



Is β -diversity of Amazonian ant and dung beetles communities elevated at rainforest edges?

Charles J. Marsh¹ | Rodrigo M. Feitosa² | Julio Louzada^{3,4} | Robert M. Ewers¹

¹Imperial College London, Ascot, Berkshire, UK

²Departamento de Zoologia, Universidade Federal do Paraná, Centro Politécnico, Curitiba, PR, Brazil

³Departamento de Biologia, Setor de Ecologia, Universidade Federal de Lavras, Lavras, Minas Gerais, Brazil

⁴Lancaster Environment Centre, Lancaster University, Lancaster, UK

Correspondence

Charles J. Marsh, Department of Plant Sciences, University of Oxford, South Parks Road, Oxford OX1 3RB, UK.
Email: charliem2003@gmail.com

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Abstract

Aim: Thousands of kilometres of rainforest edges are created every year through forest fragmentation, but we have little knowledge of the impacts of edges on spatial patterns of species turnover and nestedness components of β -diversity.

Location: A quasi-experimental landscape in the north-east Brazilian Amazon.

Methods: We sampled dung beetles and ants using a sampling design based on a fractal series of equilateral triangles that naturally allows examination at multiple spatial scales. We sampled two edge types (primary-secondary and primary-*Eucalyptus* forest) and three control sites immersed in primary, secondary and *Eucalyptus* forest. We measured β -diversity between communities across the primary forest-matrix edge and within communities at up to 1 km from the forest edge. We examined β -diversity at multiple scales by partitioning the dissimilarity matrix into fractal orders representing inter-point distances of ~32, ~100, ~316 and ~1,000 m and into turnover and nestedness components.

Results: Turnover but not nestedness was greater across the primary-*Eucalyptus* forest than primary-secondary forest edge. There was spillover of species across edges in both directions. Across edges and within controls, turnover was the main driver of β -diversity. Within community, β -diversity was increased for dung beetles at large scales (~300–1,000 m) at both edge types. This increase, however, was driven by elevated nestedness. Levels of β -diversity were affected even ~300 m into habitat interiors, but appeared to be at control levels by 1 km.

Main conclusions: The effects of edges on the spatial dynamics of community composition penetrated far beyond the typical distances at which forest structure and microclimate are altered. This indicates that for a significant proportion of Amazonian communities, the underlying processes determining diversity may be impacted by deforestation.

KEYWORDS

community dissimilarity, edge effects, Formicidae, fragmentation, Scarabaeinae, species nestedness, species turnover

1 | INTRODUCTION

The rate and spatial configuration of deforestation are causing a rapid increase in the quantity of “core” habitat being converted to “edge” habitat in the Amazon (Ewers & Laurance, 2006). Globally

70% of remaining forest is <1 km from the forest edge (Haddad et al., 2015), and it is estimated that over 35,000 km of new forest edges are created in the Brazilian Amazon every year (Numata & Cochrane, 2012), resulting in large increases in the quantity of forest that is exposed to edge effects (Ries, Fletcher, Battin, & Sisk, 2004).

Edge effects incorporate a wide range of well-established biotic and abiotic changes that occur in forest proximate to the forest-matrix boundary, where the matrix may be any natural or unnatural adjoining habitat (Laurance et al., 2002). As the forest is exposed to the matrix habitat, altered microclimatic fluxes affect the structure of the forest bordering edges (Harper et al., 2005). These structural changes cause a plethora of impacts, from populations to community-level alterations (Didham, Hammond, Lawton, Eggleton, & Stork, 1998). Although microclimatic variables typically reach normal levels within 100 m (Laurance et al., 2002), the changes to biotic communities may be much more pervasive, penetrating a kilometre or more into the forest interior (Ewers & Didham, 2008; Laurance, 2000).

The impacts of edge effects on species richness and abundance are variable, with negative, positive and neutral responses all having been found (Ries et al., 2004). This arises as edge responses, and the distances they penetrate, are typically species (Didham et al., 1998) and edge specific (Feer, 2008), meaning that the community-level diversity response is determined by the relative distribution of edge-sensitive to edge-tolerant species. For example, if no change in species richness is observed at an edge, this may be that there has been no loss of interior species, but the same pattern may also arise as the loss of an edge-avoiding species is offset by the arrival of an edge specialist (Blackwood, Smemo, Kershner, Feinstein, & Valverde-Barrantes, 2013).

Consequently, rather than examining patterns of richness across the edge, it may be more informative to examine changes in species composition, β -diversity. These changes can be described through partitioning into two components that reflect different processes, turnover and nestedness (Baselga, 2010). Spatial turnover is the replacement of species between two sites, for example, due to environmental filtering along a gradient. Nestedness is the result of species gain or loss between two sites leading to one site containing a subset of species from the other due to non-random processes such as competitive exclusions.

Typically, such studies sample across the edge using transects running perpendicular across the border. As we travel from the forest interior across the edge and into the matrix habitat, we expect a replacement of forest-interior specialists by matrix specialists, and as such, the community becomes more dissimilar to the forest-interior community (Dangerfield et al., 2003; Ewers & Didham, 2008).

However, very few studies have investigated the magnitude to which β -diversity differs within, rather than among, communities located at different distances from a forest edge. Thus, the question arises whether edge effects (and proximity to edges) per se impact rates of β -diversity. Quantifying this variation in β -diversity requires an alternative sampling design, where transects that run perpendicular to the edge must be replaced by transects that run parallel to the edge. Studies that have implemented such designs have found some (Gabriel, Roschewitz, Tschartke, & Thies, 2006), but often no evidence that β -diversity may be higher along the edges of forest than the interior (Duraes, Martins, & Vaz-de-Mello, 2005; Filgueiras et al., 2016).

A limitation of these studies is that β -diversity was analysed at a single scale, collating dissimilarities between all pairs of sample

points at the extent of the study site. For example, for a transect with regularly spaced sample points, pairwise dissimilarity between all points are averaged together, with greater weighting given to medium distances where there will be a greater number of point-to-point comparisons. Therefore, changes to levels of β -diversity at small and large distances may remain unnoticed. We, therefore, argue that it is necessary to examine β -diversity at multiple scales (Barton et al., 2013), and we suggest a novel method of decomposing the dissimilarity-distance decay curve to do so.

This study seeks to address three hypotheses. First, β -diversity within communities along the forest edge will be higher compared with β -diversity within communities of the forest interior (Filgueiras et al., 2016). This may arise through several processes. As the forest community is replaced by the matrix community, we would expect this conversion to be greater at the habitat boundary where the changes in habitat characteristics are most pronounced. Since the replacement of forest species by matrix species is unlikely to be uniform along the length of the boundary, communities will likely differ to a greater extent along the boundary compared with forest or matrix interiors. Furthermore, there may be hyperdynamism in ecological processes at habitat edges (Laurance, 2002), characterized by increased frequencies or amplitudes of species interactions and dynamics, leading to persistent, increased ecological instability (Wang & Malanson, 2008). Hyperdynamism may lead to greater fluctuations in populations and community composition (Laurance et al., 2011), and thus greater β -diversity within edge communities (Ewers & Didham, 2008).

Our second hypothesis is that the scaling of β -diversity will also be altered. The spatial autocorrelation of the mixing between primary forest and matrix communities at the edge may lead to a change in the scales at which the change in β -diversity is most pronounced. For example, a pattern of large clumps of matrix and primary forest communities along the edge would lead to lower β -diversity at fine scales but higher β -diversity at broad scales than the reference interior communities. This would be reflected by an increase in the large-scale turnover component. Alternatively, if mixing is more disordered, without distinct patches of matrix or forest communities, then we might see higher turnover at fine scales. As far as we are aware, no study of the spatial structuring of communities at edges has been previously been carried out.

Our third hypothesis is that any differences to β -diversity will be greater where the structure of the matrix differs more strongly from the structure of the forest. First, a structurally distinct matrix habitat may expose the forest edge to more pronounced variations in microclimate and, therefore, more marked edge effects (Harper et al., 2005). Second, there is likely to be a greater dissimilarity between the forest community and a matrix community in a more distinct habitat (Nichols et al., 2007). For example, Feer (2008) found dung beetle communities at the edges of secondary forest to be more similar to forest-interior communities than communities at the edges of natural savanna.

To test these hypotheses, we selected two taxa responsive to edge effects, dung beetles (Coleoptera: Scarabaeinae) and ants



(Hymenoptera: Formicidae). Both are cost-effective and efficient diversity indicator taxa (Spector, 2006) that fulfil a suite of important ecological functions (Folgarait, 1998; Nichols et al., 2008) and are highly sensitive to habitat gradients, fragmentation, and proximity to edges (e.g. Larsen, Lopera, & Forsyth, 2008; Philpott, Perfecto, Armbricht, & Parr, 2010).

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out at the Jari forestry project, an ongoing 50-year-old pulp plantation located in the north-east Amazon in Pará, Brazil (00°27'00"–01°30'00" S, 51°40'00"–53°20'00" W), which provides a large-scale quasi-experimental landscape that has been previously well-studied (Barlow, Gardner, et al., 2007). The project consists of a 1.7 Mha landholding, of which around 65,000 ha are *Eucalyptus* plantation and 45,000 ha cleared land and secondary forest as of 2011 (Figure S2.6), the rest being largely undisturbed primary forest with occasional settlements (see Barlow, Mestre, Gardner, & Peres, 2007 for greater detail).

We sampled at five sites: one control site each in the interior of *Eucalyptus*, secondary and primary forest; and two edge sites: a primary-*Eucalyptus* forest edge and a primary-secondary forest edge. Sites were located sufficiently far apart to be independent of spatial autocorrelation effects (mean distance between different sites = 16.6 km; range = 5.2–31.6 km; Koenig, 1999). Control sites were located within the deep interior of each habitat so that all points were >0.95 km from the nearest border with any adjacent habitat. Sites within secondary forest were located within a large continuous block of 17- to 25-year-old regenerating forest. Sites within *Eucalyptus* plantations were 2–3 years of age from last planting at the start of sampling (plantations are typically cut on a 4- to 6-year cycle). Edge sites were located on straight borders between primary forest and the adjacent matrix. As multiple edges may act synergistically (Laurance et al., 2011; Malcolm, 1994), the edges selected were chosen as they

extended at least 1 km in both directions beyond each end of the edge transect.

2.2 | Sampling design

Previous research found that classical sampling designs may be unsuitable for quantifying β -diversity (Marsh & Ewers, 2013). Therefore, we sampled communities using a sampling pattern based on a fractal series of equilateral triangles created explicitly for the investigation of β -diversity. The design allowed us to sample broad spatial scales while simultaneously maintaining fine-scale data at all locations (Ewers et al., 2011) and, furthermore, allows β -diversity to be naturally decomposed into multiple spatial scales. In simulations, this design was found to provide more accurate estimates of β -diversity across all spatial scales than classical designs of equivalent sampling effort (Marsh & Ewers, 2013).

For a sample design of one order, three points are located on the apices of an equilateral triangle (Figure 1b). From these three points, we can generate three estimates of community turnover and so also obtain a measure of the variance around that estimate. For two spatial scales, a second-order triangle is created, with three 1st-order triangles, and thus nine sampling points located on the apices. For three spatial scales, three second-order triangles and nine 1st-order triangles are located on the apices, and so on. This is repeated for four spatial scales, with triangles of side lengths of $10^{1.5}$, 10^2 , $10^{2.5}$ and 10^3 m. At the three control sites, we reduced the sampling effort required by replacing two of the first-order triangles with a single sampling point (Figure 1a). In this way, we were able to significantly reduce sampling effort with little loss in statistical rigour (Marsh & Ewers, 2013).

To model β -diversity within communities at set distances from the edge, we require transects running parallel to the edge. At edge sites, we achieved this by linearizing the edge of the control subsampling design to allow it to be transposed across the forest border (Figure 1b). Thus, the edge scheme may be considered as seven "transects" running parallel to the border (hereafter referred to as "distance transects"), while still maintaining the ability to estimate β -

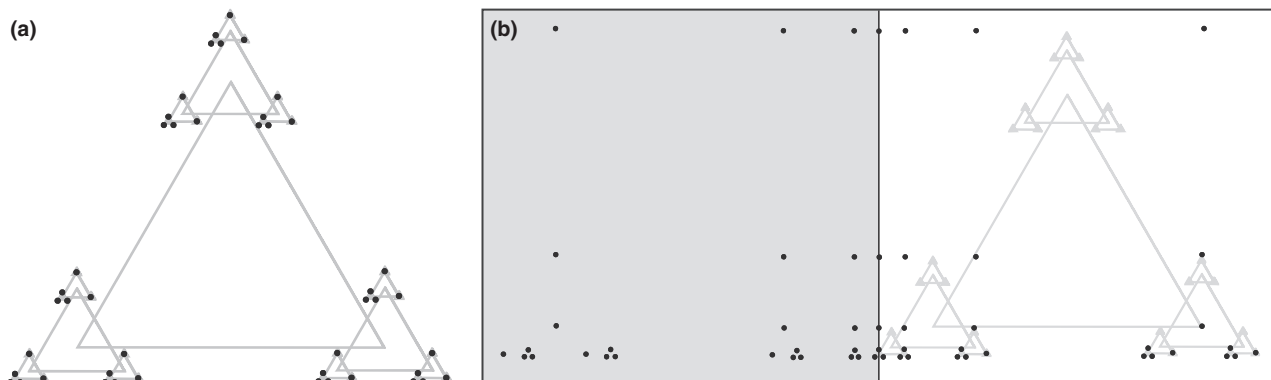


FIGURE 1 Sampling design used in the study. (a) At the control sites, sample locations (black points) were placed in a series of triangle fractals that allow for β -diversity to be estimated at four spatial scales. (b) At edge sites, this design was linearized to produce seven "distance transects" running parallel to the border between one habitat (grey) and another (white). The triangle fractal scheme is overlaid on one half to demonstrate how the same spatial scales are applied to edge sampling as control sampling

diversity at the four spatial scales. Both the distances between points at each spatial scale and the distances of each “transect” from the edge were equivalent to the spatial scales used in the control design to allow direct comparisons of spatial patterns of turnover. This allowed us to estimate β -diversity across the same four spatial scales as the control sites ($10^{1.5}$, 10^2 , $10^{2.5}$ and 10^3 m) and at four distances away from the border (10^0 , 10^2 , $10^{2.5}$ and 10^3 m) into both the forest and matrix interior. See Appendix 1 for a detailed exploration of the sampling design and its partitioning into multiple spatial scales.

The disadvantage is the intensity of sampling required to quantify β -diversity within communities at any given distance from the edge. To sample a single edge site requires 54 sampling points, whereas to quantify β -diversity across the edge requires a transect of only seven, allowing for a further seven edge replicates. However, we believe that the lack of replication is outweighed by the unique insights the design may have (Barley & Meeuwig, 2016).

2.3 | Sampling

We sampled both taxa using baited pitfalls buried flush with the ground (20 cm width, 15 cm depth), containing water with the addition of salt and detergent. For dung beetles, bait was a 20 g mix of pig and human dung in a 90:10 ratio that was found to be an optimal compromise between effectiveness and bait availability within the study area (Marsh, Louzada, Beiroz, & Ewers, 2013). Bait was suspended below a protective cover directly above the pitfall. For ants, each trap had two baits, honey and sardines, placed in separate cups in the centre of the trap. Traps were operated over a 2-day period for ants and 4 days for dung beetles traps, re-baiting and collecting contents after 2 days for the latter, which should be effective for describing the local assemblage (Gardner, Hernández, Barlow, & Peres, 2008; Lopes & Vasconcelos, 2008).

One trap was placed at each sampling point (45 at control sites, 54 at edge sites). Five points were removed from the primary-*Eucalyptus* forest edge site as they were located within a manioc plantation. Sampling was carried out once in the early dry season (July–October 2010 for beetles; November–December for ants) and then repeated in the early wet season (February–April 2011 for beetles; April–May for ants). Dung beetle specimens were sorted and oven dried at the study site, and then identified to species level and deposited at *Universidade Federal de Lavras* (UFLA), Brazil. Where species names were unknown, we identified individuals to morphospecies using the classifications of Vaz-de-Mello and Gardner (unpublished). Ants were sorted and mounted, identified to morphospecies at UFLA and deposited in the *Museu de Zoologia da Universidade de São Paulo* (MZSP) and in the Entomological Collection *Padre Jesus Santiago Moure* of the *Universidade Federal do Paraná* (DZUP), Brazil.

2.4 | Analyses

For all analyses, we pooled species collected during both sampling occasions for each trap. At edge site, distance transects were

ordered by distance into the forest interior (negative values) and away from the forest into the matrix (positive values). In each case, we fitted five potential response functions against distance from the edge (Ewers & Didham, 2006) in order of complexity: a null model (a slope of 0); a linear slope; and quadratic, exponential and logistic curves. The best model was determined through the Akaike information criterion (AIC). Where values were bounded between 0 and 1 (dissimilarities and proportions) values were first logit-transformed. It should be noted that the fitting of response functions are not determining significant relationships, but rather are meant to serve as guidelines to any emerging patterns. All analyses were carried out in program R version 2.13.1 (R Core Team, 2017) using “vegan” (Oksanen et al., 2018), “indicpecies” (De Cáceres & Legendre, 2009), “betapart” (Baselga & Orme, 2012) and “iNEXT” (Hsieh, Ma, & Chao, 2016) packages for calculating diversity measures, “minpack.lm” (Elzhov, Mullen, Spiess, & Bolker, 2015) for the optimization of function parameters, and “qpcR” (Spiess, 2014) for calculating AIC of functions.

We examined differences in diversity between transects through sample-based accumulation curves of Hill numbers, where $q = 0$ (species richness), 1 (Shannon diversity) and 2 (Simpson diversity) (Chao et al., 2014). Higher order q values are more robust to under-sampling. Curves were standardized at the maximum (for visualizing extrapolated curves) and minimum (rarefied for testing differences) observed sampling coverage, defined as the proportion of the total number of individuals in an assemblage that belong to species represented in the sample. For each distance transect and each control, we plotted rarefied diversity against distance from the forest edge. We repeated this for relative abundances, calculated as the number of individuals per trap-night for dung beetles, and for ants, the proportion of trap occurrences per trap-night as we could not always preclude recruitment. Differences in community composition were visualized from the results of non-metric multidimensional scaling (NMDS) carried out on data from all sites. Values for k were selected visually from scree plots.

We modelled β -diversity in two ways: between communities across the edge and within communities at different distances from the edge. The first analysis illustrates the turnover of forest to matrix species as we travel from the forest interior to matrix interior. The second analysis investigates if the levels and scales of turnover are affected by proximity to the forest edge. In all cases, dissimilarity was measured using presence-based Sorensen's index for both ants and dung beetles to investigate changes in community composition and abundance-based Bray–Curtis index for dung beetles only, to analyse changes to community structure. In both cases, we also partitioned total β -diversity (β_{tot}) into the component derived from species turnover (β_{turn}) and the component derived from species gain and loss or nestedness (β_{nest} , Baselga, 2010, 2017).

2.4.1 | Across edge dissimilarity

For each edge, we examined the turnover across the edge in both directions, from the interior of the primary forest to the interior of



the matrix, and vice versa. In each case, we used the transect located furthest inside the primary forest and matrix interior (i.e. 1 km), respectively, as the “reference” interior community, and we estimated dissimilarity between all pairs of sampling points in these reference communities with the sample points in each distance transect. The baseline level of turnover was estimated as the mean dissimilarity between all pairwise comparisons within the reference transect.

In order to further investigate which components of the community are changing across the forest edge, we classified all species into generalists, or primary, edge (the transect at 0 m) or matrix specialists (secondary and *Eucalyptus* forest separately). We aggregated all traps in each habitat across all sites and calculated relative abundance as the number of individuals for dung beetles or number of occupancies occurring per trap-night for ants. Habitat fidelity was calculated using Pearson's phi coefficient of association and point biserial correlation coefficient for ants and dung beetles, respectively (De Cáceres & Legendre, 2009). We assigned a species as a habitat specialist when the probability of association was $< .05$ after correcting for uneven sample sizes (Tichý & Chytrý, 2006). We then calculated the proportion of specialists and generalists in each distance transect and examined the changes in these proportions with distance from the edge.

2.4.2 | Within-community dissimilarity

To investigate β -diversity within communities at distances from the forest edge, for each distance transect we created dissimilarity matrices between all pairs of sampling points. Each matrix was then decomposed to four spatial scales naturally generated from the fractal triangles, representing the distance between points: first order = ~ 32 m (first–third quantile = 29.5–34.7 m); second order = ~ 100 m (86.8–111.6 m), third order = ~ 316 m (283.4–364.9 m); and fourth order = $\sim 1,000$ m (884.6–1,174 m). For each order, we calculated the mean and standard error around the dissimilarity values. Descriptions and visual representations of the decomposition of the dissimilarity matrices, along with histograms of between-point distances for each site, can be found in Appendix S1 in the Supporting Information.

Although this approach discards some of the pairwise dissimilarity values, the advantages are that it allows the analysis of turnover at multiple spatial scales which may highlight scale-specific changes in turnover. For example, in a scenario where communities separated by short distances became more similar but more dissimilar at large distances, multiple-site measures would be unable to detect any difference in the overall mean (but some increase in the variance around that mean). Such subtleties may be picked up by fitting a distance-decay curve (Nekola & White, 1999); however, it is unclear as to the best interpretation of the fitted curve into a metric that can be compared statistically across transects (Morlon et al., 2008). Furthermore, the slope and intercept may be confounded if dissimilarity at the shortest distances approaches one. By contrast, our approach allows us to dissect the decay curve in to multiple spatial scales,

identifying which, if any, scales have increased dissimilarity. For example, the mean dissimilarity of the first order represents dissimilarity at the finest scales (in effect “initial similarity” *sensu* Soininen, McDonald, and Hillebrand, 2007), and the mean dissimilarity of the fourth order is dissimilarity over large distances. The differences in means going from the first to the fourth orders are analogous to the slope of dissimilarity-distance decay curve.

3 | RESULTS

We captured 11,126 individuals of 79 species from 1,746 trap-nights for dung beetles and 237 species/morphospecies from 908 trap-nights for ants. Sampling coverage was high in beetles (min = 0.959, max = 0.997, mean = 0.984) but low at edges for ants (min = 0.427, max = 0.952, mean = 0.650, Table S2.1). For dung beetles, diversity was highest in primary forest, then secondary, then *Eucalyptus* forest (Figure S2.7). For ants, diversity was equivalent in primary and secondary forest (Figure S2.8). There were no clear diversity patterns across edges although there were slight decreases in dung beetle diversity across the primary–secondary forest edge. However, Simpsons and Shannon diversity increased across the primary–*Eucalyptus* edge (Figure S2.9), and there was a similar increase in standardized abundance (Figure S2.10). This was driven by the hyper-abundance of a single species, *Ateuchus irinus*, which composed some 68% of all individuals in the primary forest. NMDS plots showed some overlap between primary and secondary forest communities, but none with *Eucalyptus* (Figure S2.11). In ants at the primary–*Eucalyptus* edge, there is a rough gradient from the interior of primary forest to the interior of the matrix, but none such gradient occurred at the primary–secondary forest edge. The converse was true for dung beetles.

3.1 | Across edge dissimilarity

In both ants and dung beetles, dissimilarity increased with distance from the interior community in both directions (Figure 2). Three strong patterns emerged: (a) the increase in dissimilarity across the edge was higher in dung beetles than ants, which had generally higher levels of turnover even across short distances, although it cannot be ruled out this was due to lower sampling coverage (Figure S2.8); (b) the increase in dissimilarity across the edge was higher at the primary–*Eucalyptus* forest edge than the primary–secondary forest edge; and (c) these patterns were driven largely by the turnover component, β_{turn} , especially at the primary–*Eucalyptus* forest edge.

In general, the increase in dissimilarity across the edge was gradual rather than showing any sharp change in community composition. In primary forest, dissimilarity often approached the background rate of the interior communities by 316 m from the edge, but matrix communities were still considerably different from the matrix interior community at the same distances. In dung beetles, there was unusually low turnover within the interior primary forest of the primary–*Eucalyptus* forest edge driven by the hyper-abundance of *A. irinus*.

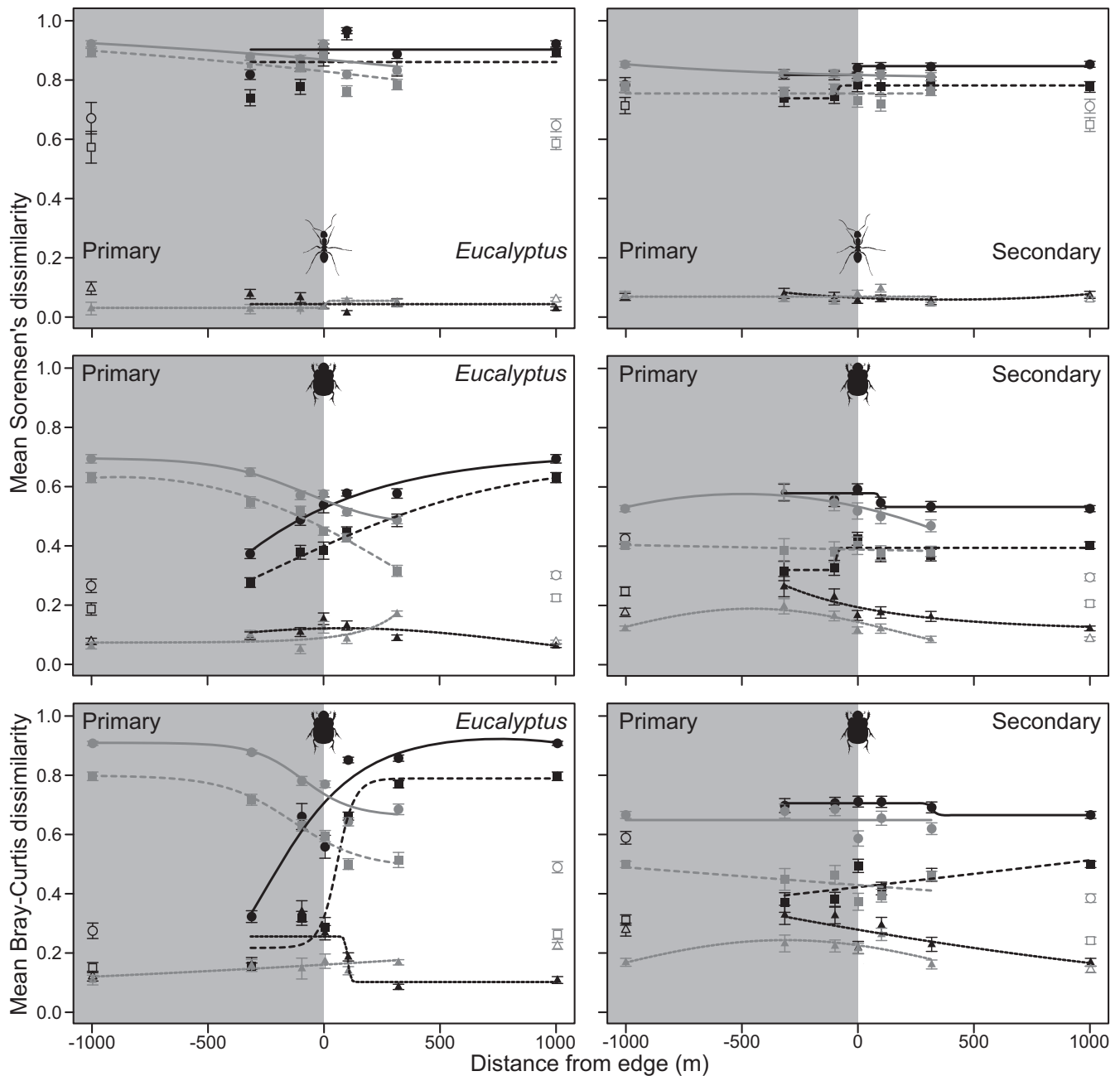


FIGURE 2 Mean (\pm SE) dissimilarity of Amazonian dung beetle and ant communities as measured through presence-based Sorensen's (ants and dung beetles) and abundance-based Bray–Curtis (dung beetles only) measures. Dissimilarity was estimated between communities sampled in transects 1 km into the interior of primary (black) and matrix forest (dark grey), and communities sampled at six distances from the forest edge. Communities were sampled both within primary forest (negative edge distances, shaded grey) and into the matrix (positive edge distances) for primary forest bordering secondary and *Eucalyptus* forest. Open circles are the mean dissimilarities measured within only communities 1 km into the interior. Total β -diversity (β_{tot} , circles, solid lines) was decomposed into turnover (β_{turn} , squares, dashed lines) and nestedness (β_{nest} , triangles, dotted lines) components. Lines represent the best-fit of five possible response functions

Habitat generalists composed the majority of all communities, especially in ants (Figure 3). Unsurprisingly, primary forest and matrix specialists increased towards the interior of the respective habitats. Secondary forest specialists were also found in large numbers inside primary forest, even 1 km into the interior, whereas fewer *Eucalyptus* forest specialists penetrated across the edge. Primary forest specialists were found in both secondary and *Eucalyptus* forest interiors.

3.2 | Within-community dissimilarity

Once again, ants had greater β -diversity in community composition at all scales than dung beetles (Figure 4). We found evidence for increased total β -diversity of community structure at edges between primary and *Eucalyptus* forest in dung beetles at large scales (fourth-order [$\sim 1,000$ m] distances) at both edges and both community

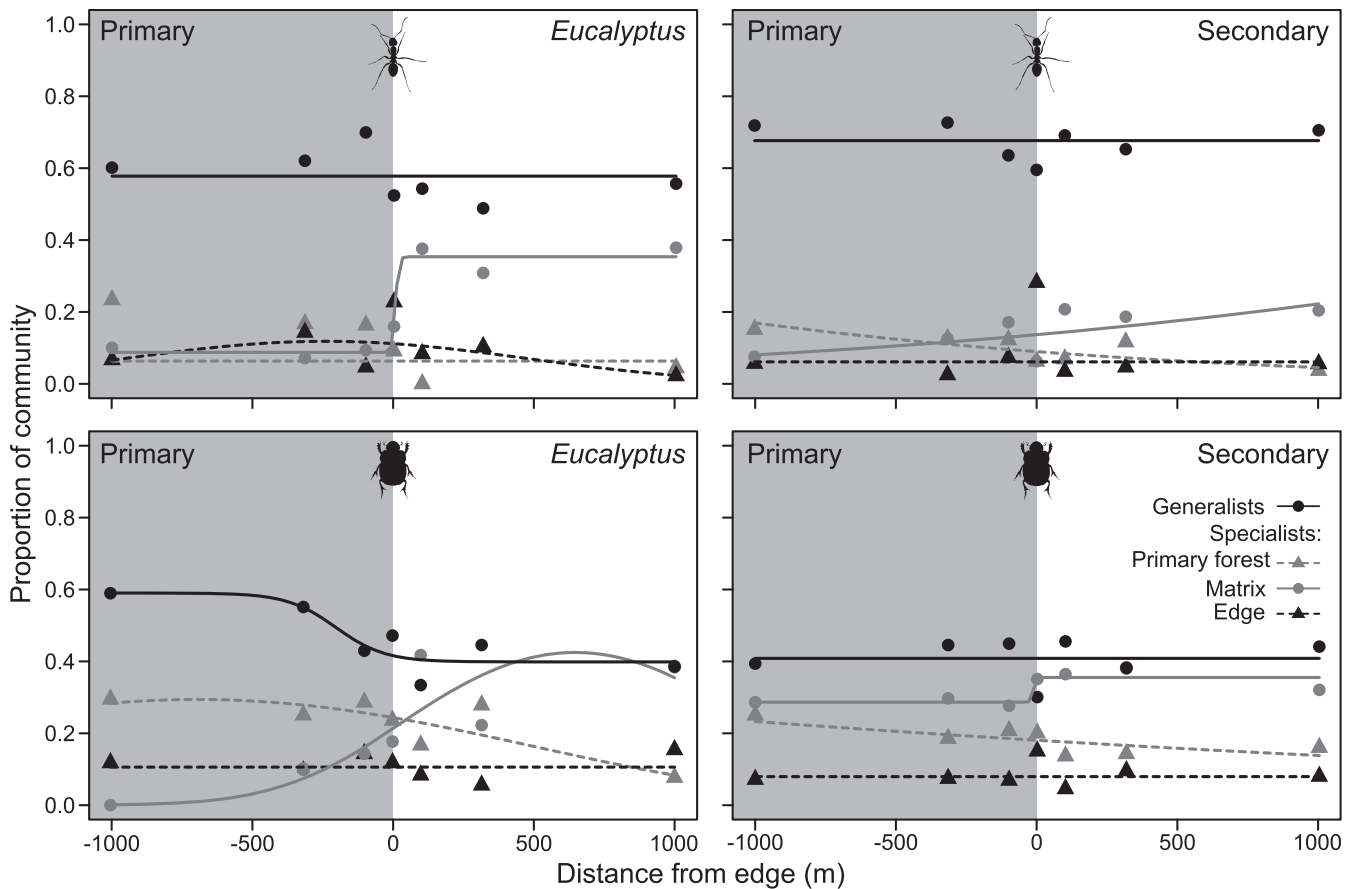


FIGURE 3 The proportion of Amazonian dung beetle and ant species categorized as generalists (black points; solid line) or matrix (grey points; solid line), primary forest (grey triangles; dashed line) or edge (black triangles; dashed lines) specialists in ant and dung beetle communities at forest edges. We estimated the proportion of specialists in communities at six distances from the forest edge both within primary forest (negative edge distances, shaded grey) and into the matrix (positive edge distances) for primary forest bordering secondary and *Eucalyptus* forest. Lines represent the best-fit of five possible response functions

structure and composition at medium-scales (third-order [~ 316 m] distances) at the primary-secondary forest edge. There were no such increases at either edge in ants. In these cases, β -diversity was elevated even 316 m into the primary forest. In the interior controls, like across edges, levels of total β -diversity were driven by turnover, with nestedness only forming a small component (Figure S2.12). However, the elevation in total β -diversity we observed within communities near edges was due to an increase in nestedness (Figure 5), whereas turnover was relatively consistent within communities across the edge (Figure 6). Where there were changes in turnover across edges, such as at fine scales in dung beetles at the primary-*Eucalyptus* forest edge, this reflected differences in turnover levels between the habitats, rather than an elevation at the edge (Figure 6).

It is possible to observe an increased turnover at edges compared with the interior controls (Figure 5) when we pull out the dissimilarities only for those two communities and examine the difference between dissimilarity over fine scales (first order [~ 32 m]) and large scales (fourth order [$\sim 1,000$ m]). These are analogous to the slope of the dissimilarity-distance curve. In both ants and dung beetles, the slope between fine scales and large scales was almost

identical for all control habitats and only the “intercept” (“initial” dissimilarity) distinguished between habitats. In both taxa, these values were higher in primary forest than *Eucalyptus* forest. Values in secondary forest were equal to primary forest for ants but similar to *Eucalyptus* forest for dung beetles. The slopes between orders at the primary-secondary forest edges were much greater than in the controls in all cases. Slopes at the primary-*Eucalyptus* edge were similarly high for dung beetle community structure, but very low for both ant and dung beetle community composition due to very high fine-scale dissimilarity.

4 | DISCUSSION

Studies investigating edge effects typically focus effort within a hundred metres of the edge within the range that microclimatic variables and habitat structure are still affected (Laurance et al., 2002), and thus where environmental edge effects will be most pronounced. However, impacts on populations and communities may be much more pervasive and pernicious. We observed altered spatial patterns in edge communities such that large-scale β -diversity could be

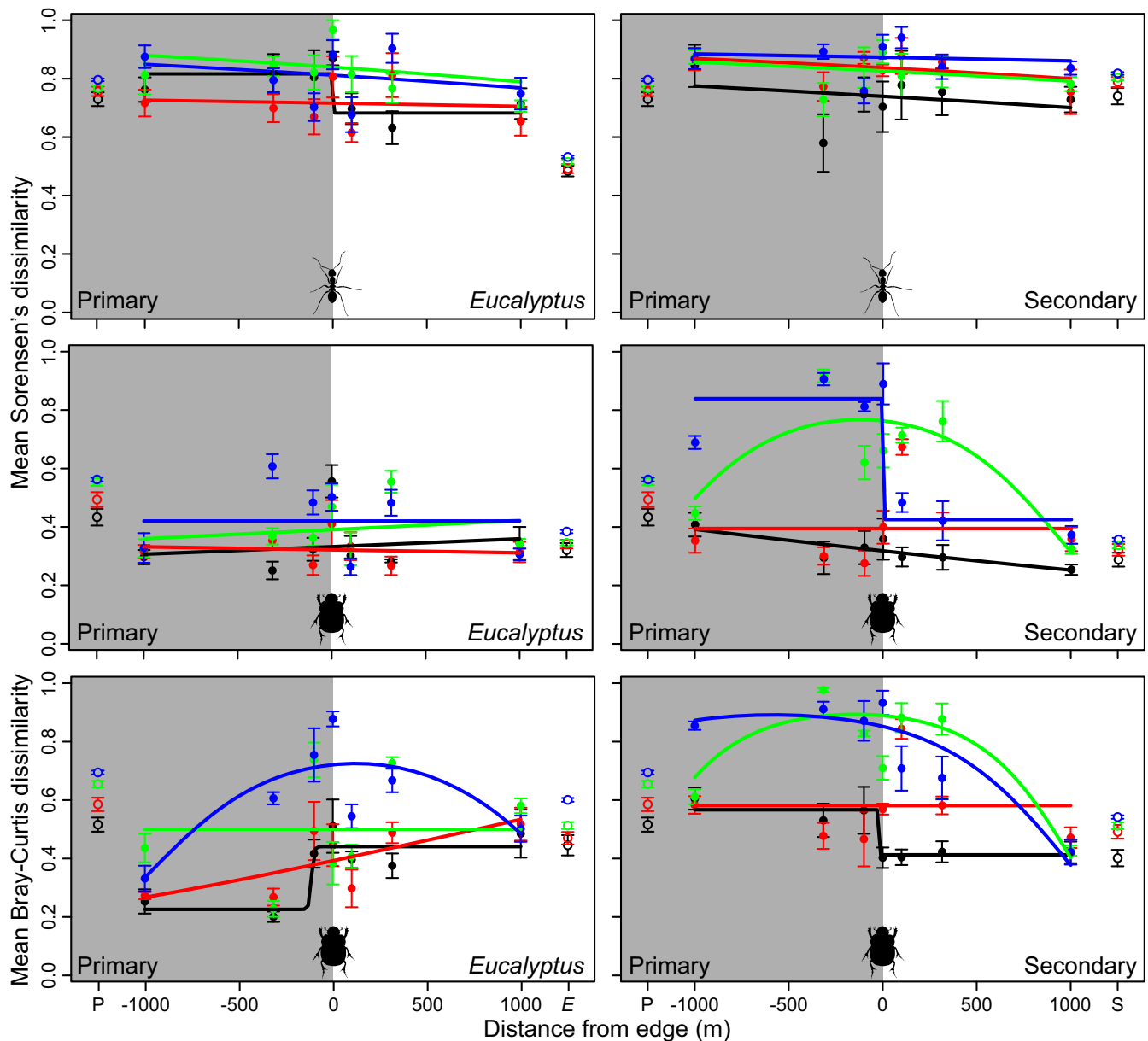


FIGURE 4 Mean (\pm SE) of presence-based Sorensen's (ants and dung beetles) and abundance-based Bray-Curtis (dung beetles only) dissimilarity between of Amazonian dung beetle and ant communities sampled at six distances from the forest edge within primary forest (negative edge distances, shaded grey) and into the matrix (positive edge distances) for primary forest bordering secondary and *Eucalyptus* forest. Each dissimilarity matrix was decomposed into four fractal orders representing distance classes between points from the first (shortest distances, black), second (red), third (green) and fourth orders (furthest distances, blue). Open circles are the mean dissimilarity within communities at 1 km. Lines represent the best-fit of five possible response functions

greater in edge habitats than would be expected in habitat interiors and so β -diversity appeared to still be increased even 316 m from the edge (Figure 4), especially at the primary-secondary forest edge in dung beetles (Figure 7).

The few studies that have investigated deeper into interior forest have found that communities may still be altered >1 km from the edge (Ewers & Didham, 2008; Laurance, 2000). As some 17% of Amazonian forest may be within 1 km of the forest edge (Numata & Cochrane, 2012), and globally this figure stands at 70% (Haddad et al., 2015), then large areas of remaining forest may experience

altered community dynamics due to edges. Furthermore, these edge forests are also more likely to experience increased anthropogenic pressures, such as hunting and fire exposure, which can double the biodiversity loss from deforestation (Barlow et al., 2016).

4.1 | Differences in β -diversity between habitats

Invertebrate communities, in particular, can be sensitive to habitat change and it is common to see the reduction in diversity and compositional changes in degraded habitats as we observed (Nichols

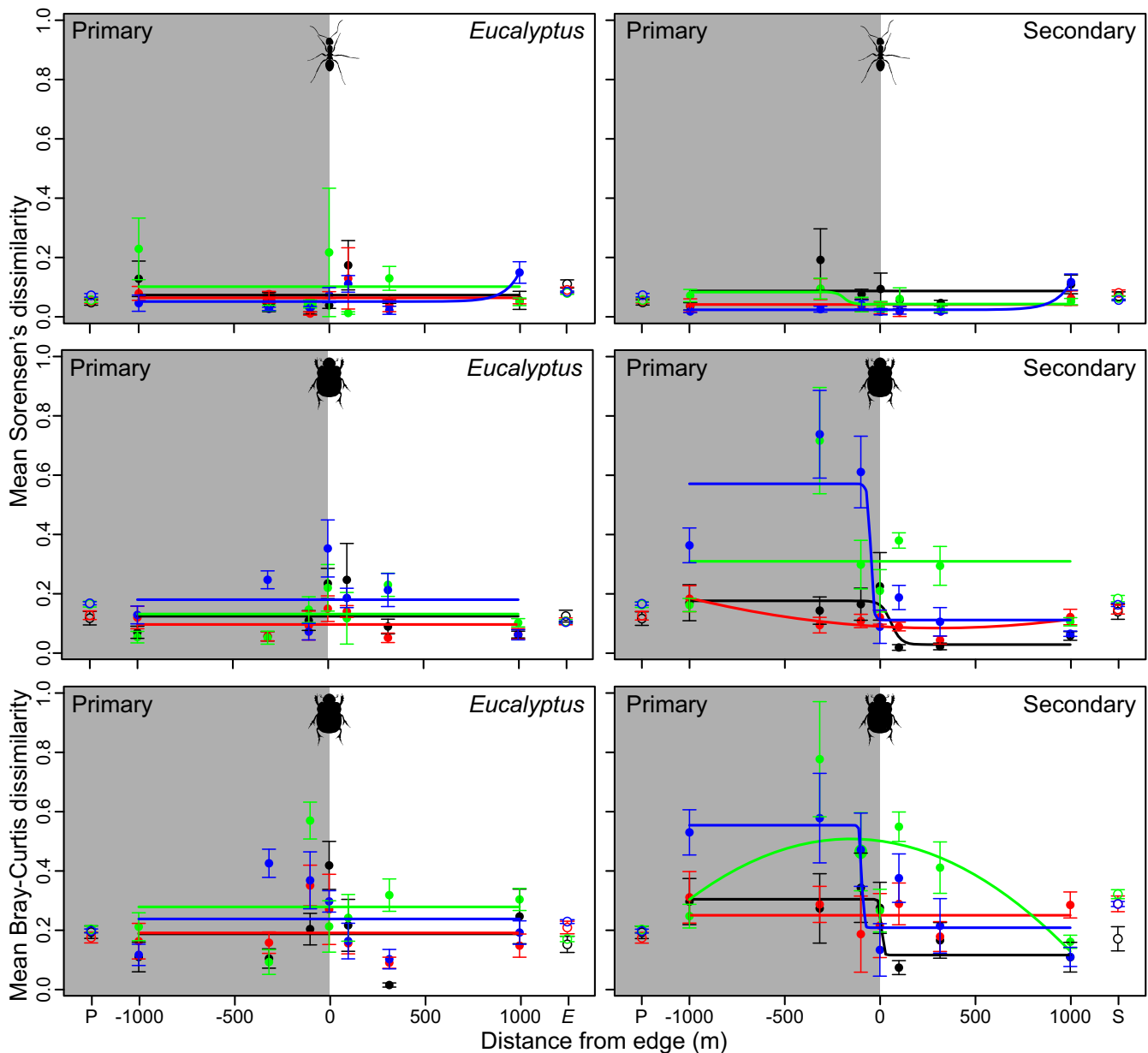


FIGURE 5 The nestedness component (β_{nest}) of mean (\pm SE) of presence-based Sorensen's (ants and dung beetles) and abundance-based Bray–Curtis (dung beetles only) dissimilarity between of Amazonian dung beetle and ant communities sampled at six distances from the forest edge within primary forest (negative edge distances, shaded grey) and into the matrix (positive edge distances) for primary forest bordering secondary and *Eucalyptus* forest. Each dissimilarity matrix was decomposed into four fractal orders representing distance classes between points from the first (shortest distances, black), second (red), third (green) and fourth orders (furthest distances, blue). Open circles are the mean dissimilarity within communities at 1 km. Lines represent the best-fit of five possible response functions

et al., 2007; Solar et al., 2016). These responses are largely driven by changes to the microclimate and vegetation composition and structure. At the study site, *Eucalyptus* forest was structurally simpler than primary forest with a lower, more open canopy leading to higher temperatures and reduced humidity (Figure S2.14), and secondary forest intermediate between the two. The high temperatures in *Eucalyptus* forest may exceed the thermal tolerances of primary forest species (Chown & Klok, 2011; Verble-Pearson, Gifford, & Yanoviak, 2015) and lead to hotter, drier soil temperatures that limit

nesting resources (Davis, Scholtz, & Deschodt, 2008; Philpott et al., 2010) or alter competitive interactions (Wittman et al., 2010). As a result, primary forest specialists penetrated only small distances across the *Eucalyptus* forest edge but were relatively frequent even 1 km into secondary forests (Figure 3). Similarly, secondary forest specialists were found even 1 km into the primary forest, and as a result, the assemblages of the primary and secondary forests were relatively similar compared with the community in *Eucalyptus* forest (Figure S2.11).

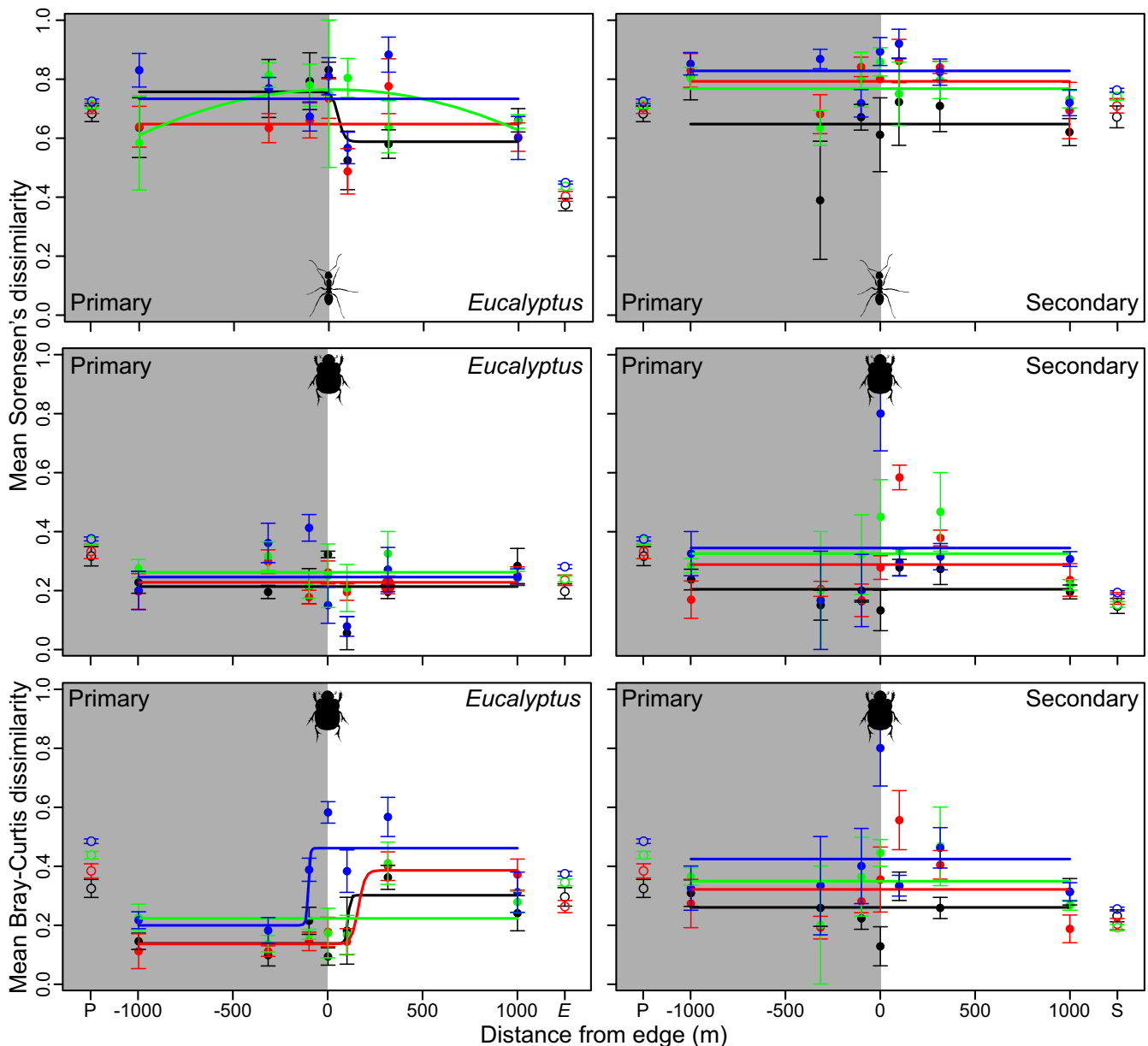


FIGURE 6 The turnover component (β_{turn}) of mean (\pm SE) of presence-based Sorensen's (ants and dung beetles) and abundance-based Bray-Curtis (dung beetles only) dissimilarity between of Amazonian dung beetle and ant communities sampled at six distances from the forest edge within primary forest (negative edge distances, shaded grey) and into the matrix (positive edge distances) for primary forest bordering secondary and *Eucalyptus* forest. Each dissimilarity matrix was decomposed into four fractal orders representing distance classes between points from the first (shortest distances, black), second (red), third (green) and fourth orders (furthest distances, blue). Open circles are the mean dissimilarity within communities at 1 km. Lines represent the best-fit of five possible response functions

Disturbed habitats may also have reduced feeding resources through reduced vegetation complexity for ants (Gibb & Parr, 2010) or for dung beetles through the reduced mammal diversity and abundance (Andresen & Laurance, 2007) at the study site (Parry, Barlow, & Peres, 2007). Consequently, disturbed habitats are generally dominated by generalist, invasive or "supertramp" species (Solar et al., 2016), with smaller body sizes (Gardner et al., 2008), higher dispersal abilities (Larsen et al., 2008) and larger niche breadths (Swihart, Lusk, Duchamp, Rizkalla, & Moore, 2006).

As a result, total β -diversity was highest in primary forest and lowest in *Eucalyptus* forest (Figure S2.12). This was largely driven by species turnover, with nestedness forming only a small component in line with most studies (Soininen, Heino, & Jianjun, 2018) and particularly ants (Luis, Silva, Souza, Solar, & Neves, 2017; Schmidt et al., 2017). In disturbed habitats turnover decreased, probably due to a larger proportion of generalist species that tolerate a broader range of conditions, reducing the effects of environmental filtering. Levels of nestedness, however, were maintained so that although overall β -diversity was reduced the

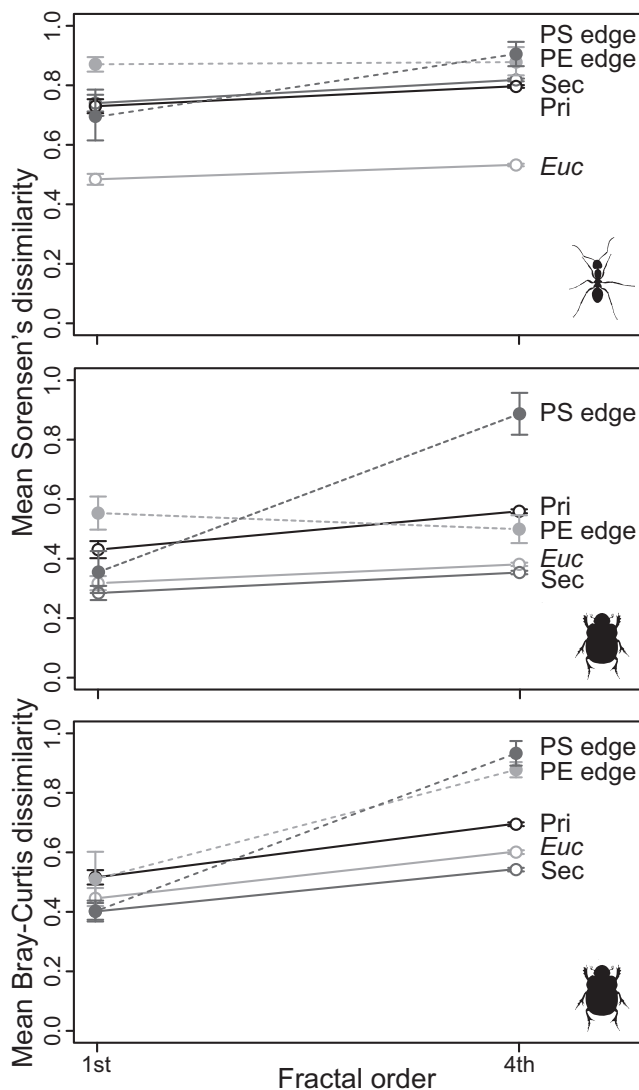


FIGURE 7 A comparison between the difference between the mean (\pm SE) of presence-based Sorensen's (ants and dung beetles) and abundance-based Bray-Curtis (dung beetles only) dissimilarity of the first (shortest inter-point distances) and fourth orders (furthest distances) between points in primary (black), secondary (dark grey) and *Eucalyptus* forest (light grey) and points on the border of the primary-*Eucalyptus* (dashed light grey) and primary-secondary forest edge (dashed dark grey)

proportion attributed to nestedness increased, a pattern observed in other Amazonian taxa (Solar et al., 2015) and evidencing a homogenization process.

4.2 | β -diversity across the edge

As a consequence of the large difference between primary and *Eucalyptus* forest communities, turnover along this habitat gradient was much higher than across the primary-secondary forest edge, where nestedness played a larger role (Figure 2). Where adjoining habitats are quite distinct from the forest, we can often see an almost complete turnover in community composition in the communities of both

ants (Ivanov & Keiper, 2010) and dung beetles (Spector & Ayzama, 2003). By contrast, secondary forests harbour a more complete subset of primary forest species than *Eucalyptus* forest in many taxa in the region, including dung beetles (Barlow, Gardner, et al., 2007; Louzada, Gardner, Peres, & Barlow, 2010), and there was some overlap between our secondary and primary forest communities for both taxa (Figure S2.11) resulting in higher values for species gain/loss across this edge.

4.3 | Effects of edge effects on within-community β -diversity

Primary forest edge communities exhibited patterns of nestedness contrasting from the expected low values. Fine-scale β -diversity was largely unaffected by edge proximity, but was elevated across larger scales (316 m and 1 km) as hypothesized (Figures 4 and 7). Unexpectedly though, the elevation was stronger at the primary-secondary than primary-*Eucalyptus* forest edge. However, unlike in habitat controls, this was a result of a large increase in the nestedness component (Figure 5) rather than any change in turnover (Figure 6), so that the nestedness component was sometimes even larger than turnover. This suggests that, as well as species replacement, differences in richness between points large distances apart were also important.

A possible explanation is that the mixing of species at the forest edge is not even along the edge's length. Instead, it suggests that there may be large patches of species originating from each community type. Within such a patch, the turnover is similar to that within the respective habitat interior, but between patches originating from opposing habitats, β -diversity would be similar to that comparing a primary forest and matrix community. This would also result in the differences in richness between points, increasing nestedness.

One possible mechanism for such a pattern could be aggressive, dominant species from disturbed habitats colonizing edge habitats, outcompeting primary forest specialists (Holway, 2005). This could potentially generate patches of communities of matrix-characteristic species of low richness in an otherwise primary forest community. At the primary-*Eucalyptus* forest edge, we may not observe this pattern as the conditions are too dissimilar to allow *Eucalyptus* species to colonize the forest habitat.

5 | CONCLUSIONS AND CONSERVATION IMPLICATIONS

We observed patterns of nestedness in primary forest close to edges quite unlike those observed in habitat interiors. This indicates that community dynamics may be altered due to edge effects even >300 m into the forest interior, possibly due to the uneven mixing of primary forest and matrix species in these habitats. Changes were particularly pronounced in primary forest bordering secondary forest, perhaps because secondary forest species are more able to tolerate primary forest conditions and vice versa. As the proportion of forest within 1 km of the edge is increasing rapidly, this may result in large

areas of remaining primary forest experiencing altered community processes. Therefore, conservation actions should carefully consider the spatial configuration of deforestation processes and remaining primary forest in order to minimize these impacts.

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ORCID

Charles J. Marsh  <http://orcid.org/0000-0002-0281-3115>

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BIOSKETCHES

Charles J. Marsh is interested in spatial ecology, focussing on the tropics, and, in particular, how ecological processes scale with observation and how we can incorporate this scaling into a better understanding of the effects of human disturbance.

Rodrigo M. Feitosa is Professor of Invertebrate Zoology and Hexapod Evolution at the Federal University of Paraná (UFPR), Brazil. His research is mainly focused on the systematics and diversity of Neotropical ants.

Author contributions: R.M.E. and C.J.M. conceived the ideas; R.M.E., J.L. and C.J.M. designed the field experiment; C.J.M. and R.M.F. identified the specimens; C.J.M. collected and analysed the data. C.J.M. led the writing with contributions from all other authors.

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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