RESEARCH ARTICLE

Insect herbivores and soil fertility drive variation in density-dependent seedling dynamics across a fragmented landscape

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Abstract

1. Habitat fragmentation is associated with decreased species diversity. However, the effects of fragmentation on the processes that maintain diversity, such as enemy-mediated negative conspecific density dependence (CDD), are largely unknown. We examined how negative CDD in seedling survival is influenced by habitat fragmentation.
2. We measured the effect of conspecific density on seedling survival of 30 species for 10 years on 25 islands in an artificially fragmented habitat and took parallel measurements of the potential drivers: soil physical and chemical properties, and insect herbivore communities.
3. Increasing densities of conspecific trees and seedlings reduced seedling survival more on larger and more isolated islands. These processes were linked to increases in insect herbivore richness on larger islands, and less fertile soils on more isolated islands.
4. *Synthesis*. Our results indicate that shifts in the abiotic and biotic conditions of fragmented habitats can modify the mechanisms thought to maintain species coexistence, perhaps contributing to the long-term decay of fragmented ecosystems, and suggesting approaches for restoration. The relationships between island configuration, and insect herbivore communities and soil properties may vary among ecosystems, which could help explain variation among studies in the effects of fragmentation on biodiversity.

KEYWORDS
anthropogenic impacts, habitat fragmentation, Janzen–Connell hypothesis, plant–enemy interactions, plant–soil interactions

1 | INTRODUCTION

Human activity is transforming a large and growing proportion of the world's forest ecosystems (Haddad et al., 2015; Laurance et al., 2012; Scott et al., 2022). A notable challenge for ecologists is assessing how well ecological theory, which has often been developed without explicitly considering anthropogenic disturbance, applies to human-modified habitats (e.g. how are coexistence mechanisms modified in human-modified habitats). Prominent among these modifications is the division of continuous forest into smaller, disconnected patches, a process known as habitat fragmentation (Haddad et al., 2015; Ma et al., 2023). Although there is debate over whether habitat

fragmentation contributes to diversity declines (Haddad et al., 2015; Riva & Fahrig, 2023), recent work indicates that decay of ecosystems in small habitat patches plays a role (small patches tend to have lower biodiversity than that expected based solely on their area) (Chase et al., 2020; Gonçalves-Souza et al., 2025; Riva & Fahrig, 2023).

One possible mechanism for ecosystem decay in fragmented forests is the disruption of interactions between plants and their enemies (e.g. plant-pathogens and insect herbivores) (Krishnadas et al., 2018; Viswanathan et al., 2020). Habitat fragmentation influences plant–enemy interactions via multiple mechanisms. There is evidence that herbivory reduces vegetation abundance and plant diversity more in degraded fragments (Morante-Filho et al., 2024; Xu et al., 2023). However, the impacts of enemies on plant diversity will depend on the distribution of their effects on common and rare plant species, which depends, in turn, on the species composition of enemy communities. There is increasing evidence that the diversity of insect herbivores, bacteria and fungi are reduced by habitat fragmentation (Grilli et al., 2017; Kiesewetter et al., 2023; Rossetti et al., 2017; Vannette et al., 2016), with dietary specialists disproportionately lost from small fragments (Bagchi et al., 2018; Mickley et al., 2025; Rossetti et al., 2017; Valladares et al., 2006). Specialist natural enemies are especially important for mediating density-dependent regulation of their host plant populations. The negative effects of host-specific natural enemies on plants tend to intensify as proximity to parent trees and conspecific density increases (Bagchi et al., 2014; Downey et al., 2018; Forrister et al., 2019), driving negative conspecific density dependence (CDD) in plant survival and growth. This negative CDD reduces the performance of locally dominant plant species and allows rarer, potentially less competitive, species to establish and persist, promoting species diversity (Connell, 1971; Janzen, 1970). Given the pivotal role that negative CDD appears to have in maintaining plant diversity (Comita et al., 2014; Hülsmann et al., 2021; LaManna et al., 2017), altering natural enemy communities in ways that weaken it in smaller and more isolated forest patches may erode diversity over the long term. Indeed, weaker negative CDD due to weaker interactions between fungal pathogens and insect herbivores and plants, and consequently lower plant diversity, has been observed at forest edges (Krishnadas et al., 2018) and in small forest patches (Viswanathan et al., 2025) at a site in South India. Understanding the extent to which fragmentation degrades enemy-mediated density dependence in general is a critical task for ecologists.

Habitat fragmentation can also affect microenvironments, with higher temperature (Ewers & Banks-Leite, 2013) and lower soil moisture (Baidya Roy, 2011) recorded in smaller forest patches, and slower nutrient cycling in smaller (Didham, 1998) and more isolated habitats (Kiesewetter et al., 2023). These shifts in environmental conditions could affect plant–enemy interactions, thereby altering CDD and the plant diversity it enhances. Both antagonistic (plant-pathogens) (Joachin et al., 2023; Liu & He, 2019; Milici et al., 2020; Rudgers et al., 2020) and mutualistic (some plant-fungi/bacteria) (Hersh et al., 2012; Revillini et al., 2016) interactions are sensitive to soil fertility and moisture, often becoming more antagonistic or less

beneficial as soil fertility and moisture increase. Wetter conditions may promote dispersal of and infection by many plant-pathogens (Barrett et al., 2009; Garrett, 1970). Furthermore, defence investment by plants tends to increase in stressful conditions, where tissue lost to enemies is more costly to replace (Fine et al., 2006; Lynn & Fridley, 2019; Moreira et al., 2018; Quigley et al., 2020). Thus, both increased soil moisture and soil fertility can enhance negative CDD (Comita et al., 2014; LaManna et al., 2016). However, some studies have found the opposite result, with stronger negative CDD in less fertile and drier areas (Brown et al., 2021; Cao et al., 2018), probably due to intensified intraspecific competition for limited resources (Tilman et al., 1982). Additionally, under certain nutrient-poor conditions, plants may prioritize growth over defence through resource allocation trade-offs to secure limited resources (Brown et al., 2021; Coley et al., 1985; Herms & Mattson, 1992; Zhong et al., 2021). Simultaneously, drought stress can exacerbate herbivory pressure on plants (Weissflog et al., 2018). The links between environmental conditions and both fragmentation and negative CDD suggest potential mechanisms through which fragmentation may affect enemy-mediated density dependence.

Here, we monitored tree communities and seedling survival of 30 species for 10 years on 25 islands of the Thousand Island Lake, China (TIL, Figure S1). We also took parallel measurements of soil fertility, soil moisture and insect herbivore communities on the islands. We used these data to ask two questions: (1) How do island area and isolation influence the effects of conspecific density on seedling survival? (2) Does variation in soil properties and insect herbivore communities associated with island area and isolation contribute to altered effects of conspecific density on seedling survival? We found that (1) the negative effects of conspecific tree density on seedling survival were stronger on larger islands; (2) conspecific seedling density had more pronounced negative effects on seedling survival on larger islands, which was linked to more species-rich insect herbivore assemblages; and (3) conspecific seedling density had stronger negative effects on seedling survival on more isolated islands, which could be attributed to reduced soil fertility on more isolated islands.

2 | MATERIALS AND METHODS

2.1 | Study site

The study was conducted within Thousand Island Lake, located in Chun'an County, Zhejiang Province, China (29°22′–29°50′N, 118°34′–119°15′E). TIL is an artificial fragmented habitat formed by the construction of a large reservoir in 1959 with 1078 land bridge islands (area ≥ 0.25 ha). The forests were cleared during dam construction, and the islands are now mostly covered with secondary successional forest dominated by *Pinus massoniana* in the tree layer, and *Loropetalum chinense* and *Vaccinium carlesii* in the understorey (Liu et al., 2018). TIL lies in the subtropical monsoon climate zone. Between 2011 and 2020, the mean annual temperature was 17.8°C

(temperature range −7.1°C–40.2°C), and the mean annual precipitation was 1428.4 mm (unpublished data). All studied islands are surrounded by water, which clearly demarcates habitat edges. No fieldwork permits or animal ethics approvals were required for this study.

2.2 | Plant community

Following Hu et al. (2016), we selected 25 islands in 2009 and measured their area and isolation (distance to mainland) using ArcGIS 9.3 (Table S1). We divided the 25 islands into two groups: the 16 small islands (area < 1 ha) and the nine large islands (area ≥ 1 ha). Plots encompassing the entire forest-covered areas (175–6950 m²) on small islands and plots ranging from 0.5 ha to 1.5 ha on large islands were divided into 5 m × 5 m subplots. The plot areas on large islands were sufficient to capture most woody plant species (Yu et al., 2012). In all plots, woody trees with a diameter at breast height (DBH) ≥ 1 cm were tagged, identified, measured and mapped. The first surveys were completed in 2009 (small islands) and 2010 (large islands). Subsequent resurveys were completed in 2014 (small islands) and 2015 (large islands) and 2019 (all islands).

2.3 | Seedling survey

We established 1–39 seedling plots (1 m × 1 m) within each island's tree plot in 2011, based on the island area and an area-dependent proportional sampling procedure (Borges et al., 2009). These seedling plots were distributed randomly and at least 10 m from the edge of the tree plots. The first survey of the total 306 seedling plots was completed in spring 2011, with subsequent surveys conducted in every fall (October) and spring (April) from 2011 to spring 2020. At each survey (total 19 surveys), all woody seedlings with DBH < 1 cm were tagged, mapped, identified to species, and their stem height and number of leaves were recorded.

2.4 | Soil properties

Soil properties were measured in 2015 (Liu et al., 2018) and 2019 (using the same methodology). Soil fertility was characterized by measurements of total carbon (TC, %), total nitrate (TN, %) and total phosphorus (TP, mg/kg). Nitrogen and phosphorus represent the most important soil-borne nutrients for plant growth (Jiang et al., 2019), and soil carbon measures the organic content of soil (Jackson et al., 2017). Soil TC/TN/TP refers to the sum of all forms of carbon/nitrogen/phosphorus elements in the soil, which can characterize the difference in nutrient pools in soils at different locations. We quantified five moisture properties (soil water holding capacity): soil maximum water holding capacity (MWHC, g/kg), capillary water holding capacity (CWHC, g/kg), mass moisture content (MMC, g/kg), water conversion factor (WCF) and soil density (SD, g/cm³). Soil water holding capacity refers to the ability of soil to absorb water. It is a combination of the capillary attraction of soil pores and the molecular attraction of soil particles. It can characterize the difference in soil moisture at different locations in the same region under various precipitation/air humidity conditions. We divided each tree plot into adjacent 10 m × 10 m soil sampling plots for small islands, and into adjacent 20 m × 20 m soil sampling plots for large islands. A subset of these sampling plots was selected for soil measurements to obtain an even coverage of the tree plot (Liu et al., 2018). We matched each seedling plot to the nearest soil sampling plot (distances ranged from 0 to 5 m) to represent the soil properties of the seedling plot (Figure S1).

One soil fertility and one soil moisture sample were taken from the centre of each 5 m × 5 m subplot in the soil sampling plot (three subplots in a 10 m × 10 m soil sampling plot, five in 20 m × 20 m). The top organic horizon was removed before soil sampling. Soil fertility samples were taken from the top 0–20 cm soil layer and passed through a sieve (2-mm mesh size). The three or five fertility samples per sampling plot were combined, air-dried (at ambient temperature), crushed, sieved (0.15-mm mesh size) and dried at 95°C to constant weight. The sample was then divided into two parts. The first 100 mg was wrapped in tin foil and used to determine the content of TC and TN by using an elemental analyser (Vario MACRO Cube, Elementar, Langenselbold, Germany) in CN mode. The second part (400 mg) was put in a digestion tube to which we added 5 mL of sulphuric acid (H_2SO_4) and 1 mL of perchloric acid ($HClO_4$). The sample was then digested with a digestion instrument at 360°C for an hour and then mixed with deionized water to a volume of 100 mL. TP content was determined by ICP-OES (Inductively Coupled Plasma Optical Emission Spectrometry, Optima 8300, PerkinElmer, Waltham, MA, USA). The soil moisture samples were collected with a 100 cm³ cutting ring. We measured each sample's moisture properties (MWHC, CWHC, MMC, WCF and SD) using the cutting ring method (Viji & Prasanna, 2012) and averaged each property across the three or five moisture samples from the same soil sampling plot. For each soil sampling plot on each island, we then averaged the data on soil properties from the two measurements (2015 and 2019).

2.5 | Insect herbivore community

We established a 20 m × 20 m subplot at a randomly chosen point within the tree plot on each island, to conduct insect community surveys from May to August 2017 (Tu et al., 2019), which align with both the active growth phase of plants and herbivore activity peaks, using both sweep net and pitfall trapping methods. Sweep net sampling was conducted at each site on a sunny morning, using a 35-cm diameter net to sweep 50 times along the two diagonal lines of the subplot. Collected insects were killed using ethyl acetate and then placed into a paper bag with a cotton layer inside. Five pitfall traps were set at the four vertices and the centre point of each subplot (25 traps per subplot or island); the pitfall traps consisted of a plastic

cup (8 cm diameter, 11 cm depth) with a rainproof cover, filled with 70% ethanol solution (40 mL). The insects were collected from the pitfall traps every 3 days to ensure adequate sampling. All insects were brought back to the laboratory and sorted to morphospecies. We calculated insect herbivore abundance (number of individuals) and richness (number of species) to represent the insect herbivore community of each island.

2.6 | Statistical analysis

For each seedling, we calculated four measures of neighbourhood density from the start of each census interval that the seedling was present: (1) the number of other conspecific seedlings within the same seedling plot (conspecific seedling density, CSD); (2) the number of all other seedlings (all species including conspecifics) within the same seedling plot (total seedling density, TSD); (3) the local density index (LDI) of conspecific trees within a 10 m radius of the focal seedling (conspecific tree density, CTD, cm^2); and (4) the LDI of all trees (all species) within a 10 m radius of the focal seedling (total tree density, TTD, cm^2). Total seedling and tree density were included to distinguish between conspecific effects and overall crowding effects. Although some previous work (Comita et al., 2014; LaManna et al., 2016) used the difference between the effects of conspecific and heterospecific densities on survival, the use of total densities simplifies interpretation because the conspecific effects are interpretable on their own (Hülsmann et al., 2024). The LDI provides an inverse-distance weighted sum of basal areas of neighbouring trees, assuming an exponential decay with distance of the effects of neighbouring trees calculated using the following function (Comita et al., 2010; Hülsmann et al., 2024):

$$LDI_i = \sum_j^n \frac{BA_{ij}}{e^{\mu \times distance_{ij}}}$$

where *BA* represents the basal area of the *j*-th tree within a 10 m radius of the focal seedling *i*, *distance* denotes the distance between the *j*-th tree and the focal seedling *i*, and *μ* represents the distance-decay coefficient. We assessed model fit using candidate values of *μ* between 0 and 0.5 in increments of 0.1 (Comita et al., 2010). The *μ* values for *LDI_conspecific* and *LDI_total* were permitted to differ in model parameterization (Hülsmann et al., 2024). The best-fit model configuration was identified through model comparison using the Akaike information criterion (AIC), with *μ_conspecific* = 0.2 and *μ_total* = 0.1 minimizing the AIC (Table S2).

Because seedling surveys were conducted more frequently than tree surveys, we interpolated tree density (both CTD and TTD) for each seedling using the following equation:

$$LDI_y = LDI_{t1} + (LDI_{t2} - LDI_{t1}) \times \frac{y - t1}{t2 - t1}$$

where *LDI* is (conspecific or total) tree density, *y* is the year of the last seedling survey, *t1* is the previous tree survey year, and *t2* is the next tree survey year.

To assess potential nonlinearity in the relationship between conspecific density and seedling survival, we fitted a binomial generalized additive mixed model (GAMM) and compared its statistical performance with the corresponding binomial generalized linear mixed model (GLMM) (Wood, 2017). Model comparison using AIC suggested the GLMM performed better than the GAMM (ΔAIC = 4.86). Subsequent analyses assumed linear relationships on the logit scale. We used the brms package (Bürkner, 2021) to fit a binomial Bayesian generalized linear hierarchical model of seedling survival as a function of the two island attributes (island area and isolation) and their interactions with the four density parameters (CSD, TSD, CTD and TTD). The model included normally distributed random intercepts for seedling plot nested within island identity, for plant species and for seedling survey time. We excluded species without variation in any one of the four density parameters and two island attributes from the analysis (e.g. species that were only observed as single seedlings).

Any effects of island attributes on CDD are likely to be mediated by intermediate variables. To identify factors that might contribute to the effects of the two island attributes on the strength of CDD, we examined the relationships between insect herbivore community and soil variable datasets and island area and isolation using the lme4 and lmerTest packages (Bates et al., 2015; Kuznetsova et al., 2017). The results of these models suggested that insect herbivore richness and abundance increased significantly with island area, and soil total phosphorus significantly decreased and capillary water holding capacity significantly increased with island isolation (Figure S2). The positive relationship between insect richness (i.e. the number of insect species) and island area appears relatively stable over time in TIL, based on other studies at the site (Luo et al., 2024; Zhang et al., 2023; Zhao et al., 2020; Zhou et al., 2017). Moreover, the spatial variation of soil total phosphorus and capillary water holding capacity among islands (4504.27 and 2016.48, respectively) was much greater than their temporal variation (200.32 and 0, respectively). Consequently, two-year surveys of soil TP/CWC and single-year sampling of insect herbivore species richness on all the islands included in the study provide a reasonable estimate of variation among islands for investigating spatial variation in CDD across the decade-long time sequence. Soil total carbon and total nitrate were positively correlated with total phosphorus (Figure S3), and the other four soil moisture properties (MWHC, MMC, −WCF and −SD, positively related to soil moisture) increased significantly with capillary water capacity (Figure S4). The analyses presented below are based on the results obtained from all the aforementioned models.

We then used structural equation models in a Bayesian framework (Bayesian SEM) (Bürkner, 2021) to estimate the direct and indirect drivers of CDD in seedling survival (Figure 1). Our main questions were whether the conspecific density effects on seedling survival depended on island attributes, and whether these effects were direct (paths (a) 2, 3 and (b) 2 in Figure 1) or indirectly mediated by insect herbivore richness, soil total phosphorus or capillary water holding capacity (paths (a) 6, 8, 9 and (b) 4, 8, 6, 10 in Figure 1). In the Bayesian SEMs, the submodel with soil total phosphorus or
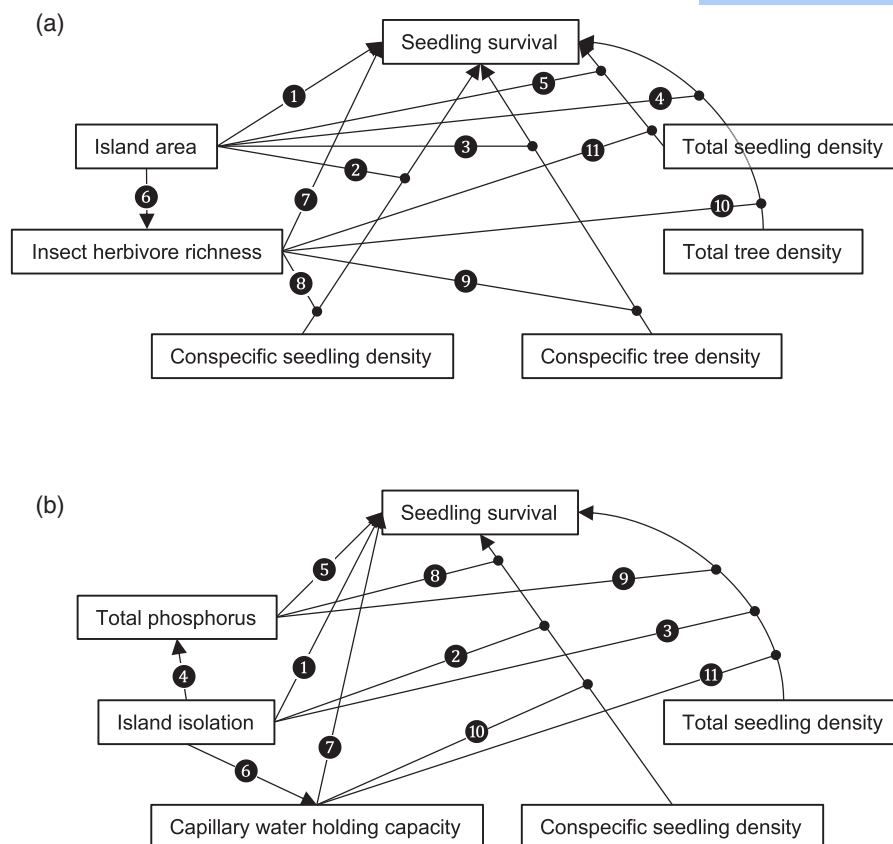
FIGURE 1 Schematic figures of the two Bayesian structural equation models (SEMs) that were used to test the drivers of conspecific density dependence (CDD) in seedling survival. The Bayesian SEMs for (a) island area and (b) island isolation. Numerical labels in the figure serve as identifiers for individual paths. Potential interactions between covariates are indicated by dots at path intersections (e.g. path (a) 2 represents an interaction between island area and conspecific seedling density in their effects on seedling survival). Total seedling and tree density were included to distinguish between conspecific effects and overall crowding effects. All paths displayed here were included in the models.

capillary water holding capacity as the response included a normally distributed random intercept for island identity, and the submodel with seedling survival status as the response included normally distributed random intercepts for seedling plot nested within island identity, for plant species and for seedling survey time. The Bayesian SEMs for island area and isolation included 9910 observations (Figure 1a) and 10,049 observations (Figure 1b), respectively (each observation is a unique combination of the 306 seedling plots nested within 25 islands, 30 plant species, 18 seedling surveys and a unique density parameter combination).

All continuous numeric variables were mean-centred and scaled by their standard deviation. The posterior of the models was explored using Hamiltonian MCMC sampling with 2000 samples from each of four chains. We confirmed model convergence by ensuring the Gelman–Rubin metric (R-hat) was less than 1.01 and an absence of divergences. Model adequacy was determined using posterior predictive graphical checks using 1000 posterior draws (Figure S5) and implemented in the performance package (Lüdecke et al., 2021). The radius for calculating CTD and TTD was set at 10 m because it resulted in better model fit than 5 m. All data analyses were performed in R 4.3.3 (R Core Team, 2024).

3 | RESULTS

The surveys identified 3641 tagged seedlings of 57 species on 306 seedling plots. Of these, 30 species (3501 seedlings; Table S3) had some variation (var > 0) in all the covariates (four density parameters and two island attributes) and therefore could be included in the analyses.

3.1 | Island attribute effects on seedling survival

Seedling survival declined with increasing island area and isolation (Figure 2a). Seedling survival also decreased as both conspecific and total tree density increased, with the former having a stronger effect (Figure 2a). The negative effects of conspecific tree density on seedling survival were more pronounced on larger islands (Figure 2c), but independent of island isolation (Figure 2e). The negative effects of conspecific seedling density on seedling survival strengthened with both increasing island area and isolation (Figure 1b,d). Total seedling density had no direct or indirect effects on seedling survival (Figure 2a).
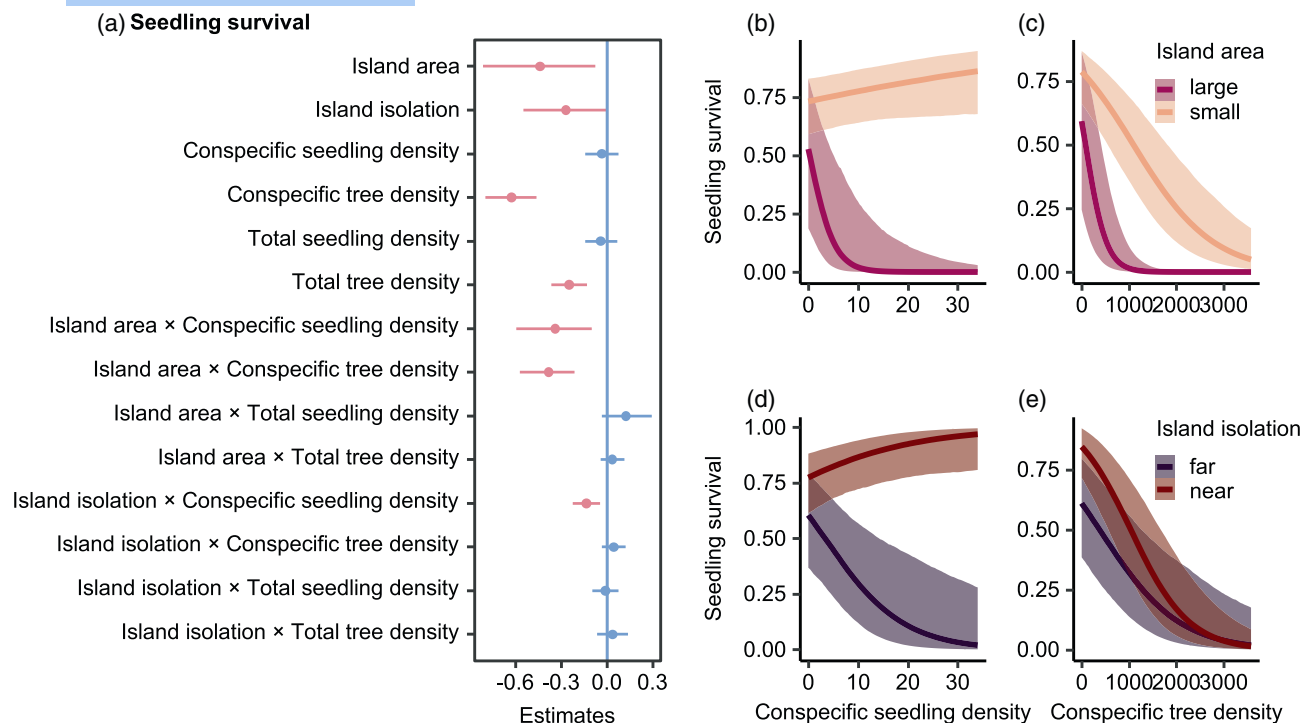
FIGURE 2 Marginal effects of island attributes and their interactions with conspecific density on seedling survival. (a) Parameter estimates of the effects on survival of the two island attributes, the four density variables, and the interactions between island attributes and density. Parameter estimates (dots) are coloured according to whether their 95% credible intervals (95% CrIs) overlap zero (blue) or not (red). (b–e) The relationships between seedling survival and conspecific seedling and tree density on islands with different attributes. Increasing conspecific seedling (b) and tree (c) density reduced seedling survival to a greater extent on large (1154 ha) islands than small islands (0.19 ha). Increasing conspecific seedling density (d) had stronger negative effects on seedling survival on islands far (4217 m) from the mainland than those near the mainland (200 m). However, the effects of conspecific tree density on seedling survival did not differ noticeably between islands of different isolation (e). The lines and shaded areas represent model predictions and 95% CrIs of the posterior distributions of the predictions, respectively.

3.2 | Mediators of island area effects on negative CDD

The effect of island area on negative conspecific seedling dependence in seedling survival appeared to be mediated by increasing species richness of insect herbivores on larger islands (Figure 3a). In our SEM, the direct path linking island area to conspecific seedling density effects on seedling survival was weak with a posterior distribution that overlapped zero ($\beta=0.074$, 95% CrI: −0.378 to 0.531). However, the indirect path, mediated by the positive relationship between island area and insect herbivore richness, was supported by the data (Figure 3a). In contrast, the negative effects of conspecific tree density on seedling survival appeared to be independent of insect herbivore richness (Figure 3a; Figure S6a,b).

3.3 | Mediators of island isolation effects on negative CDD

Conspecific seedling density had stronger negative effects on seedling survival on more isolated islands, and this relationship appeared to be mediated by decreasing soil total phosphorus on more isolated

islands (Figure 3b). More isolated islands had lower soil total phosphorus and higher soil capillary water holding capacity (Figure 3b). In our SEM, the decrease in soil total phosphorus directly reduced seedling survival and also strengthened the negative effects of conspecific seedling density on seedling survival (Figure 3b,d). Additionally, the direct effect of island isolation on seedling survival and on conspecific seedling density dependence in seedling survival was weak ($\beta=0.090$, 95% CrI: −0.374 to 0.176; $\beta=0.015$, 95% CrI = −0.090 to 0.117) (Figure 3b). Soil capillary water holding capacity had no direct or indirect effects on seedling survival (Figure 3b; Figure S6c).

4 | DISCUSSION

A large body of research indicates that plant performance declines in areas with high densities of conspecifics (negative CDD) (Comita et al., 2014) and that insect herbivores (Forrister et al., 2019; Sullivan, 2003) and fungal pathogens (Bagchi et al., 2014; Mangan et al., 2010; Packer & Clay, 2000) drive this process. This enemy-mediated negative CDD is thought to promote plant diversity (Bagchi et al., 2014; Hülsmann et al., 2021; Mangan et al., 2010). However, the implications of anthropogenic disturbance for negative CDD,
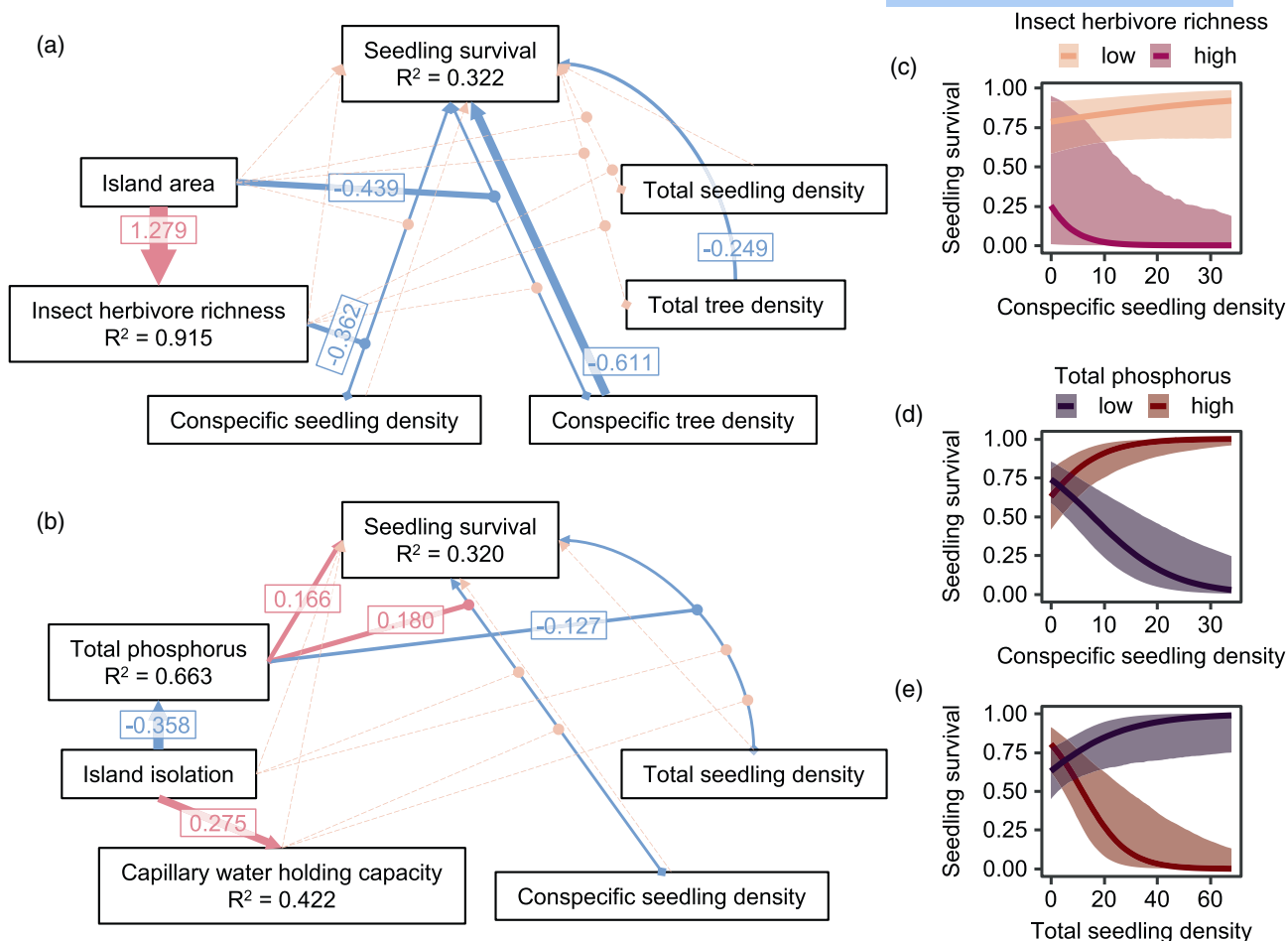
FIGURE 3 Results of the two Bayesian structural equation models (SEMs) on the drivers of negative conspecific density dependence (CDD) in seedling survival. (a) Pathways mediating the effects of island area on negative CDD in seedling survival. (b) Pathways mediating the effects of island isolation on negative CDD in seedling survival. Red arrows denote positive effects with 95% credible intervals (CrIs) that are greater than zero. Blue arrows denote negative effects with 95% CrIs less than zero (including insect herbivore richness-conspecific seedling density interaction with 94.1% CrI < 0). Yellow arrows indicate paths that received less support from the data, with 95% CrIs that overlap zero. Dots at path intersections indicate interactions between variables. Arrow widths indicate the relative strength (value in box) of well-supported paths (Figure S6 for more detail). Negative CDD in seedling survival intensified with greater insect herbivore richness (c) but diminished with elevated soil total phosphorus (d). Conversely, the adverse impact of total seedling density on seedling survival was magnified under higher soil phosphorus conditions (e). The lines and shaded areas represent model predictions and 95% CrIs of the posterior distributions of the predictions, respectively.

and hence plant diversity, remain poorly understood. In this study, in an artificially fragmented landscape, we found that conspecific seedling and tree densities reduced seedling survival and that these negative effects strengthened with increasing island area and isolation. Furthermore, we found that these effects of island area and isolation on negative CDD were mediated by shifts in insect herbivore communities (that were more species-rich on larger islands) and soil fertility (total phosphorus was more limited on isolated islands), respectively. The overall patterns suggest that fragmentation of this landscape has modified important neighbourhood interactions, partly as a result of altered soil properties and insect herbivore communities by fragmentation.

Our results build on previous work on plant–enemy interactions in fragmented landscapes (Benítez-Malvido & Lemus-Albor, 2005; Krishnadas et al., 2018; Viswanathan et al., 2019, 2020, 2025).

Previous studies have observed decreases in specialist insect herbivores with decreasing fragment area (Rossetti et al., 2017) and reduced negative conspecific density dependence due to weaker effects of specialist enemies at forest edges and in small fragments (Krishnadas et al., 2018; Viswanathan et al., 2025). In our data, stronger negative conspecific seedling density dependence in seedling survival on larger islands was associated with more species-rich insect herbivore communities (Figure 3a,c). The positive relationship between insect herbivore richness and fragment area has been repeatedly observed before (Krauss et al., 2003; Öckinger et al., 2012; Rossetti et al., 2017) and provides a plausible pathway for stronger negative conspecific effects on larger islands. In particular, the richer insect herbivore communities in larger fragments tend to include more specialists that are most likely to exert density-dependent control of their hosts (Alvarez-Loayza & Terborgh, 2011; Mickley

et al., 2025; Sullivan, 2003). In contrast to the influence of conspecific seedlings, the stronger negative effects of conspecific tree density on seedling survival on larger islands were independent of insect herbivore richness (Figure S6). Explanations of the differences between the mediation by insect herbivores of conspecific seedling and adult tree effects on seedling survival are necessarily speculative, but one possibility is limited overlap between insect herbivores consuming trees and seedlings, as has been observed in some tropical forests (Barrios, 2003; Basset et al., 1999). Further research could explore how fragmentation-associated shifts in insect herbivore diet breadth influence herbivory patterns and their relationship with tree neighbourhoods.

There is considerable evidence that the impacts of adult trees on conspecific seedlings are mediated by fungal pathogens via plant–soil feedbacks (PSF) (Eck et al., 2019; Mangan et al., 2010; McCarthy-Neumann & Kobe, 2010), and regulation of plant populations by their diseases increases with increasing fragment area (Viswanathan et al., 2019, 2025). Soil fungal communities on larger islands are more species-rich and spatially heterogeneous in TIL (Li et al., 2020). Spatial heterogeneity in soil-borne fungal communities may represent greater opportunities for seedlings to escape host-specific pathogenic fungi associated with adult conspecifics through dispersal, allowing stronger negative PSF on larger islands. Documenting the heterogeneity of soil-borne fungal communities, and the influence of that heterogeneity on plant communities, provides a promising avenue for future work.

We found stronger negative conspecific seedling density dependence in seedling survival on more isolated islands (Figure 2). This result (stronger negative CDD on more isolated islands, which could promote species diversity) runs counter to the tendency for isolated fragments to contain fewer species (Ibáñez et al., 2014), and within the TIL, island isolation is unrelated to plant species richness (Yu et al., 2012). Our SEM results suggested an association between stronger negative effects of conspecific seedling density and less fertile soils (lower TP, accompanied by lower TC and TN, Figure S3) on more isolated islands (Figure 3b). The relationship between soil fertility and island isolation within the TIL could be a result of several possible processes acting alone or in combination. First, increased island isolation has been associated with declines in insect decomposer abundance and richness within the TIL (Luo et al., 2024), which might inhibit biotic processes involved in decomposition on more isolated islands. Second, rhizosphere soil fungal richness (but not non-rhizosphere soil fungal diversity; Li et al., 2020) in the TIL decreases with increased island isolation (Guo et al., unpublished data) and is positively correlated with soil phosphorus. Negative CDD could strengthen in infertile soils because there is evidence that plants invest less in defensive traits on less fertile islands within the TIL (Zhong et al., 2021), and replacing tissue damaged by pests and pathogens is harder when resources are limited (Coley et al., 1985). These trade-offs could make plants more vulnerable to pests and pathogens, thus strengthening enemy-mediated negative conspecific seedling density dependence on less fertile islands. The positive relationship between defence

investment and nutrient availability reported from the TIL is not universal, however. High fertility areas are generally associated with investment in growth as opposed to defence (Fine et al., 2006; Lynn & Fridley, 2019), and also stronger negative CDD (LaManna et al., 2016; Zang et al., 2021), except in very infertile soils, where the relationships may reverse (Brown et al., 2021; Coley et al., 1985; Herms & Mattson, 1992; Zhong et al., 2021). On the contrary, the stronger negative conspecific seedling density dependence on more isolated islands (with less soil total phosphorus) was mainly mediated by arbuscular mycorrhizal (AM) plants rather than ectomycorrhizal (EM) plants (Lei et al., in preparation). There is evidence that under high soil phosphorus conditions, the high AM fungal colonization of plant roots is associated with providing more defence benefits and less growth benefits (Frew et al., 2023), which could weaken negative CDD in fertile soils. Arbuscular mycorrhizal plants tend to exhibit stronger negative CDD than EM plants, because EM fungi more effectively shield host plants from soil-borne pathogens than AM fungi, while also enabling slower pathogen build-up in the rhizosphere (Chen et al., 2019; Jiang et al., 2021; Liang et al., 2020; Pu et al., 2022). Furthermore, AM fungi demonstrate greater dispersal limitation under habitat fragmentation (Delavaux et al., 2021). In addition to its association with weaker negative CDD, higher soil total phosphorus was correlated with more negative effects of total seedling density (Figure 3b,e). One possible explanation is that releasing plants from phosphorus limitation intensified interspecific competition for other resources, shifting the balance of interspecific and intraspecific competition (Letten et al., 2017; Tilman et al., 1982). Shifts in the underlying relationships between soil fertility and environmental variables like island isolation, and plant defence investment, could lead to alternative relationships between environmental variables and CDD.

It is becoming increasingly clear that habitat fragmentation can erode diversity through ecosystem decay (Chase et al., 2020; Gonçalves-Souza et al., 2025), but the processes through which this ecosystem decay occurs are unresolved. In this 10-year plant community dynamics dataset, weaker negative effects of conspecific seedling density on seedling survival on smaller islands were linked to declines in insect herbivore richness. Because negative CDD contributes to maintaining the diversity of tree assemblages (Bagchi et al., 2014; Hülsmann et al., 2024; Johnson et al., 2012; Mangan et al., 2010), disrupting the process could accelerate ecosystem decay in small forest patches. Perturbations that are generally associated with fragmentation, like reduced specificity of herbivores (Bagchi et al., 2018; Martinson & Fagan, 2014; Rossetti et al., 2017) which drives negative CDD, may consistently reduce diversity in smaller or isolated habitats (Xu et al., 2023). In contrast, shifts that are particular to how fragmentation occurred (e.g. in this study islands represent mountaintops left after flooding, that may have been less fertile) will have idiosyncratic effects on diversity, which cannot be understood without reference to the underlying mechanisms. Developing a general understanding of how fragmentation influences diversity will therefore require a more mechanistic approach that concentrates on the pathways that regulate biodiversity

in both disturbed and intact ecosystems. Such a mechanistic understanding of the biological mechanisms underlying ecosystem decay in fragmented ecosystems would advance general theory about the regulation of biodiversity in natural ecosystems.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data and code supporting the findings of this study are available on Zenodo at https://doi.org/10.5281/zenodo.14044095 (Lei et al., 2025).

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REFERENCES

Alvarez-Loayza, P., & Terborgh, J. (2011). Fates of seedling carpets in an Amazonian floodplain forest: Intra-cohort competition or attack by enemies. *Journal of Ecology*, 99(4), 1045–1054. https://doi.org/10.1111/j.1365-2745.2011.01835.x

Bagchi, R., Brown, L. M., Elphick, C. S., Wagner, D. L., & Singer, M. S. (2018). Anthropogenic fragmentation of landscapes: Mechanisms for eroding the specificity of plant-herbivore interactions. *Oecologia*, 187(2), 521–533. https://doi.org/10.1007/s00442-018-4115-5

Bagchi, R., Gallery, R. E., Gripenberg, S., Gurr, S. J., Narayan, L., Addis, C. E., Freckleton, R. P., & Lewis, O. T. (2014). Pathogens and insect herbivores drive rainforest plant diversity and composition. *Nature*, 506(7486), 85–88. https://doi.org/10.1038/nature12911

Baidya Roy, S. (2011). Mesoscale moisture transport effects on forest edges in a fragmented landscape in Amazonia. *Climatic Change*, 108(3), 609–617. https://doi.org/10.1007/s10584-011-0218-2

Barrett, L. G., Kniskern, J. M., Bodenhausen, N., Zhang, W., & Bergelson, J. (2009). Continua of specificity and virulence in plant host-pathogen interactions: Causes and consequences. *New Phytologist*, 183(3), 513–529. https://doi.org/10.1111/j.1469-8137.2009.02927.x

Barrios, H. (2003). Insect herbivores feeding on conspecific seedlings and trees. In *Arthropods of tropical forests* (pp. 282–290). Cambridge University Press.

Basset, Y., Charles, E., & Novotny, V. (1999). Insect herbivores on parent trees and conspecific seedlings in a Guyana rain forest. *Selbyana*, 20(1), 146–158.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Benítez-Malvido, J., & Lemus-Albor, A. (2005). The seedling community of tropical rain forest edges and its interaction with herbivores and pathogens. *Biotropica*, 37(2), 301–313. https://doi.org/10.1111/j.1744-7429.2005.00031.x

Borges, P. A. V., Hortal, J., Gabriel, R., & Homem, N. (2009). Would species richness estimators change the observed species area relationship? *Acta Oecologica*, 35(1), 149–156. https://doi.org/10.1016/j.actao.2008.09.003

Brown, A. J., White, P. S., & Peet, R. K. (2021). Environmental context alters the magnitude of conspecific negative density dependence in a temperate forest. *Ecosphere*, 12(3), 1–13. https://doi.org/10.1002/ecs2.3406

Bürkner, P.-C. (2021). Bayesian item response modeling in R with brms and Stan. *Journal of Statistical Software*, 100(5), 1–54. https://doi.org/10.18637/jss.v100.i05

Cao, J., Zhang, C., Zhao, B., Li, X., Hou, M., & Zhao, X. (2018). Seedling density dependence regulated by population density and habitat filtering: Evidence from a mixed primary broad-leaved Korean pine forest in Northeastern China. *Annals of Forest Science*, 75(1), 25. https://doi.org/10.1007/s13595-018-0706-x

Chase, J. M., Blowes, S. A., Knight, T. M., Gerstner, K., & May, F. (2020). Ecosystem decay exacerbates biodiversity loss with habitat loss. *Nature*, 584(7820), 238–243. https://doi.org/10.1038/s41586-020-2531-2

Chen, L., Swenson, N. G., Ji, N., Mi, X., Ren, H., Guo, L., & Ma, K. (2019). Differential soil fungus accumulation and density dependence of trees in a subtropical forest. *Science*, 366(6461), 124–128. https://doi.org/10.1126/science.aau1361

Coley, P. D., Bryant, J. P., & Chapin, F. I. (1985). Resource availability and plant antiherbivore defense. *Science*, 230(4728), 895–899. https://doi.org/10.1126/science.230.4728.895

Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, 329(5989), 330–332. https://doi.org/10.1126/science.1190772

Comita, L. S., Queenborough, S. A., Murphy, S. J., Eck, J. L., Xu, K., Krishnadas, M., Beckman, N., & Zhu, Y. (2014). Testing predictions of the Janzen-Connell hypothesis: A meta-analysis of experimental evidence for distance-and density-dependent seed and seedling survival. *Journal of Ecology*, 102(4), 845–856.

Connell, J. H. (1971). On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In *Dynamics of populations* (pp. 298–312). Centre for Agricultural Publishing and Documentation. https://edepot.wur.nl/469421#page=296

Delavaux, C. S., Weigelt, P., Dawson, W., Essl, F., van Kleunen, M., König, C., Pergl, J., Pyšek, P., Stein, A., Winter, M., Taylor, A., Schultz, P. A., Whittaker, R. J., Kreft, H., & Bever, J. D. (2021). Mycorrhizal types influence Island biogeography of plants. *Communications Biology*, *4*(1), 1–8. https://doi.org/10.1038/s42003-021-02649-2

Didham, R. K. (1998). Altered leaf-litter decomposition rates in tropical forest fragments. *Oecologia*, *116*(3), 397–406. https://doi.org/10.1007/s004420050603

Downey, H., Lewis, O. T., Bonsall, M. B., Fernandez, D. C., & Gripenberg, S. (2018). Insect herbivory on seedlings of rainforest trees: Effects of density and distance of conspecific and heterospecific neighbors. *Ecology and Evolution*, *8*(24), 12702–12711. https://doi.org/10.1002/ece3.4698

Eck, J. L., Stump, S. M., Delavaux, C. S., Mangan, S. A., & Comita, L. S. (2019). Evidence of within-species specialization by soil microbes and the implications for plant community diversity. *Proceedings of the National Academy of Sciences of the United States of America*, *116*(15), 7371–7376. https://doi.org/10.1073/pnas.1810767116

Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS One*, *8*(3), e58093. https://doi.org/10.1371/journal.pone.0058093

Fine, P. V. A., Miller, Z. J., Mesones, I., Irazuzta, S., Appel, H. M., Stevens, M. H. H., Sääksjärvi, I., Schultz, J. C., & Coley, P. D. (2006). Growth-defense trade-off and habitat specialization by plants in Amazonian forests. *Ecology*, *87*(7), S150–S162. https://doi.org/10.1890/0012-9658(2006)87[150:TGTAHS]2.0.CO;2

Forrister, D. L., Endara, M.-J., Younkin, G. C., Coley, P. D., & Kursar, T. A. (2019). Herbivores as drivers of negative density dependence in tropical forest saplings. *Science*, *363*(6432), 1213–1216. https://doi.org/10.1126/science.aau9460

Frew, A., Heuck, M. K., & Aguilar-Trigueros, C. A. (2023). Host filtering, not competitive exclusion, may be the main driver of arbuscular mycorrhizal fungal community assembly under high phosphorus. *Functional Ecology*, *37*(7), 1856–1869. https://doi.org/10.1111/1365-2435.14349

Garrett, S. D. (1970). *Pathogenic root-infecting fungi*. England University Press.

Gonçalves-Souza, T., Chase, J. M., Haddad, N. M., Vancine, M. H., Didham, R. K., Melo, F. L. P., Aizen, M. A., Bernard, E., Chiarello, A. G., Faria, D., Gibb, H., de Lima, M. G., Magnago, L. F. S., Mariano-Neto, E., Nogueira, A. A., Nemésio, A., Passamani, M., Pinho, B. X., Rocha-Santos, L., ... Sanders, N. J. (2025). Species turnover does not rescue biodiversity in fragmented landscapes. *Nature*, *640*, 702–706. https://doi.org/10.1038/s41586-025-08688-7

Grilli, G., Longo, S., Huais, P., Pereyra, M., Verga, E., Urcelay, C., & Galetto, L. (2017). Fungal diversity at fragmented landscapes: Synthesis and future perspectives. *Current Opinion in Microbiology*, *37*, 161–165. https://doi.org/10.1016/j.mib.2017.09.003

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Herms, D. A., & Mattson, W. J. (1992). The dilemma of plants: To grow or defend. *The Quarterly Review of Biology*, *67*(3), 283–335. https://doi.org/10.1086/417659

Hersh, M. H., Vilgalys, R., & Clark, J. S. (2012). Evaluating the impacts of multiple generalist fungal pathogens on temperate tree seedling survival. *Ecology*, *93*(3), 511–520. https://doi.org/10.1890/11-0598.1

Hu, G., Feeley, K. J., & Yu, M. (2016). Habitat fragmentation drives plant community assembly processes across life stages. *PLoS One*, *11*(7), e0159572. https://doi.org/10.1371/journal.pone.0159572

Hülsmann, L., Chisholm, R. A., Comita, L., Visser, M. D., de Souza Leite, M., Aguilar, S., Anderson-Teixeira, K. J., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., Castaño, N., Chang-Yang, C.-H., Chuyong, G. B., Clay, K., Davies, S. J., Duque, A., Ediriweera, S., Ewango, C., Gilbert, G. S., ... Hartig, F. (2024). Latitudinal patterns in stabilizing density dependence of forest communities. *Nature*, *627*(8004), 564–571. https://doi.org/10.1038/s41586-024-07118-4

Hülsmann, L., Chisholm, R. A., & Hartig, F. (2021). Is variation in conspecific negative density dependence driving tree diversity patterns at large scales? *Trends in Ecology & Evolution*, *36*(2), 151–163. https://doi.org/10.1016/j.tree.2020.10.003

Ibáñez, I., Katz, D. S. W., Peltier, D., Wolf, S. M., & Connor Barrie, B. T. (2014). Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess-multiresponse dynamics. *Journal of Ecology*, *102*(4), 882–895. https://doi.org/10.1111/1365-2745.12223

Jackson, R. B., Lajtha, K., Crow, S. E., Hugelius, G., Kramer, M. G., & Piñeiro, G. (2017). The ecology of soil carbon: Pools, vulnerabilities, and biotic and abiotic controls. *Annual Review of Ecology, Evolution, and Systematics*, *48*(1), 419–445. https://doi.org/10.1146/annurev-ecolsys-112414-054234

Janzen, D. H. (1970). Herbivores and the number of tree species in tropical forests. *The American Naturalist*, *104*(940), 501–528. https://doi.org/10.1086/282687

Jiang, F., Lutz, J. A., Guo, Q., Hao, Z., Wang, X., Gilbert, G. S., Mao, Z., Orwig, D. A., Parker, G. G., Sang, W., Liu, Y., Tian, S., Cadotte, M. W., & Jin, G. (2021). Mycorrhizal type influences plant density dependence and species richness across 15 temperate forests. *Ecology*, *102*(3), e03259. https://doi.org/10.1002/ecy.3259

Jiang, J., Wang, Y.-P., Yang, Y., Yu, M., Wang, C., & Yan, J. (2019). Interactive effects of nitrogen and phosphorus additions on plant growth vary with ecosystem type. *Plant and Soil*, *440*(1), 523–537. https://doi.org/10.1007/s11104-019-04119-5

Joachin, J., Kritzell, C., Lagueux, E., Luecke, N. C., & Crawford, K. M. (2023). Climate change and plant-microbe interactions: Water-availability influences the effective specialization of a fungal pathogen. *Fungal Ecology*, *66*(2023), 101286. https://doi.org/10.1016/j.funeco.2023.101286

Johnson, D. J., Beaulieu, W. T., Bever, J. D., & Clay, K. (2012). Conspecific negative density dependence and forest diversity. *Science*, *336*(6083), 904–907. https://doi.org/10.1126/science.1220269

Kiesewetter, K. N., Otano, L., & Afkhami, M. E. (2023). Fragmentation disrupts microbial effects on native plant community productivity. *Journal of Ecology*, *111*(6), 1292–1307. https://doi.org/10.1111/1365-2745.14097

Krauss, J., Steffan-Dewenter, I., & Tscharntke, T. (2003). How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, *30*(6), 889–900. https://doi.org/10.1046/j.1365-2699.2003.00878.x

Krishnadas, M., Bagchi, R., Sridhara, S., & Comita, L. S. (2018). Weaker plant-enemy interactions decrease tree seedling diversity with edge-effects in a fragmented tropical forest. *Nature Communications*, *9*(1), 4523. https://doi.org/10.1038/s41467-018-06997-2

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

LaManna, J. A., Mangan, S. A., Alonso, A., Bourg, N. A., Brockelman, W. Y., Bunyavejchewin, S., Chang, L.-W., Chiang, J.-M., Chuyong, G. B., Clay, K., Condit, R., Cordell, S., Davies, S. J., Furniss, T. J., Giardina, C. P., Gunatilleke, I. A. U. N., Gunatilleke, C. V. S., He, F., Howe, R. W., ... Myers, J. A. (2017). Plant diversity increases with the strength of negative density dependence at the global scale. *Science*, *356*(6345), 1389–1392. https://doi.org/10.1126/science.aam5678

LaManna, J. A., Walton, M. L., Turner, B. L., & Myers, J. A. (2016). Negative density dependence is stronger in resource-rich environments and

diversifies communities when stronger for common but not rare species. *Ecology Letters*, 19(6), 657–667. https://doi.org/10.1111/ele.12603

Laurance, W. F., Carolina Useche, D., Rendeiro, J., Kalka, M., Bradshaw, C. J. A., Sloan, S. P., Laurance, S. G., Campbell, M., Abernethy, K., Alvarez, P., Arroyo-Rodriguez, V., Ashton, P., Benítez-Malvido, J., Blom, A., Bobo, K. S., Cannon, C. H., Cao, M., Carroll, R., Chapman, C., … Zamzani, F. (2012). Averting biodiversity collapse in tropical forest protected areas. *Nature*, 489, 290–294. https://doi.org/10.1038/nature11318

Lei, Y., Bagchi, R., Liu, J., Wang, Z., Wang, J., Hu, G., & Yu, M. (2025). Insect herbivores and soil fertility drive variation in density-dependent seedling dynamics across a fragmented landscape [dataset]. *Zenodo*. https://doi.org/10.5281/zenodo.14044095

Letten, A. D., Ke, P.-J., & Fukami, T. (2017). Linking modern coexistence theory and contemporary niche theory. *Ecological Monographs*, 87(2), 161–177. https://doi.org/10.1002/ecm.1242

Li, S.-P., Wang, P., Chen, Y., Wilson, M. C., Yang, X., Ma, C., Lu, J., Chen, X.-Y., Wu, J., Shu, W.-S., & Jiang, L. (2020). Island biogeography of soil bacteria and fungi: Similar patterns, but different mechanisms. *The ISME Journal*, 14(7), 1886–1896. https://doi.org/10.1038/s41396-020-0657-8

Liang, M., Johnson, D., Burslem, D. F. R. P., Yu, S., Fang, M., Taylor, J. D., Taylor, A. F. S., Helgason, T., & Liu, X. (2020). Soil fungal networks maintain local dominance of ectomycorrhizal trees. *Nature Communications*, 11(1), 2636. https://doi.org/10.1038/s41467-020-16507-y

Liu, J., Vellend, M., Wang, Z., & Yu, M. (2018). High beta diversity among small islands is due to environmental heterogeneity rather than ecological drift. *Journal of Biogeography*, 45(10), 2252–2261. https://doi.org/10.1111/jbi.13404

Liu, Y., & He, F. (2019). Incorporating the disease triangle framework for testing the effect of soil-borne pathogens on tree species diversity. *Functional Ecology*, 33(7), 1211–1222. https://doi.org/10.1111/1365-2435.13345

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, 6(60), 3139. https://doi.org/10.21105/joss.03139

Luo, Y., Wu, D., Weng, C., Zhou, W., Yu, M., & Zhang, A. (2024). Competitive exclusion drives termite community assembly process on islands. *Landscape Ecology*, 39(9), 161. https://doi.org/10.1007/s10980-024-01922-z

Lynn, J. S., & Fridley, J. D. (2019). Geographic patterns of plant-herbivore interactions are driven by soil fertility. *Journal of Plant Ecology*, 12(4), 653–661. https://doi.org/10.1093/jpe/rtz002

Ma, J., Li, J., Wu, W., & Liu, J. (2023). Global forest fragmentation change from 2000 to 2020. *Nature Communications*, 14(1), 3752. https://doi.org/10.1038/s41467-023-39221-x

Mangan, S. A., Herre, E. A., & Bever, J. D. (2010). Specificity between Neotropical tree seedlings and their fungal mutualists leads to plant–soil feedback. *Ecology*, 91(9), 2594–2603. https://doi.org/10.1890/09-0396.1

Martinson, H. M., & Fagan, W. F. (2014). Trophic disruption: A meta-analysis of how habitat fragmentation affects resource consumption in terrestrial arthropod systems. *Ecology Letters*, 17(9), 1178–1189. https://doi.org/10.1111/ele.12305

McCarthy-Neumann, S., & Kobe, R. K. (2010). Conspecific plant-soil feedbacks reduce survivorship and growth of tropical tree seedlings. *Journal of Ecology*, 98(2), 396–407. https://doi.org/10.1111/j.1365-2745.2009.01619.x

Mickley, J. G., Anderson, R. M., Wagner, D. L., Brown, L. M., Connors, C. J., Davis, M. L., Elphick, C. S., Kilpatrick, H., LaScaleia, M. C., Marren, C., Musavi, H., Pirtel, N. L., Weeks, K., Singer, M. S., & Bagchi, R. (2025). Underrepresentation of dietary-specialist larval lepidoptera in small forest fragments: Testing alternative mechanisms.

Journal of Animal Ecology, 94(4), 786–799. https://doi.org/10.1111/1365-2656.70020

Milici, V. R., Dalui, D., Mickley, J. G., & Bagchi, R. (2020). Responses of plant-pathogen interactions to precipitation: Implications for tropical tree richness in a changing world. *Journal of Ecology*, 108(5), 1800–1809. https://doi.org/10.1111/1365-2745.13373

Morante-Filho, J. C., Cruz, C. D., Benchimol, M., Almeida, F. V., & de Oliveira, R. A. (2024). Linking changes in landscape structure to insect herbivory in forest edges and interiors of Atlantic forest remnants. *Ecological Applications*, 34(7), e3026. https://doi.org/10.1002/eap.3026

Moreira, X., Castagneyrol, B., Abdala-Roberts, L., Berny-Mier y Teran, J. C., Timmermans, B. G. H., Bruun, H. H., Covelo, F., Glauser, G., Rasmann, S., & Tack, A. J. M. (2018). Latitudinal variation in plant chemical defences drives latitudinal patterns of leaf herbivory. *Ecography*, 41(7), 1124–1134. https://doi.org/10.1111/ecog.03326

Öckinger, E., Lindborg, R., Sjödin, N. E., & Bommarco, R. (2012). Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, 35(3), 259–267. https://doi.org/10.1111/j.1600-0587.2011.06870.x

Packer, A., & Clay, K. (2000). Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, 404(6775), 278–281. https://doi.org/10.1038/35005072

Pu, X., Weemstra, M., Jin, G., & Umaña, M. N. (2022). Tree mycorrhizal type mediates conspecific negative density dependence effects on seedling herbivory, growth, and survival. *Oecologia*, 199(4), 907–918. https://doi.org/10.1007/s00442-022-05224-6

Quigley, K. M., Griffith, D. M., Donati, G. L., & Anderson, T. M. (2020). Soil nutrients and precipitation are major drivers of global patterns of grass leaf silicification. *Ecology*, 101(6), e03006. https://doi.org/10.1002/ecy.3006

R Core Team. (2024). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Revillini, D., Gehring, C. A., & Johnson, N. C. (2016). The role of locally adapted mycorrhizas and rhizobacteria in plant-soil feedback systems. *Functional Ecology*, 30(7), 1086–1098. https://doi.org/10.1111/1365-2435.12668

Riva, F., & Fahrig, L. (2023). Landscape-scale habitat fragmentation is positively related to biodiversity, despite patch-scale ecosystem decay. *Ecology Letters*, 26(2), 268–277. https://doi.org/10.1111/ele.14145

Rossetti, M. R., Tscharntke, T., Aguilar, R., & Batáry, P. (2017). Responses of insect herbivores and herbivory to habitat fragmentation: A hierarchical meta-analysis. *Ecology Letters*, 20(2), 264–272. https://doi.org/10.1111/ele.12723

Rudgers, J. A., Afkhami, M. E., Bell-Dereske, L., Chung, Y. A., Crawford, K. M., Kivlin, S. N., Mann, M. A., & Nuñez, M. A. (2020). Climate disruption of plant-microbe interactions. *Annual Review of Ecology, Evolution, and Systematics*, 51(51), 561–586. https://doi.org/10.1146/annurev-ecolsys-011720-090819

Scott, E. R., Uriarte, M., & Bruna, E. M. (2022). Delayed effects of climate on vital rates lead to demographic divergence in Amazonian forest fragments. *Global Change Biology*, 28(2), 463–479. https://doi.org/10.1111/gcb.15900

Sullivan, J. J. (2003). Density-dependent shoot-borer herbivory increases the age of first reproduction and mortality of neotropical tree saplings. *Oecologia*, 136(1), 96–106. https://doi.org/10.1007/s00442-003-1233-4

Tilman, D., Kilham, S. S., & Kilham, P. (1982). Phytoplankton community ecology: The role of limiting nutrients. *Annual Review of Ecology and Systematics*, 13, 349–372.

Tu, T.-H., Wang, J.-R., Gu, J.-Q., Li, T.-Q., Lv, K., Zhou, G.-X., & Xu, Z.-H. (2019). Effects of habitat fragmentation on the functional diversity of insects in Thousand Island Lake, China. *Entomological Research*, 49(2), 93–104. https://doi.org/10.1111/1748-5967.12329

Valladares, G., Salvo, A., & Cagnolo, L. (2006). Habitat fragmentation effects on trophic processes of insect-plant food webs. *Conservation Biology*, 20(1), 212–217. https://doi.org/10.1111/j.1523-1739.2006.00337.x

Vannette, R. L., Leopold, D. R., & Fukami, T. (2016). Forest area and connectivity influence root-associated fungal communities in a fragmented landscape. *Ecology*, 97(9), 2374–2383. https://doi.org/10.1002/ecy.1472

Viji, R., & Prasanna, P. R. (2012). Assessment of water holding capacity of major soil series of Lalgudi, Trichy, India. *Journal of Environmental Research and Development*, 7(1A), 393–398.

Viswanathan, A., Bagchi, R., Ghazoul, J., Honwad, G., & Lewis, O. T. (2025). Impacts of forest fragmentation on interactions between plants and their insect herbivores and fungal pathogens. *Ecological Applications*, 35(3), e70025. https://doi.org/10.1002/eap.70025

Viswanathan, A., Ghazoul, J., Honwad, G., Kumar, N. A., & Bagchi, R. (2019). The effects of rainforest fragment area on the strength of plant-pathogen interactions. *Biology Letters*, 15(1), 20180493. https://doi.org/10.1098/rsbl.2018.0493

Viswanathan, A., Ghazoul, J., Lewis, O. T., Honwad, G., & Bagchi, R. (2020). Effects of forest fragment area on interactions between plants and their natural enemies: Consequences for plant diversity at multiple spatial scales. *Frontiers in Forests and Global Change*, 2, 88. https://doi.org/10.3389/ffgc.2019.00088

Weissflog, A., Markesteijn, L., Lewis, O. T., Comita, L. S., & Engelbrecht, B. M. J. (2018). Contrasting patterns of insect herbivory and predation pressure across a tropical rainfall gradient. *Biotropica*, 50(2), 302–311. https://doi.org/10.1111/btp.12513

Wood, S. N. (2017). *Generalized additive models: An Introduction with R* (2nd ed.). Chapman and Hall/CRC.

Xu, C., Silliman, B. R., Chen, J., Li, X., Thomsen, M. S., Zhang, Q., Lee, J., Lefcheck, J. S., Daleo, P., Hughes, B. B., Jones, H. P., Wang, R., Wang, S., Smith, C. S., Xi, X., Altieri, A. H., van de Koppel, J., Palmer, T. M., Liu, L., … He, Q. (2023). Herbivory limits success of vegetation restoration globally. *Science*, 382(6670), 589–594. https://doi.org/10.1126/science.add2814

Yu, M., Hu, G., Feeley, K. J., Wu, J., & Ding, P. (2012). Richness and composition of plants and birds on land-bridge islands: Effects of Island attributes and differential responses of species groups. *Journal of Biogeography*, 39(6), 1124–1133. https://doi.org/10.1111/j.1365-2699.2011.02676.x

Zang, L., Xu, H., Li, Y., & Zang, R. (2021). Conspecific negative density dependence of trees varies with plant functional traits and environmental conditions across scales in a 60-ha tropical rainforest dynamics plot. *Biotropica*, 53(2), 693–702. https://doi.org/10.1111/btp.12910

Zhang, X., Dalsgaard, B., Staab, M., Zhu, C., Zhao, Y., Gonçalves, F., Ren, P., Cai, C., Qiao, G., Ding, P., & Si, X. (2023). Habitat fragmentation increases specialization of multi-trophic interactions by high species turnover. *Proceedings of the Royal Society B: Biological Sciences*, 290(2009), 20231372. https://doi.org/10.1098/rspb.2023.1372

Zhao, Y., Dunn, R. R., Zhou, H., Si, X., & Ding, P. (2020). Island area, not isolation, drives taxonomic, phylogenetic and functional diversity of ants on land-bridge islands. *Journal of Biogeography*, 47(8), 1627–1637. https://doi.org/10.1111/jbi.13860

Zhong, L., Didham, R. K., Liu, J., Jin, Y., & Yu, M. (2021). Community re-assembly and divergence of woody plant traits in an Island-mainland system after more than 50 years of regeneration. *Diversity and Distributions*, 27(8), 1435–1448. https://doi.org/10.1111/ddi.13290

Zhou, W., Luo, Y., Zhong, L., & Pan, L. (2017). Effects of habitat fragmentation on species diversity of ground dwelling beetles in the Thousand-Island Lake region, Zhejiang, China. *Chinese Journal of Applied Ecology*, 28(2), 509–518. https://doi.org/10.13287/j.1001-9332.201702.037

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map of the Thousand Island Lake (TIL).

Figure S2. The effects of island attributes on insect herbivore community and soil variables.

Figure S3. The correlations between three soil fertility properties.

Figure S4. The correlations between five soil moisture properties.

Figure S5. The results of posterior predictive graphical check using 1000 posterior draws for the models in a Bayesian framework.

Figure S6. Results of the two Bayesian structural equation models (SEMs) on the drivers of negative CDD in seedling survival.

Table S1. Areas and distance to mainland (isolation) of the 25 study islands.

Table S2. Model comparison for optimal distance-decay coefficient μ.

Table S3. The list of the 30 plant species included in the models.