

## LETTER

## How pervasive is biotic homogenization in human-modified tropical forest landscapes?

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**Abstract**

Land-cover change and ecosystem degradation may lead to biotic homogenization, yet our understanding of this phenomenon over large spatial scales and different biotic groups remains weak. We used a multi-taxa dataset from 335 sites and 36 heterogeneous landscapes in the Brazilian Amazon to examine the potential for landscape-scale processes to modulate the cumulative effects of local disturbances. Biotic homogenization was high in production areas but much less in disturbed and regenerating forests, where high levels of among-site and among-landscape  $\beta$ -diversity appeared to attenuate species loss at larger scales. We found consistently high levels of  $\beta$ -diversity among landscapes for all land cover classes, providing support for landscape-scale divergence in species composition. Our findings support concerns that  $\beta$ -diversity has been underestimated as a driver of biodiversity change and underscore the importance of maintaining a distributed network of reserves, including remaining areas of undisturbed primary forest, but also disturbed and regenerating forests, to conserve regional biota.

**Keywords**

Amazon forest, diversity partitioning, land-cover change, landscape divergence, multi-taxa, nestedness, turnover.

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**INTRODUCTION**

Human activities have profoundly modified most ecosystems on Earth (Steffen *et al.* 2015), causing widespread loss of biodiversity (Vellend *et al.* 2007; Arroyo-Rodriguez *et al.* 2013; Newbold *et al.* 2015), changes in community structure (Dornelas *et al.* 2014), and the loss of ecosystem functions and services (Mitchell *et al.* 2015). In many places, these changes lead to taxonomic and functional simplification and the convergence of biotas within regions (McKinney & Lockwood 1999; Olden & Rooney 2006), a phenomenon known as biotic homogenization. Biotic mixing and homogenization have been reported for both aquatic and terrestrial taxa and in most of the world's ecosystems (Baiser *et al.* 2012), and represent major signals of the start of the Anthropocene, the current human-dominated geological epoch (Lewis & Maslin 2015).

Biotic homogenization is manifested as species loss, species introductions and range shifts, and changes in species abundance distributions. Such changes are often driven or exacerbated by human activities that drive land-cover change, habitat loss, habitat fragmentation, and degradation (Karp *et al.* 2012; Püttker *et al.* 2015; Thomson *et al.* 2015). Decades of research on the ecological consequences of these disturbances provide substantial evidence that land-use intensifica-

tion drives reductions in both local ( $\alpha$ ) diversity (Gibson *et al.* 2011; Newbold *et al.* 2015) and  $\beta$ -diversity (i.e. differences in species assemblage composition among sites, Whittaker 1972; Karp *et al.* 2012). As a result, the most disturbed sites are characterized by an impoverished subset of species that typically have relatively high dispersal abilities and generalist habits (Vellend *et al.* 2007; Karp *et al.* 2012). However, variability in disturbance regimes can drive divergence in the composition of species assemblages and hence an increase in  $\beta$ -diversity, such as through differing successional pathways among forest fragments (e.g. Arroyo-Rodriguez *et al.* 2013).

Work on biotic homogenization has been almost exclusively conducted at a single spatial scale on a single taxon in relatively few types of land-use. This means that the processes of biotic homogenization and divergence in assemblage composition for entire landscapes and at multiple spatial-scales are little explored (Tabarelli *et al.* 2012; Barton *et al.* 2013). There is a growing body of theory (Tscharntke *et al.* 2012) and empirical information (Pardini *et al.* 2010; Püttker *et al.* 2015) suggesting that landscape- and regional-scale processes play a critical role in determining species distributions and the persistence of biodiversity in human-modified systems. Tscharntke *et al.* (2012) predicted that local biodiversity responses might be influenced by landscape-scale differences in: (1) the spatial heterogeneity in

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types and intensities of disturbance events and (2) the interaction between disturbances and the natural environmental heterogeneity that predated human mediated modifications. Both (a) and (b) contribute to the potential for landscape-scale divergence in species composition (e.g. Laurance *et al.* 2007). Divergence for instance, is driven by the combined effects of spatially heterogeneous environmental conditions, local pressures, and dispersal limitation (Myers *et al.* 2013).

To test the extent to which landscape-moderated patterns of  $\beta$ -diversity determine landscape-wide biodiversity and modulate the effects of local-scale disturbances, we need to decompose patterns of species diversity (for multiple taxa) at several spatial scales and over broad gradients of land-use intensity and disturbance. We need to understand the extent to which variation in  $\beta$ -diversity at different spatial scales and in response to different levels of land-use intensity and disturbance is driven by species replacement (turnover) compared to variation arising from species richness (resulting in nestedness), a distinction missing from the vast majority of studies to date (Baselga 2010; Baselga & Leprieur 2015). If  $\beta$ -diversity is driven by nestedness rather than by turnover, then generalist and highly dispersive species consistently should be favoured in areas of more intense land use, resulting in biotic homogenization. This understanding is urgently needed to support practical conservation action in the humid tropics, which house the vast majority of the world's terrestrial biodiversity (e.g. Slik *et al.* 2015) but that continue to be subjected to high rates of land-use change (Hansen *et al.* 2013; Kim *et al.* 2015) and forest degradation (Asner *et al.* 2009).

Here, we undertook the first assessment of how biotic homogenization plays out at multiple scales and for multiple taxa based on data for five taxa (birds, dung beetles, plants, orchid bees, and ants) sampled in 335 sites in 36 landscapes in two regions of the Brazilian Amazon. These regions include most of the variation in land-cover classes that characterize human-modified tropical forest landscapes, including arable crops, cattle pastures, secondary forests regenerating on cleared land, and a gradient of primary forests experiencing differing degrees of anthropogenic disturbance.

We use this extensive data set to explore three hypotheses. (1)  $\beta$ -diversity, both among-sites and among-landscapes, should decline along a gradient of forest disturbance and land-use intensification (i.e. more intense human activities lead to greater biotic homogenization; Vellend *et al.* 2007; Karp *et al.* 2012). The loss of biodiversity should be attenuated at landscape scales due to the compensating effect of divergence in species composition arising from spatial heterogeneity in disturbances or from differences in initial environmental conditions (Laurance *et al.* 2007; Tschardt *et al.* 2012). (2) The importance of nestedness in determining changes in  $\beta$ -diversity, and hence the relative importance of local extinctions compared with species replacement, should increase along a disturbance gradient from undisturbed forest to disturbed and regenerating forest to production areas, and independently of scale (Baiser *et al.* 2012). And, (3) species richness at site, landscape and regional scales should decline consistently along a gradient of land-use intensification (from undisturbed to disturbed and regeneration forest, to non-forest areas; Dornelas *et al.* 2014; Newbold *et al.* 2015). However, we expected

that high levels of  $\beta$ -diversity in disturbed areas would moderate this decline in richness at larger spatial scales (Tschardt *et al.* 2012). Last, most work on the effects of land-use intensification on biodiversity considers one, or at most two, distinct taxa. This limits the extent to which deductions can be extended to biodiversity generally. Our concurrent analysis of five very different taxa provides a powerful opportunity to assess the extent to which our observations are likely to be general phenomena.

## METHODS

### Study sites

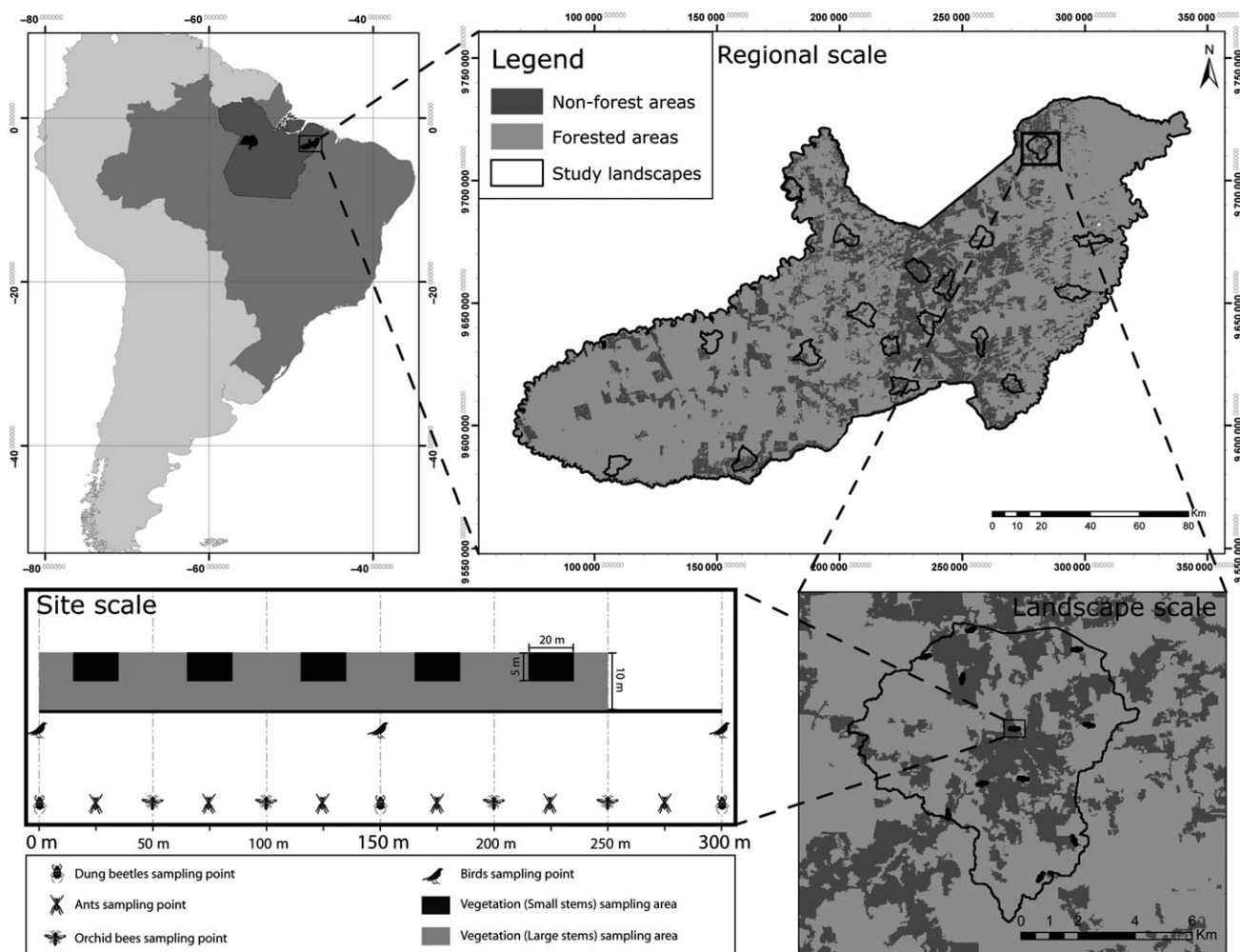
We conducted our study in two regions of Pará state, in the Brazilian Amazon: the municipality of Paragominas (hereafter PGM) and in the municipalities of Santarém, Belterra and Mojuí dos Campos (hereafter STM; Fig. 1). These two study regions, separated by *c.* 800 km encompass more than three million hectares of lowland forests and differ markedly in their human colonization history (Gardner *et al.* 2013). Although in recent decades both regions have suffered significant deforestation and forest degradation, leading to several degrees of disturbance, they still retain more than half of their native forest cover.

### Sampling design

We divided each region into third or fourth order drainage catchments (*c.* 5,000 ha; hereafter called landscapes) using the SWAT (Soil and Water Assessment Tool) model for ArcGIS 10. Eighteen landscapes were selected, covering a gradient of forest cover (from 6% to 100% forest cover) and the major land-cover classes in each region (Table 1, Gardner *et al.* 2013). Within each landscape, we allocated 8–12 transects (each 300 m long) at a density of 1 transect/400 ha and separated by  $\geq 1.5$  km. Sampling of all taxa was conducted along each transect, which formed the site-scale of our analyses. These sites were allocated in proportion to the area of forest and non-forest in a given landscape (e.g. if forest comprised 40% of the land cover in a landscape, then *c.* 40% of the sites were located randomly, with a minimum inter-site separation of 1500 m, in forest areas). Some 335 sites were sampled for plants, birds, dung beetles, ants and orchid-bees. Details of sampling techniques for each taxonomic are in the Supporting Information. Other details for methods including definitions of land-cover classes and further information on the study regions is in Gardner *et al.* (2013).

## DATA ANALYSES

Species presence-absence data were used for the main analyses, and all diversity metrics were repeated using proxies of abundance for each taxon. Our measures of abundance were the number of recorded individuals for vegetation, beetles and bees, and the number of point-counts (birds) or traps (ants) in which the species was recorded. Apart from vegetation data, these are proxies rather than true measures of abundance because the latter is very difficult to obtain for diverse tropical forest biota in



**Figure 1** Map of the sampling regions and sampling design. We stratified our sampling of all five sampled taxonomic groups within three spatial scales: regional, landscape and site. See the Supporting Information for more information on the taxa-specific sampling protocols.

**Table 1** List of sites sampled within each land-cover class in both regions

Land-cover class	Number of sampled sites		
	Acronym	PGM	STM
Primary forests			
Undisturbed	PFU	13	17
Logged	PFL	44	26
Logged-and-burnt	PFLB	44	24
Secondary forests	SEF	20	39
Pastures	PAS	51	23
Mechanized agriculture	AGR	15	19
Total number of sites		187	148

PGM = Paragominas, STM = Santarém.

multiple sites. Nevertheless, such abundance data provides a useful test of the robustness of our results and the potential for any bias in accounting for rare species (Jost 2007).

### Diversity partitioning

We defined  $\alpha_{\text{site}}$ -diversity as the average number of species per site in each land-cover class, and  $\alpha_{\text{landscape}}$ -diversity as the

total number of species per landscape for each land-cover class.  $\gamma$ -diversity ( $\gamma_{\text{region}}$ ) was the total number of species in each region per land-cover class. We calculated multiplicative  $\beta$ -diversity for each scale. Multiplicative  $\beta$  is a measure of the effective number of distinct assemblages or samples in a region (Jost 2007). Multiplicative partitioning of diversity (Whittaker 1960, 1972) uses the formula  $\gamma_{\text{region}} = \alpha_{\text{site}} \times \beta_{\text{among-sites}} \times \beta_{\text{among-landscapes}}$ , where  $\beta_{\text{among-sites}}$  is the effective number of distinct sites in a landscape and  $\beta_{\text{among-landscapes}}$  is the effective number of distinct landscapes in the entire region. We calculated all values for each land-cover class and taxonomic group separately, and used multiplicative partitioning as a measure of the magnitude of differentiation, independent of  $\alpha$ -diversity (and therefore of species loss), thus indicating the amount by which diversity (e.g. species richness) increased from local to regional scales. We computed diversity values using both species richness (Hill numbers of order 0) and the exponential of Shannon entropy (Hill numbers of order 1). While species richness includes the effect on all species irrespective of their frequency, the exponential of Shannon entropy weights species by their frequencies, reducing the influence of rare species (Chao *et al.* 2014).

Sample sizes differed for different land-cover classes because we undertook proportional (relative to forest and non-forest cover) sampling in each landscape. This could lead to biased results for analyses of  $\beta$ -diversity that may be sensitive to sample size. Therefore, we resampled the data to obtain comparable values of  $\beta$ -diversity (Baselga 2010). To calculate  $\beta_{\text{among-sites}}$  for each land-cover class, we randomly sampled without replacement three sites of the same land-cover class within each landscape 5000 times. We calculated  $\beta_{\text{among-sites}}$  by dividing  $\alpha_{\text{landscape}}$  (the cumulative species richness of the three sites) by  $\alpha_{\text{site}}$  (the average species richness per site). To calculate  $\beta_{\text{among-landscapes}}$  for each land-cover class, we randomly sampled without replacement the data selecting three landscapes with three sites each 5000 times. Therefore,  $\beta_{\text{among-landscapes}}$  was  $\gamma_{\text{region}}$  (total species richness of three landscapes) divided by  $\alpha_{\text{landscape}}$ .

### Decomposition of $\beta$ -diversity

We decomposed  $\beta_{\text{among-sites}}$  and  $\beta_{\text{among-landscapes}}$  diversities into two components: nestedness (species gain/loss) and species replacement (turnover) by calculating the multi-site Sørensen ( $\beta_{\text{SOR}}$ ) and Simpson ( $\beta_{\text{SIM}}$ ) indices (Baselga 2010, 2012).  $\beta_{\text{SOR}}$  measures total  $\beta$ -diversity, is positively related to multiplicative  $\beta$  (Pearson  $r = 0.98$ ) and includes variation in species composition from both replacement and nestedness.  $\beta_{\text{SIM}}$  is independent of variation in species richness so only measures turnover. Therefore, differences between values are representative of the nestedness component of  $\beta$ -diversity:  $\beta_{\text{NES}} = \beta_{\text{SOR}} - \beta_{\text{SIM}}$  (Baselga 2010, 2012). Multi-site  $\beta$ -diversity calculations based on the Sørensen index are sensitive to sample size, so we calculated  $\beta$ -values for all land-cover classes using a resampling procedure. We took 5000 random samples from the total number of sites of each land-cover class (Table 1) in the same way that we did for each scale of  $\beta$ -diversity to have comparable measures of  $\beta_{\text{SOR}}$  and  $\beta_{\text{SIM}}$  diversities. The percentage importance of the nestedness component ( $\beta_{\text{NES}}/\beta_{\text{SOR}}$ ) was used as a response variable for analyses. To assess the robustness of our results for the  $\beta_{\text{SOR}}$  partition, we also calculated Jaccard indices as proposed by Baselga (2012) and Carvalho *et al.* (2013). While a comparative review of these methods is beyond the scope of this article, both approaches yielded qualitatively very similar conclusions (see Legendre 2014 and Baselga & Leprieur 2015).

### Statistical analyses

We used generalized linear mixed models (GLMM, Bolker *et al.* 2009) for all diversity comparisons between land-cover classes. To investigate how  $\alpha_{\text{site}}$  and  $\gamma_{\text{region}}$  diversities differ across land-cover classes, we first standardized species richness per site for each taxon because the different taxa have very disparate levels of species richness. We divided the richness of each taxon in each individual site by the value of the richest site in the entire sample, leading to values between 0 and 1 for each taxon ( $\alpha$ -diversity). We performed the analysis using standardized values for all taxa jointly and for each taxonomic group separately. We used land-cover classes as the predictor variable and set taxonomic group, landscape identity, and region as ran-

dom effects. For  $\gamma$ -diversity, we considered the total number of species (also standardized to range between 0 and 1) in each taxonomic group and land-cover class within each landscape as the response variable, and land-cover classes as the explanatory variable, with taxon and region set as random effects. We performed pairwise contrast analyses to evaluate specific differences between land-cover classes combining the most similar classes and comparing models (Crawley 2012).

To assess how  $\beta$ -diversity was related to land-cover classes at two scales (among-sites and among-landscapes), we used the values of  $\beta$ -diversity for each taxon within each land-cover as a response variable and land-cover class as the predictor variable. Landscape and region were included as random effects for the among-site  $\beta$ -diversity, with region as a random effect for  $\beta$ -diversity among-landscapes. We performed contrast analyses in the same way as for analyses of  $\alpha_{\text{site}}$  and  $\gamma_{\text{region}}$ .

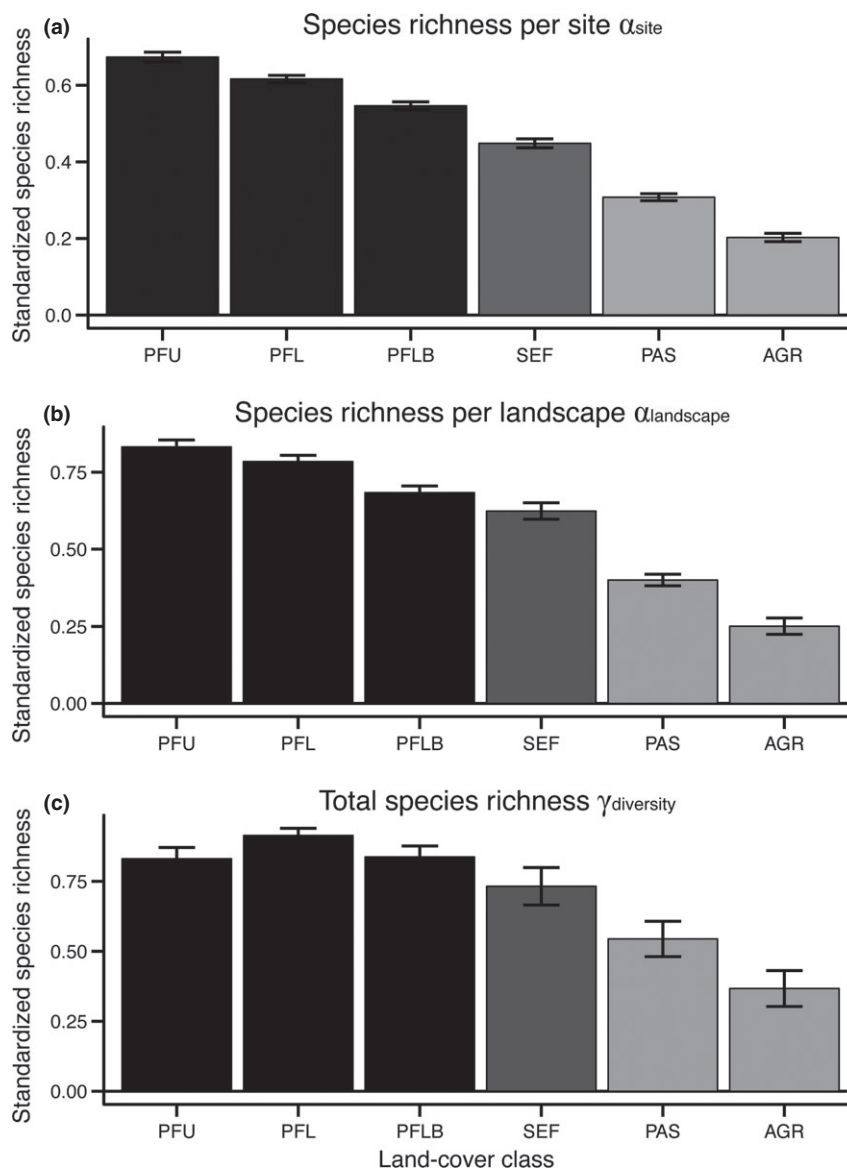
To analyse whether processes of nestedness and replacement differed among land-cover classes and among taxa, we used land-cover class as the predictor variable and used the percentage contribution of nestedness as the response variable for each taxon within each land-cover class. We did this for both among-sites and among-landscapes scales. Random effects were landscape and region for among-site  $\beta$ -diversity and region for among-landscapes  $\beta$ -diversity. We used binomial error distributions, corrected for over-dispersion if necessary by incorporating individual-level random effects in the model, and contrast analysis to discriminate among levels significance (Crawley 2012).

We used R v3.2.0 (R Core Team 2015) for all analyses. We performed residual analyses for all models and checked for the distribution of errors and over-dispersion in the data. We adjusted  $P$ -values following Benjamini & Yekutieli (2001), controlling for the probability of false discovery rate in multiple tests. Diversity partitioning and correlation analyses were conducted using the *vegan* package v2.3-0.  $\beta$ -diversity decomposition was undertaken using the *betapart* package v1.3, and GLMMs using the *lme4* package v1.1-8.

## RESULTS

### Species richness in different land-cover classes at site and landscape scales

Species richness at the site level ( $\alpha_{\text{site}}$ ) declined steadily from undisturbed forests to disturbed primary forests, secondary forests and production areas (cattle pastures and mechanized agriculture) with significant differences between all land-cover classes ( $\chi^2 = 398.92$ , d.f. = 185,  $P < 0.001$ , Fig. 2a). Species richness at the landscape level ( $\alpha_{\text{landscape}}$ ) followed a similar pattern, declining along the same gradient ( $\chi^2 = 202.86$ , d.f. = 8,  $P < 0.001$ , Fig. 2b), with significant differences between all land-cover classes apart from logged and burnt and secondary forests ( $\chi^2 = 1.21$ , d.f. = 8,  $P = 0.30$ , Fig. 2b). Species richness at the regional scale (i.e.  $\gamma_{\text{region}}$ ) differed only when comparing forest areas (of any type) with production areas (of any type) ( $\chi^2 = 42.27$ , d.f. = 5,  $P < 0.001$ , Fig. 2c). We found similar patterns and statistical results when we computed diversity measures taking species abundances or frequencies into account (exponential Shannon entropy)



**Figure 2**  $\alpha$  and  $\gamma$  components of diversity in different land-cover classes. Diversity is expressed as the standardized average species richness within each land-cover class for all taxa, and separately for  $\alpha$ -diversity-site – species richness at the site scale (a);  $\alpha$ -diversity-landscape – species richness at the landscape scale (b); and  $\gamma$ -diversity – pooled species richness at the regional scale (c). Different colours illustrate forest (black and dark grey) and non-forest land-cover classes (light grey). We used  $P < 0.05$  to determine significance levels and error bars are standard errors (for gamma they represent only maximum and minimum values, as  $n = 2$ ). Codes for land-cover classes are as Table 1.

(Fig. S1). These trends were broadly similar for each taxon, which despite individual idiosyncrasies, exhibit a general decline in species richness outside primary forests (Fig. 3).

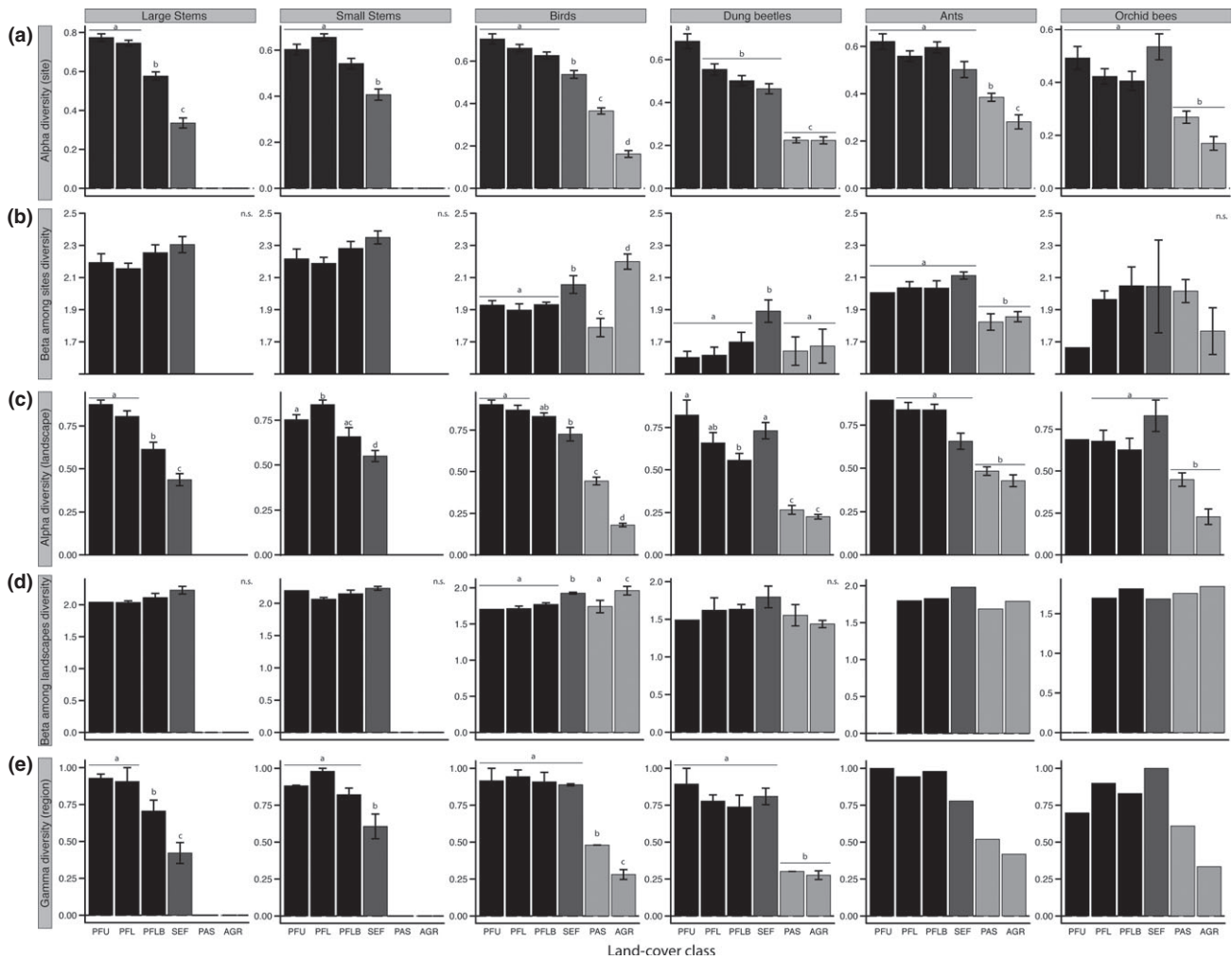
#### $\beta$ -diversity in different land-cover classes

Among-site  $\beta$ -diversity was consistently greater in forest habitats (of all types) than in production areas (of any type) ( $\chi^2_{1,8} = 12.37$ , d.f. = 10,  $P \sim 0.005$ , Fig. 4a). This pattern held when based on measures of abundance (Fig. S2a). Conversely, we found little difference in landscape-scale  $\beta$ -diversity ( $\beta_{\text{among-landscapes}}$ ) among all land-cover classes ( $\chi^2 = 9.24$ , d.f. = 6,  $P \sim 0.09$ , Fig. 4b) based only on presence-absence data. However, when proxies of abundance are accounted for there was a significant drop in  $\beta_{\text{among-landscapes}}$  when moving

from forest to non-forest land ( $\chi^2 = 15.07$ , d.f. = 6,  $P < 0.001$ , Fig. S2b). Patterns were essentially the same for each taxonomic group, although  $\beta_{\text{among-sites}}$  was somewhat greater in arable fields for birds and in secondary forests for dung beetles) (Fig. 3b and c).

#### Relative importance of nestedness and replacement contributing to $\beta$ -diversity

Species replacement accounted for the majority of  $\beta$ -diversity in all land-cover classes but the proportional contribution of nestedness increased in non-forest areas ( $\beta_{\text{SOR}}$ , Fig. 5). The contribution of nestedness to  $\beta_{\text{among-sites}}$  to total  $\beta$ -diversity showed a three-fold increase in production areas compared with forest areas ( $\chi^2 = 70.22$ , d.f. = 10,  $P < 0.001$ , Fig. 5a).



**Figure 3** Components of diversity for all taxa across all land-cover classes based on species occurrence data. Row (a), shows  $\alpha_{\text{site}}$ -diversity (i.e. average number of species per site), rows (b) and (d) show  $\beta$ -diversity among-sites and among-landscapes, row (c) shows  $\alpha_{\text{landscape}}$ -diversity (i.e. average number of species per landscape) and row (e) shows  $\gamma$ -diversity (for each region). Different colours illustrate forest (black and dark grey) and non-forest land-covers (light grey), we used  $P < 0.05$  to determine significance levels and error bars represent standard errors (bars are absent where we could only calculate a single value). Codes for land-cover classes are as Table 1.

Moreover, the contribution of nestedness to  $\beta_{\text{among-sites}}$  in disturbed and secondary forests was also significantly greater than that observed in undisturbed sites ( $\chi^2 = 4.1$ , d.f. = 10,  $P = 0.043$ , Fig. 5a). The overall pattern was broadly similar for  $\beta_{\text{among-landscapes}}$  with  $\beta$ -diversity being dominated by species replacement, but with nestedness playing a more important role in non-forest compared to forest areas ( $\chi^2 = 44.163$ , d.f. = 6,  $P < 0.001$ , Fig. 4b) but with a similar contribution for undisturbed and disturbed forest sites. Results for individual taxa broadly followed these patterns but were particularly marked for dung beetles and orchid bees for which the contribution of nestedness in production areas accounted for up to 60% of total  $\beta$  (Fig. S3).

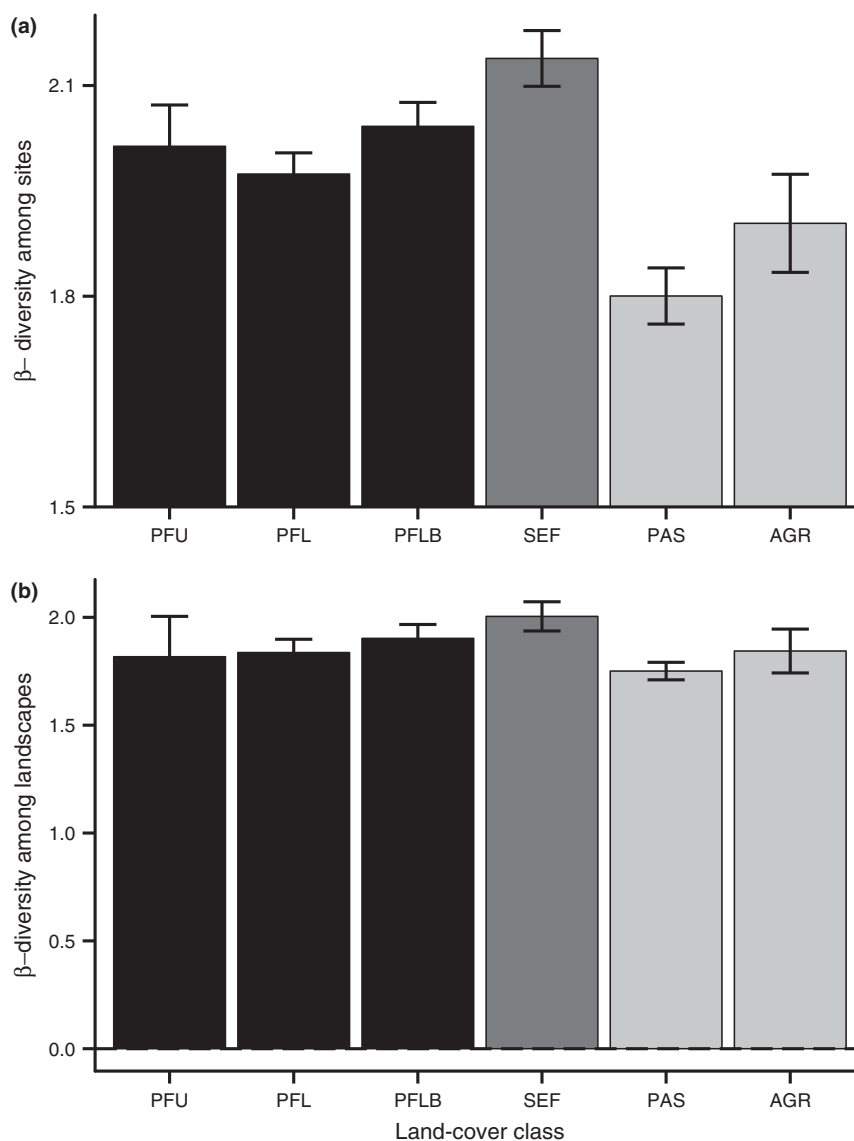
## DISCUSSION

Our assessment of patterns of diversity among multiple taxa and spatial scales in two human-modified regions of the Brazilian Amazon represents a major advance in our understanding of biotic responses to land-cover change and human-

induced forest disturbance. While we found consistent changes in  $\alpha$ -diversity in human-modified tropical landscapes, changes in  $\beta$ -diversity, and the process of biotic homogenization, were dependent on land cover and scale. Results were very similar whether based on species occurrence or on abundance or incidence data. We assess the implications of these findings in the context of our initial hypotheses by examining the new insights gained from our disturbance gradient of land-cover classes, the multiple spatial scales of our biodiversity sampling and the multi-taxonomic analysis. We consider the practical implications of our results for the conservation of forest biota in the human-modified landscapes that increasingly dominate the tropics.

### Land-cover, spatial scale and taxa-dependent patterns of biotic homogenization

$\alpha$ -diversity declined consistently along a gradient of increasing anthropogenic disturbance, which was consistent with the findings of earlier studies (e.g. Gibson *et al.* 2011; Moura



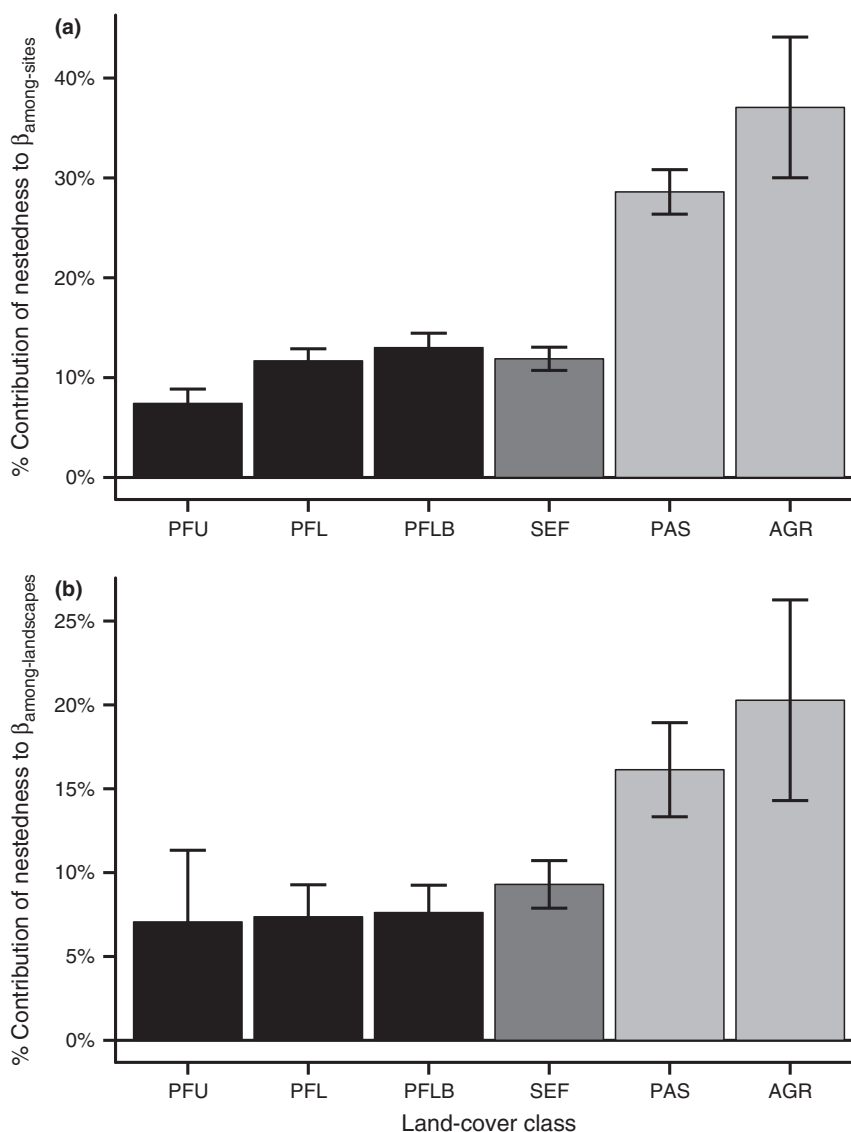
**Figure 4**  $\beta$ -diversity among sites and landscapes based on species occurrence data.  $\beta$ -diversity was calculated as the multiplicative Whittaker's  $\beta$  and sampling effort is standardized by resampling all land-cover classes to the same sample size. Data are presented as average  $\beta$ -diversity per taxon and per land-cover class for both among sites within landscapes (a) and among landscapes within regions (b). Different colours illustrate forest (black and dark grey) and non-forest land-covers (light grey), we used  $P < 0.05$  to determine significance and errors bars are standard errors. Codes for land-cover classes are as Table 1.

*et al.* 2013). However, our  $\beta$ -diversity results show how conclusions about biotic homogenization depend on both the intensity of anthropogenic disturbance and the scale of analysis.

We found strong evidence that the conversion of forests to agriculture leads to biotic homogenization by reducing  $\beta$ -diversity (c.f. Karp *et al.* 2012; Püttker *et al.* 2015). Homogenization is likely to be driven by the loss of pre-disturbance biota, followed by the colonization of generalist species with high dispersal capabilities (Bengtsson 2010). Homogenization also arises from increased homogeneity of environmental resources, which favours similar sets of species (Olden *et al.* 2004). Evidence of biotic homogenization is supported by the increasingly important contribution of nestedness to total

$\beta$ -diversity in non-forest areas, which indicates that species-poor sites are characterized by a subset of more generalized and disturbance-tolerant species due to the loss of more ecologically specialized, disturbance-intolerant and forest-dependent species (Baiser *et al.* 2012).

There was less evidence for biotic homogenization within forests, where  $\beta$ -diversity was consistently high within all disturbance classes, irrespective of taxon or the scale of analysis. This high level of community dissimilarity among forest disturbance classes may be due to pre-existing differences in environmental conditions and biota and from variability in disturbance processes and resultant spatial heterogeneity in local extinction filters (Tscharrntke *et al.* 2012). Differences in time-since-disturbance, and the frequency and intensity of



**Figure 5** Percentage contribution of the nestedness component to the total  $\beta$ -diversity observed among sites and among landscapes. Decomposition of  $\beta$ -diversity into nestedness and replacement components was computed following Baselga (2010) ( $\beta_{\text{NES}} = \beta_{\text{SOR}} - \beta_{\text{SIM}}$ ) and standardized by resampling all land-cover classes to the same sample size. Data are presented as the average percentage contribution of the nestedness component per taxon and per land-cover class for both the decomposition of  $\beta$ -diversity among sites in a landscape (a) and the decomposition of  $\beta$ -diversity among landscapes in a region (b). Different colours express forest (black and dark grey) and non-forest land-covers (light grey), we used  $P < 0.05$  to determine significance and errors bars are standard errors. Codes for land-cover classes are as Table 1.

disturbance events, may be important in maintaining  $\beta$ -diversity in all forests. For example, secondary forests maintained a high level of  $\beta$ -diversity among sites despite the initial disturbance (usually conversion to pasture or agriculture) removing the original biological communities, which reflects the importance of variation introduced by different successional pathways (e.g. Norden *et al.* 2015). Variation in the timing of disturbances may maintain  $\beta$ -diversity in forests affected by logging or fires, with longer term studies indicating a slow recovery of even the most mobile taxa (Mestre *et al.* 2013). High levels of  $\beta$ -diversity at larger spatial scales partially offset the localized loss of diversity from specific forest disturbances (Laurance *et al.* 2007), which was shown by the attenuated declines in species richness at landscape and regional scales. However, the much-reduced levels of  $\alpha$ -diversity in

disturbed and regenerating forests suggest only partial compensation. Moreover, the contribution of nestedness to among-site  $\beta$ -diversity in disturbed and regenerating forests is about twice that of undisturbed primary forests, suggesting a subtle shift towards biotic homogenization even within forests (Arroyo-Rodriguez *et al.* 2013).

While we saw consistently high levels of  $\beta$ -diversity among both sites and landscapes in remaining forest areas, we found that landscape-scale  $\beta$ -diversity remained consistently high in non-forest areas, even though such areas had much reduced  $\alpha$ -diversity. Given that turnover (replacement) in species composition accounted for most of the among-landscape  $\beta$ -diversity even in non-forest areas, this result supports the landscape divergence hypothesis (Laurance *et al.* 2007). That hypothesis asserts that disturbed areas are likely to diverge in



species composition because of differences in the effects of disturbance, or in the ways in which disturbances processes interact with underlying differences in environmental heterogeneity (see also Arroyo-Rodriguez *et al.* 2013). However, it is also the case that the contribution of nestedness to both among-site and among-landscape  $\beta$ -diversity is much greater in non-forest areas than in forest areas. While increased nestedness is an indication of increased biotic homogenization, differences in community reassembly processes (e.g. 'payment of extinction debt' and lag effects in colonization) in non-forest areas means that homogenized communities are not all nested in the same consistent fashion. This is to be expected for highly dynamic agricultural landscapes that are subject to frequent changes in cropping and land-management regimes, including fire, ploughing and cattle grazing.

The broad consistency of outcomes among taxa (Fig. 3) suggests that these general findings are likely to be typical of tropical forest biota in human-modified landscapes. However, there were some idiosyncratic differences in taxonomic responses (e.g. Barlow *et al.* 2007) that may provide insights into the nature of the biotic homogenization process. While some of the most obvious differences in diversity relate to direct consequences of land management (i.e. removal of woody vegetation from agricultural land), others results may arise from spill-over effects and the presence of occasional species (e.g. Barlow *et al.* 2010). For birds, even though there are very few species that reside in arable fields (Moura *et al.* 2013), occasional visitors from a pool of mobile species occupying adjacent habitats can contribute towards the maintenance of high apparent levels of  $\beta$ -diversity in open areas (e.g. periodic appearance of nomadic granivorous species in pastures; e.g. Lees *et al.* 2013). Similarly, invertebrate taxa sampled with baited traps may have more occasional species if some taxa are attracted from neighbouring habitats. The importance of rare and occasional species in driving high  $\beta$ -diversity in open areas was supported by the lower levels of  $\beta$ -diversity when we considered species abundance data (Fig. S4).

#### Implications for biodiversity conservation in human-modified tropical landscapes

In contrast with our observation of a consistent decline in  $\alpha$ -diversity along a gradient of increasing anthropogenic disturbance,  $\beta$ -diversity and the process of biotic homogenization depended on both land-cover class and the spatial scale of observation. These findings were supported by relatively consistent responses among diverse taxa, providing a robust basis for making recommendations for the conservation of forest biota.

Environmental laws currently governing tropical forests, such as the Brazilian Forest Code (Federal Law 12.651, 17 October 2012), focus almost exclusively on the protection of forest cover. Forest cover change is relatively easy to measure by using remote-sensing techniques, both at the scale of individual countries (e.g. PRODES-INPE 2015) and globally (Hansen *et al.* 2013). Our results support the importance of maintaining forest cover (Gardner *et al.* 2009) because all forest types were much more species rich and biologically distinct than any production areas. However, undisturbed primary

forests were consistently more diverse than forests disturbed by fragmentation, logging and fire, which underscores the urgent need to prioritize the conservation of the remaining areas of undisturbed forest where they exist (Gibson *et al.* 2011; Moura *et al.* 2013) and to minimize any further forest degradation and to restore actively already degraded areas (Malhi *et al.* 2014).

While the importance of conserving undisturbed forests is well-supported by previous work, our multi-landscape analysis provides strong additional support for the importance of maintaining a broad and distributed network of forest reserves that includes disturbed primary and secondary forests (Chazdon *et al.* 2009), especially in regions where there are no remaining undisturbed forests. This contention is supported by the high levels of among-site and among-landscape  $\beta$ -diversity we observed in all forest types and across all taxa, which are explained primarily by high levels of species replacement (*sensu* Baselga 2010). While many species may be lost from individual sites, regional biota in human-modified landscapes characterized by a heterogeneous mosaic of conserved and degraded areas of forest may be able to support much of the local biodiversity. The persistence of different taxa in disparate areas provides opportunities for both ecological recovery, through either natural processes or from strategic interventions, and for adaptation to changes (Malhi *et al.* 2014).

Our work is timely because debates about the old conservation planning contention of 'single large or several small' protected areas remain highly relevant. Our results are germane to decisions about conservation banking, offset schemes and the design of land-sparing initiatives to support both agricultural development and biodiversity conservation. One example is Brazil's legal reserve trading system (within the Forest Code) for compensation. The consistently high levels of among-landscape  $\beta$ -diversity that we report indicate that reserves should not be concentrated in one part of a region (e.g. in the form of a compensation bank) and that offset areas preferentially should be positioned within the same region for which the compensation is being made. If these suggestions are not followed, then there will be substantial losses of biodiversity. Effectively balancing conservation and rural development objectives in complex multiple-use landscapes such as those of the eastern Amazon remains a major challenge. However, our results suggest that the effectiveness of policies could be improved by considering the different effects of land-cover change and anthropogenic disturbance on patterns of biological diversity at multiple scales.

#### CONCLUSION

The paucity of studies looking at multiple scales and taxa has meant that the processes of biotic homogenization and divergence in whole landscapes are not well-understood (Tabarelli *et al.* 2012; Barton *et al.* 2013). We have disentangled some of the adverse effects of human-induced disturbances on biodiversity in tropical landscapes by exploring biotic homogenization over a broad disturbance and land-use intensity gradient and by concurrently considering multiple taxa. Our results offer strong support to theoretical predictions that landscape

processes can have a strong effect on landscape-wide biodiversity patterns (Laurance *et al.* 2007; Arroyo-Rodriguez *et al.* 2013; Barton *et al.* 2013), and that  $\beta$ -diversity has been underestimated as an important process involved in biodiversity change (Tscharntke *et al.* 2012). We show how landscape-scale differences in species assemblages for very different land-cover classes and taxa can drive landscape-wide patterns of biodiversity that may partially and temporarily offset site-scale impacts.

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## AUTHORSHIP

RRCS designed the work program, and wrote the first draft of the manuscript; JB, JF, ICGV, TAG coordinated the project; RRCS, JB, TAG, JF, JL, MM, JHS designed the experiment; RRCS, EB, ACL, MM, NGM, VHFO, JCMC collected the data; RRCS, JRT, RMN analysed the data; and all authors contributed substantially to preparing the final manuscript.

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