (Vellend *et al.* 2013; Dornelas *et al.* 2014; Newbold *et al.* 2015; Gonzalez *et al.* 2016). Some claim that there has been no overall loss in local species richness over recent times, because most loss is countered or even reversed by influx of species (Vellend *et al.* 2013; Dornelas *et al.* 2014). But others have criticised their approach for having spatial and temporal biases toward underestimating recent loss, and measuring change against inappropriate baseline conditions (Gonzalez *et al.* 2016). I contributed to work by Newbold *et al.* (2015), who took a different approach by using spatial variation rather changes over time (space-for-time approach), and estimated substantial losses to local biodiversity across the globe (see Appendix III). More recently, others have suggested that this space-for-time approach underestimates the impacts of human land use on local biodiversity (França *et al.* 2016), so the projections put forward by Newbold *et al.* (2015) may well be conservative. The state of biodiversity change we see may also depend on what type or

metric of biodiversity we measure (Pereira *et al.* 2013; McGill *et al.* 2015). Ecosystem functioning depends more on local biodiversity than global biodiversity (Cardinale *et al.* 2012; Hooper *et al.* 2012). The biodiversity-function relationships from experiments are important results whatever current changes in local biodiversity may be, but the broad consensus is that local diversity is declining and the functioning of ecosystems may be threatened. Even when local diversity is supplemented by an influx of other species, this may only delay local diversity loss (Gilbert & Levine 2013) or it may homogenise regional biodiversity (McKinney & Lockwood 1999; McGill *et al.* 2015).

What is the future?

Emerging methods

When moving into natural communities, synthetic approaches between experimental and observational study may be useful in maximising inference from complex landscapes. For example, experiments in complex landscapes inevitably impose a simplistic and discrete nature to provide more controlled study. But the discrete nature of experimental design will not reflect the landscapes in which they are situated, which may harm their ability to provide meaningful recommendations. One option may be to impose less discrete experimental treatments, for example by planting more continuous gradients of diversity in a way that fits the landscape. The landscape would then be part of the experimental design, rather than randomised away. This would pose problems for inference, as it would inevitably undermine the advantages of experiments. But the synthetic approach would be complementary to such experiments and may provide extra realism to biodiversity-function studies.

This change would also benefit from emerging analytical techniques. In the chapters presented here, there are a wide range of analyses implemented: predictive testing (using Bayesian inference), data-free simulation modelling, exploratory data analysis, and meta-analysis. There are many other analytical techniques that may become part of the ecologist's standard toolkit, often because they offer new ways to tackle the fact that ecological effects are conditional on multiple causes. Smoothing techniques such as Generalised Additive Mixed Models (GAMMs) have become very useful, and the theory behind them is becoming more complete (Wood 2006). GAMMs could utilise the continuous nature of new experiments in complex landscapes, to not only account for variation in the landscape but also capture that information for further inference. This would be useful, for example, for estimating the spatial scale of species interactions or spatial variation in diversity effects. As well as GAMMs, structural equation modelling (e.g. Grace *et al.* 2016) and quantile regression (e.g. Grubb 2016) are among the techniques that will be useful in elucidating effects in dynamic, real-world ecosystems.

Remote-sensing is another powerful tool that has emerged in recent decades, as new satellites were launched and started releasing freely available data (Pettorelli *et al.* 2014). Researchers interested in any global change can use the consistently measured, global yet finely grained, remotely sensed data to ask questions that would otherwise have been impossible to answer (Pettorelli *et al.* 2005; Asner *et al.* 2008, 2014). I have produced a tool to access and use one of these archives of remotely sensed data (Tuck *et al.* 2014a). To date, this tool has been used by over 4000 researchers.

Spanning such a broad swathe of research means having to decide what not to study. For example, adding trophic complexity beyond plant communities will improve assessments of the functional consequences of biodiversity change in complex landscapes. Food webs provide a quantitative framework to connect community ecology—the study of species richness, composition and interactions—with ecosystem ecology—the study of fluxes of energy and matter. Biodiversity-function research sits between these two fields of ecology, so using food webs to move beyond single-trophic-level communities could help build a quantitative framework for the ecosystem-level consequences of biodiversity change (Worm & Duffy 2003; Hillebrand & Cardinale 2004; Cardinale *et al.* 2006; Duffy *et al.* 2007; Thompson *et al.* 2012). These are rich areas for theory and experimentation, and challenges remain for this framework to become truly predictive. There is evidence that diversity loss among trophic groups has a greater impact on ecosystem functioning than loss within trophic groups (Duffy *et al.* 2007; Cardinale *et al.* 2012; Barnes *et al.* 2014). But the exact structure of trophic networks between consumers and predators can alter biodiversity-function relationships, and these trophic structures are not easily predicted (Yodzis 2000; Thompson *et al.* 2012; Digel *et al.* 2014).

Network complexity and the food web approach is also a frontier for species coexistence and evolutionary ecology (Chesson & Kuang 2008; Allesina & Levine 2011). It is possible that mechanisms of coexistence, functional traits, and trophic networks could be combined to model entire communities from the individual- up to the ecosystem-level, and assess the functional consequences of biodiversity change, analogous to how General Ecosystem Models simulate properties of the biosphere

(Purves *et al.* 2013). Community evolution models are a promising addition to research on community and ecosystem ecology (Loreau 2010b). These emerging models could be used to study the coevolution and maintenance of diverse food webs and its ecosystem-level properties (e.g. Brännström *et al.* 2010). They could potentially deliver a more mechanistic and predictive understanding of the structure and functioning of ecosystems (Loreau 2010a).

There is a growing trend to consider the effect of biodiversity on multiple ecosystem functions at the same time, so called multi-functionality (Hector & Bagchi 2007; Gamfeldt *et al.* 2008, 2013; Allan *et al.* 2013; Soliveres *et al.* 2016). Ecosystem multi-functionality appears to present an even stronger positive role of plant biodiversity in maintaining the functioning of ecosystems (Isbell *et al.* 2011). When considering only one ecosystem function there may be relatively few important aspects of species niches, so many may seem functionally redundant—although this may be a by-product of the types of short-term experiments most often conducted (Reich *et al.* 2012; Delgado-Baquerizo *et al.* 2016). However, when multiple ecosystem functions are considered more niches axes may be relevant and species differences become functionally important. Some have suggested that true redundancy might not exist (Loreau 2004). Important work is still needed to discover how ecosystem multi-functionality responds to biodiversity change and crucially whether any functions trade off with one another, such that biodiversity loss may harm one important function whilst not affecting or even benefitting another.

Traditional biodiversity experiments have been conducted under controlled environmental conditions and species composition treatments. The relationships that

emerge from these experiments might differ from those where the environment can vary, due to disturbances or climatic fluctuations, and species compositions can fluctuate accordingly—but the effect of environmental variation can be unexpected and depend on the ecosystem function being examined (Craven *et al.* 2016; Fischer *et al.* 2016; Flores-Moreno *et al.* 2016). Environmental changes might even result in less diverse mixtures that are originally more productive, but more vulnerable to future disturbance and hence prone to collapse (e.g. MacDougall *et al.* 2013). Measuring the effects of nonequilibrium conditions is an important step for future research in complex landscapes. This is particularly pressing in a world where human activity is rapidly changing landscapes (Drescher *et al.* 2016) and environmental extremes are becoming the norm (Fischer *et al.* 2016; Woodward *et al.* 2016).

Concluding remarks

The research presented here has helped make the study of diverse plant communities and their role in real-world ecosystems a more predictive science, rooted in mechanistic understanding. It has combined theory, experiment and observation in a range of ecosystems to improve both our fundamental understanding and our applied impact regarding the ecosystem-level consequences of global biodiversity loss. I have suggested methodological improvements to the study of natural plant communities, and used a suite of analytical techniques to inform European conservation policy and advise restoration strategies in threatened natural ecosystems. The future of biodiversity-function research is to continue down the same path: integrating multiple fields of ecology, solidifying our basic understanding of plant diversity and its role in functioning ecosystems, and verifying its relevance for the management of real-world

ecosystems. The field will need to encompass a greater diversity of taxa, trophic interactions, ecosystems, ecosystem functions, and measures of biodiversity itself. Perhaps then this research might unify ecology, from populations up to ecosystems, and become an invaluable framework for the management of our environment and global biodiversity.

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Appendix I

Sean L. Tuck, Helen R.P. Phillips, Rogier E. Hintzen, Jörn P.W. Scharlemann, Andy Purvis & Lawrence N. Hudson (2014). MODISTools – downloading and processing MODIS remotely sensed data in R.
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MODISTools – downloading and processing MODIS remotely sensed data in R

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Abstract

Remotely sensed data – available at medium to high resolution across global spatial and temporal scales – are a valuable resource for ecologists. In particular, products from NASA's MODerate-resolution Imaging Spectroradiometer (MODIS), providing twice-daily global coverage, have been widely used for ecological applications. We present *MODISTools*, an R package designed to improve the accessing, downloading, and processing of remotely sensed MODIS data. *MODISTools* automates the process of data downloading and processing from any number of locations, time periods, and MODIS products. This automation reduces the risk of human error, and the researcher effort required compared to manual per-location downloads. The package will be particularly useful for ecological studies that include multiple sites, such as meta-analyses, observation networks, and globally distributed experiments. We give examples of the simple, reproducible workflow that *MODISTools* provides and of the checks that are carried out in the process. The end product is in a format that is amenable to statistical modeling. We analyzed the relationship between species richness across multiple higher taxa observed at 526 sites in temperate forests and vegetation indices, measures of aboveground net primary productivity. We downloaded MODIS derived vegetation index time series for each location where the species richness had been sampled, and summarized the data into three measures: maximum time-series value, temporal mean, and temporal variability. On average, species richness covaried positively with our vegetation index measures. Different higher taxa show different positive relationships with vegetation indices. Models had high R^2 values, suggesting higher taxon identity and a gradient of vegetation index together explain most of the variation in species richness in our data. *MODISTools* can be used on Windows, Mac, and Linux platforms, and is available from CRAN and GitHub (https://github.com/seantuck12/MODISTools).

Introduction

Remote-sensing and ecology

Remotely sensed data – available at global scales at a fine to medium resolution, and often for free – are increasingly being used in ecology (Donoghue 2002; Kerr and Ostrovsky 2003; Bai et al. 2008; Chawla et al. 2012; Naeem et al. 2012; Sutherland et al. 2013). In particular, products derived from NASA's MODerate-resolution Imaging Spectroradiometer (MODIS) instruments (Justice et al. 1998) are a unique resource for research in many areas of ecology, conservation biology, and global change research (Table 1). Remote-sensing instruments measure physical, geochemical, and biological processes that allow us to evaluate the environment in a scalable way: from characterizing the distribution of a species or phenology of a plant community, to recording land cover change,

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Table 1. Moderate-resolution Imaging Spectroradiometer products available for download using *MODISTools*, and examples of their use. Potential summary measures are techniques that are currently used in the literature and may be incorporated into *MODISTools* in future releases. Several other methods have been proposed to summarize and thereby reduce the serial correlation in time series of remotely sensed data, including principal components analysis (PCA; (Eastman and Fulk 1993), temporal Fourier processing (e.g., Scharlemann et al. 2008), and simple metrics such as bioclimatic variables (e.g., BIOCLIM variables; Xu and Hutchinson 2011).

Code	Product	Examples of product use	Potential summary measures
MOD09/MYD09	Surface reflectance	Spatiotemporal distribution of rice phenology (Sakamoto et al. 2006) Monitoring intensification of croplands (Galford et al. 2008) Land cover mapping of Germany (Colditz et al. 2011)	NA – reflectance data from which many measures can be derived
MOD11/MYD11	Surface temperature and emissivity	Investigating the relationship between land surface temperature and vapor pressure deficit (Hashimoto et al. 2008) Calculating air surface temperature using remotely sensed data and meteorological data (Benali et al. 2012)	Degree days; length of period above temperature threshold
MOD43/MCD43	Nadir BRDF-adjusted Reflectance	Land cover mapping of South Africa (Colditz et al. 2011) Studying vegetation phenology in the United States (Zhang et al. 2003)	NA – reflectance data from which many measures can be derived
MOD13/MYD13	Vegetation Indices	Crop-related LULC classification in the U.S. Central Great Plains (Wardlow et al. 2007) GPP estimates for biomes across the conterminous US (Xiao et al. 2010) Quantifying tree cover in an African grass savanna (Gaughan et al. 2013)	Phenological measures (eg. season shift index); change vector magnitude; integrated vegetation indices
MOD15	LAI/FPAR	Comparison of products suitable for vegetation phenology (Ahl et al. 2006) GPP estimates for biomes across the conterminous US (Xiao et al. 2010)	Phenological metrics; annually integrated LAI/FPAR
MOD17	Gross primary productivity (GPP), Net photosynthesis	Calculating global terrestrial net primary production (Running et al. 2004) Validation of NPP/GPP across multiple biomes (Turner et al. 2006)	Total productivity; peak NPP; seasonality of GPP
MCD12	Land cover and change	Estimation of timber volume (Nelson et al. 2009) Presentation and validation of global land cover types (Friedl et al. 2002)	*Already functional in MODISTools*

natural or human-caused, from the ecosystem up to the global level. Several MODIS data products have been used to investigate land surface temperatures, monitor intensification of croplands, estimate volume of timber stocks, and assess change in the magnitude and frequency of fires (Table 1). Whilst it is beyond our scope to review in detail all ecological questions to which MODIS data have been applied, we discuss the relevance of MODIS data to monitoring global biodiversity change as this will be pertinent to our example analysis.

Global biodiversity is declining (Balmford et al. 2003; Gaston et al. 2003; Collen et al. 2009; Tittensor et al. in press) and is predicted to continue to decline at unprecedented rates (Pereira et al. 2010; Tittensor et al. in press). Tackling this problem requires global biodiversity monitoring, such as (Collen et al. 2009; Pereira et al. 2010) which have analyzed indicators of global biodiversity change over recent decades. At global spatial scales, the time and cost involved make field-based monitoring near impossible. Remotely sensed data with global coverage and continuous, frequent measurements over periods exceeding the lifespan of most ecological studies can help bridge this gap in biodiversity monitoring; consequently, there has been an increase in the use of remotely sensed data to project biodiversity over large extents (Fuller et al. 1998; Kerr and Ostrovsky 2003; Turner et al. 2003; Pettorelli et al. 2005; Lassau and Hochuli 2008; St-Louis et al. 2014). Combining remotely sensed data with biodiversity observations using meta-analysis (Gibson et al. 2011) or synthetic analysis (Newbold et al. 2014) has

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become more fruitful with advances in remote-sensing instruments, data archives, and error correction methods such as the bidirectional reflectance distribution function (BRDF) that removes directional effects of view angle and illumination (Nicodemus et al. 1977). Importantly, these data can now be accessed at spatial and temporal scales similar to ecological field data (Kerr and Ostrovsky 2003).

MODIS remotely sensed data

MODIS provides data with global coverage at 250 m^2, 500 m^2, and 1 km^2 spatial resolutions collected twice daily by NASA's Terra and Aqua satellites since the year 2000. Raw data from the MODIS sensors are composited to daily, 8 day, 16 day, and yearly imagery and preprocessed into discipline-specific MODIS products for atmospheric, oceanic, or land process applications. The Land Processes Distributed Active Archive Center (LP DAAC – https://lpdaac.usgs.gov) holds MODIS data on metrics of land processes such as surface reflectance, land cover/land cover change, land surface temperature and emissivity, vegetation indices (Normalized Difference Vegetation Index, NDVI, and Enhanced Vegetation Index, EVI), leaf area index and fPAR (fraction of photosynthetically active radiation), evapotranspiration, net photosynthesis, and primary productivity (https://lpdaac.usgs.gov/products/modis_products_table; examples of their usage are shown in Table 1).

Many ecological studies, such as meta-analyses, observation networks or globally distributed networks of experiments, combine information from large numbers of locations. Such studies allow comparison of patterns across space and time and estimation of global responses. They can help to identify and understand generalities (Borer et al. 2014), and synthesize the literature to predict the responses of ecological communities to global change (Newbold et al. 2013). The global coverage of remotely sensed data presents a valuable resource for global ecological studies but the existing MODIS access mechanisms make it hard to obtain the relevant data.

Despite the increasingly common use of MODIS data, there is a burden on the investigator to access, download, and store them. The Oak Ridge National Laboratory Distributed Active Archive Center (ORNL DAAC) provides online access to spatially and temporally delimited subsets (ORNL DAAC 2014). The user can download one subset at a time, via email, after manually inputting subset definitions each time. Manual input of spatial and temporal limits can be both error-prone and time-consuming. A web service is available (http://daac.ornl.gov/MODIS/MODIS-menu/modis_webservice.html) that can facilitate automation but this requires familiarity with protocols and languages such as SOAP (Simple Object Access Protocol; Gudgin et al. 2007) and XML (Extensible Markup Language), which ecologists are typically not familiar with, are time-consuming to learn and shift attention away from science.

Utilizing MODIS data with MODISTools

MODISTools – a package for the R Statistical Computing Language (R Core Team 2014) – allows MODIS data for multiple locations, time periods and products to be downloaded, and stored using a single line of R code. Downloaded data are stored in a simple, memory-efficient way that can be easily retrieved and manipulated. *MODISTools* provides functions for processing downloaded data and merging these data with the user's ecological response data, making it possible to apply MODIS data to research questions with minimal effort. By avoiding the time-consuming and often error-prone manual steps, the package simplifies access to MODIS data, thereby increasing research efficiency. *MODISTools* completes all functioning within the R environment without requiring external software.

We are aware of one other existing R package, *MODIS*, that downloads MODIS data (Mattiuzzi et al. 2013). This is geared toward use of data in a geographic information system (GIS), which often requires the user to download and interact with additional software, such as the MODIS Reprojection Tools (LP DAAC 2014). *MODISTools* completes all functioning within the R environment without requiring external software. The *MODIS* R package provides useful functions to download MODIS data at one or a few locations as raster files for use in GIS. Many users of MODIS data will require some data processing steps in a GIS environment, for example, extracting a complex shape, such as the boundary of a country or national park, from the downloaded rectangular MODIS tile. In our experience of ecological modeling, an ideal format for downloaded MODIS data has been in ASCII plain text format, which can be readily downloaded from the ORNL DAAC MODIS web service. Although *MODISTools* does not itself contain functions for GIS processing steps, it connects to a GIS environment efficiently by providing a function for creating ASCII raster grids from the downloaded files. These new files are provided with the correct MODIS projection datum (PRJ file) that allows them to be easily imported into standard GIS software.

Example analysis

We demonstrate the utility of *MODISTools* applying MODIS data to ecological questions, particularly studies involving many sites, by conducting an illustrative analysis of our own. We analyzed species richness data from

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the literature, investigating the relationship between local species richness in temperate regions and spatiotemporally matched vegetation indices. We show every step from downloading data, through data processing, and analysis; this demonstrates the value that *MODISTools* provides in each step of the method and how it can aid researchers to apply MODIS data to ecological questions in general.

Many studies have reported a positive correlation between species richness and aboveground net primary productivity, although the relationship might not be linear depending on the spatial scale (Gaston 2000). Previous studies have established a relationship between aboveground net primary productivity and vegetation indices (Reed et al. 1994; Waring et al. 2006): vegetation indices describe the greenness of the vegetation and the Normalized Difference Vegetation Index (NDVI) is one of the most commonly used (Pettorelli et al. 2005). NDVI is calculated using red and near-infrared wavelengths of light that are reflected and captured by the satellite. Chlorophyll will absorb red light, while the mesophyll structure of a leaf will scatter reflected near-infrared light. Therefore, if the proportion of reflected near-infrared light captured is greater than red light captured this represents a signal of vegetation. NDVI values increase from 0 to 1 as the amount of vegetation increases, whilst negative values indicate an absence of vegetation (Myneni et al. 1995). An extension of NDVI, the Enhanced Vegetation Index (EVI), adjusts for atmospheric aerosol interference and improves sensitivity so values do not saturate in areas of high biomass (Huete et al. 2002). Because of their relationship with aboveground net primary productivity, NDVI and EVI are often used as predictors for species richness, with good results (Hurlbert and Haskell 2003; Seto et al. 2004; Waring et al. 2006). Time series, rather than one off measurements, of vegetation indices are required to capture vegetation dynamics relevant to the species richness data, and to minimize the contamination of this signal of vegetation dynamics due to noise.

Normalized Difference Vegetation Index is publicly available from various data sets; the earliest was collected from the National Oceanic and Atmospheric Administration's Advanced Very High Resolution Radiometer (NOAA-AVHRR), with data extending back to 1981 (James and Kalluri 1994). EVI has been proposed comparatively recently, but MODIS products provide global data for both indices. As with the multitude of other products available through the LP DAAC MODIS archive, these vegetation indices can be summarized in many ways to produce measures relevant to ecological study (see Pettorelli et al. 2005 for a review of NDVI measures).

Here, we focus on three measures of NDVI and EVI time series that are calculated by *MODISTools*: the maximum value in a time series, the temporal mean, and the temporal variability (Fig. 1). The time series were smoothed with temporal interpolation, using `MODISSummaries`, prior to calculating these summary statistics. Smoothing reduces noise in the time series due to cloud cover, or high solar or scan angles (Pettorelli et al. 2005). The temporal variability can be characterized as the average temporal variation of vegetation index within a site, factoring in the minimum value: it is the time-averaged difference between the total area under the time series and the area under the minimum value in the time series. Temporal variability is of interest when comparing among sites as the average variation in a vegetation index can be equal when the mean is not, and *vice versa*. In this context, temporal variability can be seen as a measure of seasonality; higher temporal variability indicates increased change in vegetation cover from one season to another. It could alternatively represent offtake, with a higher temporal variability indicating more harvesting at a site.

These summary measures of NDVI and EVI were the explanatory variables that we related to local species rich-

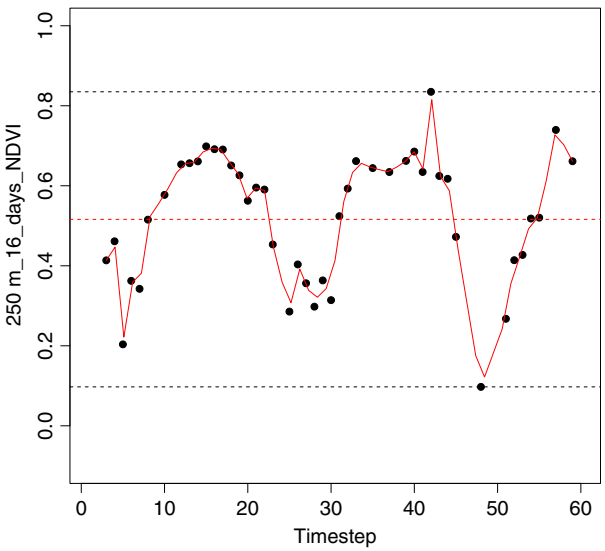

Figure 1. Time series of NDVI following a `QualityScreen`, as produced by an optional argument `DiagnosticPlots` in `MODISSummaries`, that illustrates the relationship between the three measures used: maximum time-series value, temporal mean, and temporal variability. On the y-axis is NDVI at 250 m^2 resolution (the axis label is the data band name for this Science Data Set). On the x-axis is time, with 16-day regular intervals. This time series produces a temporal variability value of 0.4. Variability is defined in the introduction of the main text. Upper black dashed line indicates the maximum value in the time series and the lower black dashed line indicates the minimum value in the time series. The solid red line indicates the interpolated values of the NDVI. Red dashed line indicates the mean of these values.

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ness across temperate forests globally. The diversity data were sampled from the PREDICTS database (www.predicts.org.uk – Newbold et al. 2014; Hudson et al. unpublished data), a compilation of data from studies worldwide that have measured diversity (of one or more species) over multiple habitat types. Data were collected from published papers and, when necessary, subdivided further into studies with distinct methodologies. Within each study, there were multiple sites where diversity (in this case species richness) was measured. Our methods detail the utility that *MODISTools* provided at each stage. We then discuss our results and reflect on the benefits of using *MODISTools* for such research and more broadly. The code used to analyze the data and a dummy data set, generated from the real data we have analyzed, are available for reproducing the entire workflow presented (see Table S1, Appendices S1–S4).

Method

Data preparation

A subset of diversity data from the PREDICTS database was extracted using the following criteria: (1) studies were within the Temperate Broadleaf and Mixed Forests Biome (as determined by the WWF biome layer, Olson et al. 2001); (2) the studies sampling period ended post 2000 (to ensure MODIS data were available); (3) studies contained more than 20 sites; and (4) studies captured a diversity metric that could be converted to species richness. The resulting data set contained 526 sites from eight different studies (Brunet et al. 2011; Buczkowski 2010; Chapman and Reich 2007; Lantschner et al. 2008; Lentini et al. 2012; Su et al. 2011; Weller and Ganzhorn 2004; Winfree et al. 2007 – Magura et al. 2010 was also considered but removed from analysis due to small sample size).

Normalized Difference Vegetation Index and EVI were downloaded for each of the 526 sites using the `MODISSubsets` function. `MODISSubsets` fetches data from the ORNL DAAC MODIS Land Product Subsets web services. The input to the function is an R data.frame or a text file specifying all sites where diversity data were collected (ST1). For each site, this data frame must specify lat/long coordinates and dates for the time series requested. End dates and optionally start dates for each time series can be specified; or, just end dates can be given with an optional time-series length that `MODISSubsets` will consistently download for when the timespan of preceding data permits. Specific column names are necessary for `MODISSubsets` to find the information it needs: "lat," "long," "end.date," and optionally "start.date". The input coordinates must be in decimal degrees format with WGS84 datum. As with any spatial data, ensuring the coordinates consistently conform to the intended datum is imperative for correctly specifying locations. *MODISTools* provides the `ConvertToDD` function to reformat coordinates into decimal degrees from either degrees minutes seconds or degrees decimal minutes. The dates can be specified in two different formats: (1) years, in which case data will be downloaded from the beginning of the year, or (2) POSIX formatted dates (YYYY-MM-DD) that allow more precise requests.

Once the time series coordinates and dates have been specified, the user must delimit the area of interest around each location, defined as the distance in kilometers around each location. Two directions must be specified, firstly in the north/south direction from the focal pixel (pixel identified by the coordinate supplied), and secondly the east/west direction. Using the values (0,0) would result in data for the focal pixel only. The values (1,1) identify an area of interest that, in addition to the focal pixel, includes surrounding pixels for 1 km in each direction. The maximum area of interest surrounding a location that can be retrieved using the ORNL DAAC MODIS web service is (100,100). This two-dimensional input means rectangles of any size smaller than the maximum area of interest can be specified. The number of pixels included in a request depends on the resolution of the data requested: for NDVI data at 250 m^2 resolution, a 2.25 × 2.25 km area, downloaded using values (1,1), will contain 81 pixels.

Users must also state what MODIS data product is required. Each data "product" released contains many variables that are stored in separate "Science Data Sets," also known as data "bands." For example, the EVI and NDVI bands that we require can be found in the vegetation indices product (MOD13Q1), alongside other variables and indicators of pixel reliability. Functions `GetProducts` and `GetBands` help specify the desired data type.

Download the data

We downloaded NDVI and EVI at 250 m^2 resolution as well as pixel reliability for these data to allow quality control before analysis. The size of area of interest used to relate vegetation indices to our diversity data may have an impact on the result. It may be that the most local conditions sufficiently explain species richness, or that the surrounding area must also be captured. We analyzed the data at both the focal pixel (`Size = c(0,0)`) and 6.25 × 6.25 km tile (`Size = c(3,3)`) scales and compared which best explained variation in species richness. The function `ExtractTile` can

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extract subsets from larger areas of interest to avoid duplicated downloads. To ensure all estimates are based on the same length of time series, we requested 3 years prior to the species richness sampling date at each site (year of sampling date plus `TimeSeriesLength` argument). The following line of code completes the download for the request described:

```
MODISSubsets(LoadDat = PREDICTS, Products =
"MOD13Q1", Bands = c("250m_16_days_NDVI",
"250m_16_days_EVI",
"250m_16_days_pixel_reliability"), Size = c(3,3),
StartDate = FALSE, TimeSeriesLength = 2)
```

For each site downloaded `MODISSubsets` saves a text file (ASCII format, comma separated, no header), with a log file listing all the unique downloads and their download status (see Table 2 for an explanation of downloaded data structure). The data saved to these files can be easily read back into R using `MODISTimeSeries`. If the input data set contains unique identifiers (IDs) for each site, these will be used as file names; if not, the function will generate unique IDs itself and use these. All files will be stored in a user-specified directory (working directory by default), and this directory path will be printed in R prior to downloading. The download speed primarily depends on server traffic at the ORNL DAAC MODIS web service, and to a lesser extent on internet connection and size of data set being downloaded. Speed can be highly variable for even the same data set. We replicated the download of our 526 sites and on one occasion it took 2–3 h and another approximately 12 h (see Table 3 for performance metrics).

No internet service can guarantee 100% availability and `MODISSubsets` employs a strategy to work around temporary loss of availability of the ORNL DAAC MODIS server and to download as many of the requested subsets as possible. If `MODISSubsets` encounters a problem, such as a loss of connection, it produces a warning message and retries that subset until either it has been downloaded or 15 min have elapsed, after which time it attempts to download the next of the requested subsets. Any error and warning messages encountered during downloading are stored in the log file so they can be traced to the problematic time series. `MODISSubsets` then attempts a second download of any subsets that could not be fetched in the first pass, minimizing the amount of missing data in the final output. `MODISSubsets` writes each unique subset (i.e., combination of lat/long location and time-series start and end dates) to a single text file, minimizing download and storage load. The text files can easily be combined into a single text file (CSV format), along with the input ecological data, facilitating modeling (see Statistical analysis). `UpdateSubsets` can also be used to complete an unfinished download, or download for new sites added to a data set.

Table 2. An explanation of the sections, for example, text string (in text), which shows the format of data subsets written in the ASCII text file outputs from `MODISSubsets`. These ASCII files can be read back into an R workspace using `read.csv("filename.asc", header = FALSE, as.is = TRUE)`. The resulting data.frame would contain columns for each section described below and rows for each date in the time series.

Section description	Example
Number of tile rows	1
Number of tile columns	1
x-coordinate (MODIS datum longitude) for lower left corner of tile	13702705
y-coordinate (MODIS datum latitude) for lower left corner of tile	−3709977
Pixel size (meters)	231.6564
Unique Identifier	MOD13Q1.A2009001.h30v12.005.2009020003129.250m_16_days_EVI
Shortname code for the MODIS product requested	MOD13Q1
Date code for this string of data, year and Julian day (A[YYYYDDD])	A2009001
Input coordinates and the width (Samp) and height (Line) in number of pixels of the tile surrounding the input coordinate	Lat-33.3636449991Lon147.548402Samp1Line1
Date–time that MODIS data product was processed (YYYYDDDHHMMSS)	2009020003129
All values following are data for each pixel in the tile (n = Samp × Line), which are ordered by row. The number of columns should equal the number of pixels in the tile – in this case 1. See `?ExtractTile` to rearrange the data back into spatially ordered tiles.	1567

Process the data

The `MODISSummaries` function collates the downloaded data and computes the per-pixel time-series summary statistics. Prior to summarizing the data, it uses the pixel reliability indicator to filter out poor-quality and missing data (data with pixel reliability values > 0 were omitted). `MODISSummaries` then assem-

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Table 3. Performance metrics for the downloading function, `MODISSubsets`, all times reported in seconds. The times reported here are for a simple subset request (one site, focal pixel only, for 1 year) using an example data.frame provided with *MODISTools* called `SubsetExample`. The effect of time-series length (3 years), tile size (2.25 × 2.25 km tile size – 81 pixels), and number of sites (four sites, using the *MODISTools* data.frame `EndCoordinatesExample`) on time taken to download is shown for multiple computers. The largest source of variation in download times will be traffic at the ORNL DAAC MODIS server, and internet connection.

System	Simple request	Time-series length	Tile size	Number of sites
MacBook Air (2013) Processor: 1.3 GHz Intel Core i5 Memory: 8 GB 1600 MHz DDR3 Software: OSX 10.9.4 Internet: up to 30 MB wireless	51.962	119.687	32.177	173.033
MacBook Pro Processor: 2.4 GHz Intel Core 2 Duo Memory: 4 GB 1067 MHz DDR3 Software: OSX 10.6.8 Internet: up to 90 MB wireless	36.887	99.253	37.093	148.616
MacBook Mini Processor: 2.6 GHz Intel Core i7 Memory: 16 GB 1600 MHz DDR3 Software: OSX 10.8.5 Internet: Network cable	47.387	112.134	39.210	158.606

bles the pixel level summary statistics with the user's data (`PREDICTS` in our example) that contain response variables and returns a data frame that can be used for statistical modeling with existing R modeling tools. Hence using two function calls, one to download data (`MODISSubsets` function call above) and the other to process data (`MODISSummaries` function call below), we generated new columns in our ecological data set that provided the explanatory variables for our analysis:

```
MODISSummaries(LoadDat = PREDICTS, Product =
"MOD13Q1", Bands = c("250m_16_days_NDVI",
"250m_16_days_EVI"), ValidRange = c(-2000,10000),
NoDataFill = -3000, ScaleFactor = 0.0001,
StartDate = FALSE, QualityScreen = TRUE,
QualityBand = "250m_16_days_pixel_reliability",
QualityThreshold = 0, Max = TRUE, Mean = TRUE,
Interpolate = TRUE, Yield = TRUE)
```

Statistical analysis

We fitted generalized linear mixed effects models to the species richness data, using a poisson error distribution with a log link function as is appropriate for count data. To avoid collinearity among explanatory variables that are based on the same data (including EVI and NDVI variables, as EVI is an extension of NDVI), each variable was fitted in a different model. To account for homogeneity among sites within a study, we fitted the study grouping variable as a random effect. The fixed effects were the remotely sensed vegetation index measures, a higher taxon factor (Aves, Coleoptera, Hymenoptera, Pinopsida), and the interaction between these effects. Models were fitted using *lme4 v1.1-6* in R (Bates et al. 2014). The R^2 for the models was calculated using the *R.squaredGLMM* function from the *MuMIn* R package (Barton 2014). R^2 is a good indication of the goodness of fit of the data to the model and a simple indicator of how well the model could be used for prediction (Nakagawa and Schielzeth 2013).

Results and Discussion

On average, species richness increased with increasing vegetation indices, as has been reported in previous studies (Waring et al. 2006). Our findings also corroborate previous results that have shown these responses to be taxa-specific (Bailey et al. 2004; Gibson et al. 2011; Newbold et al. 2013, 2014) and, although less frequent in our findings, scale-specific (Hurlbert and Haskell 2003). Overall, models at all scales produced similar R^2: values range from 0.57 to 0.83, which suggests the models explain a large amount of variation in species richness and hold some predictive power. However, rather than being definitive results, these findings are preliminary and presented here primarily to highlight the use of *MODISTools*. Thus, only a subsection of the results are discussed in the text, but additional results and figures can be found in the Supporting Information (Appendices S3, S4, and Figs. S1, S2, S3).

Species richness among all higher taxa except Aves covaried positively with maximum NDVI at the focal pixel scale, but these responses were variable so the interaction term was retained (Fig. 2). The strongest relationships estimated were for Hymenoptera and Coleoptera. Although these slope estimates should be interpreted with caution, as our data set only included 22 sites for Coleoptera, previous studies have also shown strong positive correlations of beetle species to NDVI (Lassau and Hochuli 2008). Mean NDVI at both the small and large spatial scale showed a positive correlation with species richness for all taxa except Aves (Figs. S1 and S2). All higher taxa

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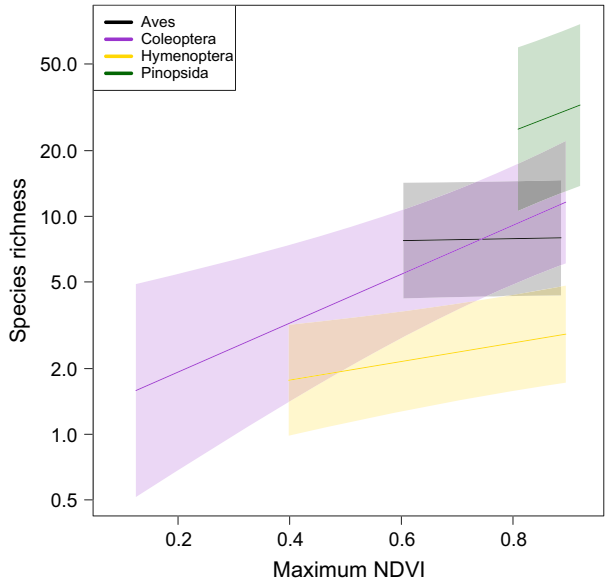

Figure 2. Responses of four taxa to changes in maximum NDVI. Aves (black line) showed no significant response to changes in maximum NDVI, while Coleoptera (purple line), Hymenoptera (yellow line) and Pinopsida (green line) showed a positive response to increasing maximum NDVI. Shaded areas indicate 95% confidence intervals.

showed similar positive correlations with NDVI variability at the focal pixel scale (Fig. S1), but with varying intercepts; the interaction was retained, however, for NDVI variability at the larger scale.

In most cases, EVI and NDVI variables produced similar patterns, but the response of Pinopsida species richness to maximum value in a time series was dependent on the vegetation index used (Figs. S2 and S3). Unlike NDVI, EVI considers the nonlinear differences between the radiative transfer of red and near-infrared light through a canopy (Pettorelli et al. 2005). This may underlie the discrepancy between vegetation indices, as conifers produce a different tree architecture and canopy structure from deciduous trees. Leaf color may also be important: The bluish color found in adult trees of some species within Pinopsida would be incorporated into the EVI, which is calculated using blue reflectance, but not NDVI.

Despite previous work showing the contrary (see Koh et al. 2006; using 1 × 1 km NDVI derived from the SPOT-VGT imaging sensor), bird species richness was not significantly affected by changes in any of the vegetation index variables, at neither the small or large spatial scales. Seto et al. (2004) found that the relationship between bird species richness and vegetation index variables strengthened as the spatial extent considered increased, possibly due to birds having larger home ranges. Therefore, the lack of relationship we found within Aves may in part be caused by analyzing our remotely sensed variables at an inappropriate spatial extent.

Conclusions

The benefits of the automated approach that *MODISTools* takes are valuable. All 526 subsets of data, for the entire timespan of interest, can be retrieved using one line of R code. Using any other method that cannot automate the process over subsets, such as the email service using the online tool, would require 526 independent subset requests to be input manually by the user: researcher time and opportunity for error would greatly increase. *MODISTools* provides a more scalable approach, so the benefit of using *MODISTools* increases with the number of subsets requested. Our tool was equally beneficial for the data processing steps (without using a GIS environment) by producing our MODIS derived variables and matching them to the species richness data, ready for ecological modeling.

The package is being actively developed, and future releases will include more product-specific post-download processing. Summaries suitable for vegetation indices, such as time-integrating vegetation indices, are already available but these will be expanded to include a range of summary functions for a wider set of MODIS products, for example, temporal Fourier processing (Scharlemann et al. 2008). Processing will become more flexible by allowing the user to write custom summary functions. Additional methods for quality control of time-series data will also be included, allowing interpolation of missing values using adjacent time-series data (Rowhani et al. 2008). The interaction between *MODISTools* and spatial processing tools, in R and GIS environments, can also be further expanded.

The current stable release of *MODISTools* is available on CRAN (http://cran.r-project.org/web/packages/) – the usual mechanism for making R packages readily available – and can be installed by running: `install.packages("MODISTools")`. The latest "in-development" version of *MODISTools* can be accessed at https://github.com/seantuck12/MODISTools. For a more in-depth walkthrough to downloading and using MODIS data with *MODISTools*, see the associated vignette by installing the package and then entering `vignette("UsingMODISTools")` into R.

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Conflict of Interest

None declared.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. R script for downloading MODIS vegetation indices for analysis.
Appendix S2. R function to create a vector of weighted means the same order as a vector.
Appendix S3. R script for analysing EVI and NDVI data for a single pixel.
Appendix S4. R script for analysing EVI and NDVI data for a 6×6 km area of interest.
Figure S1. Response of species richness to vegetation indices at the focal pixel scale.
Figure S2. Response of species richness to NDVI at the 6.25×6.25 km scale using spatially-weighted and unweighted data.
Figure S3. Response of species richness to EVI at the 6.25×6.25 km scale using spatially-weighted and unweighted data.
Table S1. Dummy ecological data set for conducting analysis.

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Appendix II

Zia Mehrabi & **Sean L. Tuck** (2015).
Relatedness is a poor predictor of negative plant–soil feedbacks.
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New Phytologist

Research

Rapid report

Relatedness is a poor predictor of negative plant–soil feedbacks

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Key words: aboveground–belowground ecology, coexistence, Darwin's naturalization hypothesis, invasion, phylogeny, soil sickness.

Summary

- Understanding the mechanisms underlying negative plant–soil feedbacks remains a critical challenge in plant ecology. If closely related species are more similar, then phylogeny could be used as a predictor for plant species interactions, simplifying our understanding of how plant–soil feedbacks structure plant communities, underlie invasive species dynamics, or reduce agricultural productivity.
- Here, we test the utility of phylogeny for predicting plant–soil feedbacks by undertaking a hierarchical Bayesian meta-analysis on all available pairwise plant–soil feedback experiments conducted over the last two decades, including 133 plant species in 329 pairwise interactions.
- We found that the sign and magnitude of plant–soil feedback effects were not explained by the phylogenetic distance separating interacting species. This result was consistent across different life forms, life cycles, provenances, and phylogenetic scales.
- Our analysis shows that, contrary to widespread assumption, relatedness is a poor predictor of plant–soil feedback effects.

Introduction

Negative plant–soil feedbacks occur when conspecific adults culture soil to the relative disadvantage of their own offspring (Bever, 1994; Mangan *et al.*, 2010; Van der Putten *et al.*, 2013). This process can maintain diversity by generating frequency-dependent population growth, and plays key roles in agriculture and invasion ecology (Packer & Clay, 2000; Klironomos, 2002; Callaway *et al.*, 2004; Petermann *et al.*, 2008; Mangan *et al.*, 2010). Two widely proposed mechanisms by which negative plant–soil feedbacks operate are through accumulation of host-specific soil borne pathogens and nutrient resource depletion (Kulmatiski *et al.*, 2008; Mangan *et al.*, 2010; Burns & Strauss, 2011; Flory & Clay, 2013; Van der Putten *et al.*, 2013). Evidence that closely related plant species are more likely to share natural enemies or resources (Darwin, 1859; Webb *et al.*, 2006; Gilbert & Webb, 2007) has led to a belief that plants will perform less well on soils cultured by more closely related species (Brandt *et al.*, 2009; Burns & Strauss, 2011; Liu *et al.*, 2012; Callaway *et al.*, 2013; Sedio & Ostling, 2013) (Fig. 1). However, discontinuities between evolutionary history, plant functional traits, and niche partitioning do not support the generalizability of this hypothesis (Mouquet *et al.*, 2012; Best *et al.*, 2013; Narwani *et al.*, 2013; Pavoine *et al.*, 2013; Kelly *et al.*, 2014). If traits responsible for resource use or host susceptibility to natural enemies are not widely conserved, or if the sum of plant–soil interactions remain neutral, relatedness may in fact be a poor predictor of negative plant–soil feedback effects.

More than two decades of plant–soil feedback research have generated sufficient number of studies to allow us to test the utility of evolutionary history for predicting negative plant–soil feedback effects. Here we present a formal meta-analysis of 329 experiments which compared the growth response of plant species to soil cultured by conspecifics relative to heterospecifics (133 plant species in 276 unique pairwise interactions). For each pairwise species interaction, we calculated Hedges' *d* standardized mean difference, where a negative effect size corresponds to a positive plant response to heterospecific-cultured soil relative to conspecific-cultured soil (i.e. a signal of negative plant–soil feedbacks). We then extracted the phylogenetic distances between species pairs in each experiment from a chronogram built using publicly available data. We meta-regressed our calculated effect sizes on the phylogenetic distance estimates by fitting a hierarchical Bayes linear model that accounts for sampling dependence (e.g. same conspecific control soils across multiple experiments), and hierarchical dependencies (e.g. multiple experiments within the same study) in the dataset (Stevens & Taylor, 2008). We estimated an

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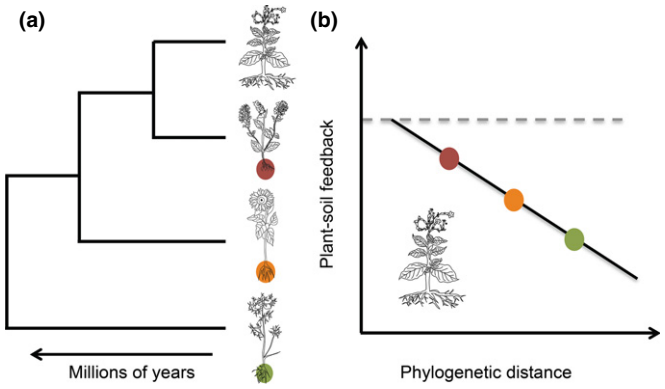

Fig. 1 The proposed relationship between phylogeny and plant–soil feedback effects. (a) The phylogenetic relationships between species; (b) the expected outcome of the interaction between a focal species and the soils of its relatives. Negative plant–soil feedbacks represent the increased performance of species on soils cultured by heterospecifics relative to conspecifics.

overall slope with 95% credible intervals to test whether phylogenetic distance between species pairs could predict negative plant–soil feedbacks, and whether this relationship differed among different subsets of our dataset: plant life forms, life cycles, and native–exotic interactions.

Materials and Methods

Study selection

We searched all published work on ISI Web of Knowledge for the last 20 yr (1993–2013) with three topic-level searches: soil*feedback*phylogeny; soil*feedback*experiment*; and plant*feedback*soil*, and screened these alongside additional references and unpublished works for studies that recorded pairwise plant–soil feedback biomass responses. A PRISMA statement, showing this flow of information through our study selection process, can be found in Supporting Information Notes S1. All studies in our final selection had data on means and standard deviations that were readily accessible from figures or through author correspondence.

Phylogeny estimation

Genbank accessions for five gene regions (ITS, *rbcL*, *matK*, *ndhF*, *trnL-F*) were retrieved for the species in the feedback experiments and individually aligned using MAFFT (v.7.205) with the l-ins-i algorithm (Katoh & Standley, 2013). Alignments were concatenated into a supermatrix and maximum-likelihood based estimation of the phylogeny performed using RAxML (v.7.0.4), optimized for each gene region under the GTR-GAMMA substitution model (Stamatakis, 2006). We restricted our search by using a constraint tree built from systematic treatments of the recognized tribes, families, orders and higher-level clades of the species in our study (Wojciechowski *et al.*, 2006; Potter *et al.*, 2007; Panero & Funk, 2008; Couvreur *et al.*, 2010; Bendiksby *et al.*, 2011; Soltis *et al.*, 2011; Grass Phylogeny Working Group II, 2012). We congruified (Eastman *et al.*, 2013) our maximum likelihood estimate with the most resolved angiosperm chronogram currently available (Tank *et al.*, 2013; Zanne *et al.*, 2013), and used penalized likelihood rate smoothing to create a time scaled phylogeny of the species in our study (Smith & O'Meara, 2012). Phylogenetic distances between species in the 329 pairwise interactions were extracted using the *cophenetic.phylo* function in the R package *ape* (Paradis *et al.*, 2004). Full details of the phylogeny estimation are presented in Supporting Information Methods S1.

Hierarchical Bayesian meta-analysis

To determine the influence of phylogeny on plant–soil feedbacks we fitted a hierarchical Bayesian model accounting for sampling and hierarchical dependencies in our data. Our model in matrix form is:

$$d = X\beta + \delta + \varepsilon \qquad \text{Eqn 1}$$

where d is the vector of effect size estimates from all the experiments; X, a design matrix with our covariates, β, a vector of parameters; δ, a vector of hierarchical errors; and ε a vector of sampling errors. It assumes the distributions:

$$\delta \sim N(0, \Delta)$$

$$\Delta = \tau^2 I + \zeta M$$

$$\varepsilon \sim N(0, V) \qquad \text{Eqn 2}$$

where V is the sampling variance-covariance matrix, with known sampling variances and covariances, Δ represents the variance and covariance among random deviations of $X\beta$ from the effect sizes being estimated. Thus, Δ is a block-diagonal matrix, with hierarchical variance τ^2 on the diagonal (I) and blocks (M) of hierarchical covariance ζ on the off-diagonal for pairs of hierarchically dependent effect sizes. We estimated the slope for phylogenetic distance with 95% credible intervals for this estimate, calculated by multiplying the posterior standard error of the coefficients by the 95% quantile of a t-distribution with N-k degrees of freedom. Our analysis was carried out using R 3.1.0 (R Core Development Team, 2013) with the R package *metahdep* (Stevens & Nicholas, 2009). Further details of the methods and our study design, including the full dataset and R code used in the paper, can be found in our Supporting Information Methods S1, Notes S2 and Table S1.

Results and Discussion

Our analyses show that phylogenetic distance between species pairs is a very poor predictor of plant–soil feedback effects (−0.00035; 95% credible interval (CI): lower = −0.00077, upper = 0.00007, n = 329; Fig. 2a). Whilst there was a moderately negative plant–soil feedback effect observed on average (−0.330; 95% CI: lower = −0.503, upper = −0.156, n = 329), variation in

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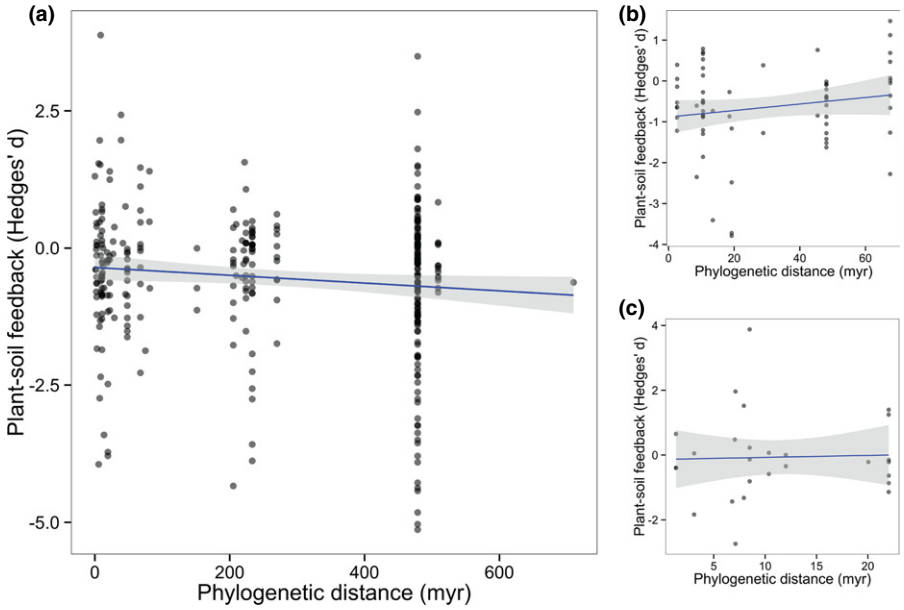

Fig. 2 (a) Relatedness is a poor predictor of negative plant–soil feedbacks. Meta-regression of 329 experimental plant–soil feedback effects against phylogenetic distance between interacting species pairs (total species = 133). There was also no relationship between relatedness and plant-soil feedbacks for closely related species interacting within two major families in our data set, (b) Poaceae and (c) Asteraceae. Unlike the estimates shown in the text, the plotted regression slope and 95% intervals assume a fixed model with no hierarchical dependence.

magnitude of this effect could not be explained by phylogenetic distance between species pairs in plant–soil feedback interactions. As life history is linked to evolution rates and niche conservatism (Petit & Hampe, 2006; Smith & Beaulieu, 2009), we may expect heterogeneity in the response such that a phylogenetic signal in negative plant–soil feedbacks is easier to detect in longer-lived species. However, despite differences in mean feedback effects within these subgroups (i.e. intercept estimates), the lack of relationship with phylogenetic distance (i.e. slope estimates) was consistent among plant life forms (grasses, herbs, shrubs and trees) and life cycles (annual, biennial and perennial) (Table 1). It is widely argued that a phylogenetic signal exists in invasiveness (Strauss *et al.*, 2006; Sol *et al.*, 2014), such that we may expect distantly related species to establish and invade ecosystems through natural enemy release. However, when we analysed whether plant–soil feedback effects created in native–exotic interactions were related to phylogenetic distance between the species pairs, we found no evidence to suggest this was the case (Table 1). Finally, it has been suggested that the effect of phylogeny may be dominant between close relatives, such that relatedness might predict plant–soil feedbacks between species interacting within taxonomic divisions such as genera or tribes within plant families (e.g. Burns & Strauss, 2011; Callaway *et al.*, 2013). However, we analysed plant–soil feedbacks from species interacting across a range of phylogenetic distances within two major plant families represented in our dataset (33 interactions within Asteraceae and 65 within Poaceae), and found the relationship between phylogenetic distance and plant–soil feedback interactions within these families was no different from that observed in the aggregate dataset (Poaceae: 0.0010; 95% CI: lower = −0.0079, upper = 0.0100, $n = 65$; Asteraceae: 0.0058; 95% CI: lower = −0.0524, upper = 0.0640, $n = 27$; Figs 2b-c). In summary, these results give little support for the notion that phylogeny can be used as a general predictor of plant–soil feedback effects.

Table 1 The effect of phylogeny on negative plant–soil feedbacks

	Intercept ± 95% CIs	Slope ± 95% CIs	*n*
Life form			
Grass	−0.32 ± 0.293	−0.0006 ± 0.001	124
Herb	−0.35 ± 0.422	−0.00009 ± 0.001	129
Shrub	−0.22 ± 0.572	−0.00009 ± 0.001	26
Tree	0.12 ± 0.607	−0.0004 ± 0.001	50
Life cycle			
Annual	−0.299 ± 0.451	−0.0001 ± 0.001	82
Biennial	−1.296 ± 1.374	0.0013 ± 0.004	9
Perennial	−0.224 ± 0.461	−0.0004 ± 0.001	238
Provenance			
Native	−0.207 ± 0.601	−0.0005 ± 0.002	296
Exotic	−0.853 ± 0.582	0.0017 ± 0.002	33

Intercept and slope estimates from the hierarchical Bayesian meta-analytic model. 95% credible intervals (CIs) for each estimate are calculated by multiplying the posterior standard error of the coefficients by the 95% quantile of a *t*-distribution with *N-k* degrees of freedom. None of the slopes showed significant effects of phylogenetic distance.

In order to check if our results were sensitive to disproportionate representation of species or phylogenetic distance levels across studies and experiments, we performed two subset analyses, re-analysing a trimmed dataset representing species in only one hierarchical grouping, and assessing the effect of unbalanced data across the range of phylogenetic distances. In order to undertake the first subset analysis with the unbiased representation of species, we trimmed the dataset to ensure species were not replicated in multiple studies, overcoming the nonindependence of multiple effect sizes for a species among studies. We selected studies for this analysis that maximized the number of total number effect sizes analysed whilst maintaining the trimming criteria. The results from this subset analysis were consistent with our initial findings: phylogenetic distance between species pairs had no effect on the magnitude of plant–soil interactions (−0.00036; 95% CI: lower = −0.00079, upper = 0.00006, $n = 287$). The second subset

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analysis, for unbiased representation of phylogenetic distance, was conducted by running 100 simulations, where an effect size for each observed value on the phylogenetic distance gradient was randomly sampled, and taking the mean and standard error for this sample of slope estimates. The results from this subset analysis were also consistent with our findings that the magnitude of plant–soil feedback observed is not dependent on phylogenetic distance (mean slope = -0.00019 ± 0.00005 standard error). We checked for bias in our models using a funnel plot combined with trim and fill assessment, and a cumulative meta-analysis approach, which evaluates how the slope of the relationship between phylogenetic distance and plant–soil feedback was influenced by experiments with high sampling variance (i.e. within-study error). The model checking and subset analyses we have conducted found little evidence for publication bias in our dataset and showed that our results were robust to biases that may exist (Supporting Information Methods S1).

There is currently much debate on the use of phylogenetic data in ecology (Mayfield & Levine, 2010; Best *et al.*, 2013; Narwani *et al.*, 2013; Pavoine *et al.*, 2013; Kelly *et al.*, 2014). The growing recognition that dissimilarity in functional traits is not related in a monotonic way to phylogenetic distance suggests that phylogeny cannot be used as a general proxy for predicting the outcome of species interactions (Best *et al.*, 2013; Pavoine *et al.*, 2013; Kelly *et al.*, 2014). The poor ability of phylogenetic distance to predict plant–soil feedbacks indicates that the traits underlying this phenomenon may be no different. Future experimental work might better focus on interactions among species at fine phylogenetic scales, and identify if and where specific traits important for plant–soil feedbacks saturate on the phylogenetic distance vs trait dissimilarity curve (e.g. Kelly *et al.*, 2014). Our meta-analysis however gives strong evidence against the general use of phylogeny for predicting plant–soil feedbacks and their associated effects on plant community assembly, plant species invasions, and agricultural soil sickness.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Table S1 Study dataset

Methods S1 Supporting methods.

Notes S1 PRISMA statement.

Notes S2 R code.

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Appendix III

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Global effects of land use on local terrestrial biodiversity

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Human activities, especially conversion and degradation of habitats, are causing global biodiversity declines. How local ecological assemblages are responding is less clear—a concern given their importance for many ecosystem functions and services. We analysed a terrestrial assemblage database of unprecedented geographic and taxonomic coverage to quantify local biodiversity responses to land use and related changes. Here we show that in the worst-affected habitats, these pressures reduce within-sample species richness by an average of 76.5%, total abundance by 39.5% and rarefaction-based richness by 40.3%. We estimate that, globally, these pressures have already slightly reduced average within-sample richness (by 13.6%), total abundance (10.7%) and rarefaction-based richness (8.1%), with changes showing marked spatial variation. Rapid further losses are predicted under a business-as-usual land-use scenario; within-sample richness is projected to fall by a further 3.4% globally by 2100, with losses concentrated in biodiverse but economically poor countries. Strong mitigation can deliver much more positive biodiversity changes (up to a 1.9% average increase) that are less strongly related to countries' socioeconomic status.

Biodiversity faces growing pressures from human actions, including habitat conversion and degradation, habitat fragmentation, climate change, harvesting and pollution[1]. As a result, global assessments show that species' extinction risk is increasing on average while population sizes are declining[1,2]. Such assessments have usually focused on data-rich vertebrates, so might not reflect broader biodiversity[3]. Furthermore, most have concentrated on the global status of species, whereas the long-term security of many ecosystem functions and services – especially in changing environments – is likely to depend upon local biodiversity[4–6]. Average trends in local diversity remain unclear: analyses of temporal changes in assemblages have suggested no systematic change in species richness[7,8], but the available times-series data might under-represent transitions between land-use types[9], and population time series suggest vertebrate populations have declined sharply in recent decades[3].

Spatial comparisons provide an alternative source of evidence on how human pressures affect biodiversity, assuming that differences in pressures have caused observed biodiversity differences between otherwise matched sites[10–12]. The prevalence of published spatial comparisons makes it possible to go beyond particular taxa or regions[11,12] to develop global, taxonomically representative models. Furthermore, the willingness of many researchers to share their raw data makes it possible to consider multiple aspects of biodiversity, rather than the single, simple metrics of most existing models[10], which cannot capture all key aspects of diversity[13].

We present the most geographically and taxonomically representative models to date of how several aspects of the composition and diversity of terrestrial assemblages respond to multiple human pressures. The explanatory variables in our models most directly measure land use and infrastructure, but might correlate[14,15] with two other important pressures, harvesting and invasive species, for which comparable high-resolution spatial data are unavailable globally. We exclude climate change effects because they are not captured well by spatial comparisons. We use our models to infer past net changes in assemblages since the year 1500, project future changes over this century under different socioeconomic scenarios of land use, and relate projected national changes in local biodiversity to socioeconomic variables and natural biodiversity.

Our models of local within-sample species richness (hereafter 'richness'), rarefaction-based species richness (hereafter 'rarefied richness'), total abundance, compositional turnover and average organism size are

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based on among-site comparisons of ecological assemblage composition collated from the literature as part of the PREDICTS project[16]. The data set consisted of 1,130,251 records of abundance and 320,924 of occurrence or species richness at 11,525 sites (2–360 sites per study, median 15; Fig. 1a). These data, from 284 publications (see Methods), represent 26,953 species (1.4% of the number formally described[17]) and 13 of the 14 terrestrial biomes (Extended Data Fig. 1). Each site was scored for six putative pressures: land use[11] and use intensity[18], land-use history[19], human population density[20], proximity to roads[21] and accessibility from the nearest large town. Random effects in our models accounted for study-level differences in response variables and sampling methods, and for the within-study spatial arrangement of sites.

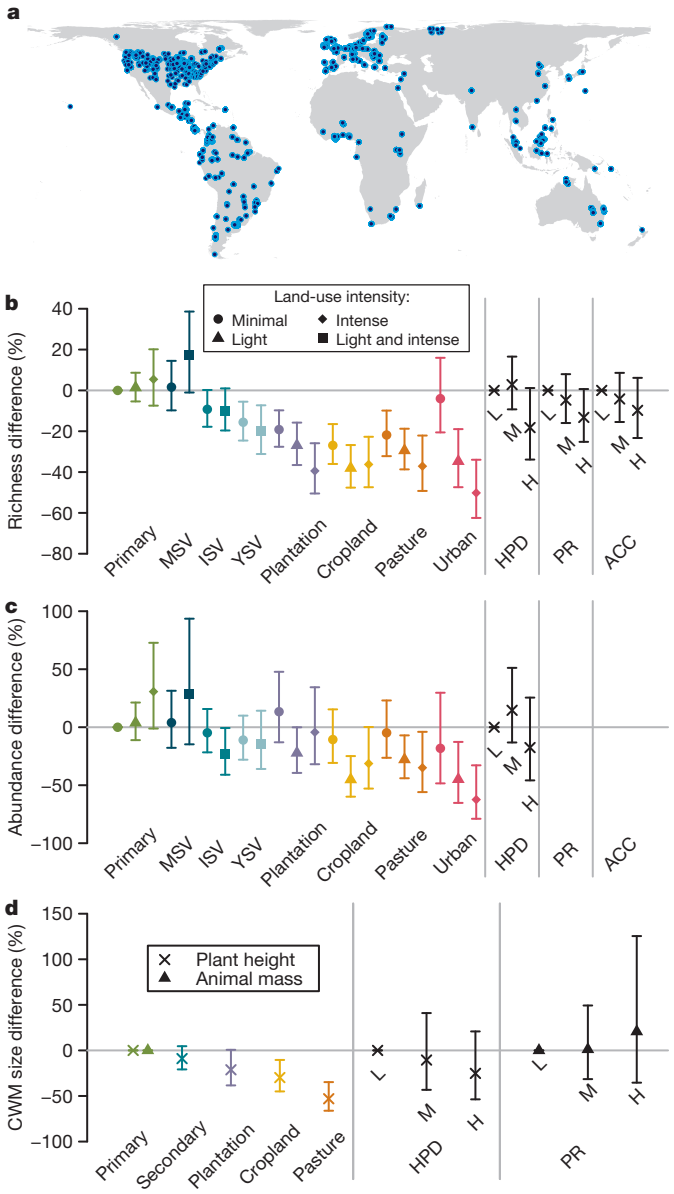

Figure 1 | Locations of sites and responses of four metrics of local diversity to human pressures. **a**, Sites used in the models. **b**–**d**, Responses[44] of richness (**b**), total abundance (**c**) and community-weighted mean (CWM) organism size—plant height (crosses) and animal mass (triangles)—(**d**) to anthropogenic variables. Error bars show 95% confidence intervals. Primary, primary vegetation; YSV, young secondary vegetation; ISV, intermediate secondary vegetation; MSV, mature secondary vegetation; plantation, plantation forest. Land-use intensity is categorized as minimal (circle), light (triangle), intense (diamond), or combined light and intense (square). HPD, human population density[45]; PR, proximity to roads[46] (as −log(distance to nearest road)); and ACC, accessibility to humans[47] (as −log(travel time to nearest major city)), are shown as fitted effects from a model with no interactions between continuous effects and land use, at the lowest (L), median (M) and highest (H) values in the data set. Sample sizes are given in full in the Methods.

Effects of pressure on site-level diversity

Local richness, rarefied richness and total abundance were most strongly influenced by land use and land-use intensity: they were substantially lower in most other land-use types than in primary vegetation, especially in intensively used areas (Fig. 1; see Supplementary Information for statistics and coefficient estimates). These results extend those of previous, geographically or taxonomically restricted, meta-analyses (for example, refs 11, 22). Other variables were weaker as main effects, but showed stronger effects in interaction (Extended Data Fig. 2) and were often significant overall (see Supplementary Information). Richness and total abundance tended to be slightly lower at the highest human population densities, and richness was lower nearer to roads and in more accessible sites (Fig. 1). Differences in richness were not driven solely by differences in abundance. Rarefied richness[23] (see Methods for details) showed weaker but mostly similar patterns, although the effects of variables other than land use and land-use intensity were not significant (Extended Data Fig. 3a, b). Under the worst combinations of pressures, our models estimated richness, rarefied richness and total abundance to be 76.5%, 40.3% and 39.5% lower, respectively, than in minimally affected sites. Effects of pressures on vertebrate, invertebrate and plant richness were statistically indistinguishable ($P > 0.05$; results not shown). The modelled coefficients were robust to efforts to correct for any publication bias (Extended Data Fig. 4). As with all studies based on data from the literature, unpublished data are almost unrepresented. Coefficients were also robust under cross-validation (Extended Data Fig. 3c, d), and the model residuals showed little spatial autocorrelation (Extended Data Fig. 5).

The importance of secondary vegetation for conservation is a hotly debated topic[11,24,25], and an important one, given that this land use will soon become the most widespread type[26]. We find that the answer depends strongly on the secondary vegetation's maturity: early-stage communities tend to be less diverse than those in primary vegetation and are compositionally distinct, but these differences are much reduced in mature secondary vegetation (Figs 1 and 2; we caution though that not all data sources clearly distinguished mature secondary from primary vegetation). This successional rise in diversity accords with a recent meta-analysis of plant communities over time[7].

Net changes in diversity provide an incomplete view of the effects of human activities on biodiversity because they ignore the replacement of original species by newcomers[8]. We therefore analysed how land use affects similarity in species composition between sites. Communities under the same land use were, as expected, the most similar (Fig. 2a). Across land uses, communities in primary vegetation were most like those in secondary vegetation, while plantation forest, pasture and cropland communities formed a different, human-dominated cluster (Fig. 2b).

Anthropogenic pressures can affect ecosystem functions and services more strongly than changes in species diversity would imply, if species' responses depend on their traits[27]. Large size is often linked to species' declines[28,29] and is important for some ecosystem processes[30]. We combined abundance data with species' average sizes to calculate site-level community-weighted mean plant height and animal mass. As in local studies[29], mean plant height was lower in human-dominated land uses than in primary and secondary vegetation, and tended to decline with increasing human population density (Fig. 1d). Most field studies focused on particular plant taxa, so this difference does not simply reflect tree removal. Average animal mass did not change consistently with land use or human population density, but increased with proximity to roads (Fig. 1d).

Models like ours that substitute space for time ignore time lags in biotic changes, which can be important[31]. We also assume that land uses

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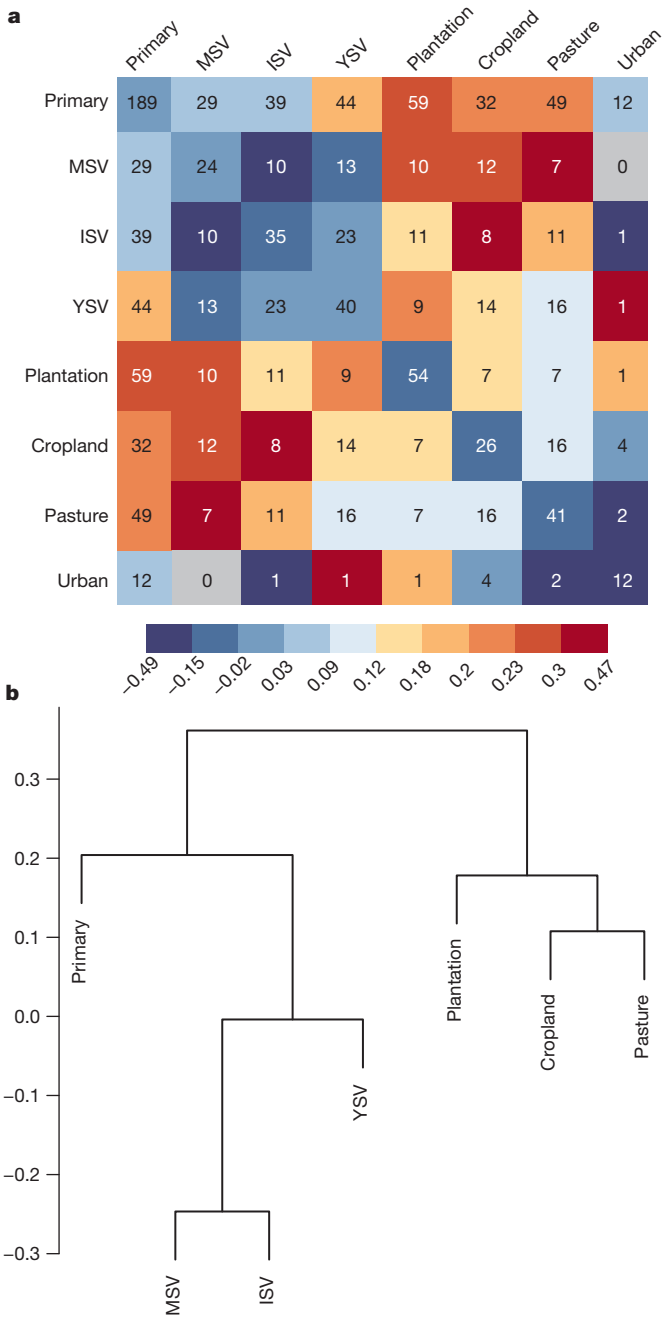

Figure 2 | Similarity in assemblage composition as a function of land use. **a**, Average dissimilarity of species composition (1 − Sørenson Index) between pairs of sites within and among land uses (shown relative to the similarity between pairs of primary-vegetation sites); blue and red colours indicate, respectively, more or less similar composition; numbers indicate numbers of studies within which comparisons could be made. **b**, Clustering of land-use types based on average compositional dissimilarity; urban sites were excluded owing to the small sample size.

are situated randomly within studies relative to sites' intrinsic suitability for biodiversity. Adding global data on other important pressures as they become available, and also incorporating climate change, will give a more complete picture of human effects on local biodiversity.

Global effects on local diversity to date

By applying our model for within-sample species richness—the most widely used and understood biodiversity measure—to maps of current pressure variables[10], we estimated the global pattern of net local changes to date in plot-level richness (Fig. 3; we did not estimate total richness within the 0.5° × 0.5° grid cells). Human-dominated areas are inferred to have lost much more local diversity than have regions where more natural vegetation remains. The worst-affected cells showed a 31% reduction in average local richness—probably enough to alter ecosystem functioning substantially[4]. Local richness increased in 1.7% of cells (by ≤4.8%). Total abundance and, less strongly, rarefied richness showed broadly similar patterns (Extended Data Fig. 6).

We applied our models to global spatial estimates of how land use and human population changed from 1500–2005 (ref. 26) (see Methods) to infer the global history of local biodiversity change. Here we focus on within-sample species richness because of its wide use and easy interpretation. Our inferences incorporate uncertainty in model parameter estimates, but not in the trajectories of the pressures themselves (which have not been assessed[32]) nor effects of changes in roads and accessibility, for which temporal estimates could not be obtained.

Richness is estimated to have declined most rapidly in the 19th and 20th centuries (Fig. 4), with other metrics showing similar responses (Extended Data Fig. 6). By 2005, we estimate that land use and related pressures had reduced local richness by an average of 13.6% (95% confidence interval (CI): 9.1–17.8%) and total abundance by 10.7% (95% CI: 3.8% gain to 23.7% reduction) compared with what they would have been in the absence of human effects. Approximately 60% of the decline in richness was independent of effects on abundance; average rarefied richness has fallen by 8.1% (95% CI: 3.5–12.9%). Although these confidence limits omit uncertainty in the projections of land use and other pressures, there is less uncertainty in estimates of current pressure levels than in changes over time[33].

Our inferences contrast with two recent analyses of community time series[7,8], which suggested no overall trend in local diversity, and with the Living Planet Index[3], which, based on vertebrate population time series, reports a much more rapid decline in abundance than we infer. Although time series potentially provide a more direct view of temporal trends than our space-for-time approach, the available data might under-represent transitions between land-use types[9]. However, our approach may underestimate additions of species through climate change and species invasion (although accessibility and proximity to roads may partly capture the latter[14,15]).

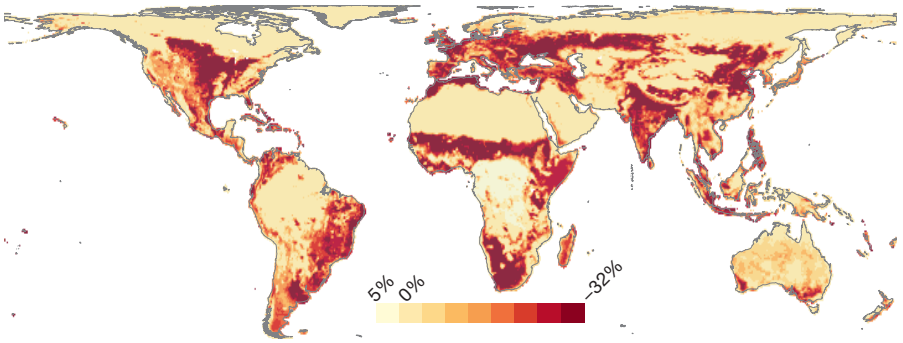

Figure 3 | Net change in local richness caused by land use and related pressures by 2000. Projections used an IMAGE reference scenario[10]. The baseline landscape was assumed to be entirely uninhabited, unused primary vegetation. Shown using a Lambert Cylindrical Equal-Area projection at 0.5° × 0.5° resolution.

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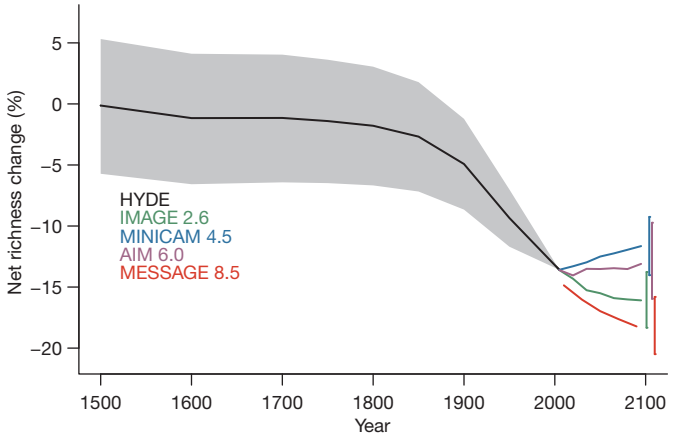

Figure 4 | Projected net change in local richness from 1500 to 2095. Future projections were based on the four RCP scenarios (Table 1). Historical (shading) and future (error bars) uncertainty is shown as 95% confidence intervals, rescaled to zero in 2005. The baseline for projections is a world entirely composed of uninhabited, unused primary vegetation; thus, the value at 1500 is not constrained to be zero because by then non-primary land uses were present (and in some regions widespread). The global average projection for MESSAGE 8.5 does not join the historical reconstruction because that scenario's human population projections start in 2010 and because human population and plantation forest extent have not been harmonized among scenarios.

Global and national projections to 2095

Global changes in local diversity from 2005 to 2095 were projected using estimated land use and human population from the four Intergovernmental Panel on Climate Change Representative Concentration Pathway (RCP) scenarios[26], which correspond to different intensities of global climate change (Table 1). Although these estimates have limitations[32], they are the most consistent available, are widely used[34], and are consistent with the historical estimates[26]. However, they—like all other global land-use projections—include no estimate of uncertainty; therefore, each of our projections must be viewed as the predicted biodiversity outcome under one particular set of land-use assumptions.

Projected net changes in average local diversity to 2095 vary widely among scenarios (Fig. 4 and Extended Data Fig. 6). The scenario with the least climate change (IMAGE 2.6) yields the second-worst outcome for biodiversity, because it assumes rapid conversion of primary vegetation, especially in the tropics, to crops and biofuels[26] (Table 1 and Extended Data Fig. 7). These projections do not imply that low-emission scenarios must entail large losses of biodiversity, but instead reflect that scenario's mitigation strategy. Indeed, in MiniCAM 4.5 (where mitigation is through carbon markets, crop improvements and diet shifts, Table 1) average richness is projected to increase (though other diversity metrics respond more weakly, Extended Data Fig. 6). The worst biodiversity outcomes arise from the scenario with most climate change (MESSAGE 8.5) in which rapid human population growth drives widespread agricultural expansion (Table 1 and Extended Data Fig. 7). This scenario, which has been characterized as 'business-as-usual'[35], most closely matches recent trends in emissions[36] and gives the worst outcomes even though our projections omit direct climate effects on local assemblages.

The global projections hide wide regional and national variation (Fig. 5 and Extended Data Fig. 8). Projections for 2095 under business-as-usual (MESSAGE 8.5) are strongly inequitable, presenting serious challenges for both sustainable development and global conservation of biodiversity (Fig. 5a). Under this scenario, European and North American countries, typically with a high Human Development Index, low native biodiversity and widespread historical land conversion, are mostly projected to gain in local richness by 2095. More naturally biodiverse but less economically developed Southeast Asian and especially sub-Saharan African countries, with more natural and semi-natural habitat, will suffer the greatest losses (Fig. 5a and Extended Data Fig. 8f).

Such globally inequitable outcomes might be avoidable. The best scenario for biodiversity (MiniCAM 4.5; Fig. 4) yielded country-level outcomes that are relatively independent of Human Development Index, native species richness (Fig. 5b) and past changes (Extended Data Fig. 8e). For local richness, outcomes under MiniCAM4.5 were better than MESSAGE 8.5 for 93% of countries worldwide (Fig. 5c).

Under AIM 6.0, most Afrotropical countries are projected to gain in local richness but heavy losses are inferred for the Indo-Malay region (Extended Data Fig. 8). Projections under IMAGE 2.6 are spatially similar to those under MESSAGE 8.5. The land-use change caused by the biofuels-based strategy in IMAGE 2.6 is projected to have a major negative effect overall on terrestrial biodiversity (Extended Data Fig. 8).

Conclusions

Many assessments of the state of biodiversity have focused on global metrics such as rates of species extinction[37], but resilient delivery of ecosystem functions and services is more likely to depend on local diversity[4–6]. Our models suggest land-use changes and associated pressures strongly reduce local terrestrial biodiversity, and we estimate global average reductions to date of 13.6% in within-sample species richness, 10.7% in total abundance and 8.1% in rarefaction-based species richness (Figs 3 and 4). Climate change, which we could not include in our

Table 1 | Key features of the four RCP scenarios

Scenario	Land use (see also Extended Data Fig. 7)	Climate and energy	Human population
IMAGE 2.6	Agriculture moves from developed to developing countries. Large increase in area of biofuel plantations. Urban extent assumed constant.	Increased energy efficiency. Increased use of carbon capture and storage, nuclear, renewable energy and biofuels. Approximately 1 °C temperature increase by 2100 compared to pre-industrial.	10.1 billion by 2100 (UN Medium variant, 2010)
MiniCAM 4.5	Carbon pricing leads to preservation of primary forest and expansion of secondary forest. Crop yield increases, improved agricultural efficiency and dietary shifts lead to decreases in cropland and pasture areas. Small increase in area of biofuel plantations. Urban extent assumed constant.	Decline in overall energy use. Decreased use of fossil fuels and increase in nuclear and renewable energy, and in carbon capture and storage. Moderate increase in use of biofuels, but limited by availability of biomass. Approximately 1.75 °C temperature increase by 2100.	Peaks above 9 billion around 2065, then declines to 8.7 billion by 2095.
AIM 6.0	Urban area increases owing to human population growth. Cropland area increases to meet food demand. Pasture area declines strongly.	Approximately 2.5 °C temperature increase by 2100.	9.1 billion by 2100 (UN Medium variant, 2004)
MESSAGE 8.5	Increasing crop yields and intensification account for much of the increased production required, but area of cropland and, to a lesser extent, pasture increases rapidly. Small increase in area of biofuel plantations. Urban area increases owing to increased population.	Small improvements in efficiency leading to high demand for energy. Conventional oil and gas become scarce, leading to shift in favour of unconventional and carbon-intensive fossil fuels. Moderate increase in use of biofuels. Approximately 4 °C increase in temperature by 2100.	12 billion by 2100.

Land-use and human population assumptions are detailed in ref. 26, energy assumptions in refs 40–42, and climate implications in ref. 43.

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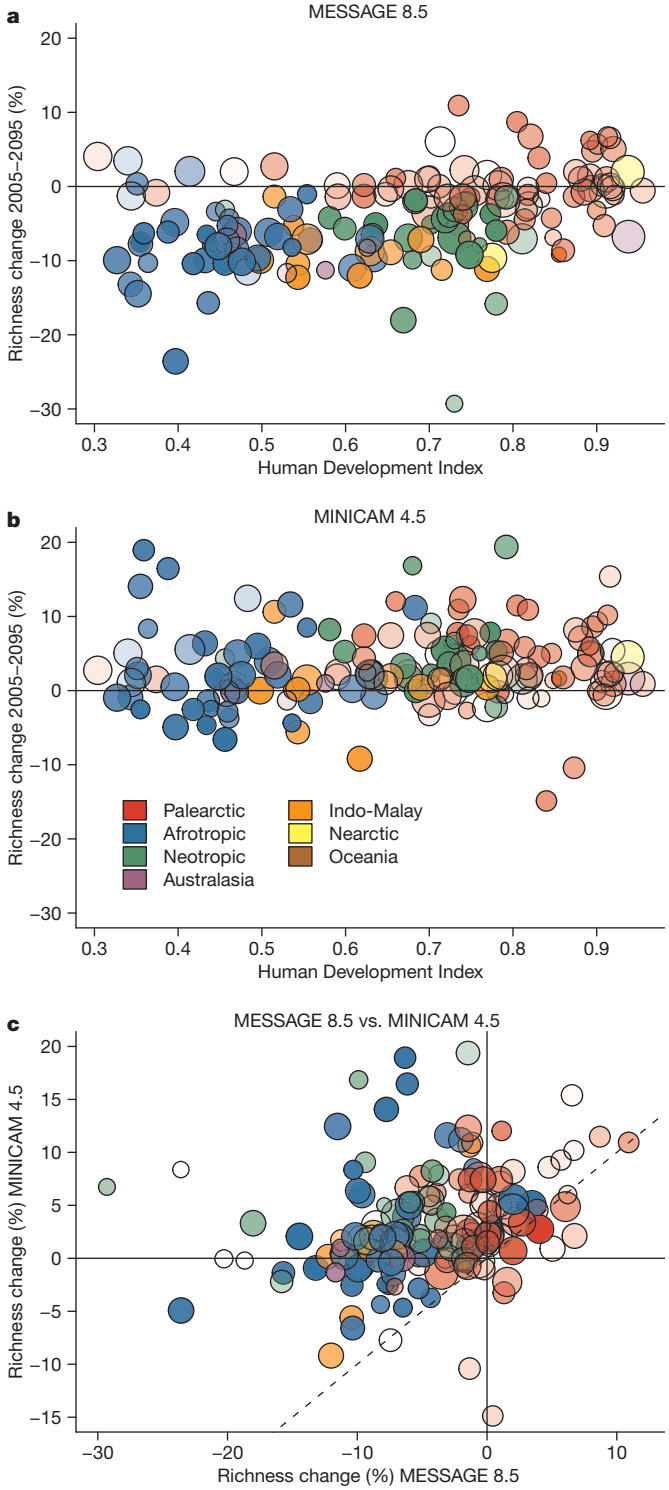

Figure 5 | Biodiversity projections at the country level. **a**, **b**, Country-level projections of average net local richness change between 2005 and 2095 under the worst (**a**, MESSAGE 8.5) and best (**b**, MiniCAM 4.5) RCP scenarios for biodiversity, shown in relation to countries' Human Development Index. Colours indicate biogeographic realms; colour intensity reflects natural vertebrate species richness (more intense colour represents higher richness); point diameter is proportional to (log) country area. **c**, Correlation between projected richness changes under the MiniCAM 4.5 and MESSAGE 8.5 scenarios, with dashed line showing equality; colours as in **a** and **b**; colour intensity is proportional to the Human Development Index (more intense colour represents higher index).

framework, is likely to exacerbate losses, especially under business-as-usual[38], although direct effects of climate change will increase local diversity in some regions[8].

It is important to remember that the habitat conversion and associated changes that reduced local biodiversity had largely positive consequences for people; agricultural intensification underpinned many countries' development. However, benefits have not been shared equally among or within countries[39]. Losses of local species richness exceeding 20% are likely to substantially impair the contribution of biodiversity to ecosystem function and services, and thus to human well-being[4]. We estimate that reductions in average plot-level species richness currently exceed this level for 28.4% of grid cells, increasing to 41.5% of cells by 2095 under business-as-usual (note that we do not estimate or project total richness across the cell). Importantly, our projections suggest that such widespread large losses are not inevitable. With concerted action and the right societal choices, global sustainability of local biodiversity may be an achievable goal.

Online Content Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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Supplementary Information is available in the online version of the paper.

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METHODS

Data collation. Between March 2012 and April 2014 we collated among-site comparisons of ecological assemblage composition from published studies (or from unpublished datasets where the methods have been published) examining the effect of human activities on more than one named taxon. A full description of how the data set was assembled and curated is presented elsewhere[16]. We define sites to be in the same study if they were sampled using the same methodology and the data were reported in the same paper; therefore, some publications contain multiple studies. After six months of broad searching, we targeted efforts towards under-represented taxa, habitat types, biomes and regions. We accepted data only from published or in-press papers, or data collected using a published methodology, and we required that the data providers agreed to our making their data publicly available at the end of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project in 2015. We accepted data only where abundance, occurrence or richness had been measured at two or more sampling locations and/or times, and where all sites were sampled using the same sampling procedure and with either the same effort or site-specific data on effort. We used geographical coordinates preferentially from the paper or supplied by data providers; but where coordinates were not thus available, we geo-referenced them from maps in the papers. The final data set came from 378 studies[48–329] and two unpublished datasets (M. E. Hanley, 2005 and 2011) that were collected with published methods[146].

Studies compared from 2 to 360 sites (median = 15; 82% had ≥5 sites); most sampled species from multiple families but fewer than half sampled multiple orders. Over 70% of sites were from studies that sampled entire communities within a taxonomic group rather than a target list of species. Removing studies having a target list did not substantially alter model coefficients (results not shown) and increased the projected global net average loss of local species richness until 2005 by 0.6%. Sites varied in the maximum linear extent sampled (median 106 m; interquartile range 50 m to 354 m). Model coefficients for the approximately 50% of studies that reported maximum linear extent were robust to its inclusion in the models (results not shown).

The great majority of listed taxa were species level, although many could not be given explicit species identifications (for example, morpho-species)[16]; henceforth we refer to distinct taxa in our data set as species. We matched taxonomic names given in the source paper to the Catalogue of Life 2013 Annual Checklist (COL)[330], obtaining the full taxonomic classification. In order to relate the taxonomic names to species-level trait databases, we generated, for each taxon, a 'best-guess' Latin binomial as: (a) the taxon name from COL if the COL query returned a species-level identification; (b) the first two words of the text returned by the COL query if this was a sub-species designation; (c) the first two words of the taxon name in the source publication if the COL query returned neither a species or sub-species name, and the taxon name in the source publication contained two or more words. Taxa that met none of these criteria were not matched to trait data, but were included in the calculation of richness and total abundance, and for estimating turnover in community composition among sites.

The resulting data set contained data for 26,953 species at 11,525 sites. For many high-diversity taxa, the database contains data for more than 1% of the number of species thought to have been formally described (Extended Data Fig. 1a). The distribution of sites among major biomes is roughly proportional to the amount of terrestrial net primary productivity (NPP) fixed within each biome (Extended Data Fig. 1b).

Site-level composition and diversity. We computed four site-level biodiversity metrics: within-sample species richness, total abundance, rarefaction-based richness and community-weighted mean organism size. These were calculated as follows.

Within-sample species richness was calculated as the number of differently-named taxa recorded at a given site in a standardised sampling unit (a measure also known as species density[331]). We gave precedence to the author's classification of species, even where a search of global databases revealed potential synonymies, because only certain taxonomic groups could be reliably matched to accepted taxonomies.

This measure of richness is appropriate for conservation questions but among-site differences could be due to effects on numbers of individuals as well as to changes in the shape of the species accumulation curve[331]. We therefore also calculated rarefaction-based species richness by taking 1,000 random samples of n individuals from each site, where n is the smallest total number of individuals recorded at any site within its study, and calculating the mean species richness across samples. This index could only be calculated for sites where, in addition to the criteria above being met, abundance was recorded as number of individuals. Rarefied species richness was rounded to the nearest integer for analysis with Poisson errors.

Total abundance was calculated as the sum of the measures of abundance of all taxa at a site; we were thus unable to estimate abundance for sites where only species occurrence or overall richness or diversity had been recorded (17% of sites). Some abundance metrics—those not reported as densities per unit time, distance, area or volume sampled—were sensitive to sampling effort. When a study reported any of these metrics and sampling effort varied among sites within a study, we corrected the raw abundance measurements for the sampling effort expended at each sampling location and time. This was done by rescaling the sampling efforts within each study so that the most heavily sampled site had a value of one (to prevent introducing additional heterogeneity into the modelled values), and then dividing the raw abundance measurements by this relative sampling effort.

Community-weighted mean organism size was calculated as the arithmetic mean of log-transformed height of plants (available for 4,235 species in our data set) or the log-transformed body mass or volume of vertebrates, beetles and hoverflies (5,236 species) present at a site, weighted by abundance[332]. Plant height data were taken from the TRY database[333]; for 61 species where plant vegetative height data were unavailable, we estimated it from generative height from a regression across the 2,554 species with estimates of both traits ($R^2 = 0.91$). Data on vertebrate body mass were taken from the PanTHERIA database for mammals[334], from BirdLife International's World Bird Database for birds, and from a wide range of published and grey-literature sources for amphibians[335–381]. Length data for reptiles were taken from published[382,383] and unpublished (S. Meiri and A. Feldman, unpublished data) sources, and converted to estimates of body mass using published length-mass allometries[384,385]. Arthropod size data (beetles and hoverflies) were collated from published sources[386,387]. Beetle length and amphibian snout-vent length values were raised to the power three so that they had the same dimensionality as the other animal size measures. For both plant height and vertebrate body mass, missing values were interpolated as the average values for congeners, since both of these traits are strongly conserved phylogenetically (Pagel's $\lambda = 0.98, 0.997, 0.93, 0.89$ for plant height, vertebrate body mass, beetle body length and hoverfly thorax volume, respectively).

Human pressure data. While many human pressures can affect local biodiversity, we focus on those that can be obtained for sites around the world and for which, as far as possible, spatiotemporal data are available for 1500–2095; this focus enables us to use our statistical models as a basis for projecting responses through time. Each site was assigned to one of eight land-use classes based on the description of the habitat given in the source paper (see Extended Data Table 1 for definitions): primary vegetation, secondary vegetation (subdivided into mature, intermediate or young secondary vegetation), plantation forest, cropland, pasture and urban[16]. These classes were selected to match the land-use classification adopted in the Intergovernmental Panel on Climate Change Representative Concentration Pathways scenarios[26] to facilitate the projection of our models onto these scenarios. Sites were also assigned to a level of human intensity of use (minimal, light or intense) within each major land-use class, also based on the description of the habitat in the source paper (see Extended Data Table 1 for definitions). The factors that determined this level depended on the land-use class (for example, bushmeat extraction and limited logging in primary and secondary vegetation, or stocking density and chemical inputs in pasture; Extended Data Table 1). Sites that could not be classified for land-use and use intensity were excluded from the analyses. The final dataset contained the following numbers of sites in each land use and land-use intensity level: primary vegetation, minimal use, 1,546 (from 183 studies); light use, 860 (76 studies); intense use, 449 (33 studies); mature secondary vegetation, minimal use, 198 (52 studies); light/intense use, 213 (23 studies); intermediate secondary vegetation, minimal use, 404 (55 studies); light/intense use, 269 (30 studies); young secondary vegetation, minimal use, 431 (50 studies); light/intense use, 331 (34 studies); plantation forest, minimal use, 356 (47 studies); light use, 402 (42 studies); intense use, 238 (29 studies); cropland, minimal use, 427 (45 studies); light use, 632 (43 studies); intense use, 703 (36 studies); pasture, minimal use, 525 (43 studies); light use, 434 (52 studies); intense use, 174 (23 studies); and urban, minimal use, 174 (23 studies); light use, 244 (26 studies); intense use, 195 (18 studies).

We overlaid our sites with available global data sets to obtain site-level estimates of human population density[45], distance to the nearest road[46] and estimated travel time to nearest population centre with greater than 50,000 inhabitants[47]. For distance to nearest road, the map of roads was first projected onto a Berhmann equal-area projection. These operations were carried out using Python code implemented using the arcpy Python module in ArcMap version 10.0 (ref. 388). In the main figures, the inverses of distance to roads and travel time to major population centre (proximity to roads and accessibility) were presented so that high values corresponded to higher hypothesized human effect. To estimate the history of human use of the landscapes within which sites were located, we calculated the number of years since the 30-arc-second grid cell containing each site became 30% covered by human land uses (cropland, pasture and urban), according to the HYDE model[389]. Co-linearity among variables describing anthropogenic change was low; the highest correlation was between land use and human population density (Pearson $R^2 = 0.31$).

Modelling site-level diversity, composition and turnover. The response of site-level diversity to the measures of anthropogenic change was modelled using generalized linear mixed effects models, implemented in the lme4 package version

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1.0-5 (ref. 44) in R version 3.0.2 (ref. 390). We first compared candidate random-effects structures using the full candidate fixed-effects structure[391]. Random-intercept terms considered in all models were the identity of the study from which data were taken, to account for study-level differences in the response variables and sampling methods used, and—within study—the spatial block in which the site was located, to account for the spatial arrangement of sites. For models of species richness (within-sample and rarefied), we also fitted an observation-level random effect (that is, site identity) to account for the overdispersion present[392]. We also considered random slopes, with respect to study, of each of the main fixed effects (land use, land-use intensity, human population density, distance to nearest road, travel time to nearest major city and time since the landscape was majority converted to human uses). Random effects were retained or discarded based on the models' Akaike Information Criterion values.

Once the best random-effects structure had been selected, we performed backward stepwise model simplification to select the best fixed-effects structure (see Supplementary Information)[391]. Human population density, distance to roads, travel time to nearest major city and time since major human use of the landscape were log transformed in the analyses, with a value of 1 added to human population density, travel time to nearest major city and time since major landscape conversion to deal with zero values. These four variables were fitted as continuous effects, with quadratic polynomials for human population, distance to roads and travel time to nearest major city, and as a linear effect for time since human landscape conversion. For variables fitted as quadratic polynomials, we also tested linear effects during the backward stepwise model selection. All continuous variables were rescaled before analysis so that values ranged between zero and one. Interaction terms were tested first, and then removed to test the main effects. All main effects that were part of significant interaction terms were retained in the final models regardless of their significance as main effects. For the model of community-weighted mean body mass and plant height, because the number of sites with data was smaller than for the other metrics, only land use (excluding urban sites, which were few), human population density and distance to roads, and no interactions, were fitted (for the model of plant height, sample sizes in each land use were: primary vegetation, 634 sites; secondary vegetation, 851 sites; plantation forest, 222 sites; cropland, 72 sites; pasture, 412 sites; and for the model of animal mass: primary vegetation, 1728 sites; secondary vegetation, 805 sites; plantation forest, 602 sites; cropland, 641 sites; pasture, 440 sites). The decision whether or not to retain terms was based on likelihood ratio tests. The coefficient estimates of the best models are shown in Fig. 1b–d and Extended Data Fig. 2, and the formulae and statistical results are shown in the Supplementary Information. To test for spatial autocorrelation in the residuals of the final best models, we calculated Moran's I values and associated P values, separately for each study considered in the models, using the spdep package version 0.5-68 (ref. 393) in R; the distribution of P values across studies was used as an indication of whether spatial autocorrelation was likely to cause a problem. This revealed that the residuals showed little spatial autocorrelation (Extended Data Fig. 5). We used cross validation to assess the robustness of model parameter estimates, first based on dividing the studies randomly into ten equal-sized sets and dropping each set in turn (Extended Data Fig. 3c), and second based on leaving out the studies from each biome in turn (Extended Data Fig. 3d).

Publication bias is a potential problem for any large-scale synthesis of data from many publications. In standard meta-analyses, funnel plots[394] can be used to test for any relationship between standard error and effect size, as a bias in effect sizes at high standard error towards more positive or more negative effects indicates a likely effect of publication bias. Creating funnel plots for our data was more complicated because ours was a site-level analysis of raw diversity estimates rather than a traditional meta-analysis. Instead we generated individual models relating diversity to land use for each study that sampled at least two sites within each of at least two land-use types. We focused on land use because: (a) there were a small number of sites included in most within-study models; and (b) the original studies focused on effects of land use, not generally on land-use intensity, human population density or distance to roads, and thus any effect of publication bias would likely be seen in the land-use coefficients. Funnel plots were generated by plotting, for each land-use type, the estimated model coefficients against the associated standard errors (Extended Data Fig. 4). There were some indications of an effect of publication bias, with less certain coefficient estimates tending to have more negative estimates for some of the land uses (Extended Data Fig. 4). However, study-level random slopes of human-dominated land uses tended to be more negative for studies that sampled more sites (Extended Data Fig. 4). It is important to emphasize that in a site-level analysis like ours, studies with fewer sites have less weight in the models. Modelled coefficient estimates were generally robust to the removal of these studies (Extended Data Fig. 4). Basing projections on coefficient estimates from models where small studies were excluded led to a less than 1% change in the estimated global richness values (results not shown). As with all studies based on data from the literature, we underrepresent unpublished data.

To model turnover of species composition between pairs of sites, we calculated average dissimilarity[23] in the lists of present species (1 − Sørensen index) between all pairs of sites within each study. For this analysis, we were only able to consider studies with more than one site in at least one of the land-use types considered. Once compositional similarity had been calculated for every pair of sites within each study, the average compositional similarity was calculated for every pair of land-use types considered within each study (including comparisons between sites in the same land-use type). Finally, the average compositional similarity was calculated for each pair of land-use types across all studies. To visualize the clustering of different land-use types in terms of community composition, we performed a hierarchical complete-linkage cluster analysis on the compositional dissimilarity (that is, 1 − similarity) matrix, using the hclust function in R version 3.0.2 (ref. 390). To test whether differences in the average geographic distance between pairs of sites in different land-use combinations affected these results, we correlated average compositional similarity with average distance between sites, for all pairwise combinations of land use (including comparisons of a land-use type with itself). Correlations between average distance and average community similarity were only very weakly negative ($R^2 = 0.001$), suggesting they do not strongly distort the comparisons of community composition. However, the fact that some land uses tend to occur more closely together than others could influence the diversity patterns seen in our models, if some land uses are typically close to high-diversity habitats and so are more likely to benefit from dispersal. For example, sites in secondary vegetation and plantation forest were closer, on average, to primary vegetation sites than were those in cropland, pasture and urban (average distances to sites in primary vegetation were: other primary vegetation sites = 7.38 km; mature secondary vegetation = 4.4 km; intermediate secondary vegetation = 3.9 km; young secondary vegetation = 6.9 km; plantation forest = 4.2 km; cropland = 16.4 km; pasture = 10.1 km; and urban = 11.4 km). Accounting for distance in such already complex models is not computationally tractable. In making the projections, we therefore implicitly assume that the average distances will not change (that is, that secondary vegetation and plantation forests will remain closer to primary vegetation than cropland, pasture and urban habitats).

Projecting the models onto spatial estimates of anthropogenic variables. We projected the best overall models of richness (within-sample and rarefied), abundance and community-weighted mean organism size onto estimates of land use, land-use intensity and human population density at $0.5^\circ \times 0.5^\circ$ resolution, using historical estimates for 1500 to 2005, and four RCP scenarios of future changes (IMAGE 2.6, MiniCAM 4.5, AIM 6.0 and MESSAGE 8.5; the names refer to the integrated assessment models used and the numbers to the amount of radiative forcing assumed in 2100)[395]. In the absence of global projections, proximity to roads and accessibility were omitted from our projections.

Estimates of land use for both the historical reconstruction and the future scenarios were taken from the harmonized land-use data accompanying the scenarios[26]. Estimates of the stage of secondary vegetation (young, intermediate or mature) are not available directly in the RCP land-use data. However, these data contain estimates of the transition each year between secondary vegetation and all other land-use types. To convert this into an estimate of the proportion of secondary vegetation in each of the stages of maturity, we considered any transition to secondary vegetation to result in secondary vegetation of age zero. Each year, this age was then incremented by one. In the absence of better information, any transitions from secondary vegetation to any other land-use type were assumed to be drawn evenly from the ages currently represented. For the purposes of the projections, secondary vegetation was considered to be young until an age of 30 years, intermediate between 30 years and 100 years, and mature thereafter. We developed C# code to convert land-use transitions into estimates of the stage structure of secondary vegetation.

Gridded temporal estimates of human population density were directly available for the HYDE historical scenario and MESSAGE future scenario. Human population trajectories in the MiniCAM model were resolved only to the level of United Nations regions[41]; we therefore downscaled these to grid cells assuming no temporal change in the spatial pattern of relative population density within regions compared to present day patterns[45], which is the method used in other RCP-scenario land-use models lacking human population data resolved to grid cells[26]. Gridded estimates of human population from the MESSAGE model were downloaded from http://www.iiasa.ac.at/web-apps/ggi/GgiDb/. For the scenarios for which human population projections were not available (IMAGE and AIM), we used country-level estimates from the 'medium' scenario of the United Nations population division[396], which gives the closest global predictions of future human population to those assumed by IMAGE and AIM[26]. These country-level estimates were downscaled to grid cells using the same method as for MiniCAM's regional projections.

Land-use intensity was an important explanatory variable in our models, but global maps of land-use intensity are not available. We therefore generated global

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estimates of current land-use intensity based on a map of 'Global Land Systems'[397], which divides coarse land-use types into sub-categories based on levels of cropland intensity, livestock densities and human population density. We mapped each Global Land Systems class onto one or more relevant combinations of our classes of land use and land-use intensity (Extended Data Table 2). The Global Land Systems data set has a spatial resolution of 5 arcmin. To calculate the proportion of each $0.5^\circ \times 0.5^\circ$ cell occupied by each land use and land-use intensity combination we calculated the proportion of 5-arcmin cells within each $0.5^\circ \times 0.5^\circ$ cell containing matching Global Land Systems categories (see legend of Extended Data Table 2 for details).

To generate past and future estimates of land-use intensity, we modelled the current proportion of each land-use type estimated to be under minimal, light or intense levels of intensity within each grid cell (one model for each intensity level), as a function of the prevalence of the land-use type within each cell and human population density, with the relationships allowed to vary among the 23 United Nations (UN) sub-regions (that is, we fitted interaction terms between UN sub-region and both the prevalence of each land-use type and human population density). UN sub-region data were taken from the world borders shapefile version 0.3 (http://thematicmapping.org/downloads/world_borders.php) and converted to a $0.5^\circ \times 0.5^\circ$ raster using ArcMap version 10.0 (ref. 388). The models were developed using generalized linear models with a binomial distribution of errors, implemented in the lme4 package version 1.0-5 (ref. 44) in R version 3.0.2 (ref. 390). The resulting models explained between 30.6% and 76.7% of the deviance in estimated current levels of intensity. Past and future land-use intensities were estimated by applying the models to the same past and future estimates of land use and human population density as above.

The scenarios gave the proportion of each grid cell estimated to be occupied by each combination of land use and land-use intensity. We did not attempt to resolve human population density within grid cells for our historical estimates or forecasts, thereby assuming it to be spatially (but not temporally) constant within each cell. The coefficients from the models of site-level diversity were thus applied to each combination of land use and intensity within each cell, with the same human population density estimate across all combinations. All predictions were expressed as a percentage net change compared with a baseline before human land-use effects on biodiversity, in which all land use was assumed to be primary vegetation of minimal intensity of use, and with a human population density of zero. Each cell's average value of net biodiversity change was calculated as the area-weighted mean value across all land uses and intensities. Global average values were calculated as mean values across all cells, weighted by cell area and an appropriate weighting factor to account for the fact that cells have different baseline levels of diversity. The weighting factors applied were: terrestrial vertebrate species richness in the case of richness, and net primary production (NPP) in the case of total abundance. No weighting factor was applied for projections of community-weighted mean plant height. Terrestrial vertebrate species richness was estimated by overlaying extent-of-occurrence range maps for mammals, birds, amphibians and reptiles, using Python code written by ourselves and implemented in ArcMap version 10.0 (ref. 388). Data on NPP were estimates of potential NPP (that is, in the absence of human effects) from the Lund-Postdam-Jena (LPJ) Dynamic Global Vegetation Model[398].

The 95% confidence intervals around the projected values of biodiversity for each combination of pressure variables were estimated based on uncertainty in the modelled coefficients. We were unable to conduct multi-model averaging to account for uncertainty in the structure of the models (that is, projections were based only on the final best model) because applying such complex mixed-effects models, based on such large data sets, to multiple scenarios of human pressure at a global scale was intractable both in terms of time and computer-memory requirements. We were also unable to account for uncertainty in the trajectories of the human pressure variables, because uncertainty estimates are not available for any of the variables considered.

To estimate average biodiversity change in individual countries, we intersected the gridded projections with the world borders shapefile (see above) using the extract function in the raster package version 2.2-12 (ref. 399) in R version 3.0.2 (ref. 390). Mean values across the cells associated with each country were calculated, weighted by cell area. To interpret the outcomes for countries in terms of their natural biodiversity, we related the country-level projections to estimates of average natural vertebrate species richness (see above). To interpret the outcomes for countries in terms of their socio-economic status, we related the projections to estimates of the Human Development Index, which is an indicator of education, life expectancy, wealth and standard of living (https://data.undp.org/).

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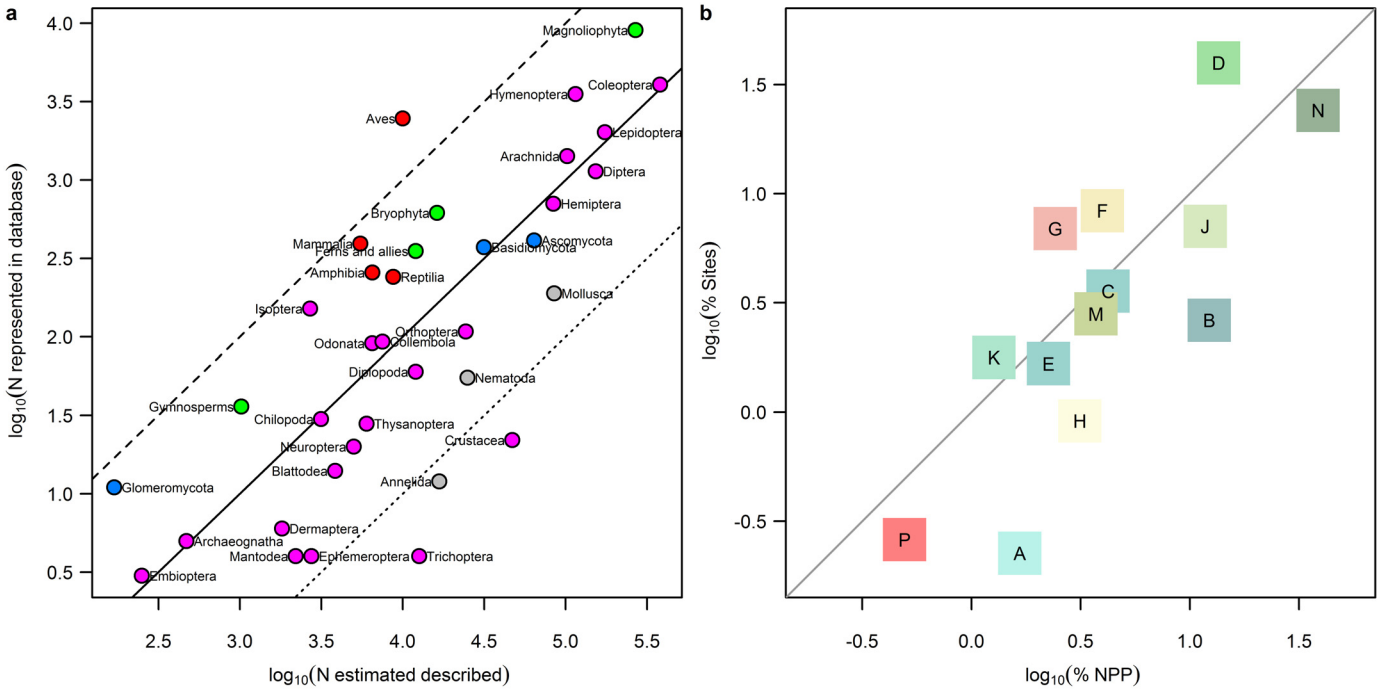

Extended Data Figure 1 | Taxonomic and geographic representativeness of the data set used. **a**, The relationship between the number of species represented in our data and the number estimated to have been described[17] for 47 major taxonomic groups. Lines show (from bottom to top) 0.1%, 1% and 10% representation of described species in our data set; magenta, invertebrates; red, vertebrates; green, plants; blue, fungi; and grey, all other taxonomic groups. **b**, The relationship across biomes[400] between the percentage of global terrestrial net primary production and the number of sites in our data set; A, tundra; B, boreal forests and taiga; C, temperate conifer forests; D, temperate broadleaf and mixed forests; E, montane grasslands and shrublands; F, temperate grasslands, savannahs and shrublands; G, Mediterranean forests, woodlands and scrub; H, deserts and xeric shrublands; J, tropical and subtropical grasslands, savannahs and shrublands; K, tropical and subtropical coniferous forests; M, tropical and subtropical dry broadleaf forests; N, tropical and subtropical moist broadleaf forests; P, mangroves; note that the flooded grasslands and savannah biome is not represented in the data set; grey line shows a 1:1 relationship.

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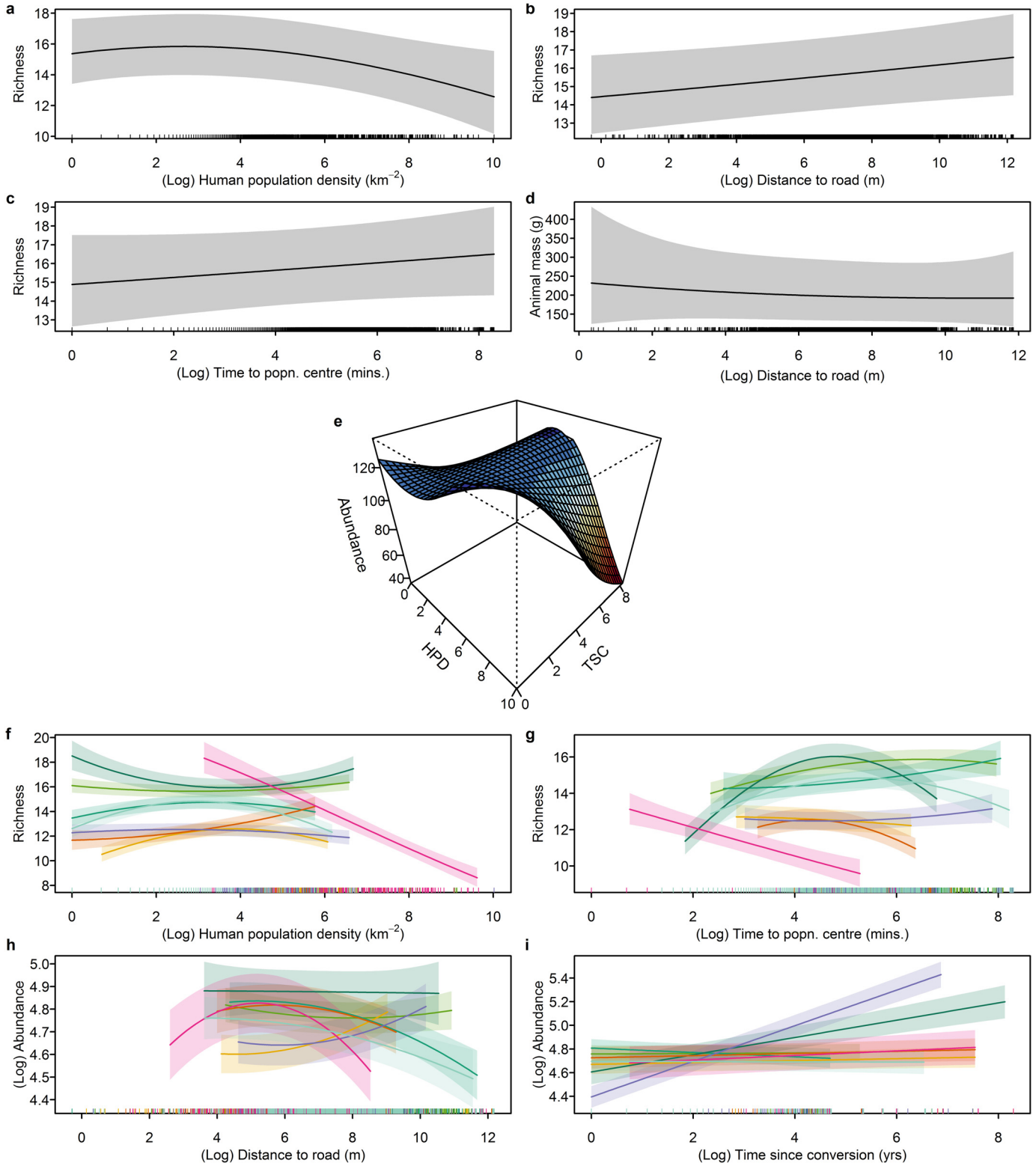

Extended Data Figure 2 | Detailed response of local diversity to human pressures. **a**–**i**, Modelled effects (controlling for land use and land-use intensity) of human population density (HPD), distance to nearest road, time since 30% conversion of a landscape to human uses (TSC) and time to nearest population centre with greater than 50,000 inhabitants (**a**–**d**), interactions between pairs of these variables (**e**), and interactions between these variables and land use (**f**–**i**) on site-level diversity. **a**–**c**, **f**, **g**, Within-sample species richness; **e**, **h**, **i**, total abundance; and **d**, community-weighted mean vertebrate body mass. Shaded polygons in **a**–**d** show 95% confidence intervals. For clarity, shaded polygons in **f**–**i** are shown as $\pm 0.5 \times$ s.e.m. Confidence intervals in **e** are omitted. Rugs along the *x* axes in the line graphs show the values of the explanatory variables represented in the data set used for modelling. Only significant effects are shown. Note that distance to nearest road and travel time to major population centre measures are the raw (log-transformed) values fitted in the models rather than the proximity to roads and accessibility values (obtained as 1 minus the former values) presented in Fig. 1. Sample sizes are given in full in the Methods.

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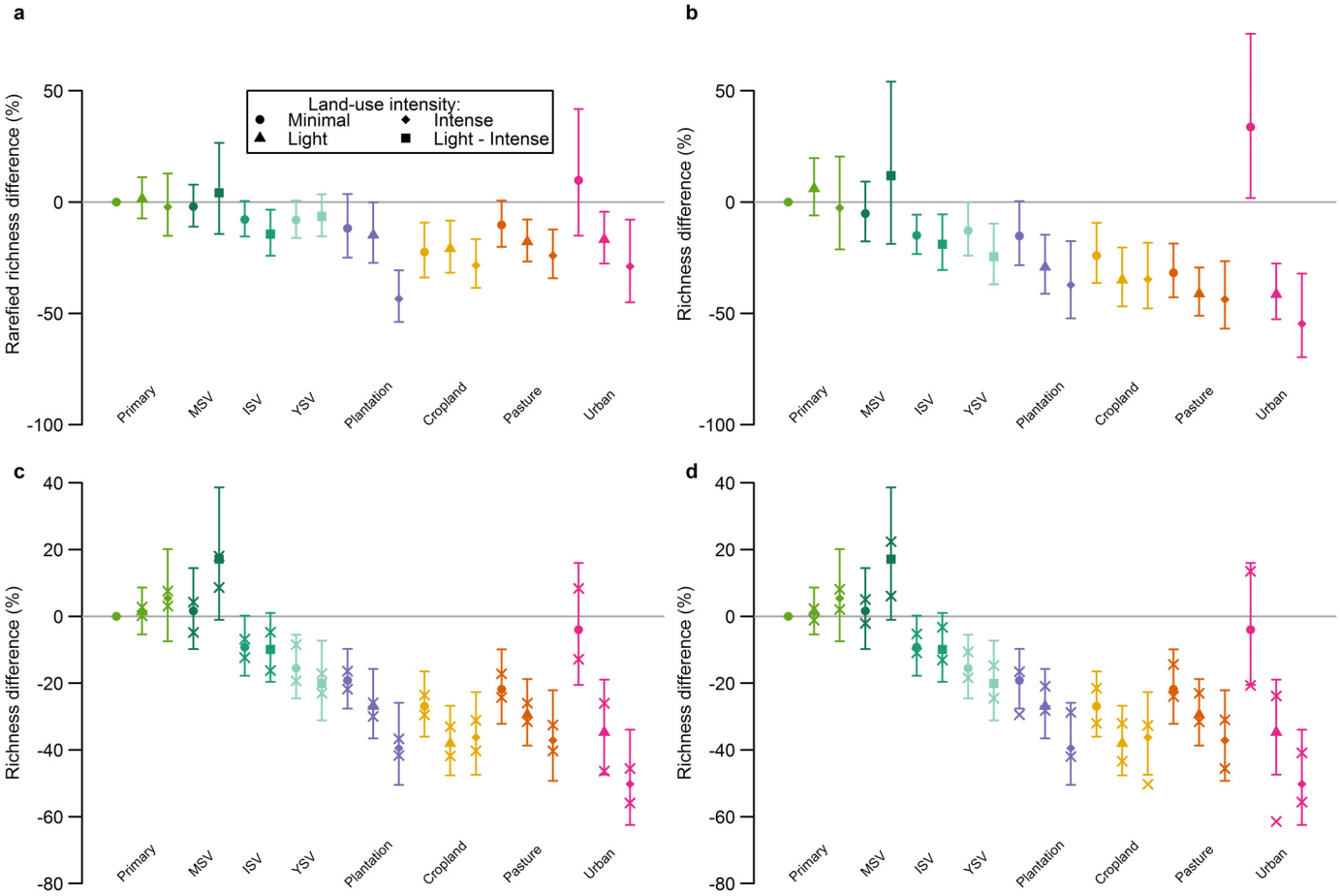

Extended Data Figure 3 | Robustness of modelled effects of human pressures. **a**, Effects of land use and land-use intensity on rarefaction-based species richness. **b**, To test that any differences between these results and the results for within-sample species richness presented in the main manuscript were not because rarefied species richness could only be calculated with a smaller data set, we also show modelled effects on within-sample species richness with the same reduced data set. **c**, **d**, Cross-validated robustness of coefficient estimates for land use and land-use intensity. Crosses show 95% confidence intervals around the coefficient estimates under tenfold cross-validation, excluding data from approximately 10% of studies at a time (**c**), and under geographical cross-validation, excluding data from one biome at a time (**d**); colours, points, error bars and land-use labels are as in Fig. 1 in the main text. Sample sizes are given in full in the Methods.

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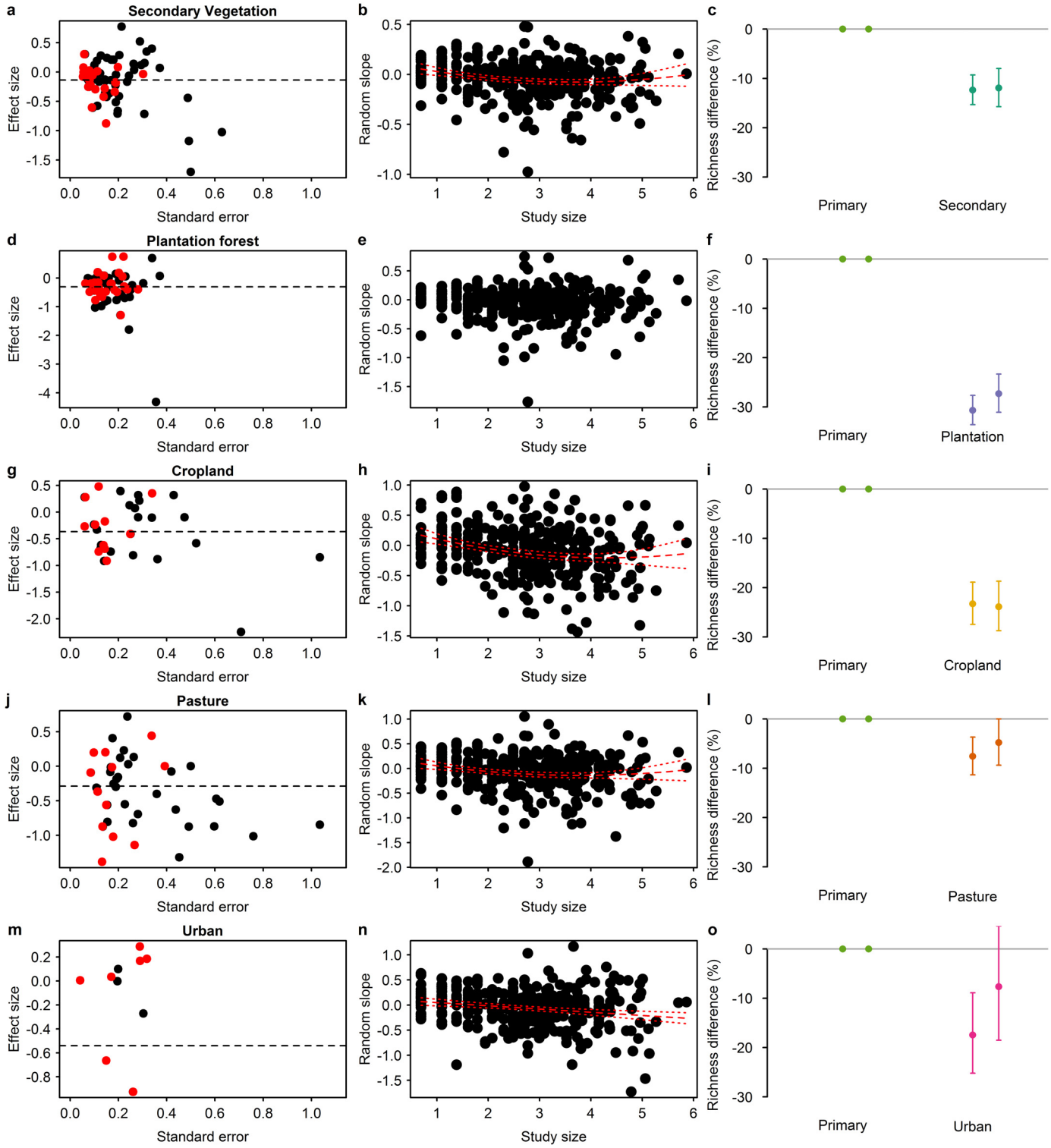

Extended Data Figure 4 | Tests of the potential for publication bias to influence the richness models and projections. Left-hand panels (**a**, **d**, **g**, **j**, **m**) show funnel plots of the relationship between the standard error around coefficient estimates (inversely related to the size of studies) and the coefficient estimates themselves for each coarse land-use type; there is evidence for publication bias with respect to some of the land-use types, as indicated by an absence of points on one or other side of zero for studies with large standard errors (but note that small studies are down-weighted in the model). Red points show studies with more than five sites in the land use in question (ten for secondary vegetation and plantation forest because there were more sites for these land uses and some studies with between five and ten sites showed variable responses); horizontal dashed lines show the modelled coefficients for each land use. Central panels (**b**, **e**, **h**, **k**, **n**) show the relationship between study size (log-transformed total number of sites) and the random slope of the land use in question with respect to study identity, from a random-slopes-and-intercepts model. Where a significant relationship was detected using a linear model, fitted values and 95% confidence intervals are shown as a red dashed line and red dotted lines, respectively. Conversely to what would be expected if publication bias was present, where significant relationships between study size and random slopes were detected, these were negative (that is, larger studies detected more negative effects). Right-hand panels (**c**, **f**, **i**, **l**, **o**) show the robustness of modelled coefficients to removal of studies with few sites in a given land use (black points in the left-hand panels). Left-hand error bars show coefficient estimates for all studies and right-hand error bars show coefficient estimates for studies with more than five sites in that land use (ten for secondary vegetation and plantation forest).

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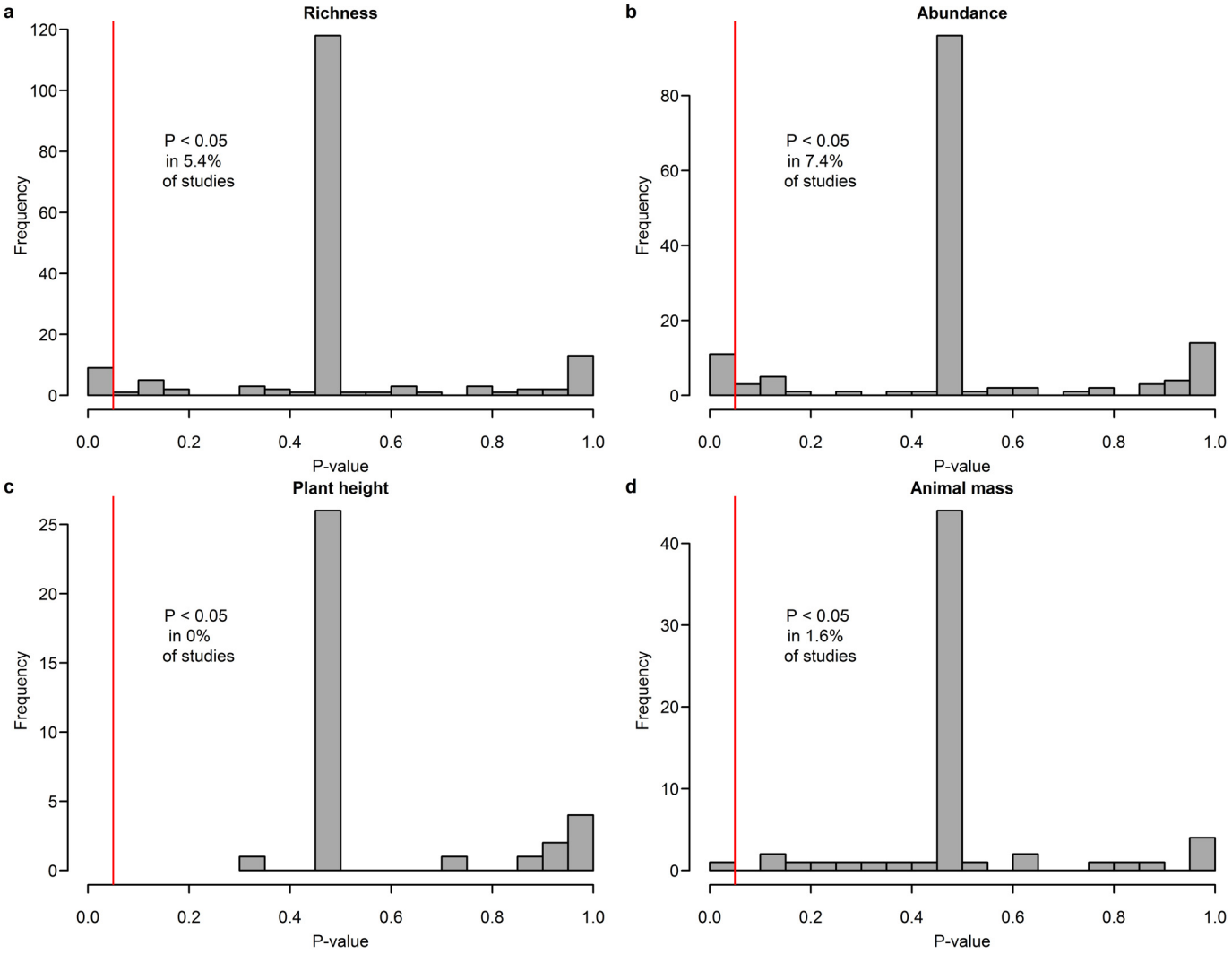

Extended Data Figure 5 | Tests for spatial autocorrelation in the model residuals. **a**–**d**, For the four main modelled metrics of site-level diversity—within-sample species richness (**a**), total abundance (**b**), community-weighted mean plant-height (**c**) and community-weighted mean animal mass (**d**)—histograms of *P* values from sets of Moran's tests for spatial autocorrelation in the residuals of the best models for individual studies are shown. The percentage of studies with significant spatial autocorrelation ($P < 0.05$; indicated by a vertical red line) is shown.

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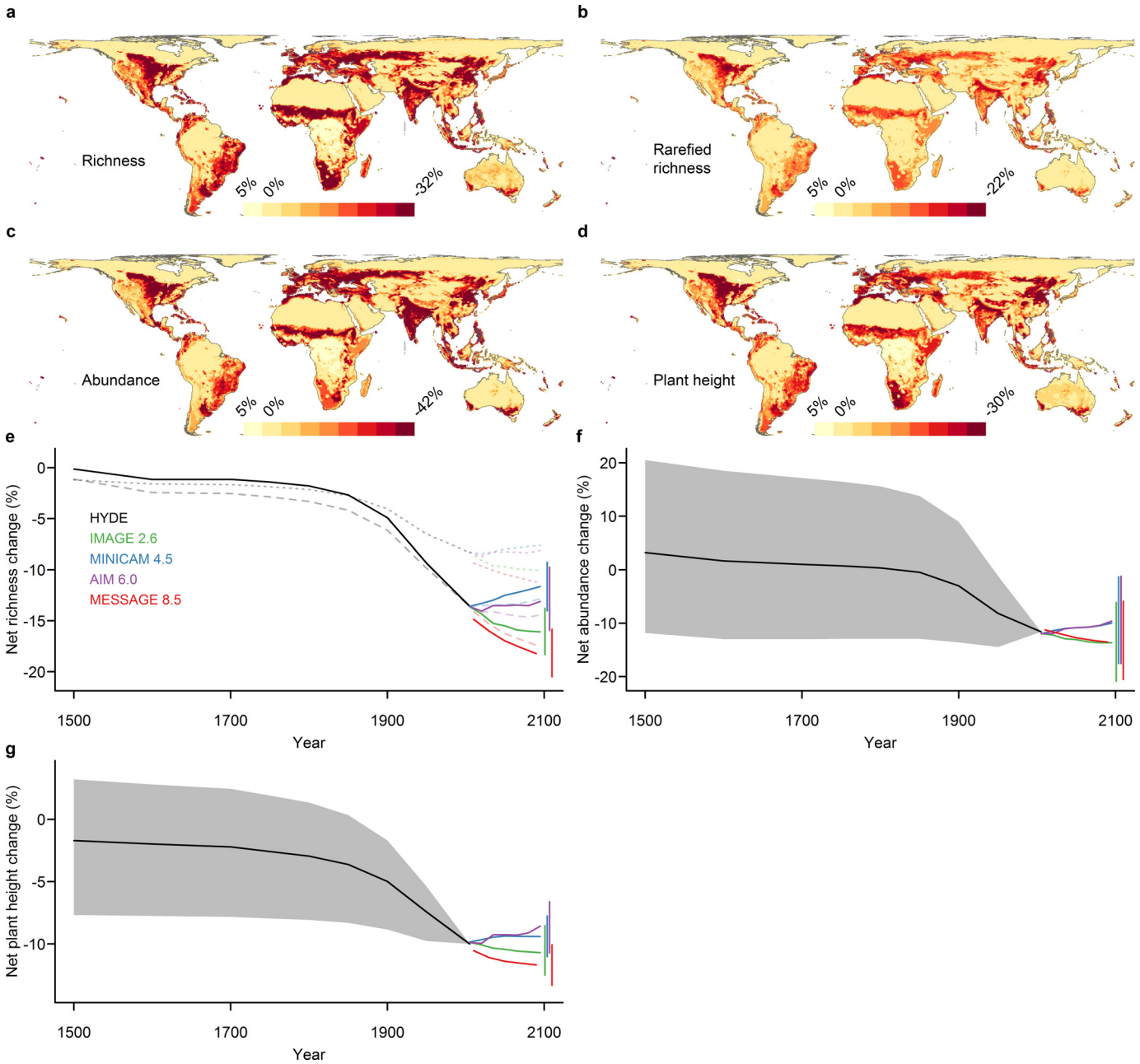

Extended Data Figure 6 | Current, past and future projections of all metrics of local biodiversity. a–d, Net change in local diversity caused by land use and related pressures by 2000 under an IMAGE reference scenario[10]. Changes in richness (**a**), rarefied richness (**b**), total abundance (**c**) and community-weighted mean plant height (**d**) are shown. Note that the values used to divide the colours are the same in all panels, but that the maximum and minimum values are different, as indicated in the legends. **e–g**, Historical and future estimates of net change in local diversity from 1500–2095, based on estimates of land-use, land-use intensity and human population density from the four RCP scenarios (Table 1). Net changes in richness (**e**), total abundance (**f**) and community-weighted mean plant height (**g**) are shown. Historical (shading) and future (error bars) uncertainty shown as 95% confidence intervals, with uncertainty rescaled to be zero in 2005 to show uncertainty in past and future change separately. The global average projection for the MESSAGE scenario does not directly join the historical reconstruction because projections start in 2010 (human population estimates are available at 15-year intervals) and because human population (and thus land-use intensity) and plantation forest extent have not been harmonized among scenarios. In panel **e**, the dashed line shows projected diversity change under land-use change only (that is, without land-use intensity and human population density, the projections of which involved simplifying assumptions), and the dotted line shows projections of rarefaction-based species richness.

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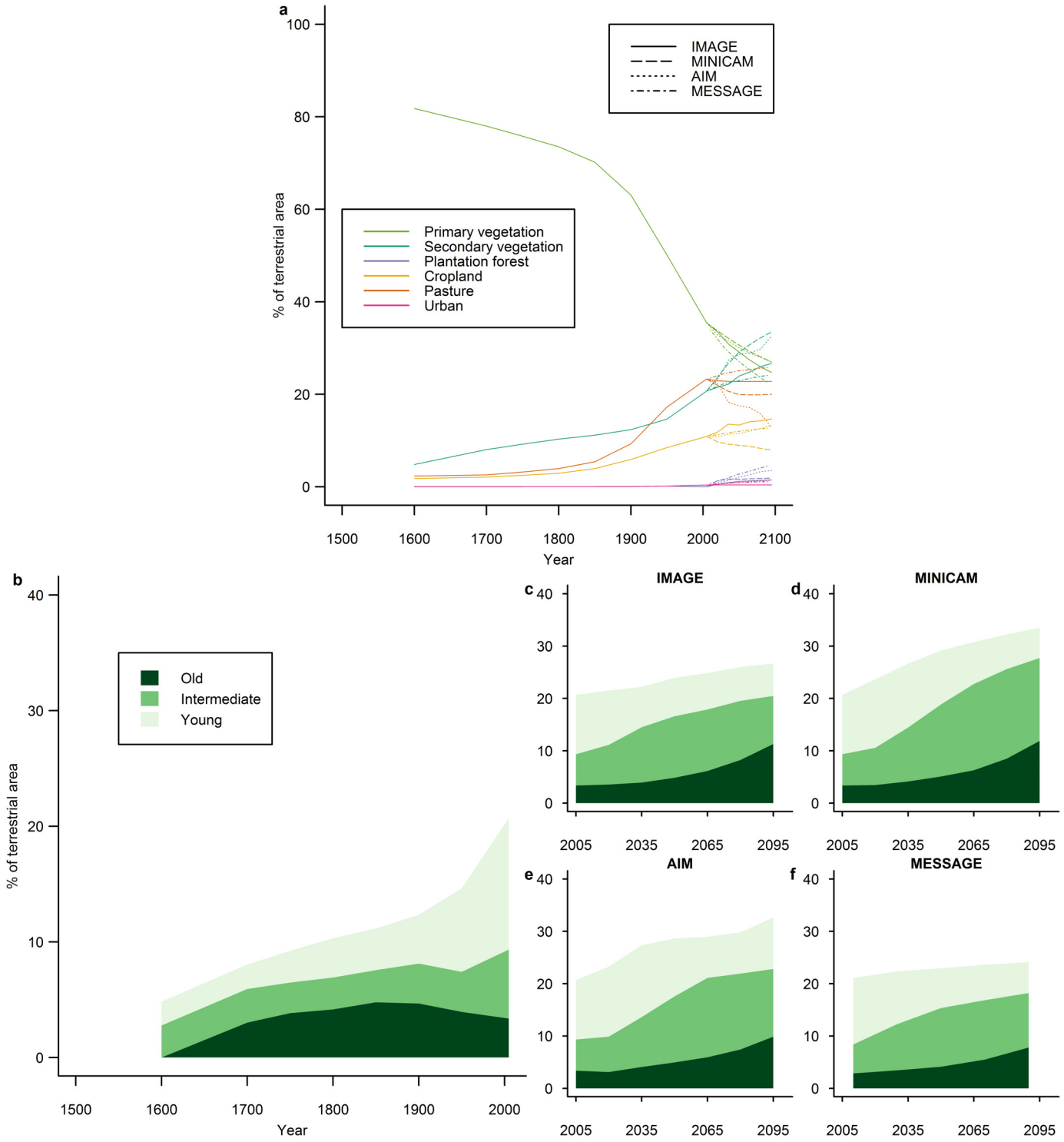

Extended Data Figure 7 | Reconstructed and projected total global land-use areas under the RCP scenarios. a, Estimated total area of the major land-use types. **b–f**, Estimated total area of secondary vegetation in different stages of recovery.

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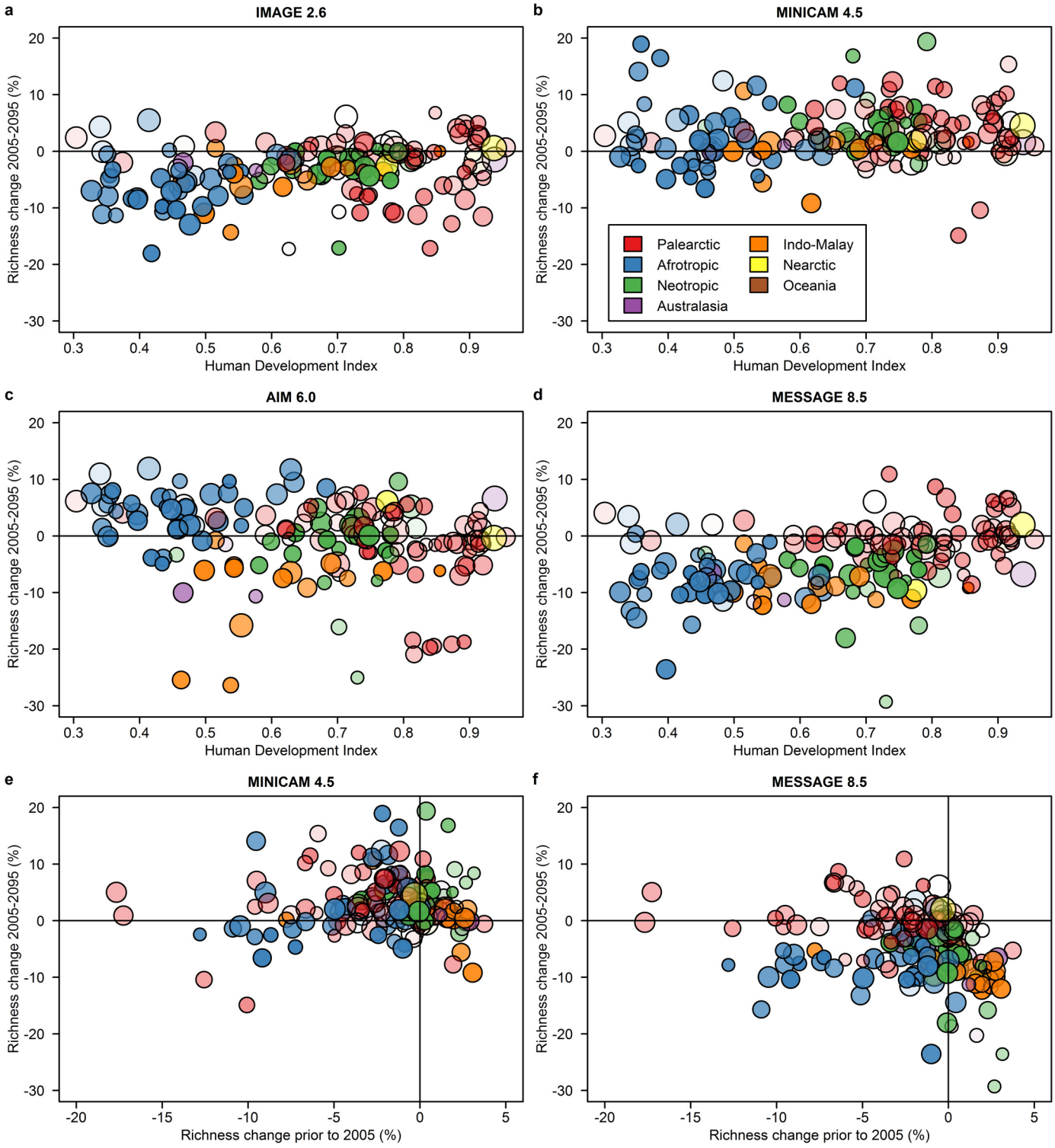

Extended Data Figure 8 | Biodiversity projections at the country level. **a**–**d**, Country-level projections of net change in local richness between 2005 and 2095 under the four RCP scenarios (IMAGE 2.6 (**a**), MiniCAM 4.5 (**b**), AIM 6.0 (**c**) and MESSAGE 8.5 (**d**)), shown in relation to the Human Development Index (an indicator of education, life expectancy, wealth and standard of living) in the most recent year for which data are available. **e**, **f**, Country-level projections of net change in local richness between 2005 and 2095 under the best- and worst-performing RCP scenarios in terms of biodiversity (MiniCAM 4.5 (**e**) and MESSAGE 8.5 (**f**), respectively), shown in relation to past change in biodiversity from a baseline with no human land-use effects to 2005 according to the HYDE land-use reconstruction. Colours indicate biogeographic realms (key in **b**); colour intensity reflects native vertebrate species richness (more intense colour represents higher species richness); point size is proportional to (log) country area.

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Extended Data Table 1 | Land use and land-use intensity classification definitions (from ref. 16)

Level 1 Land Use	Predominant Land Use	Minimal use	Light use	Intense use
No evidence of prior destruction of the vegetation	**Primary Vegetation**	Any disturbances identified are very minor (e.g., a trail or path) or very limited in the scope of their effect (e.g., hunting of a particular species of limited ecological importance).	One or more disturbances of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem. Primary sites in suburban settings are at least Light use.	One or more disturbances that are severe enough to markedly change the nature of the ecosystem; this includes clear-felling of part of the site too recently for much recovery to have occurred. Primary sites in fully urban settings should be classed as Intense use.
Recovering after destruction of the vegetation	**Mature Secondary Vegetation**			
	Intermediate Secondary Vegetation			
	Young Secondary Vegetation			
	Secondary Vegetation (indeterminate age)			
Human use (agricultural)	**Plantation forest**	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which have not been recently (< 20 years) clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no recent (< 20 years) clear-felling. Monoculture oil-palm plantations with no recent (< 20 years) clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive recent (< 20 years) clear-felling.
	Cropland	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
	Pasture	Pasture with minimal input of fertiliser and pesticide, and with low stock density (*not* high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture either with significant input of fertiliser or pesticide, or with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).	Pasture with significant input of fertiliser or pesticide, *and* with high stock density (high enough to cause significant disturbance or to stop regeneration of vegetation).
Human use (urban)	**Urban**	Extensive managed green spaces; villages.	Suburban (e.g. gardens), or small managed or unmanaged green spaces in cities.	Fully urban with no significant green spaces.

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Extended Data Table 2 | Conversion between Global Land Systems data set and our intensity classification for each major land-use type

Global Land Systems classification	Primary	Secondary	Cropland	Pasture	Urban
Cropland, extensive with few livestock	NA	NA	minimal	light	NA
Cropland, extensive with bovines, goats & sheep	NA	NA	minimal	intense	NA
Cropland, extensive with pigs & poultry	NA	NA	minimal	intense	NA
Cropland, medium intensive with few livestock	NA	NA	light	light	NA
Cropland, medium intensive with bovines, goats & sheep	NA	NA	light	intense	NA
Cropland, medium intensive with pigs & poultry	NA	NA	light	intense	NA
Cropland, intensive with few livestock	NA	NA	intense	light	NA
Cropland, intensive with bovines, goats & sheep	NA	NA	intense	intense	NA
Cropland, intensive with pigs & poultry	NA	NA	intense	intense	NA
Mosaic cropland and grassland with bovines, goats and sheep	NA	NA	intense	intense	NA
Mosaic cropland and grassland with pigs & poultry	NA	NA	intense	intense	NA
Mosaic cropland (extensive) and grassland with few livestock	NA	NA	minimal	light	NA
Mosaic cropland (medium intensive) and grassland with few livestock	NA	NA	light	light	NA
Mosaic cropland (intensive) and grassland with few livestock	NA	NA	intense	light	NA
Mosaic cropland and forest with pigs & poultry	NA	NA	intense	intense	NA
Mosaic cropland (extensive) and forest with few livestock	NA	NA	minimal	light	NA
Mosaic cropland (medium intensive) and forest with few livestock	NA	NA	light	light	NA
Mosaic cropland (intensive) and forest with few livestock	NA	NA	intense	light	NA
Dense forest	minimal	minimal	NA	NA	NA
Open forest with few livestock	light	light	NA	light	NA
Open forest with pigs & poultry	intense	intense	NA	intense	NA
Mosaic grassland and forest	minimal	minimal	NA	NA	NA
Mosaic grassland and bare	minimal	minimal	NA	NA	NA
Natural grassland	minimal	minimal	NA	NA	NA
Grassland with few livestock	NA	NA	NA	light	NA
Grassland with bovines, goats and sheep	NA	NA	NA	intense	NA
Bare	NA	NA	NA	NA	NA
Bare with few livestock	NA	NA	NA	light	NA
Peri-urban and villages	NA	NA	NA	NA	minimal
Urban	NA	NA	NA	NA	intense

To estimate proportional coverage of each intensity class for each land-use type in the $0.5^{\circ} \times 0.5^{\circ}$ grid cells used for projection, we calculated the number of finer-resolution Global Land Systems[397] cells with a matching intensity class for the land-use type in question, as a proportion of Global Land Systems cells matching any intensity class for the land-use type in question. For example, to calculate the proportion of urban land that is under intense use, we divided the number of cells with a Global Land Systems classification of 'urban' by the number of cells classified as 'urban' or 'peri-urban and villages'. None of the Global Land Systems classes could inform about the intensity of plantation forest, and so we assumed that any plantation forest was composed of equal proportions under minimal, light and intense use.

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Appendix IV

Science for Environment Policy, *8 May 2014*, *Issue 371*, *Organic farmland benefits biodiversity over the long term*, European Commission DG Environment News Alert Service. Edited by SCU, The University of the West of England, Bristol. To access articles and to subscribe, please go to http://ec.europa.eu/science-environment-policy



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European Commission

Science for Environment Policy

Organic farmland benefits biodiversity over the long term

Biodiversity on organic farms is, on average, 34% higher than on conventional farms, according to a recent study. The researchers used data from a large number of studies to show that this figure has remained stable over the last 30 years.

There is a continuing debate over whether organic farming provides greater environmental benefits than conventional farming. Previous studies have shown that organic agriculture is better for biodiversity than conventional methods. However, estimates of the benefits vary. To gain a better overview of the benefits, this research combined and analysed the results of 94 previous studies that had compared biodiversity on organic farms with that on conventional farms.

The researchers measured biodiversity in terms of 'species richness', i.e. the number of different species found. These figures were extracted from the different studies in different forms of raw data. The researchers classified the species according to their taxonomic group (arthropods, birds, microbes and plants) and also according to the function they perform, i.e. producers (plants), herbivores, pollinators, predators, decomposers (which break down dead material), and others, such as omnivores.

They also assessed the effects of land use in the surrounding landscape to see if this had an impact on species richness. Using satellite images, they estimated the proportion of arable fields and the average size of the arable fields, and used both as measures of land use intensity. They also estimated the number of habitats, e.g. wetlands, ditches and hedgerows, which is an indicator of a landscape's complexity.

Overall, the researchers found that biodiversity was, on average, 34% higher on organic farms than conventional farms. The greatest difference between farm types was found for plants; their species richness was around 70% higher on organic farms. This is probably because herbicides are not used, the researchers suggest. The species richness of arthropods, birds and microbes were also all significantly higher on organic farms compared with conventional farms, most likely due to the restricted use of pesticides on organic farms.

As a functional group, pollinators received one of the greatest benefits from organic farming, with the number of different species 50% higher on organic farms compared with conventional farms. Herbivores and predators were also more diverse on organic farms than on conventional ones.

The beneficial effect of organic farms, relative to conventional farms, was greater in more intensively-farmed landscapes, where a larger proportion of the landscape surrounding the farms was covered with arable fields. This may be because organic farms provide an 'island' or refuge for wildlife in the conventional landscape. The benefits of organic methods varied, however, depending on the species, what function they performed and the type of crops grown.

Importantly, the researchers found that the positive effects of organic methods on biodiversity remained stable over the 30 years spanning the studies included in this research. The authors of the study note that most of the data used came from research in temperate western and northern Europe and North America. Farming has been long established in these regions, and wildlife is partly adapted to extensive farming methods, although it is threatened by more recent intensive farming. It is in these regions that the application of organic farming could most clearly contribute to mitigating the agricultural impacts on biodiversity.

However, there is a lack of data from other regions, such as Asia, Africa and Australasia, and more research could help determine whether biodiversity benefits are also found in hotter climates on organic farms which grow very different crops, such as bananas or cocoa.