LETTER

Loss of functional diversity under land use intensification across multiple taxa

Dan F. B. Flynn,[1] Melanie Gogol-Prokurat,[2] Theresa Nogeire,[3] Nicole Molinari,[4] Bárbara Trautman Richers,[5] Brenda B. Lin,[1,6] Nicholas Simpson,[7] Margaret M. Mayfield[8] and Fabrice DeClerck[5,6]*

Abstract

Land use intensification can greatly reduce species richness and ecosystem functioning. However, species richness determines ecosystem functioning through the diversity and values of traits of species present. Here, we analyze changes in species richness and functional diversity (FD) at varying agricultural land use intensity levels. We test hypotheses of FD responses to land use intensification in plant, bird, and mammal communities using trait data compiled for 1600+ species. To isolate changes in FD from changes in species richness we compare the FD of communities to the null expectations of FD values. In over one-quarter of the bird and mammal communities impacted by agriculture, declines in FD were steeper than predicted by species number. In plant communities, changes in FD were indistinguishable from changes in species richness. Land use intensification can reduce the functional diversity of animal communities beyond changes in species richness alone, potentially imperiling provisioning of ecosystem services.

Keywords

Biodiversity measurement, functional redundancy, functional traits, land use change, meta-analysis.

Ecology Letters (2009) **12**: 22–33

INTRODUCTION

The conversion of land from complex natural systems to simplified agricultural ecosystems is a major cause of the current unprecedented rates of global biodiversity loss (Matson *et al.* 1997; Tscharntke *et al.* 2005). Declines in species diversity due to agricultural intensification have been documented for birds (Donald *et al.* 2001), mammals (Sotherton 1998), insects (Benton *et al.* 2002), and plants (Aebischer 1991) at national and landscape scales. Motivated by such findings, research on how species losses impact ecosystem functioning has surged. These studies have found

that declines in species richness impair ecosystem functions such as grassland production (Spehn *et al.* 2005), forest carbon storage (Bunker *et al.* 2005), resistance to plant invasion (Zavaleta & Hulvey 2004) and freshwater nutrient cycling (McIntyre *et al.* 2007). Ultimately, biodiversity losses may undermine the provisioning of ecosystem services, the ecosystem processes that support human well-being. To accurately assess how land use intensification might impinge on ecosystem services, it is essential to be able to accurately measure biological diversity relevant for ecosystem functioning.

[1]Department of Ecology, Evolution, and Environmental Biology, Columbia University, New York, NY, USA
[2]Department of Environmental Science and Policy, University of California, Davis, CA, USA
[3]Bren School of Environmental Science & Management, University of California, Santa Barbara, CA, USA
[4]Department of Ecology, Evolution & Marine Biology, University of California, Santa Barbara, CA, USA
[5]Tropical Agricultural Centre for Research and Higher Education (CATIE), Turrialba, Costa Rica
[6]The Earth Institute, Columbia University, New York, NY, USA
[7]Division of Biology, Kansas State University, Manhattan, KS, USA
[8]School of Integrative Biology, University of Queensland, Brisbane, QLD, Australia
*Correspondence: E-mail: fdeclerck@catie.ac.cr

Techniques for measuring biological diversity have developed in step with theoretical advances in linking species diversity and ecosystem function. Biodiversity-ecosystem function (BEF) studies clearly indicate that the traits of species, not just the number of taxonomic units, ultimately drive BEF relationships (Hooper *et al.* 2005). This consensus has resulted in a growing focus on the diversity and values of functional traits that influence ecosystem functioning, as a tool for explaining the role of organisms in ecosystems and the ecological impacts of their loss (Petchey & Gaston 2006). For example, in grasslands, functional group richness can be a better predictor of biomass accumulation (Tilman *et al.* 1997), resistance to plant parasites (Joshi *et al.* 2000) and decomposition rates (Scherer-Lorenzen 2008) than species richness. While there is growing evidence of how functional diversity drives ecosystem processes (but see Mokany *et al.* 2008), no clear consensus has emerged regarding how functional diversity should respond to land use changes, or indeed how best to measure functional diversity.

Until recently, functional diversity was only measured by functional group richness, where functional groups were created by grouping species according to *a priori* classification schemes, such as photosynthetic pathway (C3, C4 and CAM) and their capacity to fix atmospheric nitrogen for plants. While these groups can capture biological variation in ways relevant to BEF relationships (van Ruijven *et al.* 2003), a number of issues with functional group richness have been identified. Most notably, substantial biological variation exists within these groups, yet grouping them assumes complete equivalence between species within groups. In addition, no objective standards by which to evaluate 'correct' groupings exist. Indeed, when alternative groupings were considered for several major BEF experiments, *a priori* groups were not distinguishable from randomly constructed groups in terms of ability to predict ecosystem functioning (Wright *et al.* 2006), and alternative groupings provide even greater explanatory power (Petchey *et al.* 2004). This has lead to an increased interest in using continuous metrics of functional diversity that summarize the variation of traits in organisms. In this study, we use a dendrogram-based measure of functional diversity (FD, Petchey & Gaston 2002), which can accommodate a wide range of trait data, has desirable statistical properties, and is suitable for presence–absence community composition data. When traits are selected appropriately, this measure is a substantial improvement over simply using functional groupings to describe the functional diversity of a community, in that the assumptions of which traits are important are explicit and all the relevant information about interspecific differences is used.

A strong advantage of trait-based measures of functional diversity is the ability to examine the relationship between the number of species present and the functional diversity of a community. As functional diversity consists of the range and values of key morphological and physiological traits, communities with high numbers of species but low functional diversity can be said to have high 'functional redundancy' (Petchey *et al.* 2007). This is because high functional redundancy occurs when species overlap in their traits, which may reflect niche overlap if traits are defined in a biologically appropriate way (Díaz & Cabido 2001). Conversely, when each species present in a community represents a unique combination of traits, there is low functional redundancy. The most critical assumption in this formulation of functional redundancy is that the traits under consideration are those determining ecosystem functioning (Walker *et al.* 1999). High functional redundancy may result in limited loss of ecosystem functioning with species loss, while in communities with low functional redundancy, the loss of even a few species could have dramatic consequences for ecosystem functioning. It is also important to note that the processes which determine the trait similarity between organisms, including phylogenetic inertia and convergent evolution, are important for interpreting the meaning of functional redundancy, but these are not the focus of the present paper.

We hypothesize that the degree of functional redundancy can lead to four possible relationships between FD and species richness (S) as S changes with land use intensification (Fig. 1A–D). These hypotheses concern both the relationship between FD and S as a result of functional redundancy and the resulting pattern of FD as S changes with land use intensification:
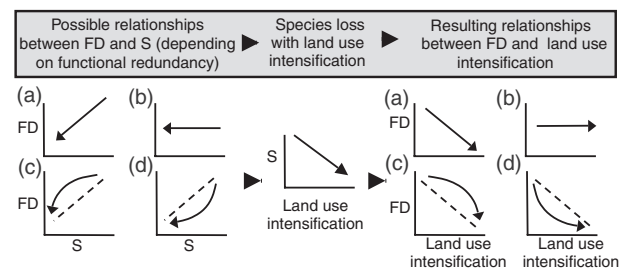
Figure 1 Hypothetical relationships between functional diversity (FD) and species richness (S; left): (a): low functional redundancy; (b): high functional redundancy; (c): functionally redundant species lost first and (d): functionally unique species lost first. Resulting relationships between FD and land use intensification (right) are mediated through the response of S to land use intensification (centre).

A. *Low functional redundancy.* S and FD will decline at the same rate; FD declines with land use intensification, but only as a result of decline in S. Species loss is random with respect to functional traits.

B. *High functional redundancy.* FD will remain constant as S declines; FD will therefore be insensitive to land use intensification, and ecosystem services may still be provided at a high level. Species loss is random with respect to functional traits.

C. *Functionally redundant species lost first.* FD declines with S, but at a much slower rate. Here, a community with high S and high redundancy in trait diversity is replaced by a community with low S but where each species is unique. Species loss is nonrandom.

D. *Functionally unique species lost first.* FD declines even more rapidly than S, possibly due to habitat filtering where species with only a specific set of traits can persist under land use intensification. Here, intensification greatly affects functional diversity even if only a few species are lost from the system. Species loss is nonrandom.

Here, we present a meta-analysis of the functional diversity along gradients of agricultural intensification in a range of communities in temperate and tropical environments in the Americas to test which of these competing hypotheses best explains patterns observed with species loss under agricultural intensification. We examine the diversity of bird, mammal, and plant communities in agricultural landscapes using both species richness (S) and functional diversity as measured by Petchey & Gaston's (2002) FD. To distinguish the hypothesized patterns (Fig. 1A–D), we use a null model approach to determine if the observed FD differs significantly from the expected FD in each community. Finally, we identify which traits are most linked with the change in FD at the different land use intensity levels, to further examine the potential consequences for provisioning of ecosystem services in agricultural landscapes.

METHODS

This study involved: (i) identifying appropriate studies of changes in species composition under differing land use intensity, (ii) assembling a database of functional traits for all species in all studies, (iii) calculating FD for all communities in each study, (iv) assessing the direction and significance of the FD change, given S and (v) evaluating the major changes in trait values and combinations following composition change.

We focused on temperate and tropical New World studies, ranging from Costa Rica to the northern United States to assess the broader question of how functional diversity has changed under land use intensification. We

identified studies appropriate for our analysis by searching the Web of Science for all available years up to December 2007 based on the key words: 'agricultur*', 'intensification', 'diversity', 'biodiversity', 'bird', 'plant' and 'mammal.' We identified additional studies by searching the bibliographies of the papers found from this search. We included all studies that reported species lists for one of the focal taxonomic groups (birds, plants or mammals) in at least two land uses under different agricultural land use intensity. In addition to published works, we sought unpublished data that met our criteria. Here we refer to a published or an unpublished work as a 'study', with the different communities surveyed in a study called a 'land use.' Following an initial review of the 108 studies identified from our search, we selected 20 studies that met all of our criteria. These included five bird studies (Best *et al.* 1995; Estrada *et al.* 1997; Daily *et al.* 2001; Estrada & Coates-Estrada 2005; Jones *et al.* 2005), with 46 land uses and 348 species; eight mammal studies (Estrada *et al.* 1994; Horvath *et al.* 2001; Daily *et al.* 2003; Naughton-Treves *et al.* 2003; Olson & Brewer 2003; Hilty & Merenlender 2004; Sullivan & Sullivan 2006; T. P. Husband & D. Abedon, unpublished data), with 39 land uses and 92 species (excluding volant species); and seven plant studies (Middleton & Merriam 1983; Jobin *et al.* 1996; Quinn 2004; Sánchez *et al.* 2005a,b; Mayfield *et al.* 2006; Smuckler & Jackson, unpublished data), with 38 land uses and 1,230 species (see Appendix S1).

Trait data

We compiled the species lists from all studies, and filled in a trait matrix for each taxonomic group (birds, mammals and plants). We define a 'trait' as a measurable aspect of an organism which impacts its interaction with the environment, its capacity to find and acquire resources, and which therefore affects the fitness of a species via its effects on growth, reproduction and survival. Here we focus on resource capture and use traits, which are the traits that can drive biodiversity and ecosystem function relationships (Spehn *et al.* 2005). Notably, here we include behavioral traits such as foraging habit of birds and location of nesting for mammals, crucial reflections of how organisms acquire resources from their environment; this definition is more inclusive than that of other authors (Violle *et al.* 2007). Our selection of traits was constrained to those traits that are commonly measured. For birds and mammals, we emphasized traits reflecting the resource use requirements of the individuals including body size, foraging habit and location, and food type. For plants, we chose anatomical and morphological traits that are tied to a species' capacity to capture resources, including height, leaf size and legume or not. Trait data were collected from published species

Table 1 Trait data used in this meta-analysis

Taxonomic group	Trait	Range or categories
Birds	Mass (ln, g)	0.96–8.80
	Feeding guild	Carnivore, herbivore, insectivore, omnivore
	Food type	Invertebrates, small fruit, seeds, nectar, fish, generalist
	Foraging location	Ground, upper canopy, shrub layer, mid-canopy, forage throughout, aquatic
	Foraging habit	Ground, leaves, perch-and-attack, stems, aerial, water, hover, soar-and-attack, other
Mammals	Mass (ln, g)	1.72–11.23
	Feeding guild	Carnivore, herbivore, insectivore, omnivore
	Food type	Invertebrates, fruit, seeds, vertebrates, vegetation
	Activity	Diurnal, nocturnal, either
	Nesting	Aquatic, arboreal, burrows, multiple, terrestrial
	Litter size	1–26
Plants	Leaf area (cm^2)	0.045–143
	Height (m)	0.11–79
	Fruit type	Fleshy, not fleshy
	Fruit length (cm)	0.015–155
	Foliage	Deciduous, evergreen
	Growth form	Tree, shrub, tall herb, low herb, grass
	Leguminous	Legume, not legume

See Appendix S2 for sources.

accounts, particularly in floras and faunas (Table 1, Appendix S2).

We chose traits that allowed an examination of how the provisioning of critical ecosystem functions might change with the loss of species with intensification, and whether the loss of functional diversity differs from expectations based on changes in species richness. Thus, the main goal was not to identify traits which determine extinction proneness under land use intensification. Such a study would require a focus on traits affecting species' response to habitat or environmental change, such dispersal, fecundity and stress tolerance (Larsen *et al.* 2005).

Land use classifications

We classified land uses from all papers into three categories: natural, semi-natural and agricultural (Appendix S1). Our land use intensity categories are defined by the relative intensity of management for agriculture, which we deter-

mined from the written descriptions or by communication with the authors. In this categorization, 'natural' communities included reference systems such as prairies, forests and marshes that were largely unaffected by agricultural activity. We defined 'semi-natural' systems as those that are largely dominated by natural vegetation, but have been modified indirectly for agricultural activities or are directly adjacent to agricultural lands, such as fallows and shelterbelts. Finally, 'agricultural' systems were those directly managed for agricultural production including row crops, pastures and shade coffee.

Importantly, for plant studies we defined agricultural communities as communities *directly adjacent to or inside of, and presumed to be greatly influenced by* agricultural land use. Meaning, we did not include crop species in this study, but focused instead on species that could be found in any of the three land use intensity categories. This choice effectively shortens the land use intensification gradient for plant studies, but avoids comparing naturally assembled plant communities with crop monocultures with zero diversity. Due to the high heterogeneity among studies, it was not possible to arrange land uses along a continuous axis of intensification.

Functional diversity measurement

We use Petchey & Gaston's (2006) FD as our index of functional diversity. This index performs well in predicting ecosystem functioning when using appropriate trait data, has logical statistical properties (namely, the addition of a species can only increase or not change the FD of the community), and does not require abundance data. This last point was important for this study, to include the largest number of studies in our meta-analysis, both those that reported abundance and those that reported only species lists. In calculating this index, multivariate distances between species from each taxonomic group in each study were calculated using Gower's distance, a metric that accommodates continuous, nominal, or ordinal data (Podani & Schmera 2006). We summarized these pair-wise distances for the total species pool of a particular study in a dendrogram, using the unweighted pair-group method with arithmetic mean (UPGMA). UPGMA gave the highest cophenetic correlation coefficient between the original distances and the distances estimated from the resulting dendrogram for all trait data sets (mammals: 0.69, birds 0.77, plants: 0.74). For each land use in a given study, we summed the branch lengths of the dendrogram corresponding to species present to calculate FD. To compare both FD and S values across studies, diversities of each land use were z-scored within each study (i.e. subtracting study mean and dividing by the study standard deviation). Thus, unstandardized trait data were used to calculate FD, and

then FD values were standardized within a study, focusing on the magnitude of change in FD across the land use intensification gradient.

To evaluate differences among studies in terms of S and FD, we binned diversity index results by land use category, and then analyzed the differences within each taxon using Kruskal–Wallis nonparametric analyses of variance (using a nonparametric test because of small sample sizes for some taxon x land use categories). As the original studies were not necessarily designed to test the effect of land use intensification on measures of diversity, it was not possible to employ meta-analysis by pooling effect strengths across studies.

Null model methods

To distinguish whether an observed change in FD was simply a product of changing S, we used a simulation approach to create a null distribution of FD values for the observed number of species. Holding species richness constant for each community in each study, we randomly selected species from the species pool (the total number of species in the study) to calculate a null FD for each community. We repeated this 1000 times to produce a distribution of null values and tested whether the actual FD for each community was significantly higher or lower than the null FD distribution, at $\alpha = 0.05$. This approach permitted us to determine if changes in FD simply reflected species richness, or if species composition and trait diversity varied in important ways along the land use intensification gradient.

Two studies required modifications of this method. In one case (Hilty & Merenlender 2004), the natural land use was excluded from the null model because all species in the local community were found in this land use, so it was not possible to create a randomized null FD. The data from one study (Best *et al.* 1995) were a compilation of several studies. Therefore, it would not have been appropriate to use all the species (144 birds) in the meta-analysis as the species pool for constructing the null communities. In this case, we ran separate null model comparisons for all 20 communities, using each of the seven communities we had classified as 'natural' as the species pool. We then used the most conservative comparison of each community's observed FD with the resulting null distributions. For all other studies, the species pool was the total of all species in that study.

Identifying changes in individual traits

Identifying which traits in each taxon remained or were lost with land use intensification gradient is not possible using the summary diversity metric FD or the null model

approach. We used a classification and regression tree approach to accomplish this. For a given study, we identified species present in at least one natural land use but absent from all agricultural land uses. We then applied regression trees, which recursively partition the predictor variables (traits) to explain the variation in the response variable, which was whether each species was present in at least one of the natural land uses, but none of the agricultural land uses. We combined data across studies, conducting a single analysis for each taxonomic group. We used the sum of squares around group means to establish splitting criteria, selected optimal tree size by K-fold cross-validation, and evaluated model fit with Pearson correlation of predicted to observed disappearance (De'ath & Fabricius 2000). All calculations and analyses were performed in the statistical programming environment R 2.6 (R Development Core Team 2008).

RESULTS

Functional diversity changes with agricultural intensification

For birds and mammals, both species richness and functional diversity declined significantly with land use intensification, while for plants no clear pattern of diversity change across the intensification gradient was observed (Fig. 2). In particular, FD values fell sharply in mammal and bird studies, but remained flat for plant studies ($P = 0.008$, 0.003 and 0.887, respectively). When plant studies were split between tree and herbaceous or understory communities, the results remained similar, with the only difference being that species richness increased significantly with increasing land use intensity for herbaceous/understory plant communities ($P = 0.029$). Thus, for birds and mammals, both the number of species in a community and trait diversity of those communities fell dramatically as land use intensification increased.

Declines in FD can be greater than expected under agricultural land use

The null model tested whether the FD in natural, semi-natural, and agricultural communities was significantly higher or lower than would be expected from a random assemblage of species from the local species pool. For bird and mammal communities, agricultural and semi-natural landscapes were more than twice as likely than natural landscapes to have a significantly lower than expected FD (30.8% vs. 13.6%). Over all studies, natural landscapes were more likely to have a significantly higher than expected FD; 10% of natural land uses had a significantly higher than random FD, while only 1% of semi-natural or agricultural
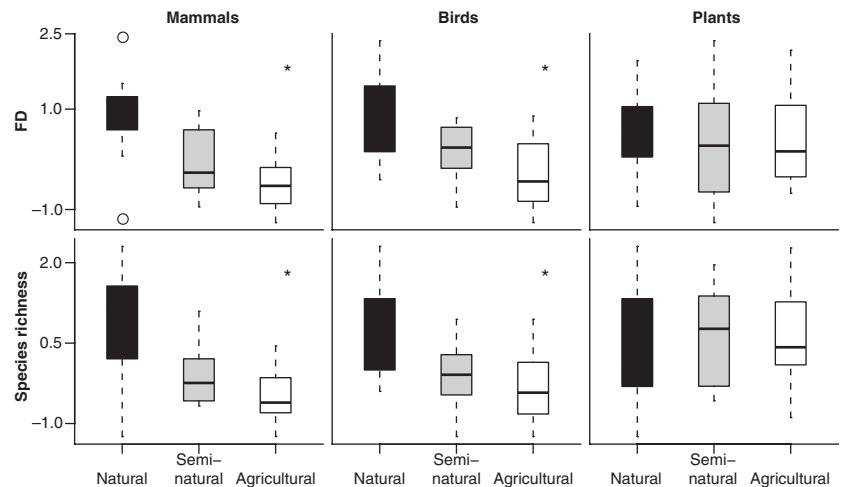
Figure 2 Petchey and Gaston's FD (top row) consistently declines with greater land use intensity for mammals and birds, and remains flat for plants. Species richness (bottom row) demonstrates similar responses to land use intensification. (*$P \leq$ 0.05, Kruskal–Wallis test).

Table 2 Percent of communities in each land use category (natural, semi-natural and agricultural) where the species assemblage had a significantly ($P \leq 0.05$) lower or higher functional diversity than would be expected from a random set of species from that study

Taxonomic group	FD lower than null expectation, % (n)			FD higher than null expectation, % (n)		
Land use category	*Natural*	*Semi-natural*	*Agricultural*	*Natural*	*Semi-natural*	*Agricultural*
Mammals	17 (2)	14 (1)	18 (3)	17 (2)	0	6 (1)
Birds	10 (1)	29 (4)	41 (9)	0	0	0
Plants	21 (4)	38 (3)	15 (3)	11 (2)	0	0

Total number of communities in each category: 41 natural, 29 semi-natural, and 59 agricultural.

land uses tested had a significantly higher than random FD (Table 2, Fig. 3). Patterns varied by taxonomic group, with birds and mammals showing the strongest patterns of lower-than-expected FD in agricultural settings, consistent with Hypothesis D (Fig. 1). Null model results for plants did not show a strong trend, with natural land uses having more communities with both higher than expected and lower than expected FD, largely consistent with Hypothesis A.

### Patterns of trait diversity loss

Regression trees revealed distinct patterns of traits lost across our intensification gradient. For birds, species present in natural but absent from agricultural communities were linked primarily by body size, and secondarily by food type and foraging habit ($R = 0.36$, $P < 0.001$; Fig. 4). Large birds (> 163 g) that were not ground or stem foragers were most likely to be absent from agricultural communities: these 50 species were primarily waterfowl and raptors (Fig. 4). For mammals, agricultural communities lacked species typified by small litter sizes (< 2.25) and specialization on fish, fruit, seeds or nuts ($R = 0.48$, $P < 0.001$). For plants, height was the most important trait, with large-

statured plants (> 1.5 m) more likely to be absent from agricultural communities ($R = 0.50$, $P < 0.001$, Fig. 4).

DISCUSSION

Land use intensification caused striking declines in functional diversity across a broad taxonomic and geographic range for birds and mammals. This analysis shows that the use of functional diversity to assess the consequences of land use change reveals that trait diversity changes largely in concert with taxonomic diversity, but that the deviations from the S – FD relationship have potentially large consequences for ecosystem functioning. The FD change could be distinguished from the change in species richness in only a minority of cases, but in those cases the observed FD was often significantly lower than would be expected by chance in agricultural communities (Hypothesis D, Fig. 1). Regression tree analysis identified distinctive patterns of traits shared by species that were present in natural but absent from agricultural land uses.

Species richness (S) is by far the most common measure of biodiversity used by scientists, conservationists, and policy makers, but here we find that the loss of functional
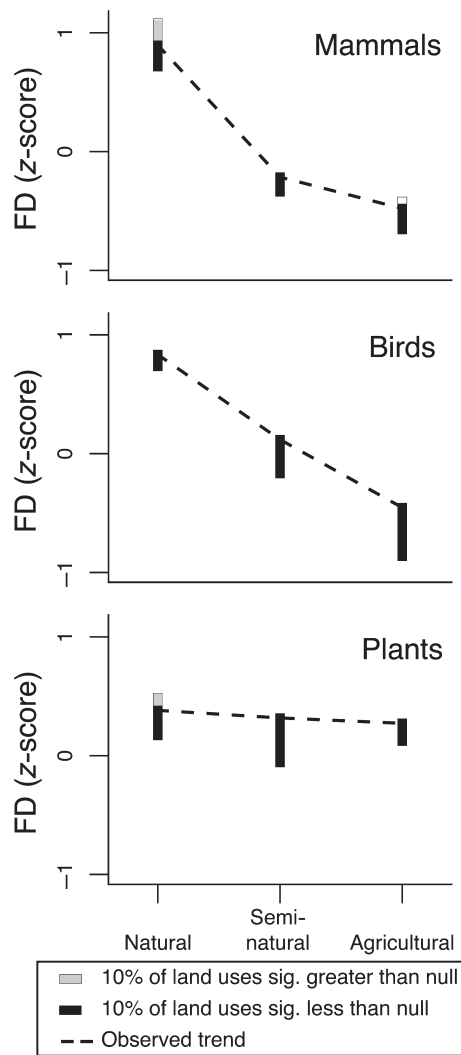
Figure 3 Summary of null model results. Mean observed FD values within land use intensity categories (dashed lines) and number of studies with greater or less FD than expected (open or filled bars, length proportional to number of studies).

diversity (FD) can be more severe than would be predicted if FD simply reflected S, although for plants it appears to adequately capture diversity variation with the land use classification used here. Similarly, other researchers have found that species richness is an inadequate measure of biodiversity in general (Wilsey 2005), and recommend using indices that account for abundance and composition of organisms. The functional diversity index used here, Petchey & Gaston's FD, does not accommodate abundance data, but was chosen over an abundance-weighted functional diversity measure like Rao's Q (Botta-Dukat 2005) in part because several of the data sources only reported species presence–absence. The use of an abundance-weighted functional diversity measure is possibly more important

when linked to a particular ecosystem function, although FD has been shown to be a better predictor of ecosystem function than species richness or functional group richness in several grassland communities (Petchey *et al.* 2004).

In most studies, functional diversity did not vary significantly from the null expectation based on randomly assembled communities. This supports Hypothesis A, where FD is simply a reflection of S. However, multiple communities were found to have a significantly lower than expected FD, especially under the higher land use intensities. This shows that with agricultural intensification, functional diversity is lost at a higher rate than would be predicted by chance if species losses were random, supporting the pattern of functionally distinct species lost first (Hypothesis D). This may be a result of functionally distinctive species being lost from agricultural landscapes more quickly than functionally similar species. This result is of great conservation concern because it demonstrates that (i) species loss with agricultural intensification may not be random; (ii) functionally unique species may be lost more quickly than functionally redundant species; and (iii) functional diversity loss does not always parallel species richness loss, therefore species richness may not be good proxy for functional diversity.

Plant studies demonstrated no overall change in FD with land use intensity, and FD values did not differ significantly from the null expectation based on species richness, supporting Hypothesis A. However, plant studies were distinct from mammal and bird studies, which compared community composition directly within agricultural land uses (e.g. the bird and mammal communities within a corn field). The plants species in the 'agricultural' category here represented communities in field margins or otherwise in close proximity to the agricultural fields, not the crops within the field. This design was employed because the goal of this study was to compare the diversity of natural-assembled communities under increasingly direct influence from agricultural activities, not to compare communities of naturally assembled communities and human-constructed communities. In addition, many of the agricultural land uses in the studies included here were monocultures, and no FD can be calculated for a single-species community.

Functional diversity measures the range and variation of traits present in a community, and therefore measures the actual features of organisms that control biotic interactions. The values of FD, as for all functional diversity metrics, strongly depend on which traits and how many traits are included. We chose traits based on resource acquisition, a process central to most biotic interactions and biodiversity-ecosystem function relationships. Our exploration of all possible trait combinations for each of the three taxa showed these results are robust to the choice of traits used (Appendix S3). Finally, while trait data compiled from the

Mammals

Birds

Plants
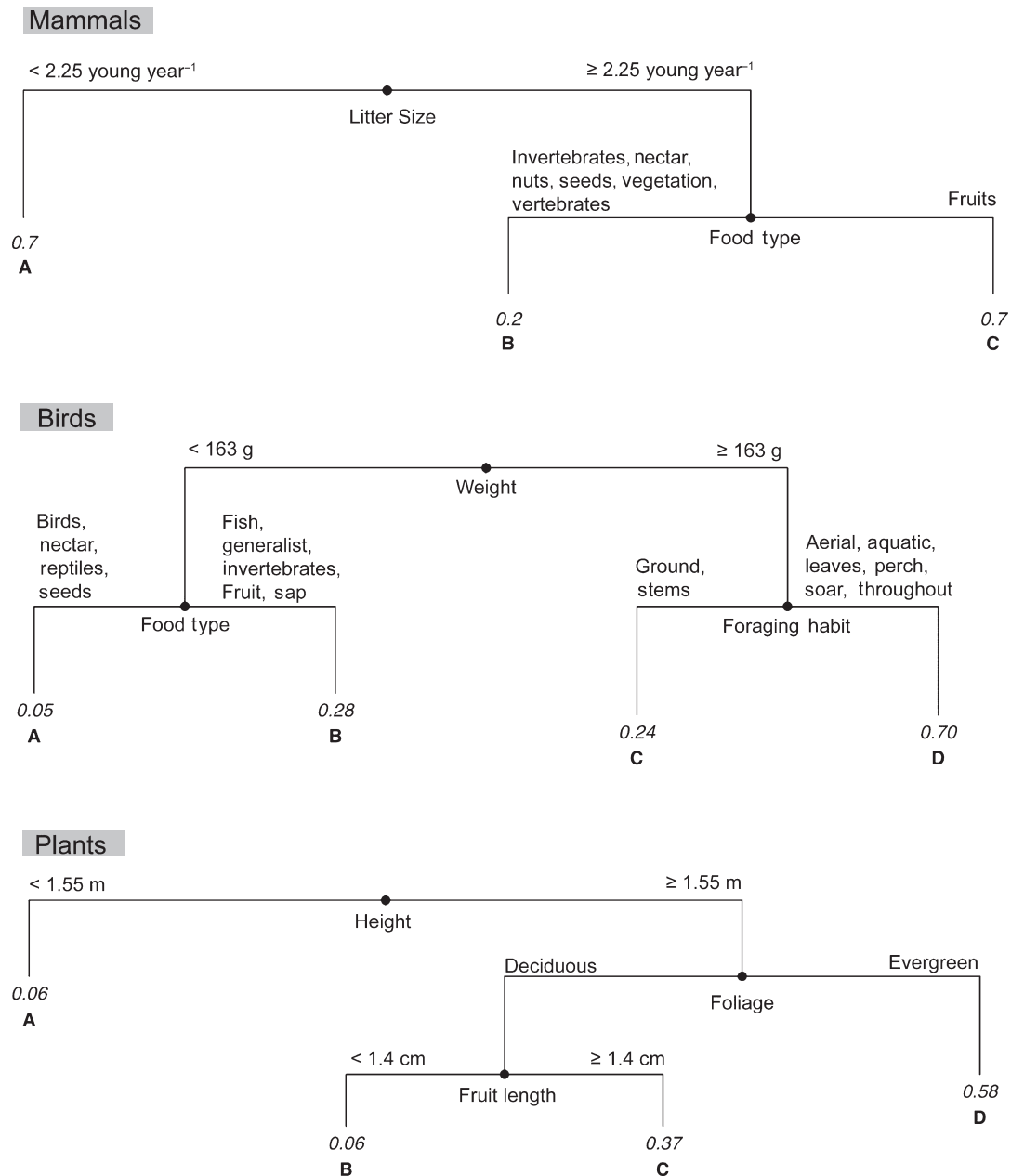
Figure 4 Regression trees identifying the trait values most closely associated with species absent from the agricultural land use category in each study. Species are sorted by traits into groups at the tips of the regression trees, and the value for each tip signifies the proportion of species in that group which were present in at least one natural land use but were extinct from agricultural land uses in each study.

literature clearly do not completely capture the true variation in biological communities, this approach allowed us to take advantage of studies that reported species composition across gradients of land use intensity. Using these literature-compiled trait data, we found that several of the traits we analyzed for birds, mammals, or plants were clearly associated with those species that were absent from the agricultural land uses.

Regression trees revealed some strong patterns of trait combination and trait value change when comparing species present in at least one natural land use but absent from all agricultural land uses in a given study (Fig. 4). For birds, 39 small- to mid-sized species, 26 of which feed primarily on seeds and 11 on nectar, persisted in agricultural areas. This finding suggests that bird-mediated pollination services may be maintained in even intensively farmed areas. Bird species

that forage in aquatic environments were disproportionately absent from agricultural land uses, a finding consistent with the understanding that wetland loss is a major driver of species loss in human-dominated landscapes. Insectivorous birds, with potential capacity to provide pest control functions, were found in both natural and agricultural sites (tips B and C in Fig. 4). This finding suggests that any pest control function provided by bird communities may be resistant to land use changes associated with agricultural intensification.

For mammals, many feeding guilds were represented in the 35 species remaining in agricultural sites (Fig. 4). These notably included species associated with humans and human settlements, including domestic dog, skunks and rodents. Felids were also maintained in agricultural areas, possibly because many of these large predators are highly mobile and habitat generalists.

The stature of plants was most closely associated with persistence in agricultural landscapes, with small plants (< 1.55 m) persisting in agricultural plots and tall plants being lost. The removal of trees and other large plants is a common practice in farm fields and thus this result is not unexpected. This does suggest that plant communities in agricultural areas provide less complex habitat, which is a potentially important factor in the loss of some animal groups from these landscapes.

Classification and regression trees have been used to identify traits associated with extinction (Olden *et al.* 2008), but here it is important to emphasize that we are not able to identify traits relating to extinction proneness under land use intensification, but rather identify the traits that are no longer present in the agricultural communities, but were present in the natural communities. This is because the agricultural communities are not necessarily subsets of the natural and semi-natural communities, and because the traits examined here are centred on resource acquisition, not necessarily on response to land use intensity. We selected traits based on their presumed influence on the provisioning of ecosystems function, but the probability of species persistence in agricultural land uses may be more determined by traits affecting dispersal, fecundity, colonization, and stress tolerance. In addition, we expect that greater-resolution trait data (beyond simply species means) and a more complete understanding of the traits necessary for coexistence in each of these studies would enhance our ability to identify which trait values were most likely to be lost under land use intensification.

Four additional issues deserve comment regarding the interpretation of these results: sampling and 'sampling effects,' the influence of phylogenetics, the definition of land use intensification categories, and the extension of this work to other taxonomic groups. First, while species richness can greatly influence ecosystem functioning, the influence of individual species being present, i.e. the sampling effect, is an important process (Cardinale *et al.* 2006), and rare species can contribute substantially to ecosystem functioning (Lyons *et al.* 2005). The influence of species composition, not just diversity, can be viewed through functional diversity, where the presence of functionally distinct species may substantially increase the community-wide trait diversity. For example, in one of the bird studies analyzed here (Jones *et al.* 2005), we found that functional diversity was higher in the margins of conventional crop fields than in those of organic crop fields; the bald eagle is the only species present in conventional field margins but not in the other communities. This species contributes a unique combination of traits to this community, and thus a single sighting of a conspicuous bird influenced the FD values for that study. Repeated sampling is necessary to fully characterize the functional composition of communities, including rare species.

In addition to these sampling issues, the interpretation of the term 'functional redundancy' must include a consideration of the evolutionary history shared between species. Here we examine the pattern of functional diversity under land use intensification, finding that functionally unique species are often absent from agricultural land uses. The process underlying the functional similarity between remaining species is also of interest, namely whether the remaining species more closely related because of phylogenetic similarity or because of convergent evolution. We found no evidence for phylogenetically determined composition change in looking at the numbers of species, genera, and families across the land use gradient in each study, as well as the ratios of species per genus and genera per family (not shown). However, this question deserves further consideration in future studies.

Land use intensification is a complex process, and can take many possible forms. In this study, we synthesized results from a wide variety of studies, including 'natural' communities ranging from wet tropical forests to prairies. While our compilation of studies includes heterogeneous land use types, the diversity metrics are only compared to values within a single study, ensuring internally consistent comparisons. Given the use of only three broad intensification categories, the consistent change in FD values for mammals and birds is remarkable. Splitting the 'agricultural' category into high- and low-intensity agriculture did not change the results (not shown), and would have involved further subjective decisions about how to categorize reported land use types. This result supports previous work showing that the FD of amphibian communities can decline substantially in logged forests, even when species richness changes little (Ernst *et al.* 2006).

Finally, we initially sought to include two additional taxonomic groups in this study, arthropods and fungi.

However, trait data for these organisms are scarce. In addition, in arthropod studies specimens are often only identified to the family level masking large species-level variation. To our knowledge, only one study has assessed changes in the functional diversity of arthropods with increasing land use intensification, finding falling functional group richness, even though species richness remains constant (Schweiger *et al.* 2007). In addition, several studies have documented declines in arthropod diversity under land use intensification (Kremen 2002; Philpott *et al.* 2008), although some arthropod communities may be insensitive to agricultural intensification (Wardle *et al.* 1999). In fungi, the problems of identifying species and assessing species traits are even more acute, and assessments of functional diversity are largely limited to categorizations into very broad functional groups, although studies have identified important changes in plant diversity and ecosystem functioning when fungal community composition is altered (Klironomos *et al.* 2000).

CONCLUSIONS

This study shows that functional diversity measurements can reveal stark declines with land use intensification for birds and mammals, in many cases following patterns of species richness change (Hypothesis A). However, in a substantial number of cases, declines in FD are distinct from changes in species diversity, declining more than expected in agricultural settings (Hypothesis D). Plant studies demonstrated little change in any measure of diversity across the land use intensity gradient, and FD values generally matched species richness values (Hypothesis A). Future work should build on direct measurements of organism traits in communities under different land use management practices, and tie these traits to specific ecosystem processes of interest. Assessing how biotic communities can provide ecosystem services relies on accurate measurement of the features of those communities, which directly contribute to ecosystem functioning; functional diversity measurement should be incorporated in such assessments.

ACKNOWLEDGMENTS

REFERENCES

Aebischer, N. (1991). Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. In: *The Ecology of Temperate Cereal Fields* (eds Firbank, L., Carter, N., Darbyshirem, J. & Potts, G.). Blackwell Scientific Publications, Oxford, pp. 305–331.

Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002). Linking agricultural practice to insect and bird populations: a historical study over three decades. *J. Appl. Ecol.*, 39, 673–687.

Best, L.B., Freemark, K.E., Dinsmore, J.J. & Camp, M. (1995). A review and synthesis of habitat use by breeding birds in agricultural landscapes of Iowa. *Am. Midl. Nat.*, 134, 1–29.

Botta-Dukat, Z. (2005). Rao's quadratic entropy as a measure of functional diversity based on multiple traits. *J. Veg. Sci.*, 16, 533–540.

Bunker, D.E., DeClerck, F., Bradford, J.C., Colwell, R.K., Perfecto, I., Phillips, O.L. *et al.* (2005). Species loss and aboveground carbon storage in a tropical forest. *Science*, 310, 1029–1031.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M. *et al.* (2006). Effects of biodiversity on the functioning of trophic groups and ecosystems. *Nature*, 443, 989–992.

Daily, G.C., Ehrlich, P.R. & Sanchez-Azofeifa, G.A. (2001). Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol. Appl.*, 11, 1–13.

Daily, G.C., Ceballos, G., Pacheco, J., Suzan, G. & Sanchez-Azofeifa, A. (2003). Countryside biogeography of neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conserv. Biol.*, 17, 1814–1826.

De'ath, G. & Fabricius, K.E. (2000). Classification and regression trees: a powerful yet simple technique for ecological data analysis. *Ecology*, 81, 3178–3192.

Díaz, S. & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646–655.

Donald, P.F., Green, R.E. & Heath, M.F. (2001). Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc. R Soc. Lond. B*, 268, 25–29.

Ernst, R., Linsenmair, K.E. & Rödel, M.-O. (2006). Diversity erosion beyond the species level: dramatic loss of functional diversity after selective logging in two tropical amphibian communities. *Biol. Conserv.*, 133, 143–155.

Estrada, A. & Coates-Estrada, R. (2005). Diversity of neotropical migratory landbird species in forest fragments and man-made vegetation of Los Tuxtlas, Mexico. *Biodivers. Conserv.*, 14, 1719–1734.

Estrada, A., Coatesestrada, R. & Meritt, D. (1994). Non-flying mammals and landscape changes in the tropical rain-forest region of Los-Tuxtlas, Mexico. *Ecography*, 17, 229–241.

Estrada, A., Coates-Estrada, R. & Meritt, D. (1997). Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. *Biodivers. Conserv.*, 6, 19–43.

Hilty, J.A. & Merenlender, A.M. (2004). Use of riparian corridors and vineyards by mammalian predators in northern California. *Conserv. Biol.*, 18, 126–135.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3–35.

Horvath, A., March, I.J. & Wolf, J.H.D. (2001). Rodent diversity and land use in Montebello, Chiapas, Mexico. *Stud. Neotrop. Fauna Environ.*, 36, 169–176.

Jobin, B., Boutin, C. & DesGranges, J.L. (1996). Animal habitats in rural Quebec: floristic analysis. *Can. J. Bot.*, 74, 323–336.

Jones, G.A., Sieving, K.E. & Jacobson, S.K. (2005). Avian diversity and functional insectivory on north-central Florida farmlands. *Conserv. Biol.*, 19, 1234–1245.

Joshi, J., Matthies, D. & Schmid, B. (2000). Root hemiparasites and plant diversity in experimental grassland communities. *J. Ecol.*, 88, 634–644.

Klironomos, J.N., McCune, J., Hart, M. & Neville, J. (2000). The influence of arbuscular mycorrhizae on the relationship between plant diversity and productivity. *Ecol. Lett.*, 3, 137–141.

Kremen, C. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl Acad. Sci. USA*, 99, 16812–16816.

Larsen, T.H., Williams, N.M. & Kremen, C. (2005). Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.*, 8, 538–547.

Lyons, K.G., Brigham, C.A., Traut, B.H. & Schwartz, M.W. (2005). Rare species and ecosystem functioning. *Conserv. Biol.*, 19, 1019–1024.

Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. (1997). Agricultural intensification and ecosystem properties. *Science*, 277, 504–509.

Mayfield, M.M., Ackerly, D. & Daily, G.C. (2006). The diversity and conservation of plant reproductive and dispersal functional traits in human-dominated tropical landscapes. *J. Ecol.*, 94, 522–536.

McIntyre, P.B., Jones, L.E., Flecker, A.S. & Vanni, M.J. (2007). Fish extinctions alter nutrient recycling in tropical freshwaters. *Proc. Natl Acad. Sci. USA*, 104, 4461–4466.

Middleton, J. & Merriam, G. (1983). Distribution of woodland species in farmland woods. *J. Appl. Ecol.*, 20, 625–644.

Mokany, K., Ash, J. & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *J. Ecol.*, 96, 884–893.

Naughton-Treves, L., Mena, J.L., Treves, A., Alvarez, N. & Radeloff, V.C. (2003). Wildlife survival beyond park boundaries: the impact of slash-and-burn agriculture and hunting on mammals in Tambopata, Peru. *Conserv. Biol.*, 17, 1106–1117.

Olden, J.D., Poff, N.L. & Bestgen, K.R. (2008). Trait synergisms and the rarity, extirpation, and extinction risk of desert fishes. *Ecology*, 89, 847–856.

Olson, R.A. & Brewer, M.J. (2003). Small mammal populations occurring in a diversified winter wheat cropping system. *Agric. Ecosyst. Environ.*, 95, 311–319.

Petchey, O.L. & Gaston, K.J. (2002). Functional diversity (FD), species richness and community composition. *Ecol. Lett.*, 5, 402–411.

Petchey, O.L. & Gaston, K.J. (2006). Functional diversity: back to basics and looking forward. *Ecol. Lett.*, 9, 741–758.

Petchey, O.L., Hector, A. & Gaston, K.J. (2004). How do different measures of functional diversity perform? *Ecology*, 85, 847–857.

Petchey, O.L., Evans, K.L., Fishburn, I.S. & Gaston, K.J. (2007). Low functional diversity and no redundancy in British avian assemblages. *J. Anim. Ecol.*, 76, 977–985.

Philpott, S.M., Arendt, W.J., Armbrecht, I., Bichier, P., Diestch, T.V., Gordon, C. *et al.* (2008). Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv. Biol.*, 22, 1093–1105.

Podani, J. & Schmera, D. (2006). On dendrogram-based measures of functional diversity. *Oikos*, 115, 179–185.

Quinn, M.A. (2004). Influence of habitat fragmentation and crop system on Columbia Basin shrubsteppe communities. *Ecol. Appl.*, 14, 1634–1655.

R Development Core Team (2008). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

van Ruijven, J., De Deyn, G.B. & Berendse, F. (2003). Diversity reduces invasibility in experimental plant communities: the role of plant species. *Ecol. Lett.*, 6, 910–918.

Sánchez, D., Harvey, C.A., Grijalva, A., Medina, A., Vilchez, S. & Hernandez, B. (2005a). Caracterización de la diversidad, densidad y estructura de la vegetación en un paisaje fragmentado de bosque seco en Rivas, Nicaragua. *Rev. Rec. Nat. Ambiente.*, 45, 91–104.

Sánchez, D.M., Harvey, C.A., Grijalva, A., Medina, A., Vílchez, S. & Hernández, B. (2005b). Diversidad, composición y estructura de la vegetación en un agropaisaje ganadero en Matiguas, Nicaragua. *Rev. Biol. Trop.*, 53, 387–414.

Scherer-Lorenzen, M. (2008). Functional diversity affects decomposition processes in experimental grasslands. *Funct. Ecol.*, 22, 547–555.

Schweiger, O., Musche, M., Bailey, D., Billeter, R., Diekotter, T., Hendrickx, F. *et al.* (2007). Functional richness of local hoverfly communities (Diptera, Syrphidae) in response to land use across temperate Europe. *Oikos*, 116, 461–472.

Sotherton, N.W. (1998). Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biol. Conserv.*, 83, 259–268.

Spehn, E.M., Hector, A., Joshi, J., Scherer-Lorenzen, M., Schmid, B., Bazeley-White, E. *et al.* (2005). Ecosystem effects of biodiversity manipulations in European grasslands. *Ecol. Monogr.*, 75, 37–63.

Sullivan, T.P. & Sullivan, D.S. (2006). Plant and small mammal diversity in orchard versus non-crop habitats. *Agric. Ecosyst. Environ.*, 116, 235–243.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.

Tscharntke, T., Klein, A.M., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecol. Lett.*, 8, 857–874.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Walker, B., Kinzig, A. & Langridge, J. (1999). Plant attribute diversity, resilience, and ecosystem function: the nature and significance of dominant and minor species. *Ecosystems*, 2, 95–113.

Wardle, D.A., Nicholson, K.S., Bonner, K.I. & Yeates, G.W. (1999). Effects of agricultural intensification on soil-associated arthropod population dynamics, community structure, diversity

and temporal variability over a seven-year period. *Soil Biol. Biochem.*, 31, 1691–1706.

Wilsey, B.J. (2005). Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology*, 86, 1178–1184.

Wright, J.P., Naeem, S., Hector, A., Lehman, C., Reich, P.B., Schmid, B. *et al.* (2006). Conventional functional classification schemes underestimate the relationship with ecosystem functioning. *Ecol. Lett.*, 9, 111–120.

Zavaleta, E.S. & Hulvey, K.B. (2004). Realistic species losses disproportionately reduce grassland resistance to biological invaders. *Science*, 306, 1175–1177.

SUPPORTING INFORMATION

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

Appendix S1 Assignment of land use intensity categories for communities analyzed in this study and full null model results.

Appendix S2 Data sources for bird, mammal, and plant traits in this study.

Appendix S3 Comparisons of FD values calculated from all possible number and combination of traits for each taxon, to FD values using all traits.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.