Paper:

Newbold, T., Hudson, L., Hill, S., Contu, S., Gray, C., Scharlemann, J., Borger, L., Phillips, H., Sheil, D., Lysenko, I. & Purvis, A. (in press). Global patterns of terrestrial assemblage turnover within and among land uses. *Ecography*

http://dx.doi.org/10.1111/ecog.01932

Global patterns of terrestrial assemblage turnover within and among land uses

Journal:	*Ecography*
Manuscript ID	ECOG-01932.R2
Wiley - Manuscript type:	Research
Date Submitted by the Author:	21-Dec-2015
Complete List of Authors:	Newbold, Tim; UNEP World Conservation Monitoring Centre, Hudson, Lawrence; Natural History Museum, Department of Life Sciences Hill, Samantha; UNEP World Conservation Monitoring Centre, ; Natural History Museum, Department of Life Sciences Contu, Sara; Natural History Museum, Department of Life Sciences Gray, Claudia; University of Sussex, School of Life Sciences Scharlemann, Jorn; University of Sussex, School of Life Sciences Borger, Luca; Swansea University, Department of Biosciences Phillips, Helen; Imperial College London, Department of Life Sciences; Natural History Museum, Department of Life Sciences Sheil, Douglas; Norwegian University of Life Sciences (NMBU), INA Lysenko, Igor; Imperial College London, Department of Life Sciences Purvis, Andy; Natural History Museum, Department of Life Sciences
Keywords:	beta diversity, land use, biodiversity
Abstract:	Land use has large effects on the diversity of ecological assemblages. Differences among land uses in the diversity of local assemblages (alpha diversity) have been quantified at a global scale. Effects on the turnover of species composition between locations (beta diversity) are less clear, with previous studies focusing on particular regions or groups of species. Using a global database on the composition of ecological assemblages in different land uses, we test for differences in the between-site turnover of species composition, within and among land-use types. Overall, we show a strong impact of land use on assemblage composition. While we find that compositional turnover within land uses does not differ strongly among land uses, human land uses and secondary vegetation in an early stage of recovery are poor at retaining the species that characterise primary vegetation. The dissimilarity of assemblages in human-impacted habitats compared with primary vegetation was more pronounced in the tropical than temperate realm. An exploratory analysis suggests that this geographic difference might be caused primarily by differences in climate seasonality and in the numbers of species sampled. Taken together the results suggest that, while small-scale beta diversity within land uses is not strongly impacted by land-use type, compositional turnover between land uses is substantial. Therefore, land-use change will lead to profound changes in the structure of ecological assemblages.

Global patterns of terrestrial assemblage turnover within and among land uses

Tim Newbold, Lawrence N. Hudson, Samantha L. L. Hill, Sara Contu, Claudia L. Gray, Jörn P. W. Scharlemann, Luca Börger, Helen R. P. Phillips, Douglas Sheil, Igor Lysenko, Andy Purvis

T. Newbold (t.newbold@ucl.ac.uk), S. L. L. Hill and J. P. W. Scharlemann, United Nations Environment Programme World Conservation Monitoring Centre, 219 Huntingdon Road, Cambridge CB3 0DL, UK. – TN, Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, Gower Street, London WC1E 6BT, UK. – L.N. Hudson, SLLH, S. Contu, H. R. P. Phillips and A. Purvis, Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK. – C. Gray and JPWS, School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK. – L. Börger, Department of Biosciences, College of Science, Swansea University, Singleton Park, Swansea SA2 8PP, UK. – HRPP, I. Lysenko and AP, Department of Life Sciences, Imperial College London, Silwood Park, London SL5 7PY, UK. – D. Sheil, Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, P.O.Box 5003, NO-1432 Ås, Norway.

Abstract

Land use has large effects on the diversity of ecological assemblages. Differences among land uses in the diversity of local assemblages (alpha diversity) have been quantified at a global scale. Effects on the turnover of species composition between locations (beta diversity) are less clear, with previous studies focusing on particular regions or groups of species. Using a global database on the composition of ecological assemblages in different land uses, we test for differences in the between-site turnover of species composition, within and among land-use types. Overall, we show a strong impact of land use on ~~the turnover of~~ assemblage composition. While we find that compositional turnover within land uses does not differ strongly among land uses, human~~-impacted~~ land uses and secondary vegetation in an early stage of recovery are poor at retaining the species that characterise primary vegetation. The dissimilarity of assemblages in human-impacted habitats compared with primary vegetation was more pronounced in the tropical than temperate realm. An exploratory analysis suggests that this geographic difference might be caused primarily by differences in climate seasonality and in the numbers of species sampled. Taken together the results suggest that, while small-scale beta diversity within land uses is not strongly impacted by land-use type, compositional turnover between land uses is substantial. Therefore, land-use change will lead to profound changes in the structure of ecological assemblages.

Introduction

The widespread modification and conversion of natural habitats is profoundly affecting the world's biodiversity (Leadley et al. 2014). Many studies have quantified the effects of land use on the diversity or composition of ecological assemblages in a particular location (alpha diversity; e.g. Gibson et al. 2011, Newbold et al. 2015). Evidence is also mounting that human activities cause "biotic homogenization"

(McKinney and Lockwood 1999, McGill et al. 2015) - reduced spatial turnover (beta diversity) of genes, species and functional groups (Olden et al. 2004). Declines in beta diversity can reduce the resilience of communities to environmental changes and alter food-web structure (Olden et al. 2004).

Land use can be a major driver of the spatial homogenization of assemblages. Studies from a wide range of countries (in Europe, North America and in ~~areas of~~ tropical forest in South America) have shown that human-modified habitats tend to show lower turnover of species composition than do undisturbed habitats (e.g. Gabriel et al. 2006, Kühn and Klotz 2006, Tylianakis et al. 2006, Clough et al. 2007, Hendrickx et al. 2007, Vellend et al. 2007). Furthermore, human-modified habitats have been shown to benefit a few widespread species at the expense of many narrowly distributed species (e.g. McKinney 2006, Schwartz et al. 2006). On the other hand, differences in beta diversity among land uses are not always found, and beta diversity can even increase with human disturbance (Tylianakis et al. 2005, Hawkins et al. 2015, Mayor et al. 2015). The response of beta diversity to land use (both magnitude and direction) varies among taxonomic groups (Fleishman et al. 2003, Clough et al. 2007, Norfolk et al. 2015). As compositional similarity between two sites is likely to decline with the distance between them (distance-decay: Nekola and White 1999), analyses of beta diversity need to consider distance, both geographical and environmental (Ferrier et al. 2007).

However, it is not clear whether the distance decay of compositional similarity is the same in different land uses~~Whether the effects on assemblage compositional similarity of distance interact with the effects of land use remains unclear~~. One previous study (McKinney 2006) compared the distance decay of compositional similarity in natural vegetation and urban habitats, using spatial comparisons of sites from around the world. At short distances, distance-decay was similar in both land uses, but at longer distances (> 1,000 km) it was shallower in urban environments (McKinney 2006). ~~It is not clear whether these results generalize to other land uses.~~

Previous studies on compositional turnover have typically focused on particular geographic regions, or on single or few taxonomic groups. This narrow focus prevents an assessment of whether any patterns are general across different regions and taxa. In particular, tropical communities are structured differently from temperate ones (Holt et al. 2013) and face different climatic conditions, but it is not known whether land use affects beta diversity similarly in these two realms.

In a previous study (Newbold et al. 2015), we showed that assemblage composition differs strongly between sites in natural vegetation and nearby sites in more disturbed land uses. However, our analysis did not account for the influence of geographical or environmental distance between sites on compositional similarity. Furthermore, no previous broad-scale study of multiple land uses has tested whether geographic distance interacts with land use to shape turnover. A better understanding of land use effects on beta diversity is needed, given its potential importance for ecosystem resilience (Olden et al. 2004).

In this study, controlling for the effects of geographic and environmental distance among sites, we tested for the first time at a global scale: 1) whether average compositional similarity differs among land uses; 2) whether distance-decay relationships differ among land uses (i.e., is there an interaction between geographic distance and land use?); 3) whether the effect of land use on average compositional similarity and on distance decay differs between the tropical and temperate realms; and 4) which factors drive any differences in the relationships between realms. The effect of land use can be divided into two components. First, patterns of compositional similarity *within* each land use inform whether general community similarity is higher on average in human-disturbed land uses, as expected from biotic homogenization theory (e.g. McKinney 2006). Second, compositional similarity between a site in primary vegetation and a site in another land use provides evidence of the extent to which human-impacted land uses retain the species composition typical of primary vegetation.

Methods

Assemblage composition data

Data on the abundance (1,520,975 records) and occurrence (417,341 further records) of species within assemblages in different land uses were taken from the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) database on 10th September 2014 (Hudson et al. 2014). These data came from 485 sources (published or in-press papers, or unpublished datasets with published methods), which sampled 14,519 sites (Fig. 1) in 85 countries and all but one of the world’s terrestrial biomes (Table 1). The data represent major taxonomic groups (including invertebrates, vertebrates, plants and fungi) in approximate proportion to the number of described species (Supplementary Material, Appendix 1~~2~~, Fig. A1a). We georeferenced all sites, using information from the source paper, the supplementary files, or by contacting the corresponding author. Studies where coordinate precision was insufficient to distinguish sites spatially were excluded. Where sampling effort differed among sites within a study and data had not already been corrected for this (<20% of studies), we adjusted abundance values assuming that recorded abundance increases linearly with effort. Sampling effort was always recorded in the same units within each study. Where effort varied in more than one dimension (e.g. number of traps and number of days on which trapping occurred), sampling effort was recorded in the smallest possible units (in the above case, trap-days). This correction ~~was applied to account for differences in sampling effort among sites within a study, but~~ does not deal with the issue of failure to detect species, ~~;~~ ~~this second issue~~ which was dealt with as far as possible by calculating a sampling-corrected measure of compositional similarity (see next section).

The data used suffer from incomplete sampling. The incompleteness of species lists will be compounded by the small spatial extent sampled in most of the studies (for 95% of sites, the maximum linear extent sampled was between 1 m and 1.6 km). Incomplete species lists will decrease recorded similarities on average, and increase variance in modelled relationships of similarity ~~with distance and land use~~ (Nekola and White 1999). The former is not a problem for this study because we were interested in differences in compositional similarity among land uses, not absolute values. However, results might be biased if sampling completeness varies among land uses~~— a potential problem for all analyses of this type.~~

Calculating compositional similarity

We calculated pairwise compositional similarity between all sites within each study in the dataset. Of the 485 studies, 444 compared sites within a single terrestrial biome~~,~~ ~~and 455 compared sites within biomes that are broadly either forested, grassland,~~

~~Mediterranean or desert environments~~. The ~~grouped~~ hierarchical structure of the data (sampled sites nested within source studies) means that it is not appropriate to compare compositional similarity between sites sampled in different studies; therefore, we used a hierarchical model structure (see ‘Statistical Analysis’ below). We selected measures to capture five different aspects of similarity (Table 2). *Sørensen similarity* captures the overlap between the sites’ lists of sampled species. *Abundance-based Sørensen similarity* considers whether shared species are abundant or rare. *Endemicity-weighted similarity* (an endemicity-weighted version of Sørensen’s index that we developed ourselves) places greater weight on species with smaller ranges. The weights were the reciprocal of the $\log_{10}$-transformed estimates of each species’ total range size.~~;~~ W~~w~~e estimated range sizes as the total land area of one-degree grid cells with records in the Global Biodiversity Information Facility (GBIF) database – queried on 2nd April 2014. We were able to obtain range-size estimates for 61% of species in the dataset, including vertebrates, invertebrates and plants. The incompleteness and biases (geographic and taxonomic) of the GBIF database will render this an imperfect measure of range size, but it captures broad trends within taxonomic groups (Newbold et al., in prep.). *Chao’s sampling-corrected similarity*, which corrects for sampling incompleteness (Chao et al. 2005, but see Beck et al. 2013 for a critique of sampling-corrected measures), requires ~~true measures of abundance (i.e.~~ integer counts of individuals~~)~~, and thus could not be calculated for studies where abundances had to be rescaled because of varying sampling effort. Finally, we calculated a modification of the incidence-based Sørensen Index that removes the measured changes in compositional similarity that are attributable solely to differences in alpha diversity (Wolda 1981, Koleff et al. 2003).~~;~~ ~~because t~~The ratio (r) of species richness in the two sites (expressed as less rich/more rich) constrains the maximum value of species-list similarity to $S_{max} = 2r/(2r+(1-r))$, so we simply divided species-list similarity by S_{max}. This is numerically equivalent to Simpson's (1943) measure of assemblage similarity (henceforth *Simpson similarity*; see Appendix 2~~3~~ for derivation). An alternative to this correction would be to employ randomization tests (Chase et al. 2011). However, ~~this~~ these would have been computationally impracticable given the very large number of pairwise comparisons of sites that we considered. The values of all compositional similarity measures used vary between 0 (entirely distinct communities) and 1 (identical communities).

We focus on the results using Sørensen similarity, because it is the simplest measure, is widely used, and can be calculated for all of our sites. Simpson similarity could also be calculated for all sites, but is less widely used and understood than the Sørensen Index, while the datasets for the other measures (which demand more detailed data) were 14-43% smaller ~~(see also Supplementary Material, Appendix 2, Fig. A2)~~, and were reduced even more for some land-use comparisons. The results for these other measures of compositional similarity are presented in the supplementary information, with notable differences highlighted in the main text.

Explanatory variables

Three explanatory variables were used to model similarity between paired sites: geographic distance, environmental distance and the combination of land uses in which sites were located (for example, primary vegetation versus cropland). Geographic distance was calculated from the sites' coordinates using the 'distm' function (with the haversine method) in the 'geosphere' package Version 1.3-8

(Hijmans 2014) in R Version 3.1.2 (R Core Team 2014). Distances between pairs of sites ~~ranged to~~ reached over 1,000 km, but 90% ~~were~~ ranged between 1 and 100 km (Supplementary Material, Appendix 1~~2~~, Fig. A2~~3~~). Environmental distance was based on elevation and four bioclimatic variables at 30-arc-second resolution (Hijmans et al. 2005): maximum temperature of the warmest month, minimum temperature of the coldest month, precipitation of the wettest month, and precipitation of the driest month. ~~These variables were downloaded from WorldClim (Hijmans et al. 2005) at 30-arc-second resolution.~~ A single measure of the environmental distance between each pair of sites was calculated from these variables using Gower distances, as implemented in the ‘FD’ package, v~~V~~ersion 1.0-12 (Laliberté et al. 2014), in R. Land use was classified as in Hudson et al. (2014): primary vegetation (sites with no record of historical destruction of natural vegetation; n = 4,451 sites), mature secondary vegetation (sites where natural vegetation has been destroyed in the past, now in a late stage of recovery, with the habitat description suggesting that ~~such that~~ vegetation architecture is approaching original complexity; n = 617), intermediate secondary vegetation (natural vegetation destroyed in the past, in an intermediate stage of recovery; n = 944), young secondary vegetation (natural vegetation destroyed in the past, in an early stage of recovery with simple vegetation architecture; n = 1,187), plantation forest (tree or shrub crops; n = 1,626), cropland (arable agriculture, with herbaceous crops; n = 2,642), pasture (livestock grazing; n = 2,350) and urban (n = 702). To explore further the results for urban environments, we additionally classified urban sites by the intensity of human use: minimally used, for large managed green spaces and villages; and substantially used, for suburban environments, small managed green spaces in cities, and fully urban environments (Hudson et al. 2014). The classification of land use and land-use intensity is necessarily subjective, but a repeatability test has suggested that different data entrants are reasonably consistent (Cohen's kappa for land use = 0.662; Hudson et al. 2014).

We were particularly interested in two aspects of compositional turnover. First, whether the similarity of ecological communities was affected by land use (objective 1); specifically, how similar are assemblages between paired sites in the same land use (objective 1a) or between a site in primary vegetation and sites in other land uses (objective 1b)? Geographic and environmental distances between sites were considered as covariates in all analyses, allowing us also to test whether the distance-decay of similarity is related to land use (objective 2). We analysed pairs of sites ~~-~~within the same land-use class to test the prediction from biotic homogenization (e.g. McKinney 2006) that distance-decay is steeper in primary vegetation than in human~~-disturbed~~ land uses~~.~~ (objective 2a). We also modelled how compositional similarity between a site in a non-primary land use and a site in primary vegetation~~,~~ is related to the combination of distance between sites and land use (objective 2b).

We ~~also~~ included realm (temperate or tropical) ~~Whether a comparison concerned the tropical or temperate realms was also considered~~ as a covariate in the analyses, to test whether the effects of land use on beta diversity are similar ~~in the different regions~~ (objective 3). Realm was classified based on the biome (Olson et al. 2001) in which the sites fell (Supplementary Material, Appendix 1~~2~~, Table A1). Sites in three of the 553 studies fell within biomes belonging to both the tropical and temperate realms; we classified these sites as temperate because they were all close to the edge of the sub-tropics (average absolute latitudes ranged from 39.4° to 44.0°) and mostly (> 80% in all three studies) within temperate biomes. ~~It is also~~

~~likely to~~Effects of land use on compositional turnover may also vary within the tropical and temperate ~~se~~ realms, for example among continents~~ or among specific biomes~~, given the known variation in the structure of ecological assemblages (e.g. Parmentier et al. 2007). However, we did not have sufficient data to analyse these differences in more detail. We also had insufficient data to test for differences among taxonomic groups.

The tropical and temperate realms differ fundamentally in species composition (Hillebrand 2004, Holt et al. 2013), landscape history (Ellis et al. 2013), topography and climate. In order to understand any differences in patterns of compositional turnover between the tropics and temperate areas (objective 4), we also conducted exploratory post-hoc analyses considering eight variables describing community composition, landscape history of sites, spatial topographic heterogeneity, climate seasonality, and possible sampling artefacts.

First, the total number of species in the regional species pool from which communities are assembled. We expect average compositional similarity to be lower and the decay of similarity with geographic distance steeper in more species-rich areas, because the sampled communities are drawn from a larger regional species pool and thus ~~will~~should be less similar to one another on average. As a proxy ~~for species-pool size, ~~we used the vertebrate species richness in the 0.5° grid cell in which the mean of a study's coordinates was located (which as expected was higher in our tropical studies than in our temperate studies: Supplementary Material, Appendix 1~~2~~, Fig. A3~~3~~a), estimated by overlaying extent of occurrence polygons from the International Union for Conservation of Nature (IUCN), BirdLife International (Birdlife International and NatureServe 2012, IUCN 2013), and separately compiled estimates of reptile species richness (provided by Shai Meiri, Tel Aviv University).

We assume that vertebrate richness is a ~~reasonable ~~useful proxy for invertebrate and plant species richness, but this may not be the case.

Second, the average endemicity (1/$\log_{10}$ range area) of species sampled in a study, weighted by species' abundance. We expect lower average compositional similarity and steeper decay of compositional similarity with distance in areas with a higher proportion of small-ranged species, given that these species ~~with small ranges ~~have lower dispersal ability (Lester et al. 2007, Laube et al. 2013). Species found in the tropics have, on average, smaller range sizes than those found in temperate regions (Rapoport's rule: Stevens 1989~~). The average endemicity of species sampled at the sites in our dataset was consistent with this rule (~~; Supplementary Material, Appendix 1~~2~~, Fig. A3~~3~~b). Range area of species was estimated as above.

Third, landscape history, which we characterised as the number of years since the 0.5° grid cell containing the central location of sites in the study was first 30% converted to human land uses (cropland, pasture and urban). This year was estimated based on the HYDE model of historical land use (Klein Goldewijk et al. 2011). We expect areas with a longer history of human use to show more biotic homogenization (higher compositional similarity and slower distance-decay) because~~:~~ the most sensitive species ~~may already ~~have already been filtered ~~out ~~from the regional species pool (Balmford 1996) while non-native species may have had longer to perfuse assemblages in secondary and primary vegetation. Conversion to human land uses took place earlier on average in temperate regions – especially in the north – than in tropical areas~~,~~ (Supplementary Material, Appendix 1~~2~~, Fig. A3~~3~~c).

Fourth, the number of species sampled by a study, which was nearly two-fold higher in the lowest ~~compared with~~than the highest latitudes (Supplementary

Material, Appendix 1~~2~~, Fig. A3~~3~~d). This latitudinal variation reflects well-known differences in ~~the~~ species richness ~~of temperate and tropical areas~~, but is much less pronounced (cf. Fig. A3~~3~~a), suggesting that temperate studies are able to sample assemblages more comprehensively. Variation in sampling completeness might cause artefactual differences in compositional similarity, with less complete sampling ~~expected to~~ leading to lower estimates of compositional similarity on average. Therefore, ~~as our fifth explanatory variable~~ we also used the ratio of the number of ~~unique~~ distinct species sampled by a study to ~~the~~ vertebrate species richness, as a rough proxy for sampling completeness. Unsurprisingly, this measure of sampling completeness correlated strongly with the number of species sampled in a study; therefore, the two variables were never considered in the same model.

Finally, we included three variables describing variation in environmental heterogeneity: temperature seasonality and precipitation seasonality, downloaded from WorldClim (Hijmans et al. 2005) at 2.5 arc-minute resolution, and topographic heterogeneity. Topographic heterogeneity was calculated from elevation data, also from WorldClim at 2.5 arc-minute resolution (Hijmans et al. 2005), using the topographic ruggedness index (Wilson et al. 2007). We expect areas with ~~higher~~ lower climate seasonality and higher topographic heterogeneity to have ~~more~~ less similar assemblages and a ~~shallower~~ steeper decay of similarity with distance~~, because species in more heterogeneous areas have evolved to tolerate a wider range of conditions (Janzen 1967)~~. Note the coarser resolution of the climate data used here to that of the climate variables used in the main models, because we were interested here in broad-scale differences among studies.

Statistical analyses

All statistical analyses were conducted in R Version 3.1.2 (R Core Team 2014). Owing to the heterogeneity ~~and grouped structure~~ of the collated datasets, the main analyses were done using hierarchical mixed-effects models (Pinheiro & Bates, 2000) as implemented in the 'lme4' Version 1.0-6 (Bates et al. 2014) package in R.~~;~~ T~~t~~hese models are robust to unbalanced designs (Pinheiro and Bates 2000), but we cannot rule out entirely the possibility for some bias in the estimated model coefficients. Analysing compositional similarity for all pairwise comparisons of sites using standard statistical approaches would entail substantial pseudo-replication. For *n* sites, there are n^2 possible comparisons, but the number of independent comparisons is 2*n*-1, given by the diagonal and off-diagonal of the matrix of all possible comparisons (Longacre et al. 2005). For pairwise comparisons of sites in the same study, the diagonal of this matrix gives the self-comparisons, so we used as independent comparisons only the first off-diagonal from a randomized site-by-site matrix for each study (Supplementary Material, Appendix 3~~1~~). This randomization was repeated to generate 100 datasets of independent comparisons, which were each used in all models~~; all models were fitted to each of the 100 randomized datasets~~.

To account for the variation among the source datasets in taxonomic groups sampled, sampling methods and level of sampling effort, the study from which the site comparisons were drawn was fitted as a random intercept in all models. There could also be a structure to the sampled sites within each study (for example where sites are sampled in a blocked design; see Hudson et al. 2014). However, including such a complex random-effects structure was not possible with our pairwise comparison data. Modelling all combinations of geographic distance, environmental distance, temperate vs. tropical realm, land use, and their interactions would have created an unmanageable number of models. Therefore, we first selected the best model from those with combinations of geographic distance, environmental distance realm and their interactions (Supplementary Material, Appendix 1~~2~~, Table A2; the model with the lowest average AIC value across the 100 randomized datasets was selected). Distance-decay curves may be best represented by either exponential or power-law functions (Nekola and White 1999, Nekola and McGill 2014). We explored both by log-transforming either similarity (exponential), or both distance and similarity (power-law); the latter was overwhelmingly supported by the data for both geographic distance (ΔAIC = -563.4) and environmental distance (ΔAIC = -232.6). Log_e-transformed distances were fitted as a linear term, because more complex functional forms were not supported by exploratory modelling.

We then fit models, all of which had the best-fitting combination of the two distance measures and realm, but with different combinations of land use, realm and their interaction (Supplementary Material, Appendix 1~~2~~, Table A2). The fits of these models to the data were compared using Akaike Information Criterion (AIC) values. To assess the support for each term in the models, we calculated the Akaike weight, *w*, for each model and summed *w* for all models containing a given term (~~following~~ Burnham and Anderson 2002).

We compared the estimated distance-decay slopes for different combinations of land uses (objective 2) using t-tests. Specifically, we asked – for a given combination of land uses – what proportion of the 100 randomized datasets yielded slopes significantly steeper or shallower than the slope for pairs of sites both in primary vegetation.

We performed a post-hoc exploration of the observed temperate/tropical differences in how land use affects compositional similarity (objective 4). Specifically we analysed within-study compositional similarities (i.e. the study-level random intercepts) between primary vegetation and the human land uses (plantation forest, cropland pasture and urban), from models with only additive effects of geographic distance and land use. Average compositional similarities across human land uses and datasets were modelled as a function of eight study-level variables: the size of the regional species pool, average endemicity, land-use history, number of sampled species, the proportion of the regional species pool sampled, temperature seasonality, precipitation seasonality, and topographic heterogeneity. In these post-hoc analyses, we fitted all possible combinations of the eight explanatory variables, except that the two collinear variables (number of species sampled and the completeness of sampling) were never fitted in the same model. Latitude (degrees of northing, as a second-order polynomial) was included in all models to control for any residual latitudinal effects. As before, the support for each model and term was evaluated with AIC values and summed AIC weights.

The explanatory variables used in these analyses of tropical-temperate differences are only proxies for the factors hypothesized to influence the observed patterns. Furthermore, owing to the complexity of the main models, which renders the effective sample size relatively low, we were only able to model effects on study-level random effects in a post-hoc analysis rather than incorporating the explanatory variables in the full models. Therefore, ~~these~~ the post-hoc analyses should be seen as exploratory pending more detailed study.

Results

Effect of land use on average similarity

Sørensen similarity declined strongly with increasing geographic distance between sites (objective 1; ΣAICw ≈ 1; Fig. 2a). This relationship differed between the tropical and temperate realms (objective 3; ΣAICw = 0.78),~~:~~ ~~pairs of nearby sites in the tropics were more similar than pairs of sites in the temperate realm, but~~with a steeper decay of similarity ~~decayed faster~~ with distance in the tropics (Fig. 2a). Sørensen similarity also declined with increasing environmental distance between sites (objective 1; ΣAICw ≈ 1; Fig. 2b), but ~~the~~ this relationship did not differ strongly between the temperate and tropical realms (ΣAICw = 0.25).

When effects of distance were controlled for, land use (within and among land uses) had a strong overall effect on Sørensen similarity (objective 1; ΣAICw ≈ 1), and the effect of land use differed strongly between the temperate and tropical realms (ΣAICw = 0.93). Similarity between pairs of sites *within* the same land use (objective 1a) did not depend strongly on which land use this was, although temperate urban sites showed a tendency toward greater self-similarity ~~similar~~ than pairs of sites in primary vegetation (Fig. 3). Other measures of compositional similarity showed similar patterns (Supplementary Material, Appendix 1~~2~~, Figs. A4~~5~~a, 5~~6~~a, 7~~8~~a), except for Chao's sampling-corrected similarity~~,~~ (which suggested that non-natural land uses had assemblages that are less self-similar than those in primary vegetation: ~~(~~Supplementary Material, Appendix 1~~2~~, Fig. A6~~7~~a); we caution that confidence intervals were wide in this model, probably because fewer sites could be included. Assemblages in human land uses had very different composition compared with those in primary vegetation (i.e. *between*-land-use comparisons; objective 1b), especially in the tropics and especially in pasture (Fig. 3b). Even secondary vegetation – especially early-stage secondary vegetation – had markedly different composition from primary vegetation (Fig. 3b). The other similarity measures showed a similar pattern (Supplementary Material, Appendix 1~~2~~, Figs. A4~~5~~-7~~8~~, panels b), but some differences are worth noting. First, for endemicity-weighted similarity, differences were generally as great in the temperate realm as in the tropics (Supplementary Material, Appendix 1~~2~~, Fig. A5~~6~~b). Second, Simpson similarity suggested little compositional turnover between primary vegetation and most land uses in the temperate realm, ~~implying that the assemblages in human land uses are nested subsets of those in primary vegetation,~~ whereas significant – though reduced – differences remained in the tropics (Supplementary Material, Appendix 1~~2~~, Fig. A7~~8~~b). ~~Again we caution that this last result is subject to a high degree of uncertainty, probably because of the small number of comparisons that could be included in this model.~~

Effect of land use on distance-decay

The decay of compositional similarity with geographic distance differed substantially among land uses (objective 2; ΣAICw = 0.88). When comparing pairs of sites in the same land use (objective 2a; Fig. 4), compositional similarity was highest at short distances, but decayed fastest with distance, in primary vegetation. In other land uses – especially plantation forest and pasture, and especially in the tropics – similarity at short distances tended to be slightly lower, while the distance-decay tended to be shallower (Fig. 4; objective 3). All other measures of compositional similarity showed very similar patterns (results not shown). The interaction between environmental distance and land use was weaker (ΣAICw = 0.56) and is not considered further~~ in this study~~.

When comparing a primary-vegetation site and a site in another land use (objective 2b; Fig. 5), compositional similarity at short distances was highest when both sites were in primary vegetation. Secondary vegetation, particularly more mature secondary vegetation, was most similar to primary vegetation, whereas human land uses had more distinct assemblages. The distance-decay was steepest when comparing primary vegetation with itself or with mature secondary vegetation, and shallower when primary sites are compared with more disturbed land uses, especially young secondary vegetation, cropland and pasture (for these land uses, the 95% confidence limits around the slope estimate crossed zero; grey shading in Fig. 5). Urban environments were unusual among the human-dominated land uses, showing a pattern much more like primary vegetation. However, there were wide confidence limits on this result, possibly because of the small number of site comparisons, or because of the variety of conditions encompassed by urban environments.

Urban environments are very heterogeneous, ranging from parks (but not remnants of primary vegetation within cities; Hudson et al. 2014) to fully built-up city centres. Sørensen similarity between urban sites and sites in primary vegetation decreased with distance very differently across this gradient, with a steep distance-decay (steeper even than primary-primary comparisons) for large green spaces and villages, but a much shallower relationship for suburban and fully urban sites (Supplementary Material, Appendix 1~~2~~, Fig. A8~~9~~).

Causes of tropical-temperate differences

In our exploratory post-hoc analyses, five variables made a substantial contribution (ΣAICw > 0.3) to explaining why assemblages in human-dominated land uses were more dissimilar to those in primary vegetation (on average) in the tropics compared with the temperate realm. Compositional dissimilarity between primary and human-dominated land uses was slightly greater where average species endemicity was higher (ΣAICw = 0.32; Fig. 6a). Compositional dissimilarity between primary and human-dominated land use was twice as high in areas of low temperature seasonality than in areas of high seasonality (ΣAICw = 0.81; Fig. 6b~~c~~), and precipitation seasonality showed a weak relationship in the same direction (ΣAICw = 0.36; Fig. 6c~~d~~). There was a weak tendency for compositional dissimilarities to be higher in studies located in areas of low regional species richness (ΣAICw = 0.37; Fig. 6d~~e~~), but a strong increase in dissimilarity with an increase in the number of species sampled by a study (ΣAICw = 0.80; Fig. 6e~~f~~). There was not a clear relationship between the strength of differences in compositional similarity and either land-use history (ΣAICw = 0.29) or the estimated completeness of species sampling (ΣAICw = 0.11).

Discussion

Overall, we show a strong impact of land use on the turnover of assemblage composition. This impact can be divided into two key patterns: ~~average~~ differences in among land uses in average beta diversity ~~among land uses~~ (controlling for geographic and environmental distance), and effects of land use on the decay of compositional similarity with geographic distance (i.e. the interaction between land use and geographic distance). We deal with each of these patterns in separate sections below. We also distinguish two types of comparison between sites: first, between sites in the same land-use type, to ask whether beta diversity varies within land uses; and second, between a site in primary vegetation and a site in another land use, to ask whether non-primary land uses retain an assemblage composition similar to that typical of primary vegetation.

~~Our analyses differ from those normally used to infer patterns of beta diversity. Many studies partition diversity into alpha diversity within sampled spatial units, and beta diversity between these units (e.g. Gabriel et al. 2006, Tylianakis et al. 2006, Clough et al. 2007). The spatial units in such studies have a fixed extent and sampled sites are often a similar distance apart, whereas our dataset was derived from many studies with different sampling designs. Therefore, we modelled the effects of land use and distance separately. This is similar to the approach taken in generalised dissimilarity modelling (GDM; Ferrier et al. 2007), with two important differences. First, GDM is based on data collected with comparable surveys. In our study the nested structure of the data necessitated the use of mixed-effects models. Second, GDM uses continuous measures of environmental similarity whereas the land-use classification on which our main results were based is discrete. Nevertheless, we also included a continuous measure of environmental distance in our models to control for differences in assemblage composition driven by climate and elevation.~~

~~The data used suffer from incomplete sampling. The incompleteness of species lists will be compounded by the small spatial extent sampled in most of the studies (for 95% of sites, the maximum linear extent sampled was between 1 m and 1.6 km). Incomplete species lists will decrease recorded similarities on average, and~~

~~increase variance in modelled relationships of similarity with distance and land use (Nekola and White 1999). The former is not a problem for this study because we were interested in differences in compositional similarity among land uses, not absolute values. However, results might be biased if sampling completeness varies among land uses – a potential problem for all analyses of this type.~~

~~We show that the response of beta diversity to land use is different between the tropical and temperate realms.~~ ~~It is also likely to vary within these realms, for example among continents or among specific biomes, given the known variation in the structure of ecological assemblages (e.g. Parmentier et al. 2007). However, we did not have sufficient data to analyse these differences in more detail.~~ ~~Furthermore, as with all large-scale synthetic analyses, we were unable to consider the local environmental factors that might shape beta diversity patterns and responses to land use.~~

Effect of land use on average similarity

The idea of human-driven biotic homogenisation (McKinney and Lockwood 1999) predicts that assemblages in more human-modified land uses will be more similar to one another than those in less modified land uses. Several studies have shown that, within land uses, more intensively used areas have lower beta diversity (e.g. Gabriel et al. 2006, Clough et al. 2007, Hendrickx et al. 2007), but comparisons among land uses ~~are~~ have been rare and results ~~have been~~ mixed (Tylianakis et al. 2005, Vellend et al. 2007). Using data from around the world and for many taxonomic groups, we found few clear, consistent differences in the average (distance-corrected) similarity of assemblages within different land uses (Fig. 3a). ~~Consistent~~

~~with a previous smaller-scale study (Kühn and Klotz 2006), temperate urban environments tended to have slightly more homogenous assemblages than other land uses (Fig. 3). Urban environments in the temperate regions are generally impacted more intensively by human activities than those in the tropics. Continued development of cities in the tropics is likely to homogenize assemblages there in the future.~~

In addition to understanding beta diversity patterns within different land uses, it is also important to ask whether land more heavily used by humans retains the assemblages typical of primary vegetation. Typically, we find that they do not, but this answer depends to some extent on the land use in question, whether sites ~~were~~ are in the tropics or temperate realm, and which measure of compositional similarity ~~was~~ is used.

Overall, the biggest influence of land use on compositional dissimilarity to primary vegetation was seen for tropical assemblages, especially in pasture. This is in contrast to the results from studies of alpha diversity, which have suggested relatively small impacts of pasture compared with other human land uses (Gibson et al. 2011, Newbold et al. 2015). Taken together these results suggest that pasture is relatively good at maintaining species numbers, but poor at retaining the species typical of primary vegetation. At least compared with tropical forest (more than four times as many of our tropical sites were from forests than from grasslands), tropical pasture is a distinct habitat type (e.g. in terms of vertical structure of the vegetation) that is unsuitable for many primary-forest species. Assemblages in secondary vegetation – especially secondary vegetation in an early stage of recovery – were also distinct compared with primary vegetation. This has previously been shown for alpha diversity (Martin et al. 2013, Newbold et al. 2015), but rarely for beta diversity (but see Vellend et al. 2007, Curran et al. 2014).

Compositional differences between primary and other land uses were smaller in the temperate realm: in fact, when accounting for the declines in compositional similarity caused by differences in alpha diversity (Simpson similarity metric), differences among temperate land uses were generally not significant. ~~This shows that non-primary habitats in the temperate realm contain more-or-less nested subsets of the species found in primary vegetation.~~ On the other hand, compositional turnover between natural vegetation and human-modified land uses in the temperate realm were stronger for endemicity-weighted similarity, suggesting that land-use-driven turnover in the temperate region is stronger among narrow-ranged species.

~~While our analysis was taxonomically broad compared with previous studies, the size of the dataset and complexity of the analyses precluded a test for differences among taxonomic groups. It is also important to note that the hierarchical structure of our analysis and the fact that most studies spanned a relatively small spatial extent (Supplementary Material, Appendix 2, Fig. A2) means that our results concern differences in similarity over short distances. A previous study found little difference in short-scale beta diversity in urban land use compared with primary vegetation, but homogenization at longer (national to continental) distances (McKinney 2006). The beta diversity of alien species has a different relationship with land use compared to native species (Kühn and Klotz 2006). Where reported, the proportion of non-native species within the studies included in our dataset was usually low (Supplementary Material, Appendix 2, Fig. A10); however, native and~~

~~alien species were distinguished in only a minority of studies, and so we could not further consider differences between them.~~

Effect of land use on the distance-decay of similarity

In addition to differences in average compositional similarity among land uses, we also find that the form of the distance-decay of compositional similarity varies with land use. Distance-decay relationships were generally steepest in primary vegetation (Fig. 4). Our results are similar to a previous study that focused on urban environments, which showed a similar decay of bird assemblage similarity with distances up to 1,000 km in natural habitat, suburbs and city centres (McKinney 2006). Although the ecological assemblages of city centres are becoming more similar to one another across large (continental or global) areas (McKinney 2006), this is not obviously the case at smaller scales. However, it is important to note that the more intensively used urban environments harbour many fewer species than primary vegetation (i.e. lower alpha diversity; Newbold et al. 2015).

It is also important to consider whether the species characteristic of primary vegetation are retained in other land uses. Comparing a site in each land use with a site in primary vegetation, in general the intercept of the distance-decay relationship was lower and the slope shallower than for primary-primary comparisons (Fig. 5). This suggests that many primary-vegetation species are lost even at small distances from primary vegetation, but probably also reflects to some extent the fact that at least in some regions the areas converted to human land uses were probably the most productive habitats. As with comparisons of compositional similarity within land uses, assemblage similarity of urban sites to primary vegetation decayed rapidly as the distance to the primary vegetation site increased. Dividing urban sites by the intensity of human use revealed that this pattern was driven by the least intensive urban environments (Supplementary Material, Appendix 1, Fig. A8), while~~.~~ more intensively used urban sites showed a pattern very similar to that for other human-dominated land uses (e.g. cropland and pasture, as shown in Figure 5). This distinction reinforces the large heterogeneity of urban environments in their effects on biodiversity (Newbold et al. 2015). We caution that analysing the effect of distance on the similarity of assemblage composition in pairs of sites is not the same as analysing the distance from a site in a non-primary land use to edge of the nearest patch of primary vegetation (e.g. Gilroy et al. 2014), which we did not have appropriate information to test. ~~The effect on biodiversity of distance to the nearest natural habitat is an important topic of study, but could not be analysed in this study because we lack information on surrounding habitat patches for most of the sites in our dataset.~~

Causes of tropical-temperate differences

Effects of land use on assemblage composition were weaker overall in the temperate than in the tropical realm (Fig. 3). The strongest correlates of the strength of compositional-similarity differences among studies were temperature seasonality and the number of species sampled.

As expected, assemblage composition differed more between primary and human-dominated land uses in studies from areas with lower temperature seasonality. It has long been suggested that species in tropical landscapes where environmental heterogeneity is lower might be more sensitive to environmental change than temperate species because they have lower tolerance of climatic variation (Janzen 1967) and a higher degree of specialization (Dyer et al. 2007). Our results support this hypothesis: controlling for the effect of latitude, assemblages in climatically (temperature and to a lesser extent precipitation) stable areas were more sensitive to land use. ~~There was also a weak tendency in the same direction with respect to precipitation seasonality.~~

Also in line with our hypotheses, differences in assemblage composition were much stronger when a larger number of species were sampled. By chance, one expects a lower similarity of assemblage composition when the sampled species are drawn from a bigger pool. It was surprising therefore to find a tendency toward larger compositional differences between primary and human-dominated land uses in areas where the species pool is smaller. However, this relationship was weak, and the estimate of the size of the regional species pool was based only on vertebrates, which might not be representative of the other taxa ~~included in our analyses of compositional differences~~considered. ~~The differences between the tropical and temperate realms in how assemblage composition responds to land use do not appear to have been driven by the completeness of sampling of the regional species pool.~~

Conclusions

We found little evidence for substantial differences in the spatial turnover of community composition *within* different land uses. ~~One exception to this general pattern was seen for urban environments in the temperate realm, where compositional similarity between sites tended to be high. The fact that this decline in~~

~~beta diversity was seen only in the temperate realm might be because cities tend to be more built-up there than in the tropics, suggesting that tropical cities could lose beta diversity in the future as they intensify.~~

Although the differences in beta diversity within land uses were small, we show that non-primary habitats are poor at retaining the species characteristic of primary vegetation. We showed a similar pattern previously (Newbold et al. 2015), but without controlling for the potentially confounding influences of either geographic or environmental distance between sites. Here we show an important influence of land use on assemblage composition even after accounting for ~~the~~ distance effect ~~of distances~~; we also find that distance-decay curves are not the same in different land uses.

~~We show that compositional turnover patterns in secondary vegetation vary with the stage of recovery of the vegetation. Young secondary vegetation exhibits a pattern similar to human-dominated land uses, whereas mature secondary vegetation is more like primary vegetation. This result confirms the importance of the stage of recovery of secondary vegetation, which has previously been shown for alpha diversity (Martin et al. 2013, Newbold et al. 2015), but rarely for beta diversity (but see Vellend et al. 2007, Curran et al. 2014).~~

In the temperate realm, compositional turnover among land uses was smaller than in the tropical realm, and could be explained mostly by loss of local (alpha) diversity. Our exploratory analyses suggest that the smaller changes in the temperate realm may be because of differences in species diversity, and in climate seasonality.

Our results suggest a mixed outcome for biodiversity under ongoing land-use change. On the one hand, within-land-use beta diversity is not strongly impacted by human land uses, at least at relatively local scales. However, human alteration of habitats has substantial effects on assemblage composition, especially in the tropics. If the species found in impacted habitats are globally more widespread, then regional or global beta and gamma diversities will still decline with the expansion of human dominated land uses (McKinney and Lockwood 1999, McKinney 2006). Overall, our results confirm that human activities are having a profound influence on the structure of terrestrial ecological assemblages worldwide.

Acknowledgements

We thank Adriana De Palma, Alexandra Robinson, Argyrios Choimes, Callum Martin, Daniel Ingram, David Laginha Pinto Correia, Di Gao, Dominic Bennett, Felicity Bedford, Gwilym Pask-Hale, Hanbin Zhang, Hannah White, Hollie Booth, Jake Simpson, Julie Day, Katia Sanchez Ortiz, Lucinda Kirkpatrick, Martin Jung, Michelle Harrison, Morgan Garon, Susan Emerson, Susy Echeverria-Londoño, Tamera Alhusseini, Victoria Kemp and Yuan Pan for help with collating the ecological assemblage data; the hundreds of contributors of the assemblage data; Rebecca Senior for help compiling the vertebrate species richness map; Shai Meiri for providing mapped estimates of reptile species richness; Andrés Baselga for noticing the equivalency between our alpha-diversity-corrected compositional similarity metric and the Simpson similarity index; and two anonymous reviewers for helpful comments on the draft of this manuscript. This study is part of the PREDICTS project, which is funded by the Natural Environment Research Council, U.K. (NERC, grant number NE/J011193/2), and which is endorsed by GEO BON. This is a contribution from the Imperial College Grand Challenges in Ecosystems and the Environment Initiative.

References

Balmford, A. 1996. Extinction filters and current resilience: the significance of past selection pressures for conservation biology. - Trends Ecol. Evol. 11: 193–196.

Bates, D. et al. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-6.

Beck, J., Holloway, J. D. and Schwanghart, W. 2013. Undersampling and the measurement of beta diversity. - Methods Ecol. Evol. 4: 370–382.

Birdlife International and NatureServe 2012. Bird species distribution maps of the world. Version 2.0.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. - Springer.

Chao, A. et al. 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. - Ecol. Lett. 8: 148–159.

Chase, J. M. et al. 2011. Using null models to disentangle variation in community dissimilarity from variation in α-diversity. - Ecosphere 2: 24.

Clough, Y. et al. 2007. Alpha and beta diversity of arthropods and plants in organically and conventionally managed wheat fields. - J. Appl. Ecol. 44: 804–812.

Curran, M. et al. 2014. Is there any empirical support for biodiversity offset policy? - Ecol. Appl. 24: 617–632.

Dyer, L. A. et al. 2007. Host specificity of Lepidoptera in tropical and temperate forests. - Nature 448: 696–699.

Ellis, E. C. et al. 2013. Used planet: a global history. - Proc. Natl. Acad. Sci. U. S. A. 110: 7978–85.

Ferrier, S. et al. 2007. Using generalized dissimilarity modelling to analyse and predict patterns of beta diversity in regional biodiversity assessment. - Divers. Distrib. 13: 252–264.

Fleishman, E. et al. 2003. Effects of spatial scale and taxonomic group on partitioning of butterfly and bird diversity in the Great Basin, USA. - Landsc. Ecol. 18: 675–685.

Gabriel, D. et al. 2006. Beta diversity at different spatial scales: plant communities in organic and conventional agriculture. - Ecol. Appl. 16: 2011–2021.

Gibson, L. et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. - Nature 478: 378–381.

Gilroy, J. J. et al. 2014. Effect of scale on trait predictors of species responses to agriculture. - Conserv. Biol. 29: 463–472.

Hawkins, C. P. et al. 2015. Environmental disturbance can increase beta diversity of stream macroinvertebrate assemblages. - Glob. Ecol. Biogeogr. 24: 483–494.

Hendrickx, F. et al. 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes. - J. Appl. Ecol. 44: 340–351.

Hijmans, R. J. 2015. geosphere: Spherical Trigonometry. R package version 1.4-3.

Hijmans, R. J. et al. 2005. Very high resolution interpolated climate surfaces for global land areas. - Int. J. Climatol. 25: 1965–1978.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. - Am. Nat. 163: 192–211.

Holt, B. G. et al. 2013. An update of Wallace's zoogeographic regions of the world. - Science 339: 74–78.

Hudson, L. N. et al. 2014. The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. - Ecol. Evol. 4: 4701–4735.

IUCN 2013. The IUCN Red List of Threatened Species. Version 2013.7.

Janzen, D. H. 1967. Why Mountain Passes are Higher in the Tropics. - Am. Nat. 101: 233–249.

Klein Goldewijk, K. et al. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. - Glob. Ecol. Biogeogr. 20: 73–86.

Koleff, P. et al. 2003. Measuring beta diversity for presence–absence data. - J. Anim. Ecol. 72: 367–382.

Kühn, I. and Klotz, S. 2006. Urbanization and homogenization - Comparing the floras of urban and rural areas in Germany. - Biol. Conserv. 127: 292–300.

Laliberté, E. et al. 2014. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Laube, I. et al. 2013. Towards a more mechanistic understanding of traits and range sizes. - Glob. Ecol. Biogeogr. 22: 233–241.

Leadley, P. W. et al. 2014. Progress towards the Aichi Biodiversity Targets: An Assessment of Biodiversity Trends, Policy Scenarios and Key Actions.

Lester, S. E. et al. 2007. The relationship between dispersal ability and geographic range size. - Ecol. Lett. 10: 745–758.

Longacre, A. et al. 2005. Linear independence of pairwise comparisons of DNA microarray data. - J. Bioinform. Comput. Biol. 3: 1243–1262.

Martin, P. A. et al. 2013. Carbon pools recover more quickly than plant biodiversity in tropical secondary forests. - Proc. R. Soc. London Ser. B Biol. Sci. 280: 20132236.

Mayor, S. J. et al. 2015. Limited impacts of extensive human land use on dominance, specialization, and biotic homogenization in boreal plant communities. - BMC Ecol. 15: 5.

McGill, B. J. et al. 2015. Fifteen forms of biodiversity trend in the Anthropocene. - Trends Ecol. Evol. 30: 104–113.

McKinney, M. L. 2006. Urbanization as a major cause of biotic homogenization. - Biol. Conserv. 127: 247–260.

McKinney, M. L. and Lockwood, J. L. 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. - Trends Ecol. Evol. 14: 450–453.

Nekola, J. C. and White, P. S. 1999. The distance decay of similarity in biogeography and ecology. - J. Biogeogr. 26: 867–878.

Nekola, J. C. and McGill, B. J. 2014. Scale dependency in the functional form of the distance decay relationship. - Ecography 37: 309–320.

Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. - Nature 520: 45–50.

Norfolk, O. et al. 2015. Contrasting patterns of turnover between plants, pollinators and their interactions. - Divers. Distrib. 21: 405–415.

Olden, J. D. et al. 2004. Ecological and evolutionary consequences of biotic homogenization. - Trends Ecol. Evol. 19: 18–24.

Olson, D. M. et al. 2001. Terrestrial ecoregions of the world: a new map of life on Earth. - Bioscience 51: 933–938.

Parmentier, I. et al. 2007. The odd man out? Might climate explain the lower tree α-diversity of African rain forests relative to Amazonian rain forests? - J. Ecol. 95: 1058–1071.

Pinheiro, J. and Bates, D. M. 2000. Mixed-Effects Models in S and S-PLUS. - Springer.

R Core Team 2015. R: A Language and Environment for Statistical Computing. - R Foundation for Statistical Computing.

Schwartz, M. W. et al. 2006. Biotic homogenization of the California flora in urban and urbanizing regions. - Biol. Conserv. 127: 282–291.

Simpson, G. G. 1943. Mammals and the nature of continents. - Am. J. Sci. 241: 1–31.

Stevens, G. C. 1989. The latitudinal gradient in geographic range: how so many species coexist in the tropics. - Am. Nat. 133: 240–256.

Tylianakis, J. M. et al. 2005. Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. - Ecology 86: 3296–3302.

Tylianakis, J. M. et al. 2006. Spatial scale of observation affects α, β and γ diversity of cavity-nesting bees and wasps across a tropical land-use gradient. - J. Biogeogr. 33: 1295–1304.

Vellend, M. et al. 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use. - J. Ecol. 95: 565–573.

Wilson, M. F. J. et al. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. - Marine Geodesy 30: 3-35.

Wolda, H. 1981. Similarity indices, sample size and diversity. - Oecologia 50: 296–302.

Supplementary material (Appendix EXXXXX at <www.oikosoffice.lu.se/appendix>).

Appendix 1–3.

Figure Legends

Figure 1. Location of the 485 studies. The diameter of the points is proportional to the number of sites sampled within each study (14,519 in total) for which we could calculate species-list similarity and diversity-corrected similarity; fewer sites could be used for the other metrics ~~(Supplementary Material, Appendix 2, Fig. A2)~~. The points are translucent, so areas of darker colour contain overlapping studies. Shown in a Cylindrical Equal Area projection.

Figure 2. Relationship between compositional similarity and: a) geographic distance; and b) environmental distance between sites. The effect of geographic distance differed between the tropical (solid line) and temperate (dashed line) realms. Shading indicates ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables.

Figure 3. Average compositional similarity of a) pairs of sites in the same land use and b) pairs of sites, one in primary vegetation and one in each other land use, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals, based on AIC-weighted averages of models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. The dashed line shows the average compositional similarity of pairs of sites in the tropics, both in primary vegetation. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate

secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

Figure 4. Relationships between compositional similarity and geographic distance between sites, for comparisons of pairs of sites both in a single land-use type, for tropical (solid lines) and temperate (dashed lines) studies. Shading indicates ±95% confidence intervals. Horizontal lines show the average compositional similarity of pairs of sites 50 m apart and both in primary vegetation, in tropical (solid lines) and temperate (dashed lines) studies. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Triangles (filled = tropical, open = temperate) indicate (by opacity) the number of randomized datasets where the relationship had a significantly shallower (upward-facing triangles) or steeper (downward-facing triangles) slope compared with the slope for the comparison of two sites in primary vegetation.

Figure 5. Relationships between compositional similarity and geographic distance between sites, for comparisons of pairs of sites one in primary vegetation and one in each other land use, for tropical (solid lines) and temperate (dashed lines) studies. Plotting conventions and symbols as in Fig. 4.

Figure 6. Relationships between the study-level difference in compositional similarity between human land uses and primary vegetation, and: a) the average endemicity of species sampled in the study; b) temperature seasonality; c) precipitation seasonality; d) the richness of the landscape species pool; and e) the number of

species sampled by the study. Study-level compositional differences were calculated as the average study-level random slope for land-use comparisons of primary vegetation with a human land use (across studies these have a mean of zero) minus the average fixed effect for human land uses. More negative values indicate a greater decline in compositional similarity in human land uses compared with primary vegetation. The solid lines represent the model-fitted relationship, and the dashed lines 95% confidence intervals, both calculated as AIC-weighted averages and ranges (respectively) from across models fitting all possible combinations of explanatory variables.

Tables

Table 1. Numbers of sampled sites in each terrestrial biome.

Biome	Number of sites
Boreal forests/taiga	346
Deserts & xeric shrublands	188
Flooded grasslands & savannas	0
Mangroves	23
Mediterranean forests, woodlands & scrub	778
Montane grasslands & shrublands	372
Temperate broadleaf and mixed forests	4657
Temperate conifer forests	315
Temperate grasslands, savannas & shrublands	923
Tropical & subtropical coniferous forests	180
Tropical & subtropical dry broadleaf forests	407
Tropical & subtropical grasslands, savannas & shrublands	923
Tropical & subtropical moist broadleaf forests	4198
Tundra	26

Biomes were derived from the WWF terrestrial ecosystems of the world dataset (Olson et al., 2001).

Table 2. Metrics of compositional similarity used.

	Formula	Name, reference and description	Label
1.	$S_i = \frac{2a}{2a + b + c}$	Sørense~~o~~n’s incidence-based index (Mueller-Dombois and Ellenberg 1974). *a* is the number of species recorded at both sites, *b* and *c* are the numbers of species recorded at one site and the other, respectively	Sørensen similarity
2.	$S_a = \frac{2UV}{U + V}$	Abundance-corrected Sørensen index (Chao et al. 2005). *U* is the sum of the relative abundances at one of the sites of the species recorded at both sites, *V* is the sum of the relative abundances at the other of the sites of species recorded at both sites	Abundance-based Sørensen similarity

3.	$S_e = \frac{2w_a}{2w_a + w_b + w_c}$	w_a is the sum of the weights of the species recorded at both sites, and w_b and w_c are the sums of the weights of the species recorded only at one site and the other, respectively. The weights are the reciprocal of the $\log_{10}$-transformed estimates of the sum of species' geographic range sizes	Endemicity-weighted similarity
4.	$S_{Chao} = \frac{2\hat{U}\hat{V}}{\hat{U} + \hat{V}}$ $\hat{U} = \sum_{i=1}^{D_{12}} \frac{X_i}{n} + \frac{m-1}{m} \frac{f_{+1}}{2f_{+2}} \sum_{i=1}^{D_{12}} \frac{X_i}{n} I(Y_i = 1)$ $\hat{V} = \sum_{i=1}^{D_{12}} \frac{Y_i}{m} + \frac{(n-1)}{n} \frac{f_{1+}}{2f_{2+}} \sum_{i=1}^{D_{12}} \frac{Y_i}{m} I(X_i = 1)$	Sampling-corrected Sørensen Index (Chao et al. 2005). *n* and *m* are the total numbers of individuals recorded at the first and second sites respectively; for each species *i* among all of those recorded at both sites (D_{12}), X_i and Y_i are the numbers of	Chao's sampling-corrected similarity

		individuals recorded in the first and second sites respectively, f_{1+} is the number of species with 1 individual and f_{2+} the number of species with 2 individuals recorded at site 1, and f_{+1} and f_{+2} the number of species with 1 or 2 individuals, respectively, recorded at site 2.	
5.	$S_{Corr} = \frac{S_i}{S_{max}}$ $S_{max} = \frac{2r}{2r + (1 - r)}$ $r = \frac{a+b}{a+c}$, where $b < c$ Therefore, $S_{Corr} = 1 - \frac{b}{a+b}$, which is Simpson (Simpson 1943) similarity (see Supplementary Material, Appendix 2~~3~~ for full derivation).	S_i is as under 1 above, and r is the ratio of the number of species recorded at the ~~least~~ less speciose site to the number recorded at the ~~most~~ more speciose site in the pair of sites being compared. This is equivalent to Simpson (Simpson 1943) similarity.	Simpson similarity

The metrics used were all derivatives of the Sorensen Index: the original version based only on the incidence of species (S_i); one that accounts for abundance differences (S_a); one that we developed that weights by species range size (S_e); one that accounts for incompleteness of sampling (S_{Chao}); and one that corrects for differences caused only by the relative alpha diversities of the sampled sites (S_{corr}).

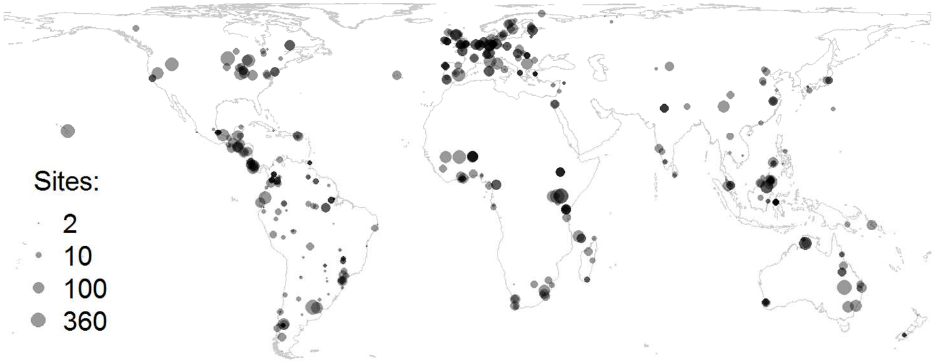


Figure 1. Location of the 485 studies. The diameter of the points is proportional to the number of sites sampled within each study (14,519 in total) for which we could calculate species-list similarity and diversity-corrected similarity; fewer sites could be used for the other metrics. The points are translucent, so areas of darker colour contain overlapping studies. Shown in a Cylindrical Equal Area projection.
124x59mm (300 x 300 DPI)

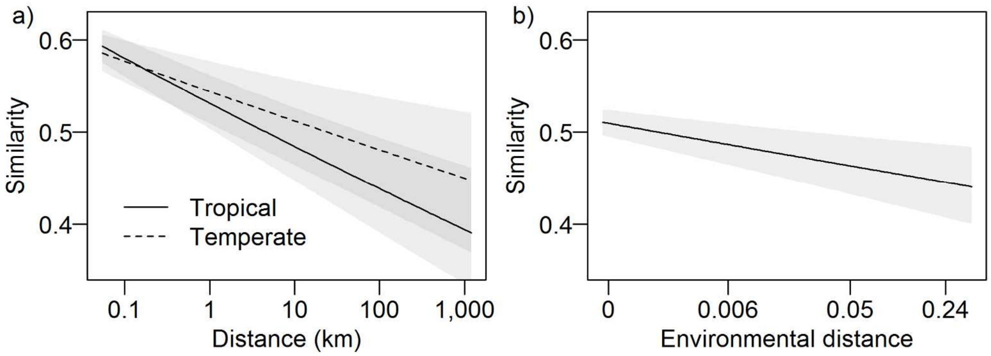


Figure 2. Relationship between compositional similarity and: a) geographic distance; and b) environmental distance between sites. The effect of geographic distance differed between the tropical (solid line) and temperate (dashed line) realms. Shading indicates ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables.

174x64mm (300 x 300 DPI)

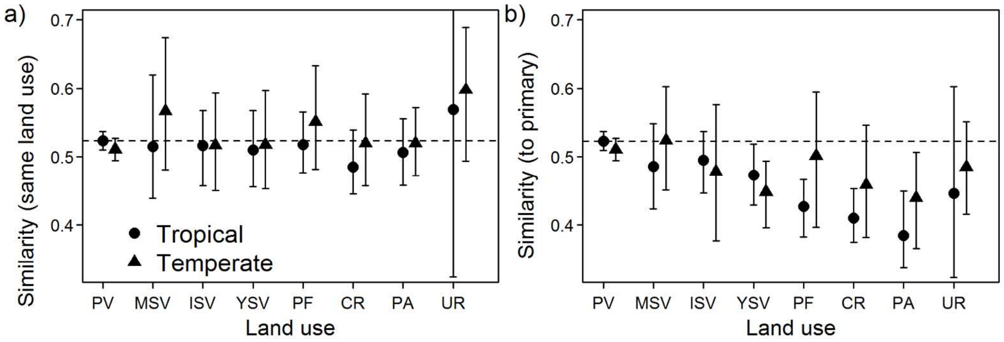


Figure 3. Average compositional similarity of a) pairs of sites in the same land use and b) pairs of sites, one in primary vegetation and one in each other land use, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals, based on AIC-weighted averages of models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. The dashed line shows the average compositional similarity of pairs of sites in the tropics, both in primary vegetation. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.
174x59mm (300 x 300 DPI)

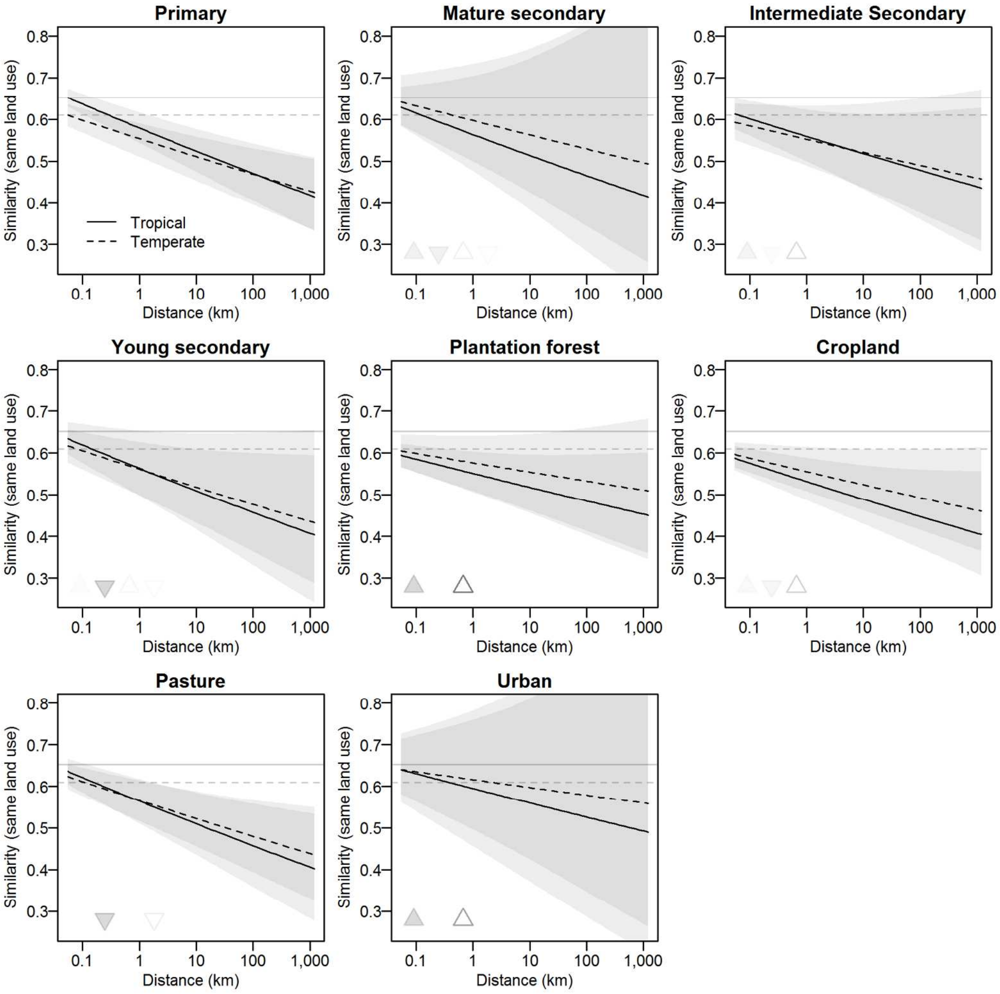


Figure 4. Relationships between compositional similarity and geographic distance between sites, for comparisons of pairs of sites both in a single land-use type, for tropical (solid lines) and temperate (dashed lines) studies. Shading indicates ±95% confidence intervals. Horizontal lines show the average compositional similarity of pairs of sites 50 m apart and both in primary vegetation, in tropical (solid lines) and temperate (dashed lines) studies. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Triangles (filled = tropical, open = temperate) indicate (by opacity) the number of randomized datasets where the relationship had a significantly shallower (upward-facing triangles) or steeper (downward-facing triangles) slope compared with the slope for the comparison of two sites in primary vegetation.
174x174mm (300 x 300 DPI)

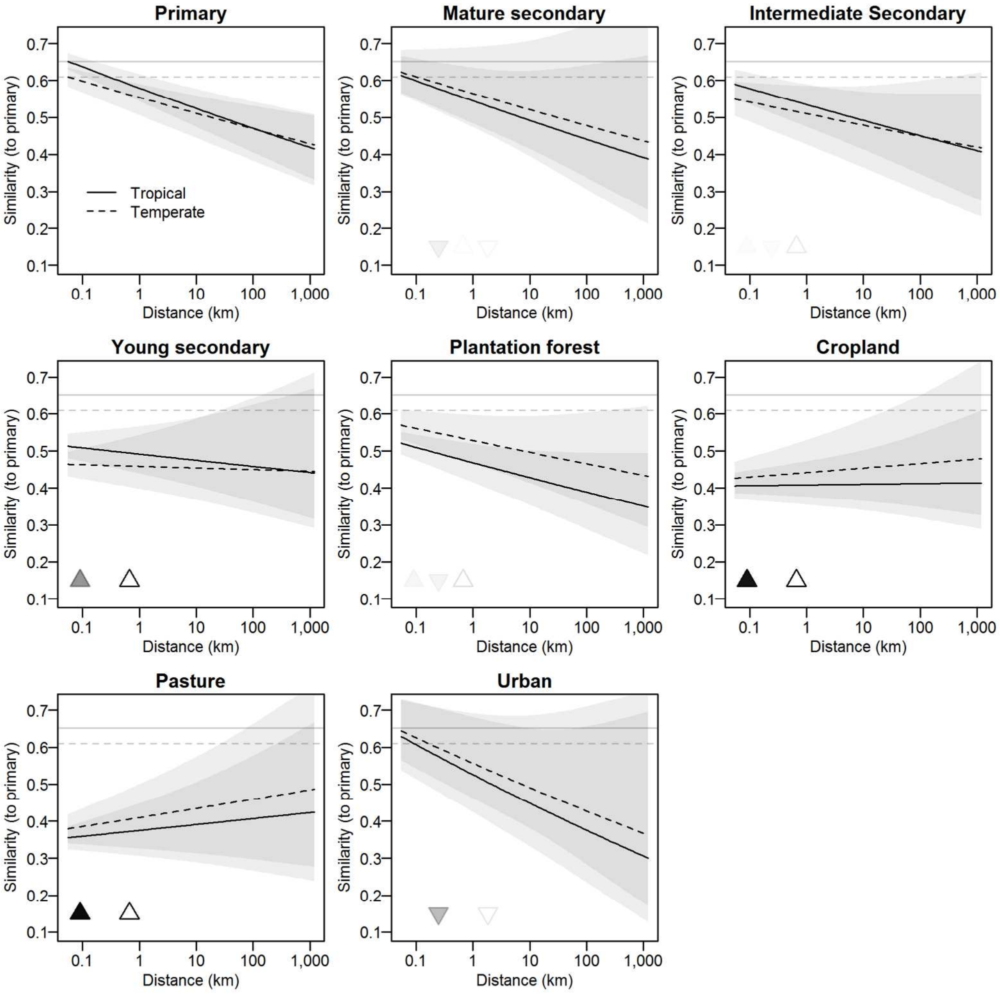


Figure 5. Relationships between compositional similarity and geographic distance between sites, for comparisons of pairs of sites one in primary vegetation and one in each other land use, for tropical (solid lines) and temperate (dashed lines) studies. Plotting conventions and symbols as in Fig. 4.
174x174mm (300 x 300 DPI)

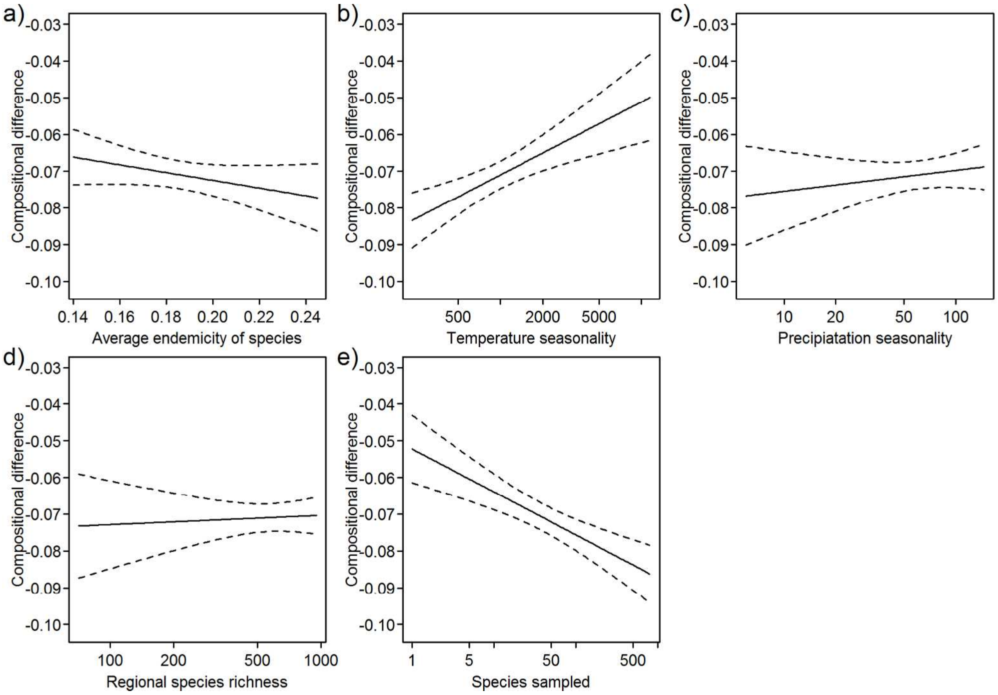


Figure 6. Relationships between the study-level difference in compositional similarity between human land uses and primary vegetation, and: a) the average endemicity of species sampled in the study; b) temperature seasonality; c) precipitation seasonality; d) the richness of the landscape species pool; and e) the number of species sampled by the study. Study-level compositional differences were calculated as the average study-level random slope for land-use comparisons of primary vegetation with a human land use (across studies these have a mean of zero) minus the average fixed effect for human land uses. More negative values indicate a greater decline in compositional similarity in human land uses compared with primary vegetation. The solid lines represent the model-fitted relationship, and the dashed lines 95% confidence intervals, both calculated as AIC-weighted averages and ranges (respectively) from across models fitting all possible combinations of explanatory variables.
174x119mm (300 x 300 DPI)

Supplementary Material

Appendix 1~~2~~. Supporting tables and figures

Table A1. Classification scheme used to derive Realm (tropical vs. temperate) depending on the biome in which sites within a study were located.

Biome	Realm
Tropical and Subtropical Moist Broadleaf Forests	Tropical
Tropical and Subtropical Dry Broadleaf Forests	Tropical
Tropical and Subtropical Coniferous Forests	Tropical
Temperate Broadleaf and Mixed Forests	Temperate
Temperate Conifer Forests	Temperate
Boreal Forests/Taiga	Temperate
Tropical and Subtropical Grasslands, Savannas and Shrublands	Tropical
Temperate Grasslands, Savannas and Shrublands	Temperate
Flooded Grasslands and Savannas	NA
Montane Grasslands and Shrublands	Depends on latitude
Tundra	Temperate
Mediterranean Forests, Woodlands and Scrub	Temperate

Table A2. Candidate models considered. Models prefixed ‘D’ were fitted first and used to select the most explanatory combination of geographic distance (‘LogDist’), environmental distance (‘LogEnvDist’), tropical vs. temperate realm (‘Realm’), and their pairwise interactions (indicated by a ‘:’). The best-fitting (from the model with the lowest average AIC value) combination of these terms (‘Distances’) was then used as the most simple of a set of models (prefixed ‘LU’) comparing combinations of land use (‘LandUse’), realm and their interaction.

Model ID	Formula
D0	1
D1	LogDist
D2	LogEnvDist
D3	LogDist+LogEnvDist
D4	Realm
D5	LogDist+Realm+LogDist:Realm
D6	LogEnvDist +Realm+LogEnvDist:Realm
D7	LogDist+LogEnvDist+Realm+LogDist:Realm
D8	LogDist+LogEnvDist+Realm+LogEnvDist:Realm

D9	LogDist+LogEnvDist+Realm+LogDist:Realm+LogEnvDist:Realm
LU0	Distances
LU1	Distances+LandUse
LU2	Distances+LandUse+LandUse:Realm
LU3	Distances+LandUse+LandUse:LogDist
LU4	Distances+LandUse+LandUse:LogEnvDist
LU5	Distances+LandUse+LandUse:Realm+LandUse:LogDist
LU6	Distances+LandUse+LandUse:Realm+LandUse:LogEnvDist
LU7	Distances+LandUse+LandUse:LogDist+LandUse:LogEnvDist
LU8	Distances+LandUse+LandUse:Realm+LandUse:LogDist+LandUse:LogEnvDist

Table A3. AIC weights for all terms in the models of all measures of compositional similarity

Term	Similarity measure				
	Sørensen	Abundance-based Sørensen	Endemicity-weighted	Chao sampling-corrected	Simpson
Land use	≈ 1	≈ 1	≈ 1	≈ 1	≈ 1
Land use:Realm	0.93	0.73	0.74	0.61	0.81
Geographical distance:Land use	0.88	0.89	0.86	0.46	0.35
Environmental distance: Land use	0.56	0.40	0.62	0.01	0.24

AIC weights were calculated for each model, and then summed across all models containing a term, following (Burnham and Anderson 2002).

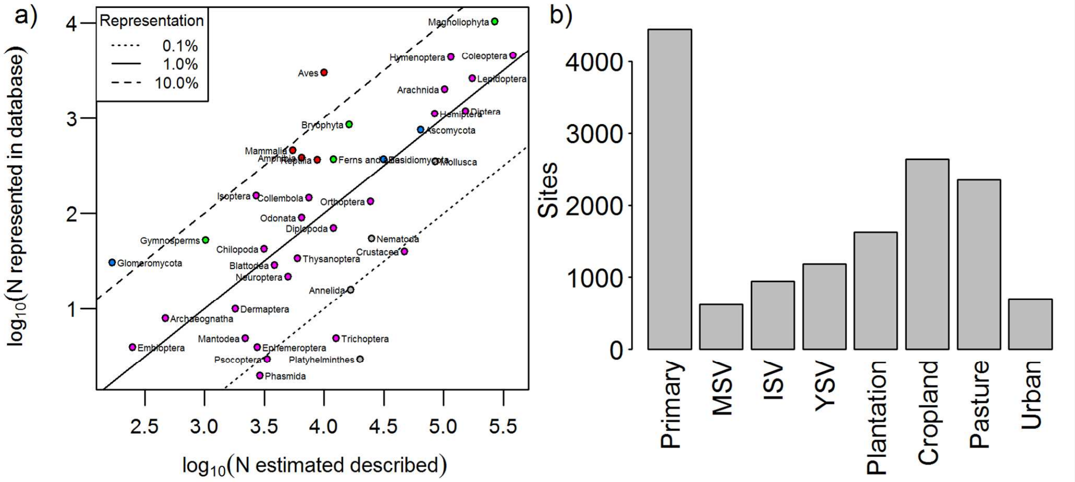
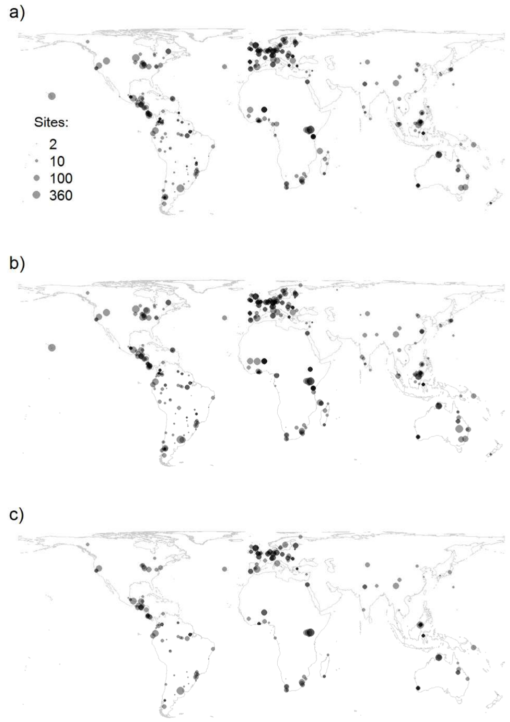


Figure A1. a) The distribution among major taxonomic groups of the number of records in our dataset, in relation to the number of species in those groups estimated to have been described by science. Colours indicate higher-level taxonomic groupings (magenta = invertebrates; red = vertebrates; green = plants; blue = fungi; grey = other). Lines indicate different percentages of described species represented in the dataset. b) The distribution of sampled sites among the land uses considered in this study. See (Hudson et al. 2014) for more details.



Formatted: Font: (Default) Times New Roman

~~**Figure A2.** Location of studies for which the alternative metrics of compositional similarity could be calculated: a) 431 studies for abundance-based similarity; b) 427 for endemicity-weighted similarity; and c) 240 for sampling-corrected similarity. The diameter of the points is proportional to the number of sites sampled within each study and for which the given metric could be calculated (13,635 in total for abundance-based similarity, 14,468 for endemicity-weighted similarity, and 8394 for sampling-corrected similarity). The points are translucent, so areas of darker colour contain overlapping studies. Shown in a Cylindrical Equal Area projection.~~

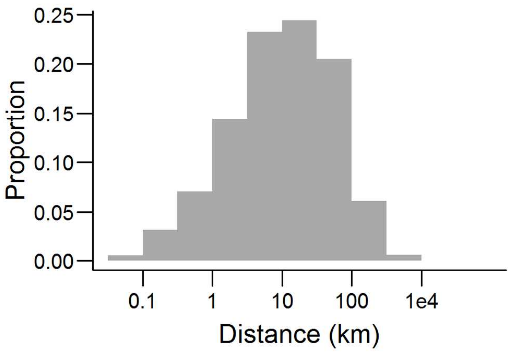


Figure A2~~3~~. Distribution of pairwise geographic distances among sites. Distances were calculated using the ‘distm’ function in the ‘geosphere’ package Version 1.3-8 (Hijmans 2014) in R Version 3.0.2 (R Core Team 2014).

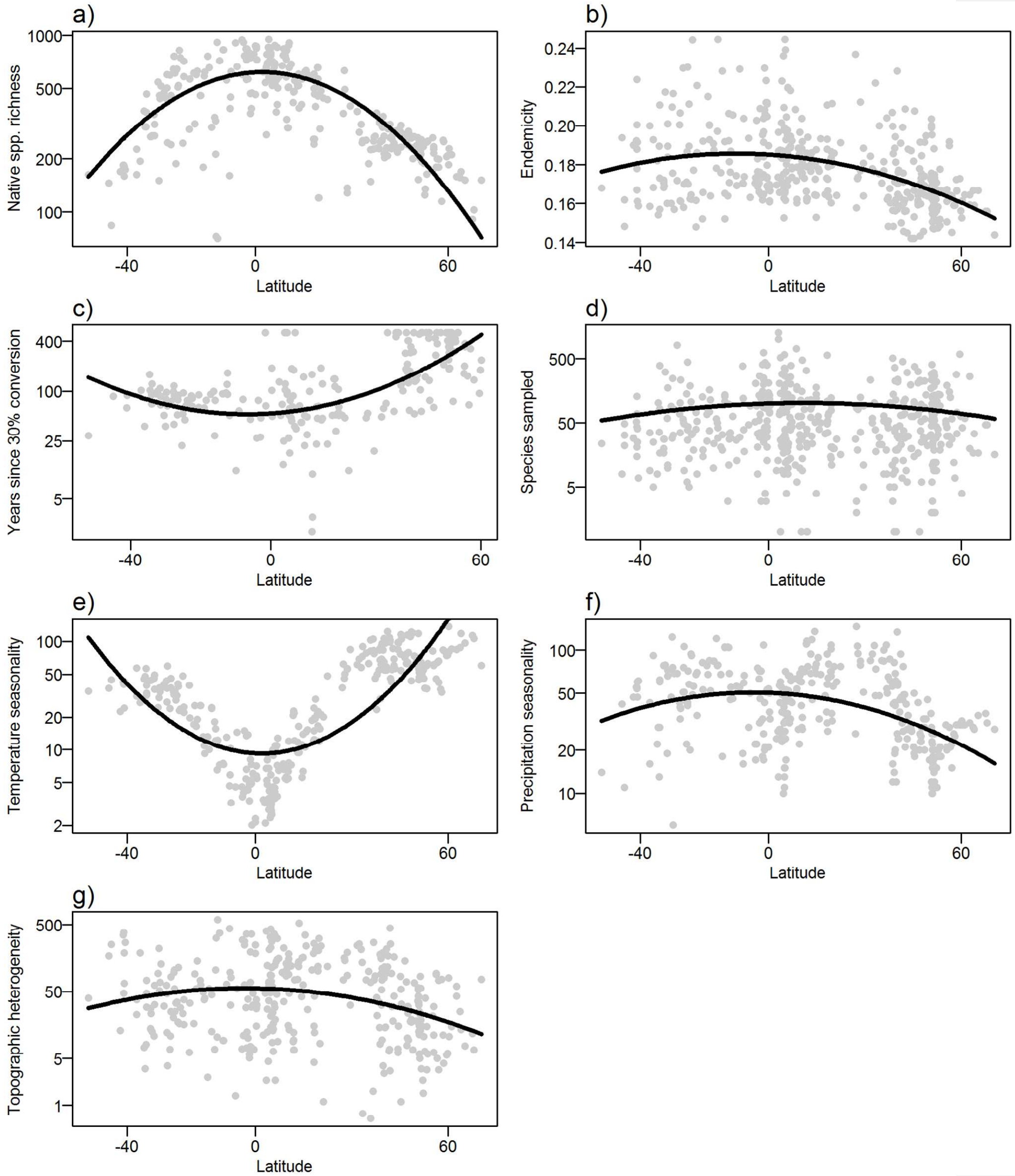


Figure A34. Variation with latitude of several variables that might explain differences between the tropical and temperate realms in observed patterns of compositional turnover: a) native (vertebrate) species richness; b) average endemicity of species in the study, as the reciprocal of the average (log$_{10}$) range size of species; c) the number of years since the landscape was 30% converted to human uses, based on the HYDE model (Klein Goldewijk et al. 2011); d) the number of species sampled by the study; e) the seasonality of temperature in the study region; f) the seasonality of precipitation in the study region; and g) the topographic heterogeneity of the study region, as measured using the topographic ruggedness index (Wilson et al. 2007). In all cases a quadratic model relating each variable to latitude better explained the data (lower AIC value) than a linear or null model.

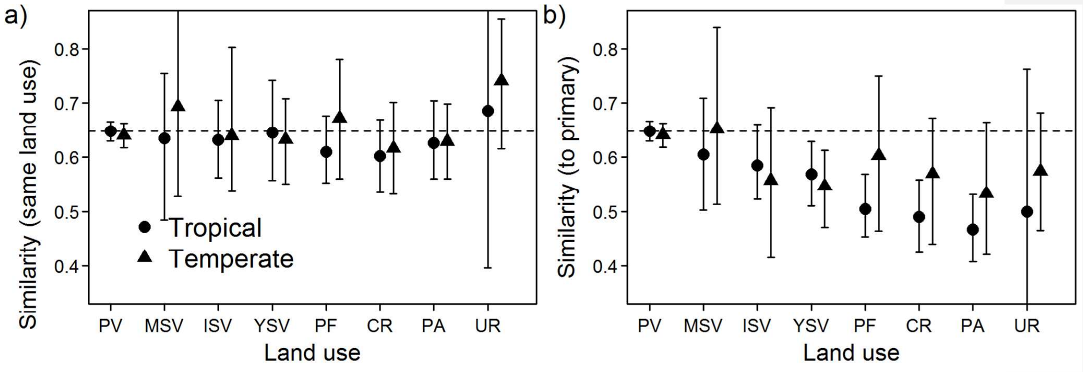


Figure A4~~5~~. Average abundance-based Sørensen similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

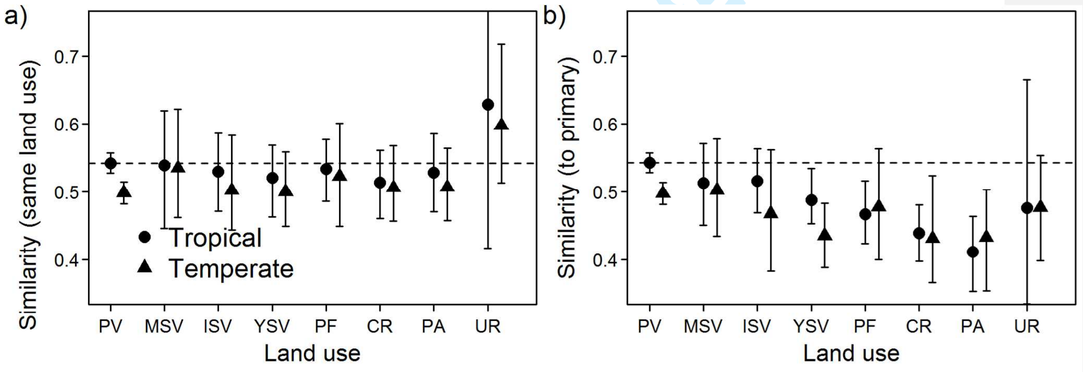


Figure A5~~6~~. Average endemicity-weighted similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

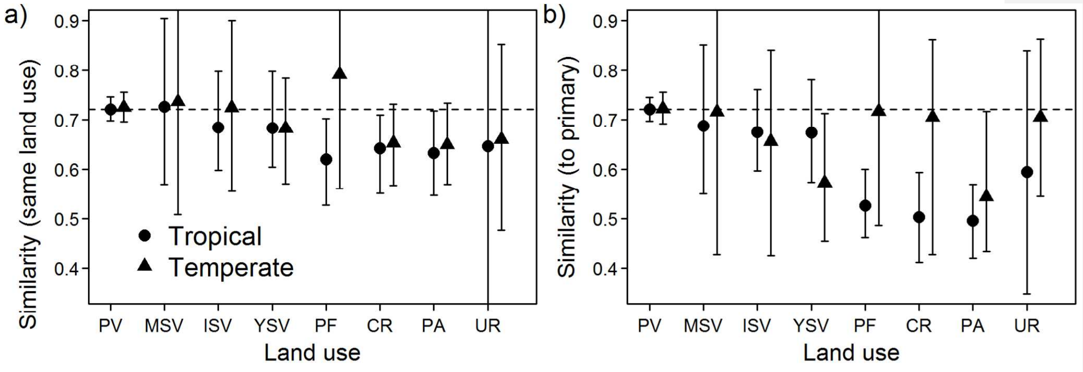


Figure A6~~7~~. Average sampling-corrected similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

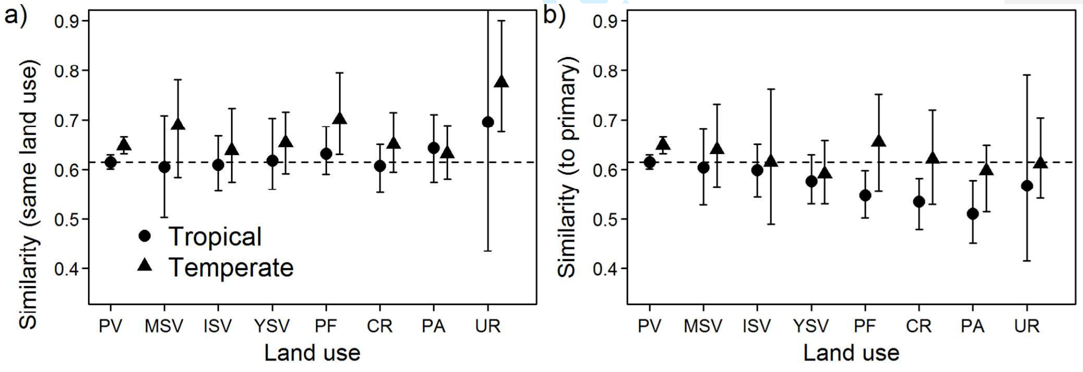


Figure A7~~8~~. Average Simpson (Simpson 1943) similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

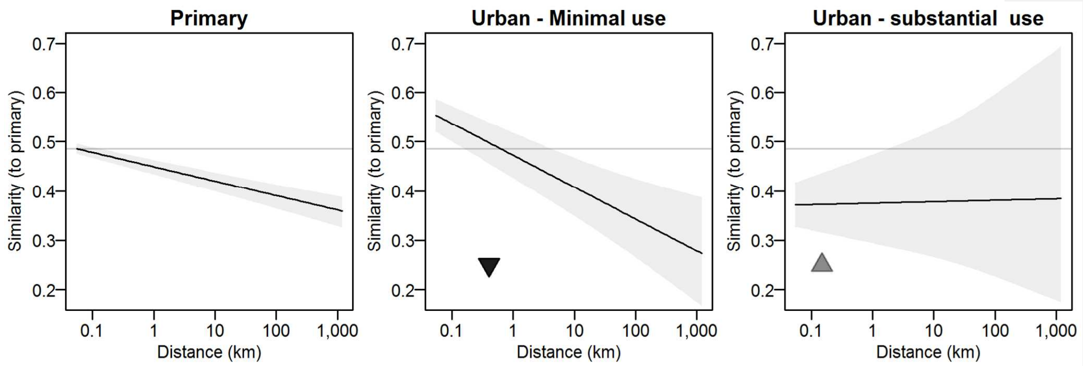
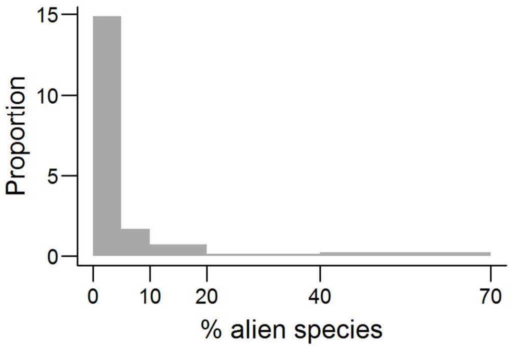


Figure A8~~9~~. Relationships between compositional similarity and geographic distance between sites, for comparisons of pairs of sites one in primary vegetation and one in either primary vegetation or urban land use, with urban land use divided into minimal (middle panel) or substantial (right-hand panel) human intensity of use. Shading indicates ±95% confidence intervals. Horizontal lines show the average compositional similarity of pairs of sites 50 m apart and both in primary vegetation. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Filled triangles indicate (by opacity) the proportion of randomized datasets where the relationship had a significantly shallower (upward-facing triangles) or steeper (downward-facing triangles) slope compared with the slope for the comparison of two sites in primary vegetation. Note that sites were not divided by tropical or temperate realm for this analysis.



~~**Figure A10.** For 70 studies where all species were indicated as being either alien or native, the distribution across studies of the proportion of species that were alien.~~

Formatted: Font: (Default) Times New Roman

Appendix 2~~3~~. Proof that correcting Sørensen Index by the maximum possible value given the alpha diversity ratio yields the Simpson similarity index

As one of our metrics of compositional similarity we correct the Sørensen Index, dividing it by the maximum possible value given the ratio of species richness recorded in each of the two sites being compared:

$$S_{corr} = \frac{S_i}{S_{max}},$$

where S_i is the Sørensen Index:

$$S_i = \frac{2a}{2a+b+c},$$

where *a* is the number of species shared between both sites, and *b* and *c* are the numbers of species recorded at one or other site respectively.

The maximum possible value of the Sørensen Index (S_{max}) is:

$$S_{max} = \frac{2r}{2r+(1-r)},$$

where *r* is the ratio of species richness recorded at each site (expressed as less rich/more rich). We show in the succeeding proof that S_{corr} is equivalent to the Simpson similarity index (Simpson 1943).

$r = \frac{a+b}{a+c}$, where b < c.

Substituting this for *r* gives:

$$S_{max} = \frac{\frac{2a+2b}{a+c}}{\frac{2a+2b}{a+c}+\frac{a+c}{a+c}-\frac{a+b}{a+c}} = \frac{\frac{2a+2b}{a+c}}{\frac{2a+b+c}{a+c}} = \frac{2a+2b}{2a+b+c},$$

Therefore:

$$S_{corr} = \frac{\frac{2a}{2a+b+c}}{\frac{2a+2b}{2a+b+c}} = \frac{a}{a+b} = 1 - \frac{b}{a+b},$$

which is the Simpson pairwise similarity index (Simpson 1943, Baselga 2010).

Appendix 3~~1~~. Randomization and data-selection methods for generating independent pairwise comparisons

For an example study (AD1_2002__Vazquez 1), the site-by-site matrix of Sørensen index values is as follows:

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1	NA	0.409938	0.348387	0.369427	0.429448	0.337662	0.31579	0.348387
2	0.409938	NA	0.5	0.548387	0.5	0.440678	0.45614	0.6
3	0.348387	0.5	NA	0.535714	0.516129	0.490566	0.509804	0.481482
4	0.369427	0.548387	0.535714	NA	0.46875	0.4	0.45283	0.571429
5	0.429448	0.5	0.516129	0.46875	NA	0.42623	0.440678	0.548387
6	0.337662	0.440678	0.490566	0.4	0.42623	NA	0.28	0.415094
7	0.31579	0.45614	0.509804	0.45283	0.440678	0.28	NA	0.392157
8	0.348387	0.6	0.481482	0.571429	0.548387	0.415094	0.392157	NA

To generate independent pairwise comparisons, this matrix was first randomized:

	2	6	8	7	1	4	5	3
2	NA	0.440678	0.6	0.45614	0.409938	0.548387	0.5	0.5
6	0.440678	NA	0.415094	0.28	0.337662	0.4	0.42623	0.490566
8	0.6	0.415094	NA	0.392157	0.348387	0.571429	0.548387	0.481482
7	0.45614	0.28	0.392157	NA	0.31579	0.45283	0.440678	0.509804
1	0.409938	0.337662	0.348387	0.31579	NA	0.369427	0.429448	0.348387
4	0.548387	0.4	0.571429	0.45283	0.369427	NA	0.46875	0.535714
5	0.5	0.42623	0.548387	0.440678	0.429448	0.46875	NA	0.516129
3	0.5	0.490566	0.481482	0.509804	0.348387	0.535714	0.516129	NA

Then data from the first off-diagonal were selected as independent contrasts:

	2	6	8	7	1	4	5	3
2	NA	0.440678	0.6	0.45614	0.409938	0.548387	0.5	0.5
6	0.440678	NA	0.415094	0.28	0.337662	0.4	0.42623	0.490566
8	0.6	0.415094	NA	0.392157	0.348387	0.571429	0.548387	0.481482
7	0.45614	0.28	0.392157	NA	0.31579	0.45283	0.440678	0.509804
1	0.409938	0.337662	0.348387	0.31579	NA	0.369427	0.429448	0.348387
4	0.548387	0.4	0.571429	0.45283	0.369427	NA	0.46875	0.535714
5	0.5	0.42623	0.548387	0.440678	0.429448	0.46875	NA	0.516129
3	0.5	0.490566	0.481482	0.509804	0.348387	0.535714	0.516129	NA

This process was repeated to generate 100 randomized datasets of independent comparisons.

Supplementary References

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. - Glob. Ecol. Biogeogr. 19: 134–143.
Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. - Springer.
Hijmans, R. J. 2015. geosphere: Spherical Trigonometry. R package version 1.4-3.
Hudson, L. N. et al. 2014. The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. - Ecol. Evol. 4: 4701–4735.
Klein Goldewijk, K. et al. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. - Glob. Ecol. Biogeogr. 20: 73–86.
R Core Team 2014. R: A Language and Environment for Statistical Computing. - R Foundation for Statistical Computing.

Simpson, G. G. 1943. Mammals and the nature of continents. - Am. J. Sci. 241: 1–31.

Wilson, M. F. J. et al. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. - Marine Geodesy 30: 3-35.

Supplementary Material

Appendix 1. Supporting tables and figures

Table A1. Classification scheme used to derive Realm (tropical vs. temperate) depending on the biome in which sites within a study were located.

Biome	Realm
Tropical and Subtropical Moist Broadleaf Forests	Tropical
Tropical and Subtropical Dry Broadleaf Forests	Tropical
Tropical and Subtropical Coniferous Forests	Tropical
Temperate Broadleaf and Mixed Forests	Temperate
Temperate Conifer Forests	Temperate
Boreal Forests/Taiga	Temperate
Tropical and Subtropical Grasslands, Savannas and Shrublands	Tropical
Temperate Grasslands, Savannas and Shrublands	Temperate
Flooded Grasslands and Savannas	NA
Montane Grasslands and Shrublands	Depends on latitude
Tundra	Temperate
Mediterranean Forests, Woodlands and Scrub	Temperate

Table A2. Candidate models considered. Models prefixed ‘D’ were fitted first and used to select the most explanatory combination of geographic distance (‘LogDist’), environmental distance (‘LogEnvDist’), tropical vs. temperate realm (‘Realm’), and their pairwise interactions (indicated by a ‘:’). The best-fitting (from the model with the lowest average AIC value) combination of these terms (‘Distances’) was then used as the most simple of a set of models (prefixed ‘LU’) comparing combinations of land use (‘LandUse’), realm and their interaction.

Model ID	Formula
D0	1
D1	LogDist
D2	LogEnvDist
D3	LogDist+LogEnvDist
D4	Realm
D5	LogDist+Realm+LogDist:Realm
D6	LogEnvDist +Realm+LogEnvDist:Realm
D7	LogDist+LogEnvDist+Realm+LogDist:Realm
D8	LogDist+LogEnvDist+Realm+LogEnvDist:Realm

D9	LogDist+LogEnvDist+Realm+LogDist:Realm+LogEnvDist:Realm
LU0	Distances
LU1	Distances+LandUse
LU2	Distances+LandUse+LandUse:Realm
LU3	Distances+LandUse+LandUse:LogDist
LU4	Distances+LandUse+LandUse:LogEnvDist
LU5	Distances+LandUse+LandUse:Realm+LandUse:LogDist
LU6	Distances+LandUse+LandUse:Realm+LandUse:LogEnvDist
LU7	Distances+LandUse+LandUse:LogDist+LandUse:LogEnvDist
LU8	Distances+LandUse+LandUse:Realm+LandUse:LogDist+LandUse:LogEnvDist

Table A3. AIC weights for all terms in the models of all measures of compositional similarity

Term	Similarity measure				
	Sørensen	Abundance-based Sørensen	Endemicity-weighted	Chao sampling-corrected	Simpson
Land use	≈ 1	≈ 1	≈ 1	≈ 1	≈ 1
Land use:Realm	0.93	0.73	0.74	0.61	0.81
Geographical distance:Land use	0.88	0.89	0.86	0.46	0.35
Environmental distance: Land use	0.56	0.40	0.62	0.01	0.24

AIC weights were calculated for each model, and then summed across all models containing a term, following (Burnham and Anderson 2002).

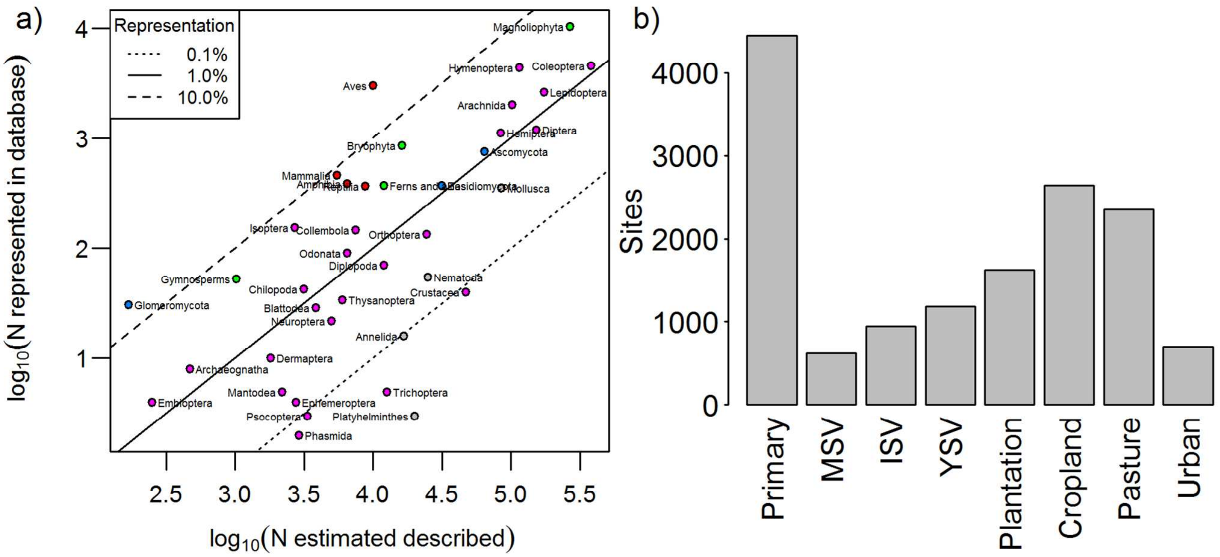


Figure A1. a) The distribution among major taxonomic groups of the number of records in our dataset, in relation to the number of species in those groups estimated to have been described by science. Colours indicate higher-level taxonomic groupings (magenta = invertebrates; red = vertebrates; green = plants; blue = fungi; grey = other). Lines indicate different percentages of described species represented in the dataset. b) The distribution of sampled sites among the land uses considered in this study. See (Hudson et al. 2014) for more details.

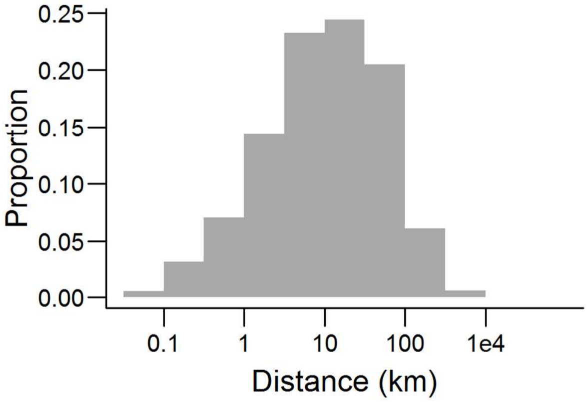


Figure A2. Distribution of pairwise geographic distances among sites. Distances were calculated using the 'distm' function in the 'geosphere' package Version 1.3-8 (Hijmans 2014) in R Version 3.0.2 (R Core Team 2014).

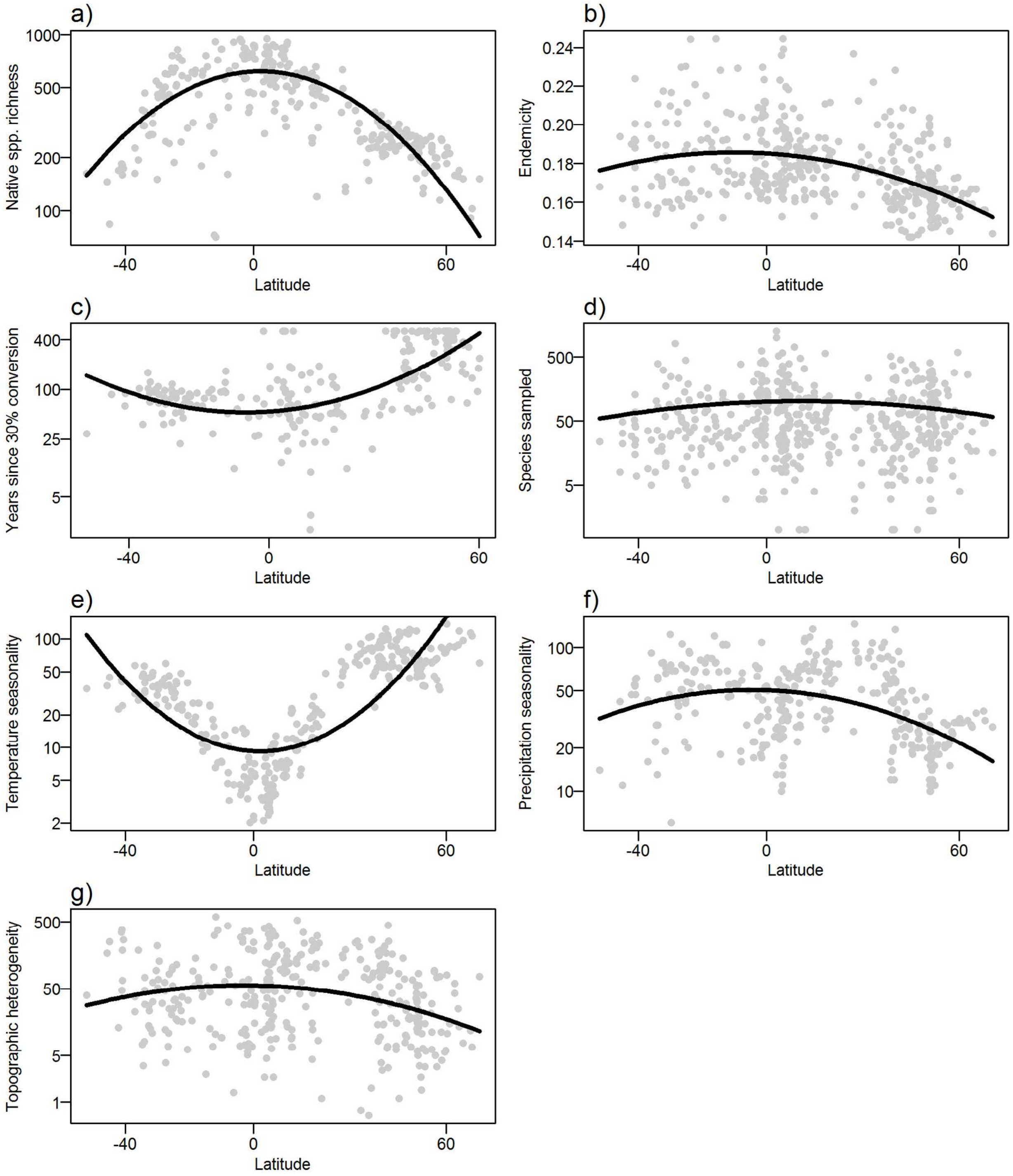


Figure A3. Variation with latitude of several variables that might explain differences between the tropical and temperate realms in observed patterns of compositional turnover: a) native (vertebrate) species richness; b) average endemicity of species in the study, as the reciprocal of the average ($\log_{10}$) range size of species; c) the number of years since the landscape was 30% converted to human uses, based on the HYDE model (Klein Goldewijk et al. 2011); d) the number of species sampled by the study; e) the seasonality of temperature in the study region; f) the seasonality of precipitation in the study region; and g) the topographic heterogeneity of the study region, as measured using the topographic ruggedness index (Wilson et al. 2007). In all cases a quadratic model relating each variable to latitude better explained the data (lower AIC value) than a linear or null model.

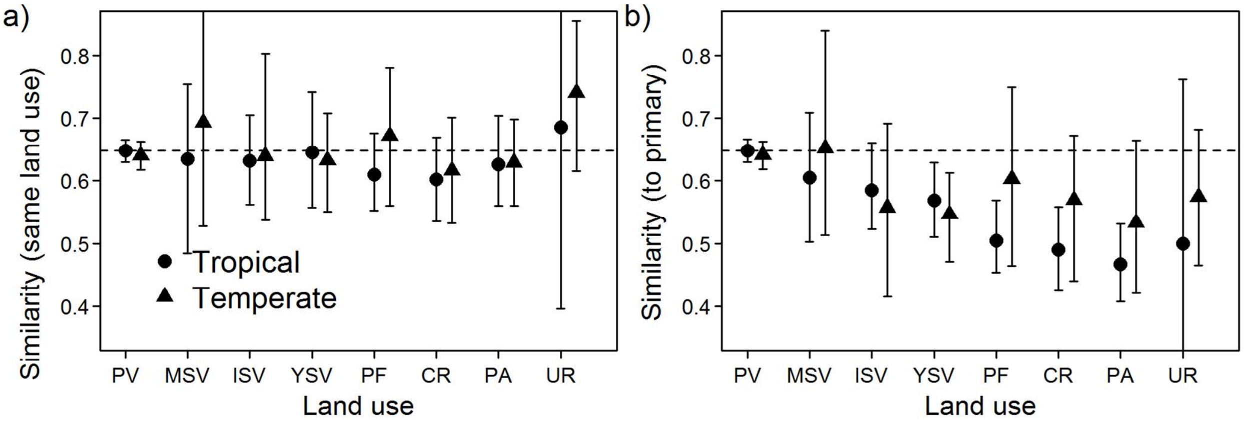


Figure A4. Average abundance-based Sørensen similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

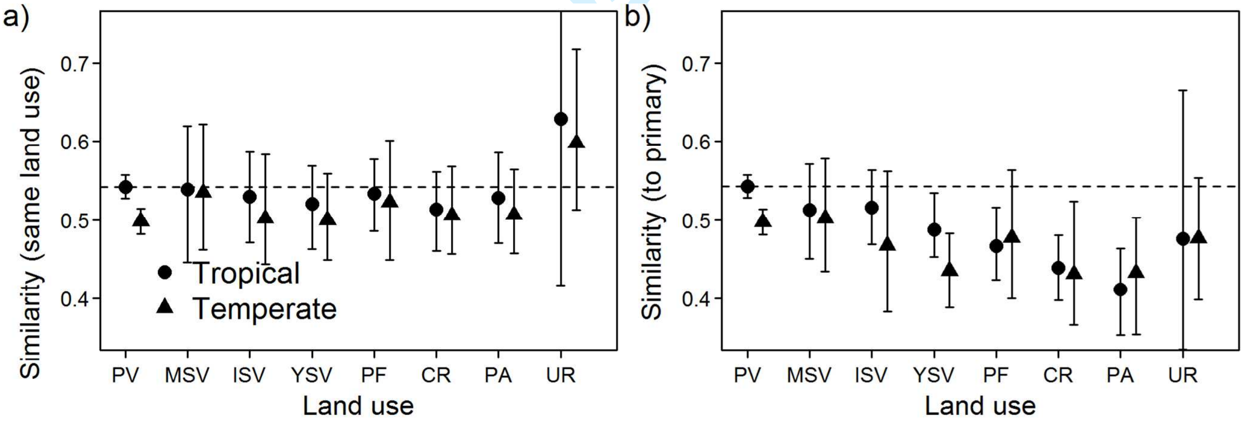


Figure A5. Average endemicity-weighted similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

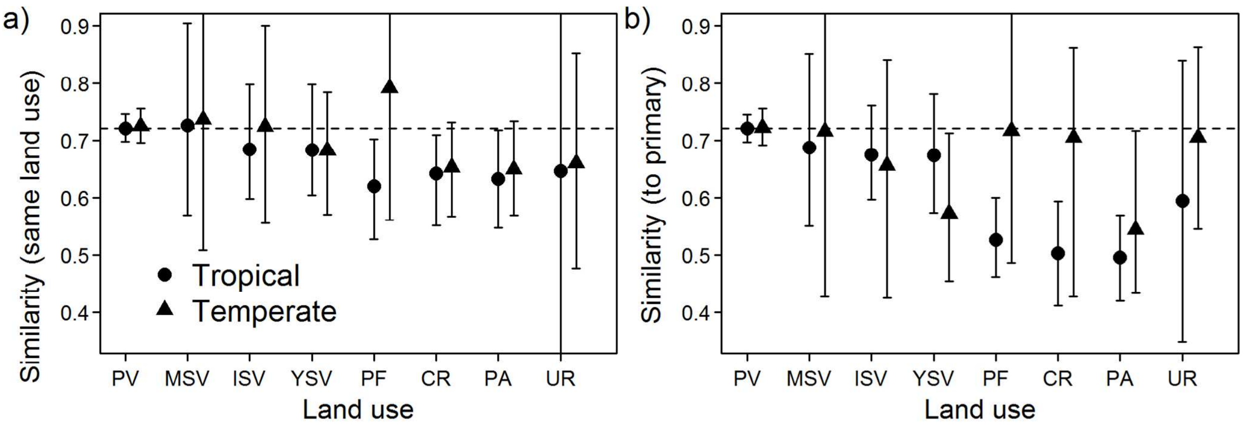


Figure A6. Average sampling-corrected similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

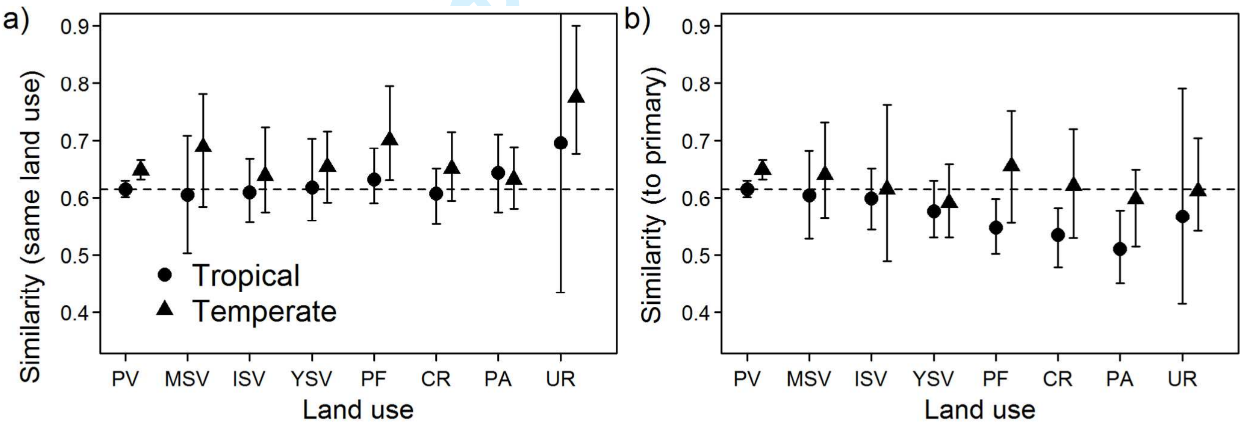


Figure A7. Average Simpson (Simpson 1943) similarity of a) pairs of sites in the same land use and b) pairs of sites, one in each land use compared with a site in primary vegetation, for tropical (circles) and temperate (triangles) studies. Error bars show ±95% confidence intervals. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Model-estimated compositional similarity here was for sites at the median distance apart. PV = primary vegetation; MSV = mature secondary vegetation; ISV = intermediate secondary vegetation; YSV = young secondary vegetation; PF = plantation forest; CR = cropland; PA = pasture; UR = urban.

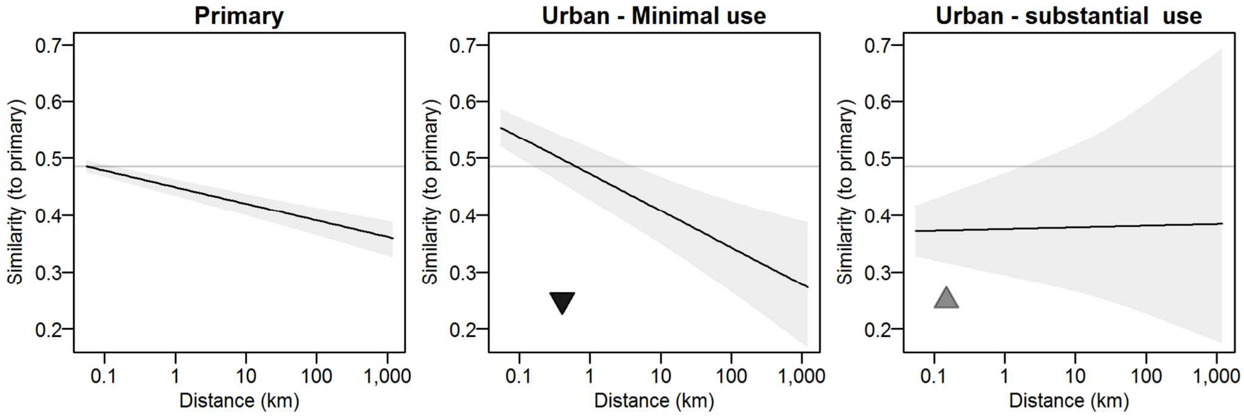


Figure A8. Relationships between compositional similarity and geographic distance between sites, for comparisons of pairs of sites one in primary vegetation and one in either primary vegetation or urban land use, with urban land use divided into minimal (middle panel) or substantial (right-hand panel) human intensity of use. Shading indicates ±95% confidence intervals. Horizontal lines show the average compositional similarity of pairs of sites 50 m apart and both in primary vegetation. Model fit and uncertainty are AIC-weighted averages and ranges (respectively) across models fitting all possible combinations of explanatory variables. Filled triangles indicate (by opacity) the proportion of randomized datasets where the relationship had a significantly shallower (upward-facing triangles) or steeper (downward-facing triangles) slope compared with the slope for the comparison of two sites in primary vegetation. Note that sites were not divided by tropical or temperate realm for this analysis.

Appendix 2. Proof that correcting Sørensen Index by the maximum possible value given the alpha diversity ratio yields the Simpson similarity index

As one of our metrics of compositional similarity we correct the Sørensen Index, dividing it by the maximum possible value given the ratio of species richness recorded in each of the two sites being compared:

$$S_{corr} = \frac{S_i}{S_{max}},$$

where S_i is the Sørensen Index:

$$S_i = \frac{2a}{2a+b+c},$$

where *a* is the number of species shared between both sites, and *b* and *c* are the numbers of species recorded at one or other site respectively.

The maximum possible value of the Sørensen Index (S_{max}) is:

$$S_{max} = \frac{2r}{2r+(1-r)},$$

where *r* is the ratio of species richness recorded at each site (expressed as less rich/more rich). We show in the succeeding proof that S_{corr} is equivalent to the Simpson similarity index (Simpson 1943).

$r = \frac{a+b}{a+c}$, where b < c.

Substituting this for *r* gives:

$$S_{max} = \frac{\frac{2a+2b}{a+c}}{\frac{2a+2b}{a+c}+\frac{a+c}{a+c}-\frac{a+b}{a+c}} = \frac{\frac{2a+2b}{a+c}}{\frac{2a+b+c}{a+c}} = \frac{2a+2b}{2a+b+c},$$

Therefore:

$$S_{corr} = \frac{\frac{2a}{2a+b+c}}{\frac{2a+2b}{2a+b+c}} = \frac{a}{a+b} = 1 - \frac{b}{a+b},$$

which is the Simpson pairwise similarity index (Simpson 1943, Baselga 2010).

Appendix 3. Randomization and data-selection methods for generating independent pairwise comparisons

For an example study (AD1_2002__Vazquez 1), the site-by-site matrix of Sørensen index values is as follows:

	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
1	NA	0.409938	0.348387	0.369427	0.429448	0.337662	0.31579	0.348387
2	0.409938	NA	0.5	0.548387	0.5	0.440678	0.45614	0.6
3	0.348387	0.5	NA	0.535714	0.516129	0.490566	0.509804	0.481482
4	0.369427	0.548387	0.535714	NA	0.46875	0.4	0.45283	0.571429
5	0.429448	0.5	0.516129	0.46875	NA	0.42623	0.440678	0.548387
6	0.337662	0.440678	0.490566	0.4	0.42623	NA	0.28	0.415094
7	0.31579	0.45614	0.509804	0.45283	0.440678	0.28	NA	0.392157
8	0.348387	0.6	0.481482	0.571429	0.548387	0.415094	0.392157	NA

To generate independent pairwise comparisons, this matrix was first randomized:

	2	**6**	**8**	**7**	**1**	**4**	**5**	**3**
2	NA	0.440678	0.6	0.45614	0.409938	0.548387	0.5	0.5
6	0.440678	NA	0.415094	0.28	0.337662	0.4	0.42623	0.490566
8	0.6	0.415094	NA	0.392157	0.348387	0.571429	0.548387	0.481482
7	0.45614	0.28	0.392157	NA	0.31579	0.45283	0.440678	0.509804
1	0.409938	0.337662	0.348387	0.31579	NA	0.369427	0.429448	0.348387
4	0.548387	0.4	0.571429	0.45283	0.369427	NA	0.46875	0.535714
5	0.5	0.42623	0.548387	0.440678	0.429448	0.46875	NA	0.516129
3	0.5	0.490566	0.481482	0.509804	0.348387	0.535714	0.516129	NA

Then data from the first off-diagonal were selected as independent contrasts:

	2	**6**	**8**	**7**	**1**	**4**	**5**	**3**
2	NA	0.440678	0.6	0.45614	0.409938	0.548387	0.5	0.5
6	0.440678	NA	0.415094	0.28	0.337662	0.4	0.42623	0.490566
8	0.6	0.415094	NA	0.392157	0.348387	0.571429	0.548387	0.481482
7	0.45614	0.28	0.392157	NA	0.31579	0.45283	0.440678	0.509804
1	0.409938	0.337662	0.348387	0.31579	NA	0.369427	0.429448	0.348387
4	0.548387	0.4	0.571429	0.45283	0.369427	NA	0.46875	0.535714
5	0.5	0.42623	0.548387	0.440678	0.429448	0.46875	NA	0.516129
3	0.5	0.490566	0.481482	0.509804	0.348387	0.535714	0.516129	NA

This process was repeated to generate 100 randomized datasets of independent comparisons.

Supplementary References

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. - Glob. Ecol. Biogeogr. 19: 134–143.

Burnham, K. P. and Anderson, D. R. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. - Springer.

Hijmans, R. J. 2015. geosphere: Spherical Trigonometry. R package version 1.4-3.

Hudson, L. N. et al. 2014. The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. - Ecol. Evol. 4: 4701–4735.

Klein Goldewijk, K. et al. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. - Glob. Ecol. Biogeogr. 20: 73–86.

R Core Team 2014. R: A Language and Environment for Statistical Computing. - R Foundation for Statistical Computing.

Simpson, G. G. 1943. Mammals and the nature of continents. - Am. J. Sci. 241: 1–31.

Wilson, M. F. J. et al. 2007. Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. - Marine Geodesy 30: 3-35.