LETTER

Land-use intensification reduces functional redundancy and response diversity in plant communities

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Abstract

Ecosystem resilience depends on functional redundancy (the number of species contributing similarly to an ecosystem function) and response diversity (how functionally similar species respond differently to disturbance). Here, we explore how land-use change impacts these attributes in plant communities, using data from 18 land-use intensity gradients that represent five biomes and > 2800 species. We identify functional groups using multivariate analysis of plant traits which influence ecosystem processes. Functional redundancy is calculated as the species richness within each group, and response diversity as the multivariate within-group dispersion in response trait space, using traits that influence responses to disturbances. Meta-analysis across all datasets showed that land-use intensification significantly reduced both functional redundancy and response diversity, although specific relationships varied considerably among the different land-use gradients. These results indicate that intensified management of ecosystems for resource extraction can increase their vulnerability to future disturbances.

Keywords

Functional diversity, land-use change, redundancy, resilience, response diversity.

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INTRODUCTION

The unprecedented rates and global extent of current biodiversity loss (Pimm *et al.* 1995) have prompted a rapidly growing body of research exploring its functional consequences (Chapin *et al.* 2000; Loreau *et al.* 2001; Hooper *et al.* 2005). Although experimental studies have shown positive relationships between biodiversity and the rates or stability of various ecosystem functions (Balvanera *et al.* 2006), many of these studies have been criticized as marginally relevant to policy and management because they used random synthetic assemblages of species without considering the

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actual drivers of biodiversity loss (Srivastava & Vellend 2005; but see Larsen *et al.* 2005). Moreover, most of these studies have presented species richness as their only measure of biodiversity (Balvanera *et al.* 2006) and did not assess functional diversity as a more direct and mechanistic link to ecosystem processes (Díaz & Cabido 2001; Hooper *et al.* 2005).

In particular, a key aspect of functional diversity that has generated much interest is the variability of responses to disturbances among species that contribute similarly to ecosystem function (Chapin *et al.* 1997; Yachi & Loreau 1999; Norberg *et al.* 2001; Naeem & Wright 2003). This important yet largely unexplored facet of functional diversity has been termed 'response diversity', and is considered crucial for ecosystem renewal and reorganization following disturbances (Chapin *et al.* 1997; Elmqvist *et al.* 2003). Response diversity represents the first safeguard against the loss of ecosystem functions and services in a changing world (Elmqvist *et al.* 2003; Folke *et al.* 2004). For example, in Californian serpentine grasslands, long-term studies over > 20 years showed that diverse responses of component species to rainfall variation and prolonged drought resulted in greater stability of primary production in the face of changing external conditions (Hobbs *et al.* 2007).

Response diversity has developed from the earlier concept of functional redundancy (Walker 1992; Lawton & Brown 1993; Naeem 1998). If there are sets of co-existing species whose ecological effects are similar, then any given species pool may be classified into 'functional effect groups', based on the traits which determine these effects (Hooper *et al.* 2002; Lavorel & Garnier 2002). The degree of redundancy within a functional effect group is the number of species it contains (Walker 1992; Naeem 1998). High redundancy provides resilience (sometimes called 'insurance') against the loss of functions and services provided by that group if different species show compensatory responses following environmental change (Naeem 1998). This view, however, is only valid if species richness corresponds directly to response diversity. This relationship cannot be assumed. If, for example, a large number of species within an effect group respond similarly to disturbance or environmental change, then functional redundancy would appear to be high even though response diversity is low (Elmqvist *et al.* 2003).

Despite calls to quantify how human-driven changes in biodiversity alter the ability of ecosystems to cope with future environmental change (e.g. Chapin *et al.* 1997; Scheffer *et al.* 2001; Folke *et al.* 2004; Foley *et al.* 2005), conceptual and theoretical development still greatly outpaces empirical application. So far, some field studies have demonstrated the existence of response diversity in plant or animal communities by observing responses to an anthropogenic disturbance event, but none has yet asked how

response diversity itself can be altered by human activities. For example, Walker *et al.* (1999) found evidence for response diversity in an Australian rangeland by observing that minor plant species took over the functional roles of the dominant species following long-term grazing. Similarly, native bee communities in watermelon fields were shown to harbour elements of differing responses following the partial clearance of adjacent native vegetation cover, stabilizing pollination services to crops (Winfree & Kremen 2009). While both studies have illustrated response diversity, neither has attempted to quantify how it can be impacted.

Globally, changing land-use patterns is the most important driver of biodiversity loss (Sala *et al.* 2000). Land-use change involves two main impacts on the biosphere: conversion (i.e. natural habitats altered for human use) and intensification (e.g. greater intensity and/or frequency of disturbance, increased use of external inputs; Foley *et al.* 2005). While the global impact of land-use change on species loss can be quantified (Pimm & Raven 2000), its impacts on functional diversity and the long-term provisioning of ecosystem services remain much less clear. Recent studies have demonstrated changes in functional diversity of plant or animal assemblages in human-modified landscapes (e.g. Mayfield *et al.* 2006; Flynn *et al.* 2009), but none has yet examined how land-use change affects response diversity in particular.

In this paper, we explore how land-use change impacts plant functional redundancy and response diversity through a meta-analysis of 18 land-use intensity gradients from five biomes and nine countries, comprising more than 2800 species (Fig. 1). The intensification gradients include forest conversion to pasture, rangeland development and logging regimes differing in intensity or frequency. We follow a hierarchical effect–response functional trait framework (Hooper *et al.* 2002) to measure response diversity based on the distinction between effect traits and response traits (Hooper *et al.* 2002; Lavorel & Garnier 2002; Naeem & Wright 2003; Suding *et al.* 2008). We first classify species within each land-use intensity gradient into functional effect groups, using 12 traits that affect biogeochemical processes. We then quantify the response diversity of each effect group as the dispersion of its constituent species in response trait space, using 12 traits that affect plant responses to disturbances. We show that land-use intensification generally leads to reductions in both response diversity and functional redundancy, thereby reducing ecosystem resilience to future disturbances.

MATERIAL AND METHODS

The data used in this study came from 18 land-use intensity gradients (Tables S1 and S2), each from geographically
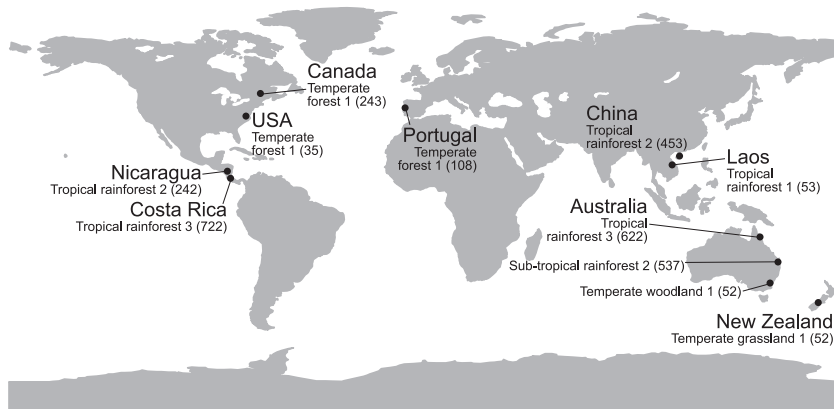
Figure 1 Map of study regions contributing to this meta-analysis. The map shows the major biome of each region, the number of distinct land-use intensity gradients and total number of species (in parentheses).

distinct landscapes within 10 different regions around the globe (Fig. 1). These 18 studies covered five biomes (tropical rainforest, sub-tropical rainforest, temperate forest, temperate woodland and temperate grassland) in a total of nine countries (Australia, Canada, China, Costa Rica, Laos, New Zealand, Nicaragua, Portugal and the United States of America; Fig. 1). Datasets used in this study were made available to us by participants in an ARC-NZ Research Network for Vegetation Function working group. To identify appropriate datasets, co-ordinators of this working group approached ecologists who had published results on plant species and functional diversity from human-altered landscapes. We aimed to identify appropriate datasets from diverse regions of the world and did not aim to obtain more than three datasets for any one global region. Of the datasets initially made available for this project by our colleagues, 18 studies proved appropriate for analysis. Datasets were used for our analyses if they included a survey of plant communities within a well-defined local geographic region, across plots representing a gradient of at least three land-use intensities relevant to that landscape (Table S2), e.g. from primary rainforest to logged sites or shifting cultivation fallows, or from ungrazed sub-alpine grasslands to heavily fertilized and grazed sites, and had equal sampling at each plot. Land-use intensity was ranked on an ordinal scale specific to each landscape according to the intensity and/or frequency of disturbance (i.e. biomass removal) and external inputs (e.g. fertilizer). Vegetation was surveyed in 1–24 plots per land-use intensity, depending on the study (Table S2). Within each study, standardized sampling methods were used to ensure consistent sampling of all plots. The vegetation surveys included all vascular terrestrial species, except in six studies which focused on particular life-forms (e.g. herbaceous or trees/shrubs) or plants within given size limits (e.g. all plants > 1 cm diameter at breast height; Table S1). Details of each land-use intensity gradient can be found in Table S2.

Plant functional traits

We compiled a common set of standardized functional traits (Table 1) to allow meaningful comparisons between the 18 datasets used in this study. In many cases, trait data were transformed and/or reclassified using traits gathered for the original studies. When this was not possible new trait data were obtained from published sources or from herbarium specimens. Each individual study had between seven and 16 of a possible 22 traits (Tables S1 and S3). Across all datasets, our functional trait analysis included 2871 species from 1290 genera and 255 families. Principal data sources and references for each study are given in Table S4.

A crucial step in our methodological approach was to distinguish between effect and response traits (Table 1). This distinction is fundamental to the concept of response diversity (Hooper *et al.* 2002; Naeem & Wright 2003). Effect traits were defined as traits that influence biogeochemical processes, while response traits were primarily regenerative traits that influence how species respond to disturbances (Lavorel & Garnier 2002). Distinguishing between effect and response traits can be challenging (Suding *et al.* 2008). To guide our assessment, we followed the recommendations of Cornelissen *et al.* (2003) for which traits fall into these categories. We designated 13 effect and 12 response traits, three of which were classified as relevant to both categories (Table 1).

Response diversity and functional redundancy

Our methodological approaches to measuring functional redundancy and response diversity are illustrated in Figs S1 and S2, respectively. For each dataset, we first computed a Gower dissimilarity matrix between all species (Figs S1a and S2a), using effect traits (Table 1). We chose this measure because it allows mixed variable types (continuous, ordinal, and categorical), as well as missing values (Legendre &

Table 1 Plant functional effect (E) and response (R) traits used in the analysis, and number of studies that included each trait

Functional trait	E/R	Type	Unit	No. studies
Growth form	E	Nominal	–	17
Height	E	Continuous	m	15
Leaf dry matter content	E	Continuous	mg g^{-1}	2
Leaf nitrogen concentration	E	Continuous	mg g^{-1}	1
Leaf phenology	E	Nominal	–	11
Leaf phosphorous concentration	E	Continuous	mg g^{-1}	1
Leaf size	E	Continuous	mm^2	14
Leaf sulphur concentration	E	Continuous	mg g^{-1}	1
Photosynthetic pathway	E/R	Nominal	–	8
Specific leaf area	E	Continuous	m^2 kg^{-1}	10
Wood density	E	Continuous	g cm^{-3}	12
Nutrient uptake strategy	E/R	Nominal	–	13
Age of reproduction	R	Ordinal	–	1
Clonality	R	Nominal	–	10
Dispersal mode	R	Nominal	–	18
Lifespan	R	Ordinal	–	8
Maximum propagule longevity	R	Ordinal	–	7
Physical defence	R	Nominal	–	14
Pollination syndrome	R	Nominal	–	15
Raunkiaer life form*	E/R	Nominal	–	7
Resprouting ability	R	Nominal	–	9
Seed mass	R	Continuous	mg	17

Traits were measured and classified as effect and/or response traits (Cornelissen *et al.* 2003). *Raunkiaer life form was used as an effect trait (as well as response) for only two datasets (Canada and USA), to better resolve the classification.

Legendre 1998). We selected the effect traits from the list in Table 1, excluding any traits that had very low coverage (> 50% missing values) or showed little or no variability; this was done on a per study basis.

We classified species into functional effect groups using Ward's minimum variance clustering on the Gower dissimilarity matrix computed from effect traits (Figs S1b and S2b). Ward's clustering method minimizes within-group sums of squares and tends to form hyperspherical clusters with roughly the same number of species per cluster if species are evenly distributed in trait space (Legendre & Legendre 1998). The actual number of effect groups for each dataset was determined by visual inspection of the clustering dendrogram according to expert botanical knowledge, following Aubin *et al.* (2009). To facilitate group identification, mean trait values (and modes for categorical traits) for all effect groups are given in Table S5.

We assigned effect group membership to all species present in each plot (Figs S1c and S2d) and measured the functional redundancy (number of species within an effect group; Fig. S1d) and the response diversity of each effect group in each plot (Fig. S2d–e). We quantified response diversity of each effect group by measuring the multivariate functional dispersion (FDis; Laliberté & Legendre 2009) of its constituent species in response trait space, based on a

Gower dissimilarity matrix of species computed from response traits (Table 1). As with effect traits, the number and identity of response traits varied by dataset (Tables S1 and S3). Because FDis is the average distance of individual species to their group centroid in response trait space, it is little influenced by species number (Laliberté & Legendre 2009), contrary to other indices such as functional richness (Villéger *et al.* 2008) or functional attribute diversity (FAD; Walker *et al.* 1999) which are strongly positively influenced by the number of species. Therefore, our use of FDis ensured that our response diversity measure was not trivially related to functional redundancy. Our index of response diversity was purposefully not weighted by species relative abundances because rare species may contribute substantially to resilience (Walker *et al.* 1999). A decrease in multivariate dispersion in response trait space (i.e. a loss of response diversity) for a given effect group means that its composition has shifted towards species that are more similar to each other in how they respond to disturbance, thereby indicating a loss of resilience. If, in a given plot, an effect group contained no species or only one species (in which case no multivariate dispersion can be computed), it was assigned a response diversity value of zero. We provide R (R Development Core Team 2009) code to implement our response diversity approach as Appendix S1.

Meta-analysis

For each of the 18 datasets (Table S1), we used all effect groups from all plots as individual observations. Therefore, the total number of observations is equal to the number of effect groups multiplied by the total number of plots, each plot representing an independent measurement. First, we ranked response diversity and functional redundancy between plots within each effect group to control for intergroup differences (e.g. as 1–10 if there were 10 plots; Figs S1d and S2e). We then computed the Pearson correlation coefficient between land-use intensity (ordinal variable with different number of classes, depending on the dataset; see Table S1) and either ranked within-group response diversity (Fig. S2f) or ranked within-group functional redundancy (Fig. S1e). This is conceptually equivalent to using the Spearman rank correlation with the exception that ranking occurs within each group and not across all groups. We used correlation coefficients as effect sizes in a formal meta-analysis across all datasets using the random-effect DerSimonian-Laird (DSL) approach (Schulze 2004). Our aims with these meta-analyses were: (1) to estimate the mean effect of land-use intensification on response diversity and functional redundancy across all studies and (2) to test the null hypotheses that land-use intensification has no effect on response diversity or functional redundancy.

In contrast to meta-analytical approaches based on fixed-effect models, the DSL approach is more conservative and shows an acceptable Type-I error rate when individual studies differ substantially (Schulze 2004). Importantly, fixed-effect models limit inference to the sample in hand, while random-effect models allow more general inferences about a wider population. In the DSL approach, correlations are first transformed using Fisher's z-transformation

$$z_r = \frac{1}{2} \quad ln\left(\frac{1+r}{1-r}\right)$$

where r is the Pearson correlation coefficient. The asymptotic variance of z_r is calculated as $v_z = 1/(n-3)$, where n is the sample size (number of effect groups × number of plots; Figs S1e and S2f). Unlike r which is bounded between −1 and 1, z_r ranges from -∞ to +∞. Negative values of z_r indicate a negative association between response diversity (or functional redundancy) and land-use intensity. The mean effect size $\bar{z}_r$ represents the average relationship between land-use intensity and the response diversity or functional redundancy of all effect groups from all 18 studies. z_r and 95% confidence intervals were computed as described by Schulze (2004). We used the 'metacor' package (Laliberté 2009) to perform meta-analysis.

Null models

To explore whether changes in response diversity could be distinguished from changes in functional redundancy, we used a null model approach. For each effect group in each community, we generated a null distribution of 999 response diversity values by randomly selecting species within the entire group while holding species number (i.e. functional redundancy) constant. We then tested whether the observed response diversity value for that effect group within each land-use was lower than the null distribution at $\alpha = 0.05$. We excluded groups containing zero or only one species, or groups containing all possible species from that group, because no meaningful null distributions could be generated in these cases. A larger occurrence of cases where response diversity is significantly ($P \leq 0.05$) lower than expected from the null distribution following land-use intensification would suggest the creation of novel environmental filters limiting the breadth of species responses to disturbances within effect groups.

RESULTS

The number of functional effect groups identified in each study ranged from two to 11 (Table S5), based on multivariate clustering analyses. Functional effect groups were generally distinguished by growth form, with further subdivisions provided by differences in nutrient uptake strategy, height, specific leaf area or photosynthetic pathway (Table S5). For each study, the average species richness per land-use intensity class is given in Table S6.

Land-use intensification was associated with an overall loss of functional redundancy in 13 of 18 datasets, with z_r values ranging from −1.234 to 0.122 (Fig. 2a). Nine of the 13 negative z_r values, and only one of the five positive z_r values, were significantly ($P \leq 0.05$) different from zero (Fig. 2a). The mean effect size $\bar{z}_r$ was −0.286 and differed significantly from zero ($P \leq 0.0001$; Fig. 2a), leading to the rejection of no change and to the conclusion that functional redundancy declined at higher land-use intensities on average.

The relationship between land-use intensity and the response diversity of all effect groups within a given dataset was negative in nine of 18 datasets and ranged from −0.430 to 0.201 (Fig. 2b), although only five of the negative and one of the positive z_r values were significantly ($P \leq 0.05$) different from zero (Fig. 2b). The mean effect size $\bar{z}_r$ was −0.089, leading to rejection of the null hypothesis of no change in response diversity under land-use intensification ($P = 0.046$; Fig. 2b). This indicates that overall, and within several of the ecosystems studied, response diversity was reduced as land-use intensified.
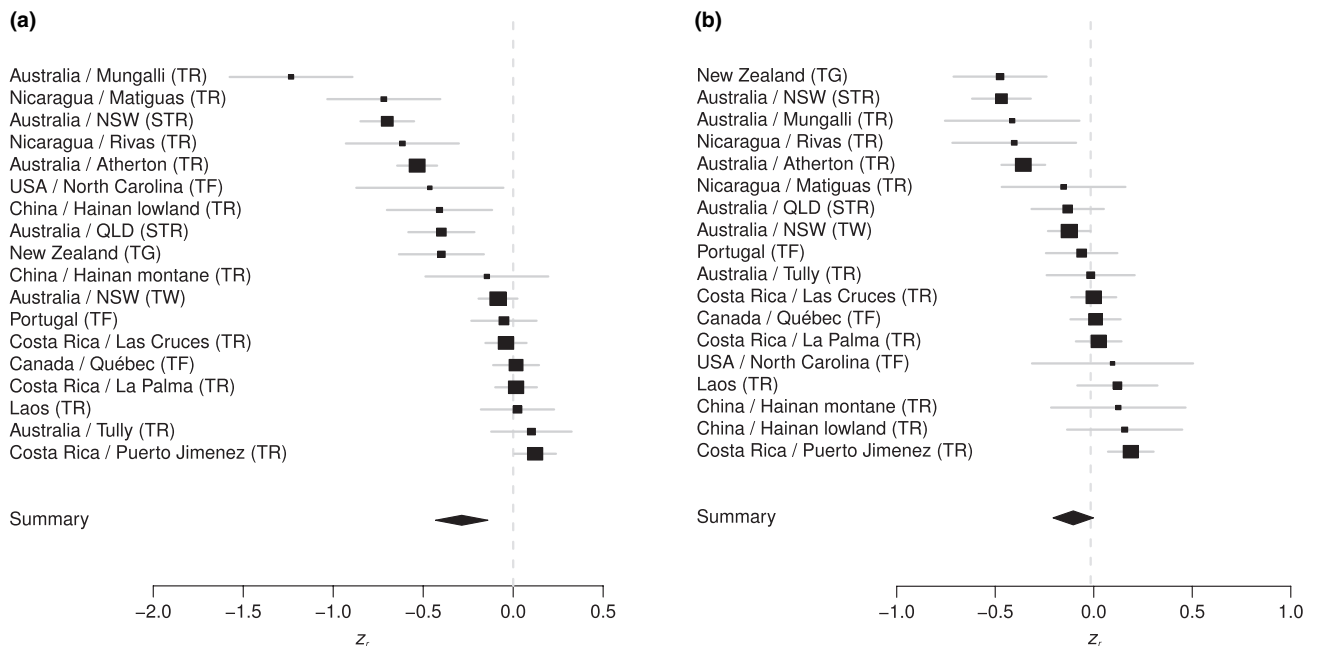
Figure 2 Meta-analyses of the effect of land-use intensification on (a) functional redundancy and (b) response diversity along 18 land-use intensity gradients. Effect sizes z_r are z-transformed Pearson correlation coefficients (r) between land-use intensity and ranked within-group functional redundancy or response diversity, following the DerSimonian-Laird (DSL) approach. A negative value of z_r indicates a decrease in functional redundancy or response diversity as land-use intensifies. Box size is proportional to the weight given to each study, based on sample size and variance. Grey lines are 95% CI. The dashed grey line represents the null hypothesis. The summary statistic (mean effect size $\bar{z}_r$) is represented by a black diamond whose width corresponds to its 95% CI. TR, tropical rainforest; STR, sub-tropical rainforest; TG, temperate grassland; TW, temperate woodland; TF, temperate forest.

Although the FDis index used to measure response diversity is by construction little influenced by species richness (Laliberté & Legendre 2009), meta-analysis showed that response diversity and functional redundancy were positively associated in 14 of 18 studies ($\bar{z}_r = 0.631$, $P \leq 0.0001$; Fig. S3). This was reflected in the similarity of results for functional redundancy (Fig. 2a) and response diversity (Fig. 2b). We found no evidence that response diversity was lower than expected from a null distribution as land-use intensified (Fig. 3). On the contrary, in more than half of the studies (10 out of 18) response diversity was lower than expected most frequently in the least modified habitats (Fig. 3).

While meta-analysis pointed to general reductions in functional redundancy and response diversity under land-use intensification, patterns of individual effect groups included positive, negative, and more complex relationships (Figs 4 and S4). Studies where land-use intensification led to relatively consistent reductions in the response diversity of individual effect groups (e.g. Australia/NSW sub-tropical rainforest and New Zealand grassland; Fig. 4) were the exception rather than the rule, as it was far more common for reductions in some groups to co-occur with minor or even large increases in others (Fig. 4). Similarly varied

results were obtained for functional redundancy, although several studies showed more consistent reductions across groups (Fig. S4).

DISCUSSION

Our meta-analysis shows that overall, and for the majority of studies considered, land-use intensification reduced functional redundancy and the diversity of responses to disturbance within groups of plants that have similar effects on biogeochemical processes (functional effect groups). Given the importance of functional redundancy and response diversity to ecosystem resilience (Walker 1995; Elmqvist et al. 2003; Folke et al. 2004), our results suggest that land-use intensification increases the vulnerability of functional effect groups to future disturbances. This occurs by reducing the number of species in each group (functional redundancy) and by reducing the response trait dispersion of each functional group (response diversity). These results support the view that maximizing commodity supply (e.g. food, fuel, fibre and timber) in the short term through intensified land management may jeopardize the long-term provisioning of ecosystem functions or services (Foley et al. 2005).
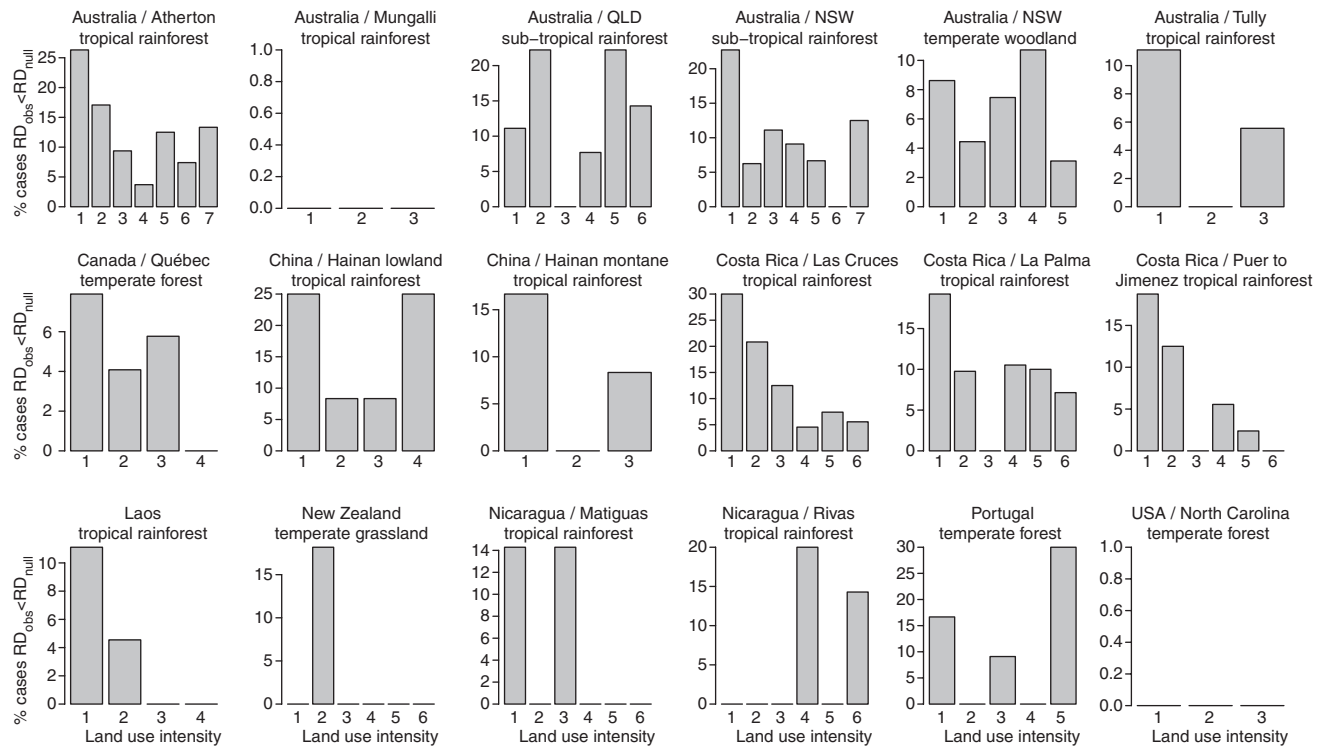
Figure 3 Percent of cases in each land-use intensity class where an effect group had a significantly ($P \leq 0.05$) lower response diversity than would be expected from a null distribution of values (representing random sampling of the same number of species as observed in each effect group in each land-use class).

It is also important to recognize that ecosystems support multiple functions simultaneously and require greater biodiversity than would be needed to sustain a single service (Hector & Bagchi 2007). This capacity for provision of multiple services is best represented in our studies by the consideration of diverse traits and their distributions in trait space. Because different functions are affected by variably distinct or overlapping sets of species, a focus on individual processes in isolation will underestimate levels of biodiversity required to maintain multifunctional ecosystems. As such, while this study does not address the resilience of any single service, our results do support the notion that the resilience of the suite of services offered by natural and semi-natural systems is impacted by land-use intensification.

The observed loss of functional redundancy is consistent with existing views of land-use intensification as one of the most important drivers of species loss worldwide, through its simplification of ecosystem structure (Pimm & Raven 2000; Sala *et al.* 2000). For example, loss of functional redundancy in bird communities following land-use intensification in south-eastern Australia has been attributed to habitat simplification at the landscape scale (Fischer *et al.* 2007). The more striking result to emerge from this study is the loss of response diversity under land-use intensification. The response diversity index (i.e. FDis; Laliberté &

Legendre 2009) used in the present study in theory should be minorly influenced by functional redundancy. However, in practice we found the two measures to be positively associated. Moreover, response diversity was not lower than expected from a null distribution as land-use intensified; in fact, the opposite pattern was often observed. Taken together, these results invite the interpretation that sampling effects are the predominant cause of observed losses in response diversity under land-use intensification, where lower species richness decreases the probability of observing species with extreme trait values, tending to a narrower distribution. However, it is also possible that the response traits are the objects of selection and that species loss occurs because the traits are nonviable under changed conditions. It is not possible to distinguish these alternative interpretations with these analyses.

Our results do show that response diversity can increase or remain similar even concurrent with declines in functional redundancy, as seen for several individual effect groups, and also at the study-level in four datasets that showed increases in response diversity with land-use intensification despite losses in functional redundancy (Fig. 2). Although such cases were rare, this suggests that response diversity can be maintained with lower levels of
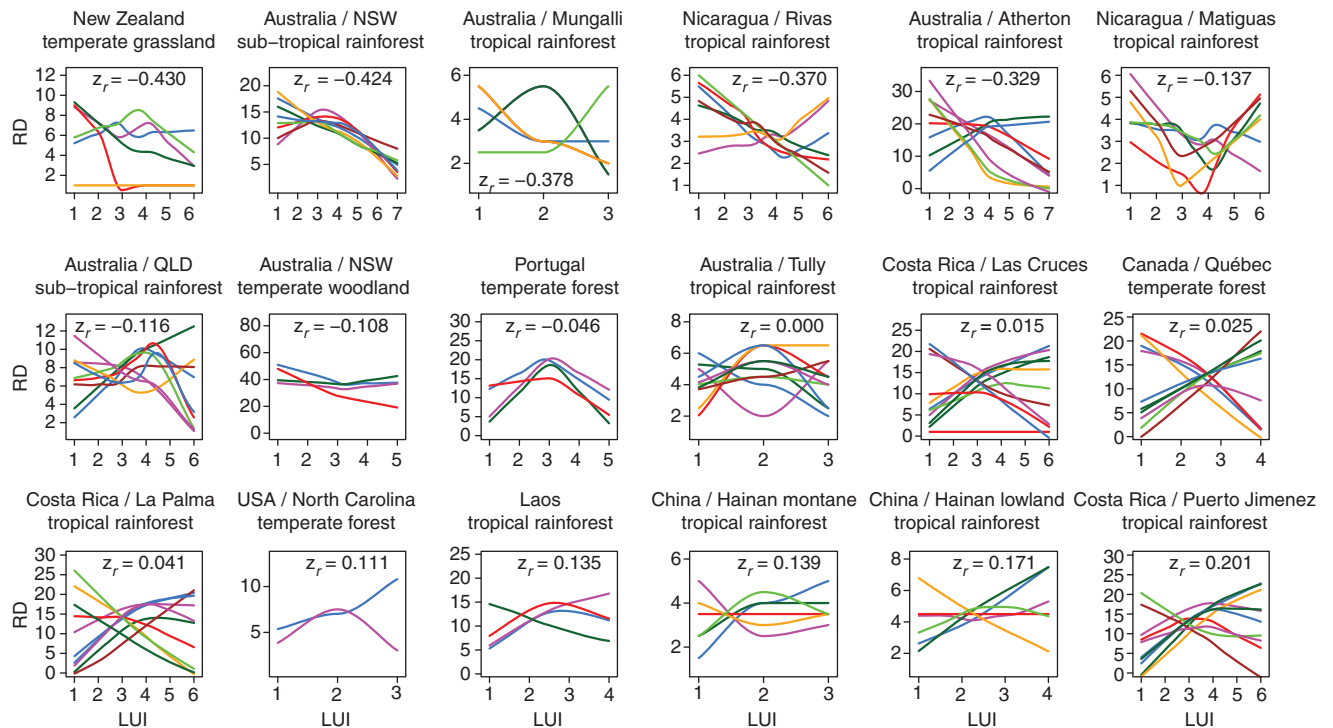
Figure 4 Response diversity (RD) of individual functional effect groups under increasing land-use intensity (LUI) for each of the 18 studies. For clarity, individual data points are omitted and only loess-smoothed curves are shown (span = 0.9). In each graph, curves of different colours represent different effect groups. RD is ranked within each effect group. z_r, the effect size used in the meta-analysis, is the z-transformed Pearson correlation coefficient (r) between RD and LUI computed from all effect groups. Graphs are laid out in increasing order of z_r, from left to right.

species richness if the remaining species are widely dispersed in response trait space.

Several studies showed no net impact of land-use intensification on response diversity or functional redundancy, and one even showed increases in both variables (Costa Rica/Puerto Jimenez). This may reflect, however, the focus of the Costa Rican studies on herb/shrub life-forms within a formerly forested landscape, where land-use intensification effectively corresponds to removal of trees and prevention of their re-establishment. This major, selective change in ecosystem structure may result from an alteration of environmental filters that enables the establishment of herbaceous species with wider trait distributions than observed in closed forest (Mayfield *et al.* 2005, 2006). Extensive variation across effect groups and ecosystems suggests that the trajectories of change under land-use intensification depend jointly on the existing flora and disturbance regimes. Exploring which factors determined the response of individual effect groups to land-use intensification should be fertile ground for future empirical work, alongside questions on what parts of the response trait space are maintained or lost, and on the roles of spatial context and colonization in the resilience of a focal ecosystem.

This study provides the first examination of how land-use change impacts response diversity. While it offers new insight, our effect–response framework presents some methodological challenges. First, it requires the assembly of a complete effect and response functional trait database for all (or most) species present in a community. This task may become easier as trait datasets covering large numbers of species are made accessible to the wider scientific community (e.g. Kleyer *et al.* 2008). Second, functional classifications should be based on traits that relate as directly as possible to an ecosystem function of interest (Naeem & Wright 2003), yet we rarely know *a priori* exactly which traits are the most important (Petchey & Gaston 2006). Furthermore, we need to be sure that our response traits actually reflect differential responses to disturbances. Finally, classifying species into functional effect groups assumes some level of functional redundancy (Naeem & Wright 2003), but this should not always be taken for granted (Micheli & Halpern 2005; Petchey *et al.* 2007), even in high-diversity systems (Bellwood *et al.* 2003). Indeed, redundancy is specific to particular functions and depends on the traits selected and methods for classification (Rosenfeld 2002). Identifying effect groups involves an element of subjectivity, although decisions are based on the

best-available ecological knowledge of the species considered (Aubin *et al.* 2009).

In this study, we classified species based on their effect on biogeochemical processes such as primary productivity, litter decomposition and nutrient cycling. The reason for this is twofold. First, many ecosystem services directly depend on biogeochemical processes (Díaz *et al.* 2007; Quétier *et al.* 2007). Second, focusing on the traits that influence biogeochemical processes, on which some scientific consensus has emerged (Cornelissen *et al.* 2003), yielded a common currency for exploring changes in response diversity and functional redundancy under land-use intensification across a wide range of different ecosystems and biomes. An emerging frontier for further research will be a more targeted application of our methodological framework to groups of species that perform specific provisioning (e.g. forage production), cultural (e.g. native biodiversity) or regulating (e.g. flood interception) ecosystem services. Although recent progress has been made in identifying the links between plant traits and specific ecosystem services (Quétier *et al.* 2007), this remains an important challenge for improving our understanding of how humans impact natural ecosystems (Díaz *et al.* 2007).

There is an urgent need for ecologists to measure and predict how human activities erode response diversity and ecosystem resilience (Scheffer *et al.* 2001; Elmqvist *et al.* 2003; Folke *et al.* 2004) to detect early signs of ecological change before abrupt shifts occur (Scheffer *et al.* 2001). Through meta-analysis of 18 land-use intensity gradients from five biomes and nine countries, we showed that land-use intensification was generally associated with a reduction in functional redundancy and response diversity within groups of species that make similar contributions to ecosystem processes. Therefore, land-use intensification may decrease the resilience of ecosystems to future disturbances. Despite this general finding, responses of individual effect groups to land-use intensification within and across studies varied widely. Understanding the drivers of these patterns is a key direction for future research, especially to assess trade-offs or interdependence among ecosystem services under land-use change (DeFries *et al.* 2004; Foley *et al.* 2005) Quantifying response diversity within groups of species that perform particular services is a promising approach for assessing how vulnerable these services will be in an uncertain future, but more work is needed to develop our understanding of the environmental filters that are involved in land-use change and the consequences of losing response diversity through human pressures.

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SUPPORTING INFORMATION

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

Figure S1 Summary of methodological approach for functional redundancy.

Figure S2 Summary of methodological approach for response diversity.

Figure S3 Association between response diversity and functional redundancy.

Figure S4 Functional redundancy of individual effect groups under land-use intensification.

Table S1 Summary of the 18 datasets.

Table S2 Detailed characteristics of the 18 datasets.

Table S3 Functional traits used in each study.

Table S4 References for trait data.

Table S5 Characteristics of individual effect groups.

Table S6 Average species richness per land-use intensity class, for each of 18 land-use intensity gradients.

Appendix S1 R script for measuring response diversity.

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