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Many losers and few winners in dung beetle responses to Amazonian forest fragmentation

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ABSTRACT

Tropical forest fragmentation is expected to result in the loss of forest-dependent species ('losers') and proliferation of disturbance-tolerant species ('winners'). Here, we use multi-species occupancy modelling to quantify the effects of fragmentation on Amazonian dung beetles at the species and community level. We investigate the relationship between species' habitat preferences and fragmentation responses to understand how interspecific variation in fragmentation responses translates into patterns of alpha and beta diversity. We sampled dung beetles within 21 forest patches and 2 continuous forests. For each site, we quantified three fragmentation metrics (area, shape, and surrounding forest amount) and modelled their effects on species occurrence and community properties. Most species were most likely to occur within large forest patches, while surrounding forest amount had a positive impact on all species. Over 80 % of species were forest specialists and species' area responses were positively correlated with their level of forest specialization. Observed species-level responses were reflected at the community level, with greater representation of forest specialists in larger forest patches up to an 88-ha threshold, stabilizing thereafter; this threshold was met by only 1 % of patches in the landscape. Species richness also increased with patch area, although surrounding forest amount had a greater positive impact. Communities were structured by a gradient of species turnover from small to large patches, and among more isolated patches. Our findings show that most Amazonian dung beetle species become 'losers' within fragmented landscapes, particularly forest specialists. We recommend landscape-scale planning to retain forest connectivity including large forest remnants.

1. Introduction

The extent of tropical deforestation is nearing a critical point, beyond which all remaining tracts of tropical forest are expected to be rapidly fragmented (Taubert et al., 2018). Although fragmentation exerts severe impacts on tropical forest biodiversity, these effects vary widely among species (Ewers and Didham, 2006a; Haddad et al., 2015). Despite this, fragmentation ecology has historically focused on patterns of species richness (MacArthur and Wilson, 1963; Fahrig, 2003), providing little insight into the identity and prevalence of those species occurring within fragmented landscapes (Hanski, 2015; Fletcher et al., 2018). Several approaches have been proposed to deal with this shortcoming, including the use of beta-diversity metrics (Banks-Leite et al., 2012), analyses of patterns of species-specific occurrence (Hanski, 2015) and modelling forest specialist assemblages separately (Matthews et al., 2014). Here, we combine these approaches to investigate how and why species-level fragmentation responses vary within an Amazonian dung beetle fauna, and how this variation translates into changes in assemblage structure.

One factor often posited to determine how species respond to fragmentation is their level of forest specificity (Keinath et al., 2016; Pfeifer et al., 2017). Alongside reductions in the size and proximity of forest patches, fragmentation alters the biotic and abiotic properties of forest

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habitat through edge-effects (Ewers and Didham, 2006a). While many forest specialists are unable to tolerate these altered conditions, the same habitat alterations can enable the infiltration of forest patches by habitat generalists and open-habitat species from the surrounding matrix (Pfeifer et al., 2017). Furthermore, as forest becomes more fragmented, the distance between remaining forest patches often increases, as intermediate areas are replaced by matrix habitat (Taubert et al., 2018; Chetcuti et al., 2021). Resultant reductions in landscape connectivity are likely to have severe impacts on forest specialist species due to their relative intolerance to matrix conditions, limiting their ability to recolonise patches where fragmentation effects have led to localised extinction. Conversely, generalist and matrix tolerant species, which are better able to traverse the matrix, may successfully expand their distribution in the landscape (de Souza Leite et al., 2021). Accordingly, community decay within fragmented tropical forests is expected to be a non-random process, characterized by the proliferation of a few disturbance-tolerant ‘winner’ species and the extirpation of forest specialist ‘loser’ species (Tabarelli et al., 2012). Quantifying the relationship between species’ level of forest specificity and their fragmentation responses can therefore identify species of conservation concern and elucidate changes in autecological composition arising from fragmentation.

At the community level, the systematic replacement of forest specialists by generalists and open-habitat species is likely to result in a pattern of species turnover from large to small forest remnants (Tabarelli et al., 2012), as the forest core-to-edge ratio decreases. Alternatively, fragmented communities may be structured through a pattern of nested species loss, whereby communities within small forest patches represent a subset of those species found within larger, more speciose patches (Patterson, 1987). Nestedness and turnover are not mutually exclusive, and quantifying the relative contributions of both processes can provide valuable insight into how biodiversity is lost within fragmented landscapes (Banks-Leite et al., 2012; Jones et al., 2021), particularly when comparing patterns of β-diversity among several whole assemblages and their forest specialist subsets. For instance, where forest specialists within small patches have been replaced by generalists and open-habitat species, we may expect to see lower turnover and higher nestedness in the forest specialist subset compared to the overall community.

The increasingly fragmented Brazilian Amazon now contains ~9 million isolated forest patches (Montibeller et al., 2020), which have been gradually colonised by open-habitat species of several vertebrate taxa, including amphibians (Bitar et al., 2015) and mammals (Santos-Filho et al., 2012; Palmeirim et al., 2020). However, the mechanisms through which habitat fragmentation restructures Amazonian invertebrate communities remain poorly understood. This is concerning given that invertebrates perform irreplaceable ecosystem functions within tropical forests (Cardoso et al., 2011). For instance, dung beetles make vital contributions to nutrient cycling and secondary seed dispersal (Nichols et al., 2008), and their species richness often declines with decreasing patch area (Filgueiras et al., 2011). Atlantic Forest dung beetle assemblages also show patterns of species turnover from small to large forest patches, mediated by the contrasting influence of edge effects on forest specialists and disturbance-tolerant species (Filgueiras et al., 2016). However, the mechanisms driving variability in patterns of dung beetle species occurrence, and resultant changes in the structure of patch assemblages, within Amazonian fragmented landscapes are unclear.

In this study, we use multi-species occupancy modelling to assess the impact of habitat fragmentation on an Amazonian dung beetle assemblage at the species and community levels (Filgueiras et al., 2016). We sampled dung beetles in 21 forest patches and two continuous forests within a hyperfragmented region of the southern Brazilian Amazon, and quantified the effects of patch area, surrounding forest amount, and shape (a proxy for edge-effects) on the dung beetle species occurrence and community structure. We also defined a new index to quantify the forest specificity of the observed dung beetle species, based on their abundance within core forest, forest edge and matrix habitat. Using the species and community-level fragmentation responses and our forest specificity index, we address three questions: 1) are dung beetle species’ responses to forest fragmentation linked to their level of forest specificity?; 2) do patterns of species richness and β-diversity differ between the entire assemblage and only forest specialists?; and 3) do reductions in forest patch size and the amount of surrounding forest reduce the representation of forest specialist species and, conversely, increase the representation of generalist/open-habitat species?

2. Methods

2.1. Study area

Our study was conducted within a ~2700 km^2 landscape surrounding Alta Floresta, Mato Grosso, Brazil (−9.8744°S, −56.082°W; Fig. 1). The landscape historically consisted of continuous upland forest until the late 1970s, when a new road connected the region to expanding agricultural frontiers further south (Oliveira-Filho, 2001). Resultant deforestation saw forest cover decline from 91.1 % to 41.7 % between 1984 and 2004 as ~3600 km^2 of primary forest was converted into grazelands (Michalski et al., 2008). At the time of this study, the landscape contained several thousand forest patches of variable size, each embedded within a matrix almost invariably consisting of managed cattle pasture (Michalski et al., 2008) (Fig. 1).

We selected 21 forest patches within a 50-km radius of Alta Floresta and covering a maximum range of size (1.76–12,699.6 Ha), shape (1.27–2.05 Shape index), and isolation (0–71.7 × 10^6 Surrounding Forest Amount index; see Section 2.3 and Table B1) for sampling. All sampled forest patches were surrounded by a matrix of managed cattle pasture (Michalski and Peres, 2005). To provide a control from which to assess the impacts of fragmentation, we additionally sampled two continuous forest sites within the landscape (Fig. 1). Most of the sampled patches were isolated within a ~ 12-year period between the early 1980s and 2000 (Michalski et al., 2008), several years before sampling for this study.

2.2. Dung beetle sampling

We sampled each forest site between March and June 2008. Dung beetles were captured using pitfall traps, consisting of a 1 L cup, buried so the rim was level with the ground, partially filled with water and detergent, and baited with human dung, which was placed in a small plastic cup suspended above the trap. We placed pitfall trap arrays at both the centre and edge of each forest site: central arrays consisted of six pitfall traps in a hexagonal arrangement, with 10-m spacing; edge arrays consisted of three pitfall traps, spaced equidistantly along a 30-m line transect running parallel to, and 10-m in from, the forest edge. We placed one trap array at the edge and one at the centre within each patch smaller than 200 ha, and one at the edge and two at the centre of patches >200 ha and the continuous forests. We defined the centre of continuous forests as at least 1 km from the nearest natural forest edge (e.g., riverbank). We also sampled dung beetles within the pasture matrix adjacent to each forest site using arrays identical to those at forest edges but placed 50-m into the matrix. Traps were deployed for a total of 48 h. Dung beetle specimens were identified at *Laboratório* de Ecologia e Conservação de Invertebrados (Universidade Federal de Lavras) and incorporated at Setor de Entomologia da Coleção Zoológica (Universidade Federal de Mato Grosso, CEMT). The data have not been used in any form for prior research. A list of observed species is provided in Table B2.

2.3. Fragmentation metrics

We quantified the morphology and configuration of forest patches within the Alta Floresta landscape using 30-m resolution land-cover data

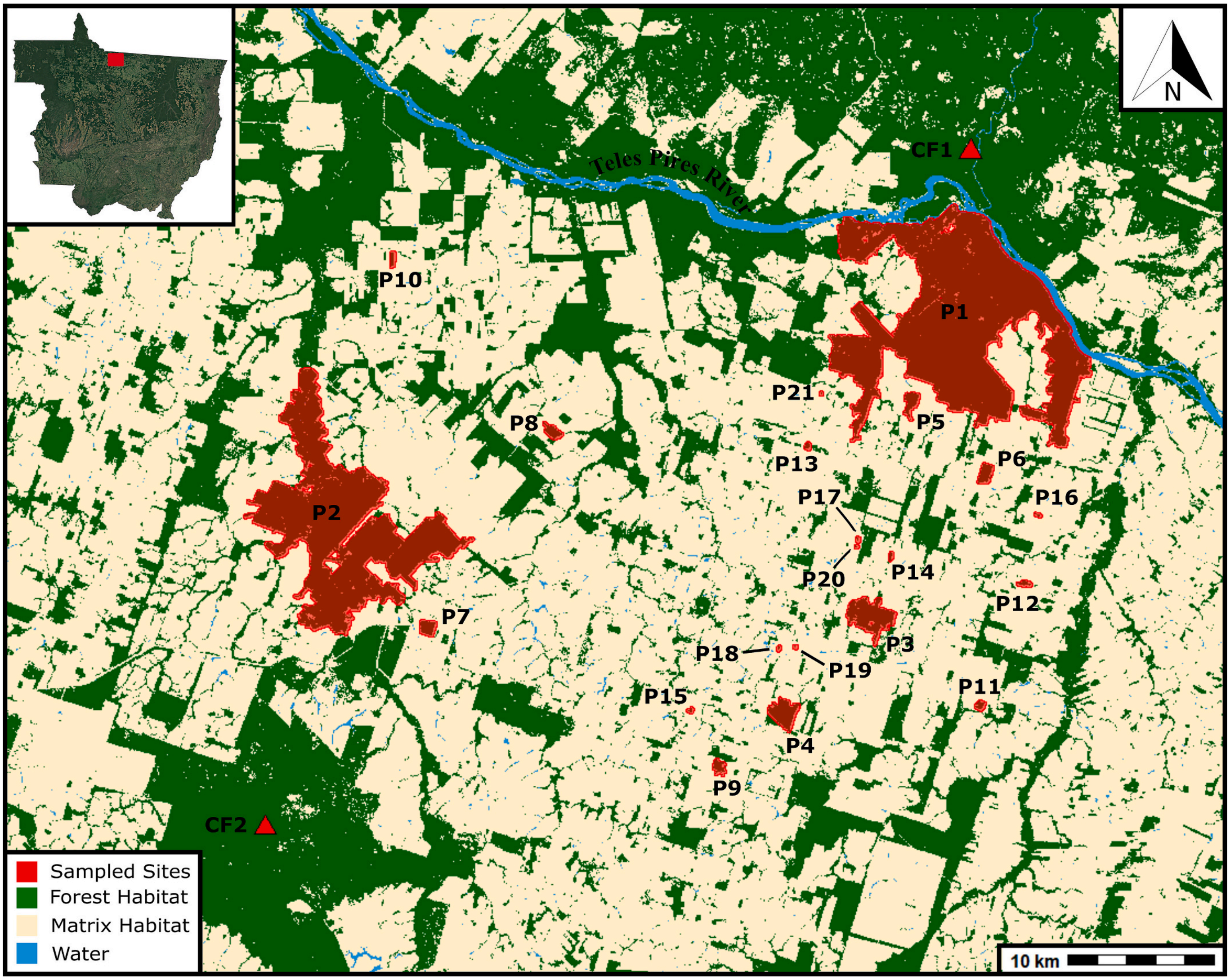

Fig. 1. The southern Amazonian study landscape in Alta Floresta, Mato Grosso, Brazil. Inset map shows the location of the study landscape (red square) in northern Mato Grosso. The 21 sampled forest patches are highlighted in red, each with a 100-m radial buffer. Patch labels are numbered in order of decreasing area. Red triangles denote the location of one of the trap arrays placed at the core of each continuous forest. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

from the same year as sampling (Souza et al., 2020). As Brazilian legislation requires landowners to set-aside forest buffers along rivers and perennial streams, several survey sites were connected to other forest patches by riparian forest corridors (Michalski and Peres, 2005) (Fig. 1). To delineate forest patches accounting for this partial connectivity, we used the marker-controlled watershed transformation to separate patches connected by corridors below a certain width. A detailed description of this method is provided in Appendix A.

We calculated three fragmentation metrics for each forest patch: area, shape, and an index of surrounding forest amount (Table B1). For forest amount, we calculated values within six different-sized radial buffers around each patch (100, 200, 500, 750, 1000, and 2500-m) and used a sensitivity analysis to select the most informative buffer size for dung beetle occupancy (see Section 2.5). Because the full extent of continuous forests cannot be discretized, we assigned control sites values for area (AREA) and surrounding forest amount (AMOUNT) one order of magnitude greater than those of the largest sampled forest fragment, and a maximally compact shape value (SHAPE) of 1 (Table B1). We subsequently log-transformed ($\log_n x + 1$) AREA and AMOUNT to improve model fits, and then centred and standardized each metric to enable us to assess their relative effects on species occurrence and community structure.

2.4. *Species forest specificities*

We defined a new index to quantify the forest specificity of each dung beetle species based on the proportion of their total abundance captured within matrix, forest edge and core forest (i.e., centre traps) habitat across all sites combined. First, to account for unequal sampling effort between habitats, we standardized the abundance of each species captured in each habitat by the number of traps placed in that habitat. We then calculated the Forest Specificity Index (FSI) of each species *i*, which we defined as:

$$\mathrm{FSI_i} = \frac{\left(\mathrm{PA_{i,m}} - \mathrm{PA_{i,e}}\right) + \left(\mathrm{PA_{i,c}} - \mathrm{PA_{i,e}}\right) - 1}{2}$$

Where $PA_{i,m}$, $PA_{i,e}$ and $PA_{i,c}$ represent the proportional standardized abundance of species *i* captured within matrix, forest edge and core forest habitat, respectively. Our index ranged between 0.0 and 1.0, indicating species exclusively captured in matrix and core forest habitat, respectively. An FSI value of 0.5 would indicate a species was equally common in core forest and matrix habitat. Intermediate values would indicate proportional weighting of species abundance toward core forest (>0.5) or matrix habitat (<0.5). We identified forest specialists as species that were never captured in the matrix (Fig. B1).

Palmeirim et al. (2021) used a similar metric to quantify the forest specificity of Amazonian mammal species within fragmented landscapes, basing their metric on raw species abundance counts within forest and matrix habitat. However, where two species occurred solely in forest habitat, but differed in abundance, using raw abundance resulted in the more abundant species being assigned a greater forest preference score, despite both species arguably exhibiting an identical level of forest specificity. By using proportional abundances, we avoided confounding interspecific variation in forest specificity and abundance.

2.5. Occupancy model

2.5.1. Model structure

We used a Bayesian multi-species occupancy model to estimate species-specific occurrence and detection probabilities, enabling us to assess patterns of species occurrence while accounting for imperfect detection in our sampling (Zipkin et al., 2009). Rarefaction suggested that sampling captured >93 % of species within each habitat type, across all sites combined (Hsieh et al., 2016) (Table B3). We therefore opted to only model the observed species (i.e., occupancy model without data augmentation). We modelled occurrence and detection probabilities at the forest site level, combining captures from traps located at the centre and edge of each forest site. To limit model uncertainty, we excluded matrix samples from modelling, as differences in species occurrence between forest and matrix habitats were expected a-priori and sampling was not designed to quantify the habitat characteristics likely to affect dung beetle occurrence within the matrix. Our model included 83 species, each detected at least once within forest sites. As occupancy models require repeat samples to estimate detection probabilities, we treated each trap within each site as individual sampling replicates (Dorazio et al., 2011). Therefore, we used a total of 9 trap replicates for each patch <200 ha and 15 trap replicates for continuous forests and patches larger than >200 ha.

We fit our model to a detection/non-detection array $Y_{i,j,k}$, with elements indicating whether each species i was detected within trap k in site j. We assumed our observed species detections $y_{i,j,k}$ to result from the imperfect observation of the true occurrence state $z_{i,j}$, a binary indicator of whether species i was truly present within site j. Therefore, we modelled our capture records as the outcome of trap-level Bernoulli trials:

$$y_{i,j,k} \sim \mathrm{Bernoulli}\left(\theta_{i,j,k} \cdot z_{i,j}\right)$$

Where, $\theta_{i,j,k}$ denotes the probability of detection of species i in trap k within site j. We then modelled true species occurrences as a site-level Bernoulli process:

$$z_{i,j} \sim \mathrm{Bernoulli}\left(\psi_{i,j}\right)$$

Where, $\psi_{i,j}$ represents the occurrence probability for species i in site j.

Species-specific detection and occurrence probabilities were specified as outcomes of the linear effects of trap and site-level covariates. We modelled species occurrence probabilities as a linear function of our fragmentation metrics, using a logit link:

$$Logit\left(\psi_{i,j}\right) = \delta_i + \beta 1_i \cdot AREA_j + \beta 2_i \cdot AMOUNT_j + \beta 3_i \cdot SHAPE_j$$

To select the most informative buffer size for AMOUNT, we used the Watanabe–Akaike information criterion (WAIC) to compare six versions of our model, sequentially including the AMOUNT index from each buffer size (Watanabe, 2010). After comparing the WAIC scores, we opted to retain the AMOUNT index from the 100-m buffers for all further analyses (Table B4). We also used WAIC to assess the performance of the full occurrence model, and all possible univariate and bivariate models. As the difference in WAIC scores between the full model and best scoring model was minimal (ΔWAIC <2; Table B4), we opted to retain the full model for analysis.

As capture prevalence of many species varied between forest core and edge habitat (Fig. B1), we assumed species detection probabilities may vary similarly. Thus, we converted trap position to a binary variable (POSITION: Core = 0, Edge = 1) and included this as a linear term in our model of species detection probabilities, using a logit link function:

$$\mathrm{Logit}\left(\theta_{i,j,k}\right) = \lambda_i + \beta 1_i \cdot \mathrm{POSITION}_{j,k}$$

We specified a joint-bivariate normal prior for the occurrence δ_i and detection λ_i model intercepts, under the rationale that more common species (i.e., with greater occurrence probability) were more likely to be detected by our sampling (Zipkin et al., 2009):

$$[\delta_i, \lambda_i | \Sigma] \sim N(0, \Sigma)$$

Here, Σ represents a 2 × 2 matrix containing the variance components of occurrence (σ_δ^2) and detection (σ_λ^2) among all species, and the covariance between the two parameters ($\sigma_{\delta\lambda}$). We incorporated hierarchical structuring by drawing all species-level parameters from community-level hyperparameter distributions (Dorazio et al., 2006; Zipkin et al., 2009), the latter specified as uninformative beta priors (1,1) for intercept hyperparameter means, normal priors (0,0.1) for slope coefficient hyperparameter means, and uniform priors (0,5) for hyperparameter variance components.

2.5.2. Derived community parameters

While multi-species occupancy models do not directly estimate community properties, community metrics can be derived as a function of posterior species-level parameters, thereby also quantifying uncertainty in metric estimates (Filgueiras et al., 2016; Zipkin et al., 2009). We thus calculated the following community metrics for each sampled site, in each model iteration:

1. Species richness: number of species *N* estimated to occur within each site:

$$N_j = \sum_{i=1}^{83} z_{i,j}$$

2. β-diversity between each pair of sites: overall pairwise dissimilarity (Sørensen dissimilarity) and its partitioned turnover and nestedness components (Baselga, 2010).
3. Community average forest specificity (cFSI): mean FSI index across all species estimated to occur within each site, weighted by their site-specific occurrence probability to account for variation in prevalence:

$$\mathrm{cFSI}_j = \frac{\sum_{i=1}^{83}\left(\psi_{i,j} \cdot z_{i,j}\right) \times \mathrm{FSI}_i}{\sum_{i=1}^{83}\left(\psi_{i,j} \cdot z_{i,j}\right)}$$

To quantify interspecific variability in forest specificity, we also calculated the occupancy-weighted standard deviation of cFSI for each site.

To determine whether impacts of fragmentation differed between forest specialists and the overall community, we recalculated species richness and the β-diversity metrics including only forest specialists, thus deriving a total of 10 site-level community metrics. Finally, we calculated the Sørensen, turnover and nestedness-resultant dissimilarity across the entire landscape (i.e., multi-site dissimilarity (Baselga, 2010)), for both forest specialists and all species combined.

2.5.3. Model fitting

We fitted our occupancy model using the 'nimble' package in R (de Valpine et al., 2022; R Core Team, 2022). Inference was derived from 4 chains of 150,000 Markov Chain Monte Carlo (MCMC) iterations, each with a burn-in of 50,000 and a thinning factor of 20. We assessed model convergence using the Gelman-Rubin Diagnostic, where values <1.1 indicate proper convergence (Gelman and Rubin, 1992).

2.6. Modelling community properties

To assess the effects of fragmentation metrics on dung beetle community structure we used Bayesian two-step regressions (Kéry and Royle, 2016), fitting separate models for each community metric, and for the overall and forest specialist communities. In all instances, we modelled the mean posterior values for each community metric x at each site j (or between each pair of sites for β-diversity metrics) as a normally distributed random variable $M_{x,j}$. For species richness, *cFSI* and the standard deviation of *cFSI*, we assumed the metric estimates to arise from the sum of the linear effects of each of our derived fragmentation metrics μ and estimation uncertainty, quantified as the posterior standard deviation of the metric estimates σ, so that:

$$M_{x,j} \sim N\left(\mu_{x,j}, \sigma_{x,j}\right)$$

$$\mu_{x,j} = \alpha0_x + \alpha1_x \cdot AREA_{x,j} + \alpha2_x \cdot SHAPE_{x,j} + \alpha3_x \cdot AMOUNT_{x,j} + \varepsilon_{x,j}$$

Where, ε represents residual error. We used a logit link function in our models of the cFSI metrics, as these were constrained to values between 0 and 1, and included a quadratic term for the effect of AREA, after visual inspection of the relationships. As the effect of AREA on cFSI increased to a plateau, we additionally implemented a changepoint regression to estimate the patch size at which AREA no longer influenced cFSI (Rukhin and Vajda, 1997), with AREA as the sole predictor. We tested whether the inclusion of a quadratic term for AREA improved performance of our models of species richness using WAIC but found no significant improvement over models including only the linear effect of AREA (ΔWAIC <2; Table B5). Finally, we modelled overall and forest specialist richness with AREA as a sole predictor (i.e., Species-Area Relationship (MacArthur and Wilson, 1963)).

To quantify the effect of fragmentation on β-diversity, we created pairwise absolute environmental distance matrices for AREA, SHAPE and AMOUNT across all sites, using untransformed values, and included these as predictor variables in models of pairwise β-diversity metrics. As community dissimilarity is often correlated with geographic distance (Nekola and White, 1999), we also included a geographic distance matrix in all models. Prior to analysis, we log-transformed (log x + 1) the AREA and AMOUNT matrices, and then centred and standardized all distance matrices. We used a logit link function in all β-diversity models. We used WAIC to compare versions of our β-diversity models including either a linear or quadratic effect of the pairwise difference in AREA. Based on the results, we opted to include a quadratic term for AREA in our models of species turnover only (see Table B5).

To determine whether the effects of fragmentation differed between the two communities, we refitted the richness and β-diversity models to a concatenated dataset of the metric estimates for both assemblages. We additionally included interaction terms between each of our fragmentation metrics and a binary community variable (COMMUNITY: OVERALL = 0; FOREST SPECIALIST = 1), which was also included as a fixed effect. Where the 90 % credible intervals of the interaction terms or the community effect overlapped 0, we took this to indicate there was no significant difference between the communities in the corresponding coefficient.

2.7. Species occurrence patterns

To investigate the relationship between species' fragmentation responses, quantified as the posterior means of the occurrence model coefficients (δ_i, $\beta1_i$, $\beta2_i$, $\beta3_i$), and their FSI, we constructed four Bayesian two-step regressions using the same framework as the community-level models, with FSIas a sole predictor variable in each case. We again inferred 'significance' of coefficients whenever their 90 % Bayesian credible intervals excluded 0.

Full specification for all models is available in Appendix C.

3. Results

3.1. Sampling and imperfect detection

We captured 24,941 dung beetles (Forest = 24,032; Matrix = 909), representing 86 species (including 33 morphospecies) and 19 genera (Table B2). Occupancy modelling suggested that observed site-level species richness underestimated true richness by 5.44 ± 2.0 species on average (mean of median richness estimates ± SD; Fig. B2). The estimated number of sites occupied by each species was an average of 1.19 ± 1.42 (mean of median estimates ± SD) higher than observed (Fig. B3).

3.2. Patterns of species occurrence

FSI values of the observed species ranged from 0 to 1, including 28 species captured exclusively within core forest ($FSI_i = 1.0$) and three species captured exclusively within matrix habitat ($FSI_i = 0.0$). In total, 46 species exhibited preference toward core forest ($0.5 < FSI_i < 1$) and nine species exhibited preference toward matrix habitat ($0 < FSI_i < 0.5$). Sixty-seven species were never observed in the matrix and were classified as forest specialists (Fig. B1).

Across all 83 modelled species, species occurrence probability tended to increase with both patch size (mean of mean $\beta1_i$ estimates = 0.26) and surrounding forest amount (mean $\beta2_i = 0.61$). We also found a negative association with patch shape complexity, although the effect size was small (mean $\beta3_i = -0.03$; Fig. B4). Increasing forest patch size had a positive effect on the occurrence probability of 56 species and a negative effect on 27 species (range of mean β estimates = −1.04–1.68), while all modelled species showed a positive response to surrounding forest amount (mean β range = 0.54–0.68). Patch shape complexity had a negative effect on the occurrence probability of 73 species and a positive effect on 10 species, although the magnitude of these effects was small (mean β range = −0.11–0.08; Fig. B4).

Across all modelled species, we observed a significant positive effect of FSI on species' responses to patch size (mean β coefficient = 0.16), so that species with a preference for core forest tended to be more likely to occur within large forest patches, while matrix-tolerant species were more likely to occur within small patches (Fig. 2). FSI had no significant effect on species' responses to surrounding forest amount, patch shape, or species' average occurrence probability (Fig. B5).

3.3. Community properties

3.3.1. Species richness

Our species-area relationships indicated that patch size had a significantly positive impact on species richness (OVERALL: mean β = 2.62; FOREST SPECIALISTS: mean β = 2.39), but this effect did not differ significantly between the overall and forest specialist assemblages (Fig. 3a-c). In our multivariate models, the mean effect of patch size on species richness was notably greater than zero for both assemblage types, but these effects were not significant. Local assemblages were, however, significantly more species-rich in less isolated patches (i.e., those surrounded by more forest habitat) for both the overall (mean β = 7.47) and forest specialist assemblages (mean β = 6.34; Fig. 3d). Area effects were substantially weaker than those of surrounding forest

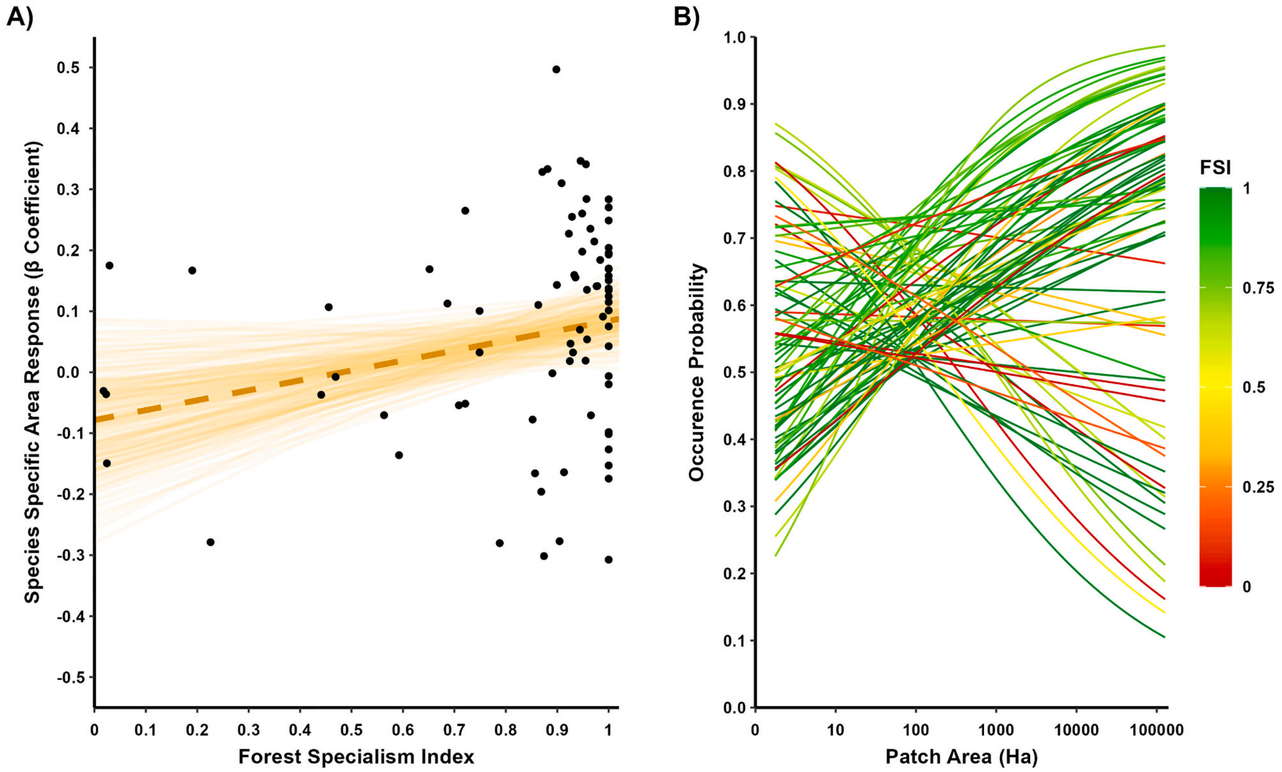

Fig. 2. Effect of species-specific Forest Specificity Index (FSI) values on species responses to forest patch area. A) Bayesian two-step regression of the effect of species' FSI on their mean posterior area response from the multi-species occupancy model. Dashed line represents the posterior mean intercept and slope estimates. Faint lines represent a random sample of the posterior coefficient estimates. B) Mean estimated change in species-specific occurrence probabilities with patch area. Each line represents one species. Lines are colour-coded by the FSI score of different species.

amount across both assemblages. The effects of fragmentation metrics on species richness did not differ significantly between the two assemblage types (Table B6).

3.3.2. *β-diversity*

In both the overall and forest specialist assemblages, pairwise Sorenson dissimilarity was significantly positively associated with pairwise differences in patch size (Overall: mean $\beta = 0.15$; Forest specialists: mean $\beta = 0.21$), but significantly negatively associated with pairwise differences in surrounding forest amount (Overall: mean $\beta = -0.15$; Forest specialists: mean $\beta = -0.21$; Fig. 4a, Fig. B6). The magnitude of the effects of patch size and surrounding forest amount on Sorenson dissimilarity were similar within both communities. Species turnover was also significantly negatively associated with pairwise differences in surrounding forest amount (Overall: mean $\beta = -0.32$; Forest specialists: mean $\beta = -0.40$; Fig. B6). Pairwise difference in patch size exhibited a positive, curvilinear relationship with species turnover in both communities, so that the rate of increase in turnover increased with pairwise differences in patch area over 100 Ha (Fig. 4). Nestedness-resultant dissimilarity was significantly positively associated with pairwise differences in surrounding forest amount in both communities (Overall: mean $\beta = 0.35$; Forest specialists: mean $\beta = 0.36$; Fig. B6).

Species turnover accounted for a greater proportion of pairwise (Fig. 4b-c) and landscape-scale (mean posterior estimates: Overall: Sorenson = 0.82, Turnover = 0.72, Nestedness = 0.10; Forest specialists: Sorenson = 0.83, Turnover = 0.72, Nestedness = 0.12) community dissimilarity than nestedness in both the overall and forest specialist communities. None of the fragmentation effects on β-diversity differed significantly between the overall and forest specialist communities (Table B6), although community itself had a significant positive effect on Sorenson (mean β coefficient = 0.11) and nestedness-resultant dissimilarity (mean β coefficient = 0.14), suggesting that total pairwise dissimilarity and nestedness were greater across forest specialist assemblages than for all species combined, although these effects were small (Fig. 4; Table B6). Multi-site β-diversity did not differ significantly between the two communities (overlapping 90 % credible intervals).

3.3.3. *Community-level forest specificity*

We found a curvilinear relationship between cFSI and patch size, with the representation of beetle species exhibiting preference for core forest habitat increasing from small- to medium-sized patches. The slope then lessened and became slightly negative in patches larger than ~100 ha. Patch shape and surrounding forest amount did not have a significant effect on cFSI (Fig. 5). The association between patch size and cFSI was better explained by our changepoint model, which suggested that cFSI increased with patch area until a threshold of 88.45 ha (mean posterior estimate) and then plateaued (Fig. B7). Variability in FSI was similar within all sites, reflected in the small range of standard deviations of cFSI (range of mean cFSI SD estimates = 0.17–0.23), which was unaffected by our fragmentation metrics (Fig. B8).

4. Discussion

Our results indicate that forest fragmentation resulted in local extinctions in almost all dung beetle species in the Alta Floresta landscape. Local extinctions were particularly prevalent within the cattle pastures that now dominate the region (Michalski et al., 2008); over 80 % of all species were never detected in the matrix, a proportion similar to that in Amazonian forest-pasture landscapes elsewhere (Silva et al., 2017). Within forest patches, most species showed increasing occupancy with patch area and surrounding forest amount, in line with previous findings that area and isolation effects are the leading drivers of dung beetle species losses within fragmented tropical forest landscapes (Filgueiras et al., 2011; Larsen et al., 2007; Storck-Tonon et al., 2020). Importantly,

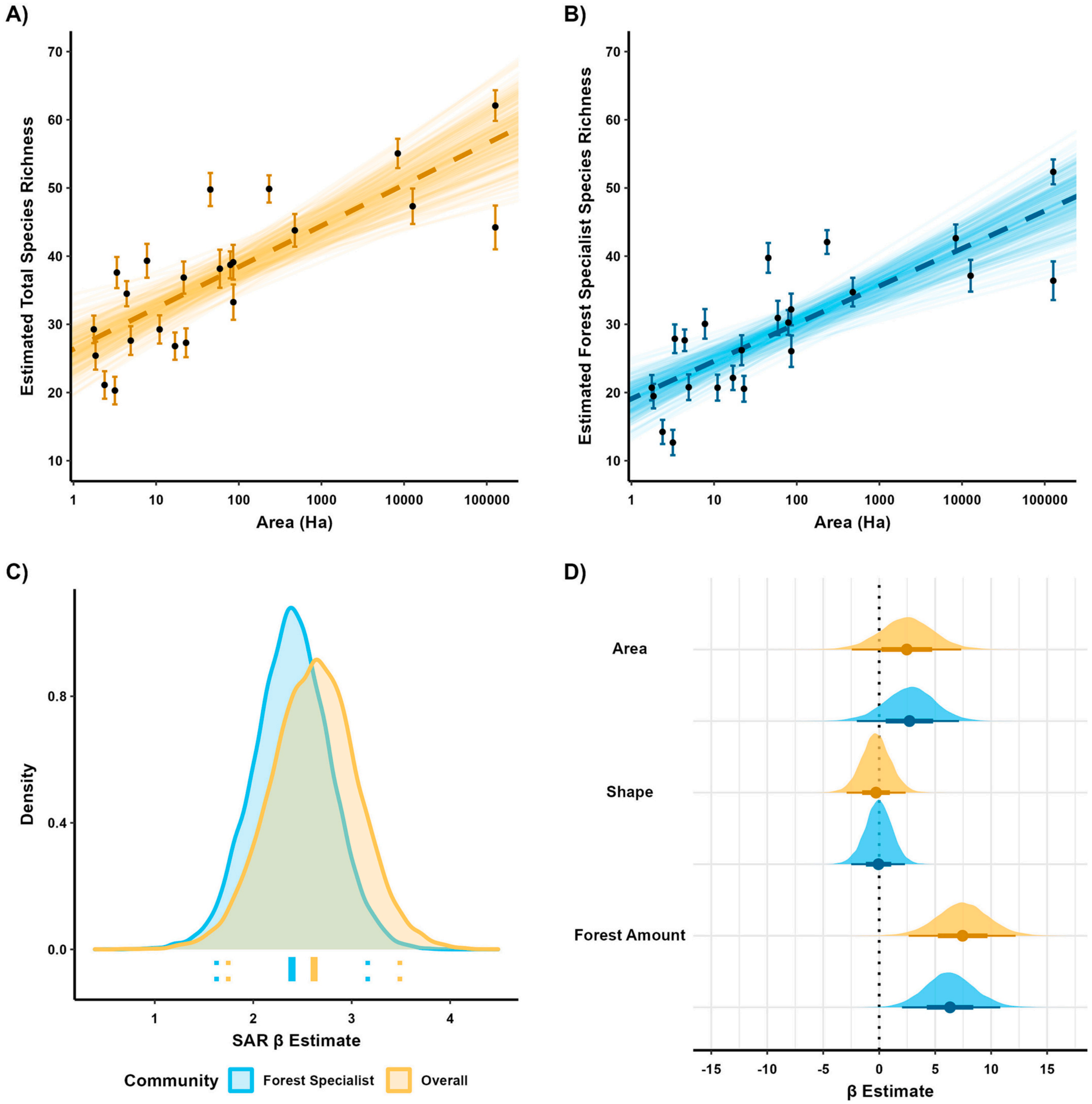

Fig. 3. Species-area relationships (A, B, C) and the results of our multivariate models of species richness (D). A) Species-Area Relationship (SAR) for the overall community (all species combined); and B) only forest specialist species. In A and B, dashed lines represent the posterior mean intercept and slope estimates, and faint lines represent a random sample of the posterior coefficient estimates. C) Density plot of the posterior SAR slope coefficient estimates for the forest specialist and overall communities. Solid and dotted lines represent the mean coefficient estimate and the 90 % credible intervals, respectively. D) Density plots of the posterior slope coefficient estimates from our multivariate models of species richness. Dots represent the posterior mean coefficient estimates and whiskers represent the 50 % (thick whisker) and 90 % (thin whisker) credible intervals.

species' area responses were positively correlated with their degree of forest specificity, and the assemblage-level representation of forest specialists decreased markedly in patches smaller than 88.5 ha. Communities were primarily structured by a pattern of species turnover, indicative of small and isolated fragments becoming increasingly compositionally different to the original forest habitats, likely through the colonisation of non-forest specialists. However, there were no differences in patterns of community structure between the overall community and its forest specialist subset.

4.1. *Species-level fragmentation responses*

Declining patch sizes led to an overall reduction in the occurrence probability of forest specialist species and increases in ubiquitous matrix-tolerant species (Fig. 2). Interestingly, the magnitude of positive area responses was generally greater than that of negative area

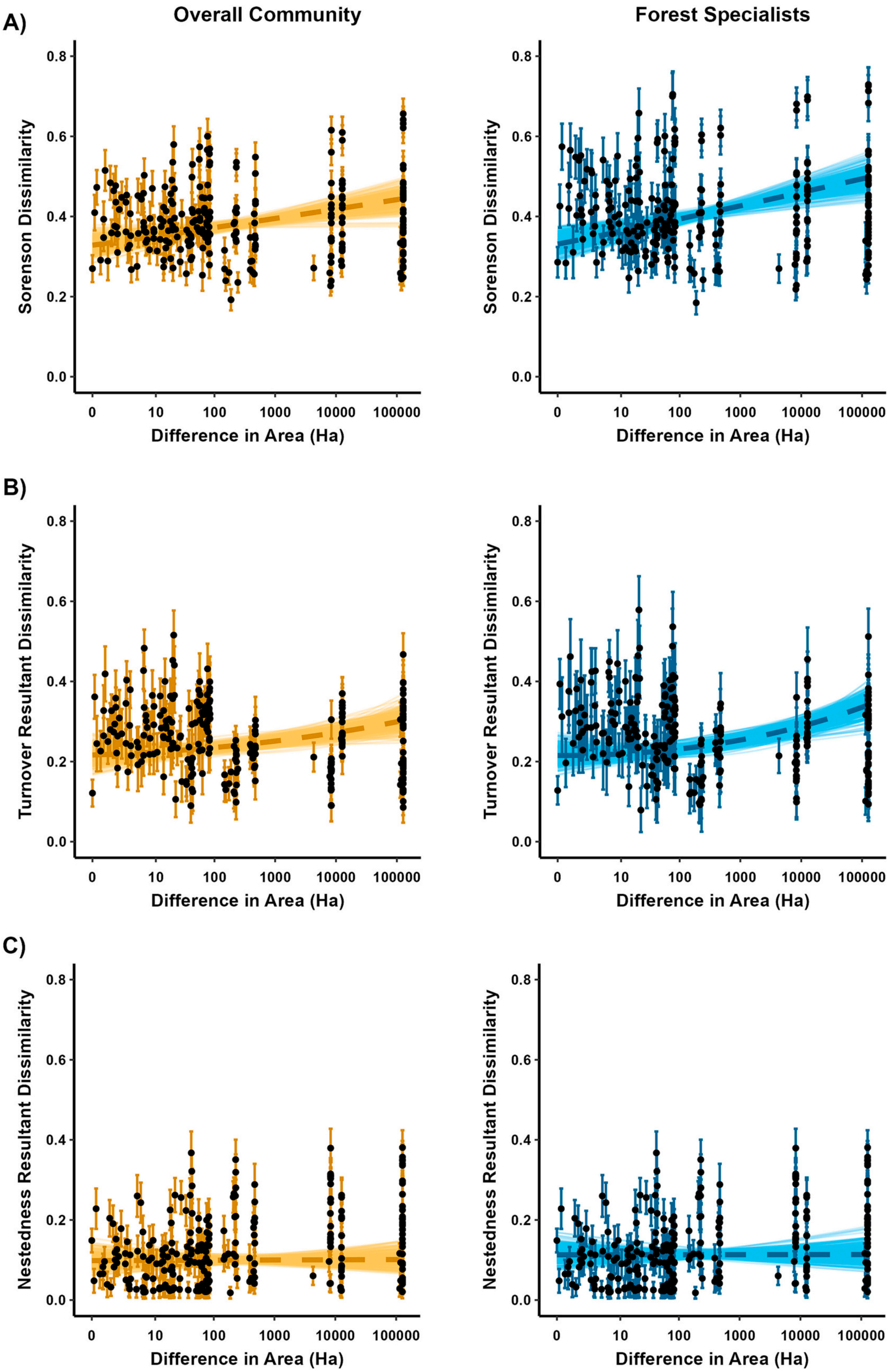

Fig. 4. Effects of pairwise differences in forest patch size on pairwise Sorenson dissimilarity (A), species turnover (B), and nestedness (C), for both the overall and forest specialist communities. Estimated effects were obtained from multivariate models including all pairwise fragmentation metrics and the pairwise geographic distances between forest sites as predictors. Dashed lines represent the posterior mean intercept and slope estimates. Faint lines represent a random sample of the posterior coefficient estimates. Error bars represent the 90 % credible intervals of the β-diversity metric estimates.

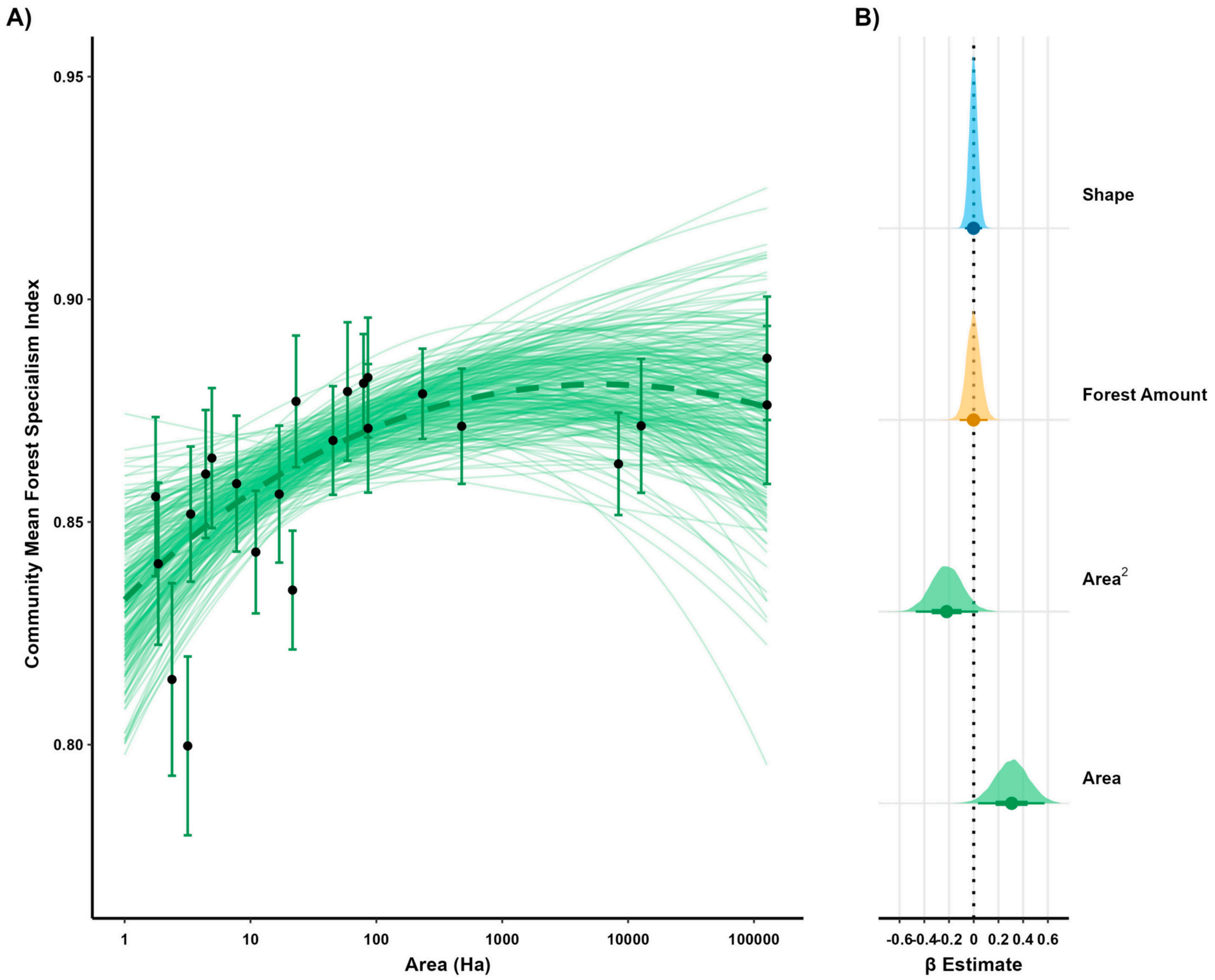

Fig. 5. The effect of each of our fragmentation metrics on community weighted mean Forest Specificity Index (cFSI). A) The quadratic relationship between cFSI and forest patch size obtained from a Bayesian two-step regression model including all fragmentation metrics as predictors. Dashed line represents the posterior mean intercept and slope estimates. Faint lines represent a random sample of the posterior coefficient estimates. Error bars represent the 90 % credible intervals of the cFSI estimates. B) The posterior distribution of the coefficient estimates for the effects of each of our fragmentation metrics on cFSI. Dots represent the posterior mean coefficient estimates and whiskers represent the 50 % (thick whisker) and 90 % (thin whisker) credible intervals.

responses (Fig. B4), suggesting that patch size was a greater limiting factor for species with larger spatial requirements. This is consistent with previous studies showing that forest specialist dung beetles are more sensitive to fragmentation than generalist species (Pinto Leite et al., 2018; Silva et al., 2019) and that a subset of species is confined to continuous forest and the largest habitat remnants (Larsen et al., 2007; Driscoll and Weir, 2005). These trends are concerning given that large forest tracts within the Alta Floresta landscape continue to be converted into smaller patches (Palmeirim et al., 2020; Michalski et al., 2008), a pattern that is widespread throughout the Amazon (Montibeller et al., 2020).

The pervasive effect of surrounding forest amount across our sampled species suggests that inter-patch dispersal may be a key limiting factor for species occurrence. We found that the size and proximity of forests within a 100-m radius of each patch had the greatest influence on species occurrence, a relatively short distance compared to the >1 km buffers often used in other studies (Jones et al., 2021; Palmeirim et al., 2020). Our buffer size aligns with the known dispersal ranges of dung beetles: although some beetles may disperse up to 1.7 km (Cultid-Medina et al., 2015), most tropical forest species only travel 50–100-m within a few days (Silva and Hernández, 2015). Dispersal capacities may also be limited by the relative hostility of the cattle pasture matrix (Silva et al., 2017; Nogueira et al., 2021): forest specialist dung beetles rarely traverse open-habitat matrix areas (Nichols et al., 2008; Silva et al., 2017; Pinto Leite et al., 2018) and closed-canopy habitat has been shown to be more permeable (Sánchez-de-Jesús et al., 2015). Wide forest habitat corridors can facilitate dispersal across forest patches and are compatible with landowner compliance with legally required set-asides (Zimbres et al., 2018). Forest specialist dung beetles in Borneo have been shown to use habitat corridors (Gray et al., 2021), but further research is required to determine the extent of corridor use by Amazonian species.

Among forest specialists, 40 % were only detected within core forest habitat (Fig. B1) and were thus likely to be edge-sensitive (Pfeifer et al., 2017). However, patch shape, a proxy of the extent of edge effects, had minimal influence on species' occurrence. Given that the core-to-edge ratio increases with forest patch size, patch size itself may have captured some variation in species occurrence resulting from edge effects (Jones et al., 2021; Banks-Leite et al., 2010). Indeed, previous studies have shown a substantial species turnover in Amazonian dung beetle communities along forest edge-interior gradients (Silva et al., 2017; Marsh et al., 2018). Further work may help elucidate the separate contributions of edge and area effects to species-specific patterns of dung beetle occurrence along forest edge gradients (Ewers and Didham, 2006b), particularly in forest-pasture mosaics, where data are lacking. This could include the use of interaction terms between patch size and shape to elucidate any synergistic effects of the two variables. As our sample size (23 sites) was insufficient to incorporate such an interaction term, we also recommend future studies sample a larger number of forest sites to leverage greater statistical power.

4.2. Community-level fragmentation responses

Our finding of a marked decline in forest specialist representation in patches below a threshold of 88.5-ha is nearly identical to the 84-ha extinction threshold detected for sensitive dung beetle species in Venezuelan land-bridge forest islands (Larsen et al., 2007). This is similar to the patch sizes required by sensitive species of large-bodied tropical taxa, including birds (Jones et al., 2021) and mammals (Michalski and Peres, 2007), which would typically be expected to have much larger spatial requirements (Crooks et al., 2017). Forest specialist dung beetles thus show a strong and potentially nonlinear response to habitat patch size, whether this be due to their own habitat requirements or their dependence on large-bodied vertebrates for dung (Bogoni et al., 2019). Based on our delineated forest map, only 1 % of patches within the Alta Floresta landscape would meet the area threshold required to maintain a naturalistic community of forest specialist species. Even patches around this size-threshold would be expected to lose 12 forest specialist species, and 13 species overall, compared to continuous forest. Nonetheless, as is common of most fragmented tropical forest landscapes (Taubert et al., 2018), there are relatively few large forest remnants within the Alta Floresta region, and there is therefore residual uncertainty about species occurrence within forest between 500 and 8000 Ha (Fig. 3). Future research may thus help to determine whether intermediate sized forest patches may also serve as a haven for sensitive species.

Community dissimilarity was largely driven by species turnover, suggesting that β-diversity contributed substantially to regional species richness, reflecting patterns observed among dung beetle assemblages in fragmented Atlantic Forest (Filgueiras et al., 2016). Turnover increased with the pairwise difference in patch size in the overall and forest specialist assemblages. Given the low contributions of nestedness to community structuring across both assemblages, our results indicate that community composition varied substantially along the gradient of patch size, with small habitat patches hosting a substantially different set of species to large patches and continuous forests. Therefore, although small patches may make contributions to regional richness, their conservation value is likely limited, given that the species they retain are unlikely to be typical of natural forest communities. Indeed, while patterns of β-diversity did not differ between the overall and forest specialist assemblages, the positive association between patch size and forest specialist richness, and the reduction in community mean FSI observed within patches <88.5 Ha, would suggest that forest specialist species were lost within small forest patches, likely being replaced by disturbance-tolerant species.

In contrast to previous studies, which generally find that effects of fragmentation are more severe among forest specialists (Matthews et al., 2014), community patterns were consistent between the overall and forest specialist dung beetle communities. While our findings could suggest that impacts of habitat fragmentation on dung beetles are unrelated to species' forest specificity values at the community level, the observed trends are more likely because >80 % of all studied species were classified as forest specialists, thereby making a disproportionate contribution to community structuring. Furthermore, many forest specialist species may already have been extirpated from the largest forest patches and continuous forest sites, given that our sampling was conducted 32 years after deforestation began within the Alta Floresta landscape (Oliveira-Filho, 2001), thereby homogenising community composition between small and large patches (Matthews et al., 2014). Nonetheless, while the sampled patches were isolated within a relatively short period of each other, and several years before sampling occurred, there is currently little information on how Amazonian dung beetle assemblages change through time after initial isolation. The substantial proportion of dung beetle species classified as forest specialists may thus also reflect species extinction debts that have yet to be realised, with concomitant effects on the assemblage level trends observed here (Krauss et al., 2010). Further investigation focusing on how changes in tropical forest dung beetle assemblage structure and species-specific occurrence manifest through time after fragmentation may could elucidate the effects of patch size, shape and isolation (Krauss et al., 2010).

To our knowledge, this is the first study to model the relationship between invertebrate species' level of forest specificity and their fragmentation responses, and to compare patterns of beta diversity between an overall invertebrate community and its forest specialist subset. It is thus uncertain whether the observed lack of difference fragmentation effects on the overall and forest specialist communities reflects a wider trend in fragmented invertebrate communities, and further research may help clarify how the relationship between species' forest specificity values and fragmentation responses vary geographically and taxonomically among invertebrate communities. By enabling researchers to quantify levels of forest specificity based on primary data alone, our forest specificity index may serve as a useful tool for this purpose, in combination with occupancy modelling. Nonetheless, researchers may wish to consider some adjustments to sampling. For instance, the relatively lower sampling effort within matrix habitat may have led to the misclassification of some species that can use matrix habitat as forest specialists, with concomitant effects on the observed community trends. Although sample coverage was generally high within matrix habitat sampled here (Table B3), future studies may wish to use a more equally distributed sampling design. Furthermore, it is important to consider that while rarefaction suggested our sampling was >93 % complete within all habitats (Table B3), this only represents the percentage of species that were susceptible to capture using pitfall traps baited with human dung. Human dung is known to attract most Amazonian dung beetle species (Marsh et al., 2013) and we were satisfied that sampling was thus sufficient to link species and community level fragmentation responses. However, where studies aim to analyse dung beetle assemblages in their entirety, researchers may also consider using a mixture of dung bait (Marsh et al., 2013) and deploying other trap types in combination with pitfalls, such as flight intercept traps.

4.3. Conclusions

Forest cover is essential for the persistence of almost all Amazonian dung beetle species studied here. As total forest cover and forest patch sizes continue to decline throughout the Amazon (Montibeller et al., 2020), the amount of forest habitat within proximity of each patch will decline concomitantly (Taubert et al., 2018). Our findings suggest that the resulting combination of area and isolation effects amounts to a 'perfect storm' for Amazonian dung beetles, resulting in widespread local extinctions of all species that utilise forest habitat, especially forest specialists. Accordingly, to retain dung beetle diversity and associated ecosystem services, we suggest that focus should be placed on maintaining large forest tracts of at least 88 ha, but ideally >1000 ha, within close proximity (<100 m) to each other. Further research exploring ways to facilitate inter-patch dispersal of insect faunas is essential to optimise landscape design within expanding deforestation frontiers. Finally, regional dung beetle diversity would also benefit from conservation efforts targeting forest specialist species.

CRediT authorship contribution statement

Ciar D. Noble: Conceptualization, Methodology, Software, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **James J. Gilroy:** Conceptualization, Validation, Writing – review & editing, Supervision. **Erika Berenguer:** Investigation, Data curation. **Fernando Z. Vaz-de-Mello:** Investigation, Data curation, Resources. **Carlos A. Peres:** Conceptualization, Methodology, Data curation, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The code for all statistical models is provided as a supplement in Appendix C. All other code is available from the correspondence author upon request. The data used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110024.

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