Stochastic dispersal assembly dominates tropical invertebrate community assembly regardless of land use intensity.

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Abstract

Understanding how community assembly processes drive biodiversity patterns is a central goal of community ecology. While it is generally accepted that ecological communities are assembled by both stochastic and deterministic processes, quantifying their relative importance remains challenging. Even fewer studies have investigated how the relative importance of stochastic and deterministic community assembly processes vary among taxa and along gradients of habitat degradation. Using data on 1,002 invertebrate species across six taxonomic groups in Malaysian Borneo, we quantified the importance of stochastic and deterministic community assembly processes across a gradient of logging intensity. Dispersal limitation was the dominant process at all levels of logging intensity. The relationship between logging and community assembly varied depending on the specific combination of taxa and stochasticity metric used, but, in general, the processes that govern invertebrate community assembly were remarkably robust to changes in land use intensity.

Introduction

Community assembly processes drive biodiversity patterns, and a key goal in community ecology is to quantify the relative importance of different community assembly processes. Simultaneously, it is well-documented that land use changes impact biodiversity (Newbold et al. 2015), but it is much less well-known that they can also affect community assembly mechanisms (Wearn et al. 2019). Currently, therefore, we have a strong awareness of the patterns of biodiversity change that are generated by land use change (Newbold et al), but little understanding of the extent to which the fundamental community assembly processes that create that change are impacted. Moreover, the specific assembly processes generating ecological communities may differ between taxa due to differences in trait evolution (Weiher et al. 2011), meaning studies examining land use impacts on the assembly processes of mammals (Wearn et al. 2019) may provide little insight into the impacts on other taxa. Attempts to rely on natural ecological processes to restore biodiversity rely, by definition, on naturally occurring community assembly processes (Palmer et al. 1997, Hilderbrand et al. 2005). It is therefore of fundamental importance that we gain a deeper understanding of whether those assembly processes in modified habitats are the same or different to those observed in primary habitats.

It is generally accepted that both stochastic (neutral, random) and deterministic (niche, non-random) processes are simultaneously involved in structuring ecological communities (Adler et al. 2007), with the two sets of processes sitting at opposite ends of a continuum. Real-world communities exist somewhere between these two extremes (Gravel et al. 2006, Kitching 2013). Ecological stochasticity, henceforth referred to as 'stochasticity', can be defined as random changes in community composition that operate independently of taxonomic identity, and forms the basis of neutral theory (Gravel et al. 2006, Ellwood et al. 2009, Zhou & Ning 2017). Neutral theory makes the extreme assumption that all individuals within a particular trophic level are ecologically equivalent, and emphasises the importance of stochastic processes such as ecological drift (random fluctuations in birth, death, immigration, and speciation rates) and dispersal that operate independently of taxonomic identity (Rosindell et al. 2011). By contrast, determinism can be defined as non-random changes in community composition that can be predicted based on species' identities and niches (Vellend & Agrawal 2010), and is broadly described as niche theory which assumes that deterministic processes, such as selection, play a fundamental role in driving community assembly (Chesson 2000).

There has been long-standing debate over the relative influence of stochastic and deterministic processes on community assembly (Connor & Simberloff 1979). Numerous studies have investigated the relative importance of stochasticity and determinism in different environments (e.g. Ellwood et al. 2009, Caruso et al. 2012, Shipley et al. 2012, Ortega-Martínez et al. 2020, Valdivia et al. 2021). However, an understanding of the effects of land use change on the relative importance of stochastic and deterministic community

assembly processes is largely absent, despite its potential importance. If community assembly processes exhibit hysteresis, then recovering an ecological community in a modified habitat might rely on different assembly processes than those that exist in primary habitats (Andersen et al. 2009, Suding & Hobbs 2009). Therefore, our understanding of primary community assembly may give information that at best is irrelevant, or at worst directly misleading, when it comes to planning the restoration of modified communities. We therefore need to characterise how community assembly mechanisms might change across gradients of habitat degradation.

Logging is a major driver of habitat degradation across many of the world's most productive and biodiverse tropical forest ecosystems (Laurance 2015). The tropical forests of Borneo have been subject to rapid and widespread logging since the early 1970s. Between 1973 and 2010, there was an estimated 30 % decline in the extent of Borneo's intact forests (Gaveau et al. 2014). Logging often results in a heterogeneous landscape, with habitat patches connected spatially but affected by different logging intensities (Berry et al. 2008). This can result in gradients of disturbance intensity, which are a frequent consequence of land use change in the tropics (Wearn et al. 2019).

There is uncertainty over how logging might affect stochastic and deterministic community assembly processes, with little in the way of direct evidence. Logging has been shown to result in the spatial homogenization of moth assemblages in Borneo, and stochastic turnover of plant species can drive deterministic turnover of these moth assemblages (Kitching et al. 2013). However the effect of logging on the balance between stochastic and deterministic processes has seldom been investigated for a variety of taxa. Döbert et al. (2017) showed that understorey plant communities in tropical Bornean forests tend to be more stochastically assembled at higher logging intensities. By contrast, Wearn et al. (2019) showed that, as logging intensity increases, environmental control on the community assembly of mammals gets more important and spatial control on community assembly gets less important. This implies that deterministic niche assembly becomes more important with logging. There is broader conceptual and empirical support for determinism having higher relative importance in logged forests, which tend to have harsher environmental conditions compared to primary forests. Harsher environmental conditions can inflict a deterministic filter on community assembly, thus increasing the importance of deterministic processes, which has been demonstrated across a variety of taxa and regions (Chase 2007, Lepori & Malmqvist 2009, Chase & Myers 2011, Ding et al. 2012, Wearn et al. 2019, Li et al. 2021, Hu et al. 2022).

There is further uncertainty over how taxonomic groups might differ in their community assembly processes. For example, Aslani et al. (2022) documented variation in the relative importance of ecological processes among taxonomic groups in the soil eukaryome, which could be due to differences in body size or niche breadth (Aslani et al. 2022). These differences in assembly processes may also exist among different invertebrate taxa. For example, Sattler et al. (2010) demonstrated that deterministic

environmental variables explain <6 % of variance in bee communities and ~10 % of variance in spider communities, suggesting that stochastic processes are highly important but that their exact importance may vary depending on which taxa are investigated (Sattler et al. 2010). However, other studies have explained higher percentages of variance in spider communities (Jeanneret et al. 2003, Muff et al. 2009, Pozzi & Borcard 2001), which may be attributable to working in different environments. We therefore need to consider how different taxonomic groups might differ in the balance of stochastic and deterministic assembly processes. In microbial communities, generalist taxa have been shown to contribute more to stochastic processes, and specialist taxa to contribute more to deterministic processes, because specialists tend to have narrower tolerance to environmental changes (Liao et al. 2016, Xu et al. 2022). Similarly, studies on microbial communities have shown that rare taxa, which have narrower niche breadths, are more deterministically assembled while abundant taxa with wider niche breadths are more stochastically assembled (Gao et al. 2020, Yang et al. 2022). There has not, to our knowledge, been a similar study directly investigating among-taxa variation in stochastic and deterministic assembly processes for invertebrate communities.

There is a long-standing need to evaluate the relative importance of stochastic and deterministic processes along environmental gradients and among taxa (Weiher et al. 2011). Here, we address that knowledge gap by examining the balance of stochastic and deterministic contributions to community assembly, as well as the contribution of a suite of individual community assembly processes, to six invertebrate taxa across a gradient of logging intensity in Malaysia. Our data encompass a comprehensive gradient of logging intensity, from areas that have never experienced logging to areas that have been salvage logged. We quantified the contribution of a suite of community assembly mechanisms for a range of invertebrate taxa including three groups of beetles, along with ants, Orthoptera and spiders. Together, these taxonomic groups encompass a range of trophic levels and are of immense ecological importance (Barlow & Woiwod 1989, Didham et al. 1998, Grimaldi et al. 2005, Nyffeler & Birkhofer 2017, Oumarou Ngoute et al. 2020). We use our data to test two hypotheses: (1) Stochastic processes will decrease in importance as logging intensity increases, as logged forest should have harsher deterministic niche constraints than primary forest; and (2) Specialist taxa will be less stochastic than generalist taxa as specialists are expected to be more strongly affected by deterministic environmental filtering. Finally, we investigate whether the relative importance of different community assembly processes varies across a gradient of logging intensity for different invertebrate taxa.

Methods

Data collection

The study sites were located within the Stability of Altered Forest Ecosystems (SAFE) project (4° 38′ N to 4° 46′ N, 116° 57′ to 117° 42′ E), a large-scale ecological experiment encompassing a gradient of land use intensities in the lowland tropical forests of Sabah, Malaysian Borneo (Ewers et al. 2011). We used data from 14 out of the 17 experimental sampling blocks at SAFE (Ewers et al. 2011), excluding three blocks located in oil palm plantation. Ten sampling blocks were located in twice-logged forests and four were located in protected areas. Two of these protected area blocks were in the Maliau Basin Conservation area and have never experienced logging, while the other two had experienced light logging through both legal and illegal processes. Each sampling block comprised a set of 4 – 43 sampling sites (mean = 21). We grouped invertebrate samples collected within each block which we considered as one local community for analysis. The aggregation of all local communities across all sampling blocks was considered to represent the metacommunity.

Above-ground carbon density (ACD), calculated from LiDAR surveys and summarized at 1 hectare resolution in 2014, was used to quantify logging intensity (Jucker et al. 2018, Swinfield et al. 2020): a higher above-ground carbon density corresponds to a lower logging intensity. ACD was log-transformed to generate a more uniform spread of logging intensity values. The sampling blocks covered a wide range of logging intensities, with average above-ground carbon densities ranging from around 15 $t.C.ha^{-1}$ in heavily logged locations, to over 200 $t.C.ha^{-1}$ in the protected areas. Not all invertebrate taxa were sampled at the same subset of sampling points per block. For analysis, then, we calculated the average ACD per sampling block separately for each taxon, taking as inputs the ACD values for the specific subset of sampling sites where that taxon was collected.

We combined community composition data collected from six invertebrate taxa: three groups of beetles, plus ants, spiders and Orthoptera. Different groups had different sample sizes and not all groups were sampled in all 14 sampling blocks (Table S1, Figure S1). Beetles were sampled between 2011 and 2013 using combination pitfall-malaise traps in all 14 sampling blocks. Three different groups of beetles were sampled: Curculionoidea (weevils), Staphylinidae (rove beetles) and Scarabaeoidea (scarabs) (Sharp et al. 2018, 2019). Because of differences in their trophic levels, each group was considered a separate taxon and was analysed separately. Weevils are predominantly herbivorous; most scarabs in our dataset are dung-feeders, and rove beetles can belong to several feeding guilds. Beetles were identified primarily to morphospecies, except some scarabs which were identified to species. Ants were sampled between December 2011 and June 2012 in 12 sampling blocks using 12cm x 14cm plastic cards, which were laid flat in the leaf litter and baited with 30 compressed dried earthworm pellets. The number of ants entering each card was observed and recorded for 40 minutes, and individuals were identified to morphospecies (Fayle et al. 2019). Spider

abundance data were collected in 2015 in 10 sampling blocks by beating plant foliage for 20 minutes at each site. Spiders were identified to family, then separated into morphospecies by genitalia dissections and DNA barcoding using the CO1 gene (Maunsell et al. 2020). Finally, Orthoptera were sampled in 2015 by sweep netting along 100 m transects in 6 sampling blocks. Orthoptera were identified to family, then separated into morphospecies using identification guides (Hardwick et al. 2022).

Stochasticity metrics

There are different ways for communities to express stochasticity, so there is value in assessing multiple metrics of stochasticity on the same communities (Vellend & Agrawal 2010). We chose to quantify stochasticity using three different null-model based mathematical frameworks that summarise stochasticity both at the community level and at the level of individual species.

First, we employed the normalised stochasticity ratio (NST) (Ning et al. 2019). NST values are normalised on a scale from 0 to 1, with 0.5 as the boundary between more stochastic (>0.5) and more deterministic (<0.5) community assembly. NST is based on pairwise community dissimilarity measures, for which there are many competing metrics. We used Ružička dissimilarity which was shown to have the highest accuracy and precision when the NST was developed (Ning et al. 2019). NST compares the observed dissimilarity of the real community with the null expected dissimilarity for 1,000 randomised communities (Ning et al. 2019). To generate the random metacommunities for the null expectation, the default null model algorithm was used. This algorithm is based on fixed taxa richness and proportional taxa occurrence frequency (Ning et al., 2019).

Second, we used the Raup-Crick metric (RC) (Raup & Crick 1979, Chase et al. 2011). While NST is based on the magnitude of the difference between observed and null expected community composition, RC is based on the statistical significance of this difference and is robust to variations in local species richness among communities. RC indicates whether the community is more dissimilar (RC closer to 1) or more similar (RC closer to -1) than null expectation. Values close to 0 indicate a community composition that is close to what would be expected if community assembly was random, and therefore reflect a high importance of stochastic processes (Chase et al. 2011). We used the absolute value of RC because we were expressly interested in the balance of stochastic *versus* deterministic processes, and this transformation ensured values were bounded at 0 and 1. We then reversed the direction of |RC| to ensure it scaled in the same direction as NST and NTP, with values closer to 1 indicating more stochastic community assembly and values closer to 0 indicating more deterministic community assembly.

Finally, we calculated the neutral taxa percentage (NTP) (Burns et al. 2016). NTP is the proportion of species with occurrence frequencies that could be predicted by Sloan's neutral model (Sloan et al. 2006, 2007), which quantifies the relationship between the occurrence frequencies of taxa in a set of local communities and their abundances across the metacommunity (Burns et al. 2016). 'Neutral taxa' are those whose

observed occurrence frequencies are within one confidence interval of that which would be expected by Sloan's neutral model. The proportion of neutral taxa was weighted according to the abundance of individuals in each taxon, and was used to assess stochasticity at the level of individual species (Burns et al. 2016).

All three stochasticity metrics were calculated from a separate community composition (site × species) matrix for each of the six taxa. We calculated stochasticity metrics for all sites in the composition matrix, and grouped sites together by sampling block to calculate the mean of each stochasticity metric for each sampling block.

Community assembly processes

To further characterise the drivers of community assembly along the logging gradient, we quantified the relative importance of a suite of stochastic and deterministic community processes. We examined three stochastic processes (dispersal limitation, homogenizing dispersal and drift) and two deterministic processes (homogeneous selection and heterogeneous selection) (Stegen et al. 2013, Ning et al. 2020). Heterogeneous selection is selection under heterogeneous abiotic and biotic conditions in space and time that leads to high phylogenetic compositional variation among local communities. Whereas homogeneous selection takes place under homogeneous conditions and leads to low phylogenetic compositional variation. Dispersal limitation refers to the situation where low levels of dispersal among local communities constrains the exchange of organisms between these communities, leading to high levels of spatial turnover. Homogenizing dispersal is the opposite situation where high levels of dispersal result in little turnover among communities. Communities that are not dominated by selection or dispersal are designated as being governed by drift (Stegen et al. 2013, Ning et al. 2020).

The proportional contribution of each of these five community assembly mechanisms was inferred through phylogenetic bin-based null model analysis (iCAMP) (Stegen et al. 2013, Ning et al. 2020). For each of the six groups of taxa, we used iCAMP to calculate the relative importance of each process for all pairwise comparisons between all sites regardless of logging intensity. We then grouped sites by sampling block and calculated the mean relative importance of each process for each taxa x sampling block combination.

The iCAMP framework divides taxa into groups ('bins') based on their phylogenetic relationships, then identifies the dominant community assembly process in each bin. Phylogenies were not available for the taxa included in this study, so we used a taxonomy tree as a surrogate. Taxa were divided into bins based on taxonomic identity (Table S2, Figure S3), and bins with fewer than the minimum number of taxa (n = 9) were merged into the bin to which they were most closely related (Ning et al. 2020). The number of randomisations used for the null model analysis was 500.

To calculate the relative importance of community assembly processes, iCAMP uses null model analysis of phylogenetic diversity (beta net relatedness index, βNRI) and taxonomic β-diversity (modified Raup-Crick metric, RC) to identify the process governing each bin. For each bin, the fraction of pairwise comparisons between sites with βNRI < -1.96 was considered as the percentage contribution of pairwise comparisons dominated by homogeneous selection, and those with βNRI > +1.96 as the percentage contribution of heterogeneous selection. Pairwise comparisons with -1.96 ≤ βNRI ≤ +1.96 were further partitioned using RC. The fraction of pairwise comparisons with RC <- 0.95 indicates the percentage contribution of homogenizing dispersal, while those with RC > +0.95 indicates the percentage contribution of dispersal limitation. The remaining pairwise comparisons with βNRI ≤ |1.96| and RC ≤ |0.95| were considered to represent the contribution of drift, which includes ecological drift and other processes such as diversification, weak selection and weak dispersal. The fractions of each process across all bins were then weighted by the relative abundance of each bin (Stegen et al. 2013, Ning et al. 2020).

Statistical analysis

All data analysis was conducted using R version 4.1.0 (R Core Team 2022). NST and RC stochasticity metrics were calculated using the NST package (Ning et al. 2019), while NTP and iCAMP metrics were calculated using iCAMP (Ning et al. 2020).

To see how species identity changed across the gradient of logging intensity, we compared the Bray-Curtis similarity of each sampling block to old-growth forest using the vegan package (Oksanen et al. 2022), and used beta regression (Cribari-Neto & Zeileis 2010) to assess the effect of ACD on Bray-Curtis similarity.

We calculated the mean of each stochasticity metric (NST, |RC| and NTP) and of each community assembly process (heterogeneous selection, homogeneous selection, dispersal limitation, homogenizing dispersal and drift) for each taxa x sampling block combination, and estimated 95 % quantiles of these means using bootstrapping; we sampled the values used to calculate the mean 1000 times with replacement, then took the 5th and 95th quantiles of this distribution.

One-sample *t*-tests were used to compare the overall unweighted mean NST, |RC| and NTP across all taxa to 0.5, which we used as an arbitrary boundary point separating stochastic (>0.5) from deterministic (<0.5) community assembly processes. ANOVA tests were used to test for significant differences in NST, |RC| and NTP among taxa.

To investigate the effect of logging on the importance of stochasticity we used beta regression. To see how this relationship varies among taxa, we fitted another beta regression model for each stochasticity metric with taxon, ACD and their interaction as predictors of stochasticity. A similar analysis was conducted to investigate the effect of logging on the relative importance of each community assembly process, however

Dirichlet regression was used instead of beta regression as Dirichlet regression is appropriate for proportions with more than two categories (Douma & Weedon 2019).

To gain a taxa-independent metric reflecting the overall change in the relative importance of the five community assembly processes across the logging gradient, we combined the slopes for all taxa to give a weighted summary mean of the slopes for each process, using a method similar to a fixed effects meta-analysis, adapted from (Borenstein et al. 2010). We also combined the mean relative importance of each of the five processes and each of the three stochasticity metrics to give a weighted summary mean for all taxa using the following method adapted from (Borenstein et al. 2010):

For each group of taxa (i), the weight (w) is the inverse of the variance for that group of taxa $w_i = \frac{1}{v_i}$. The variance (v) is the range of the 95% confidence intervals. $\overline{M}$ is the overall weighted mean for all groups of taxa combined, it is analogous to the combined effect size in a meta-analysis. $\overline{M}$ is calculated as $\overline{M} = \frac{\sum_{i=1}^{k} w_i m_i}{\sum_{i=1}^{k} w_i}$, where m is the mean relative importance or slope for each group of taxa, analogous to the effect size of each study in a meta-analysis, and w_i is the weight assigned to group i, and k is the number of groups of taxa (k = 6).

Results

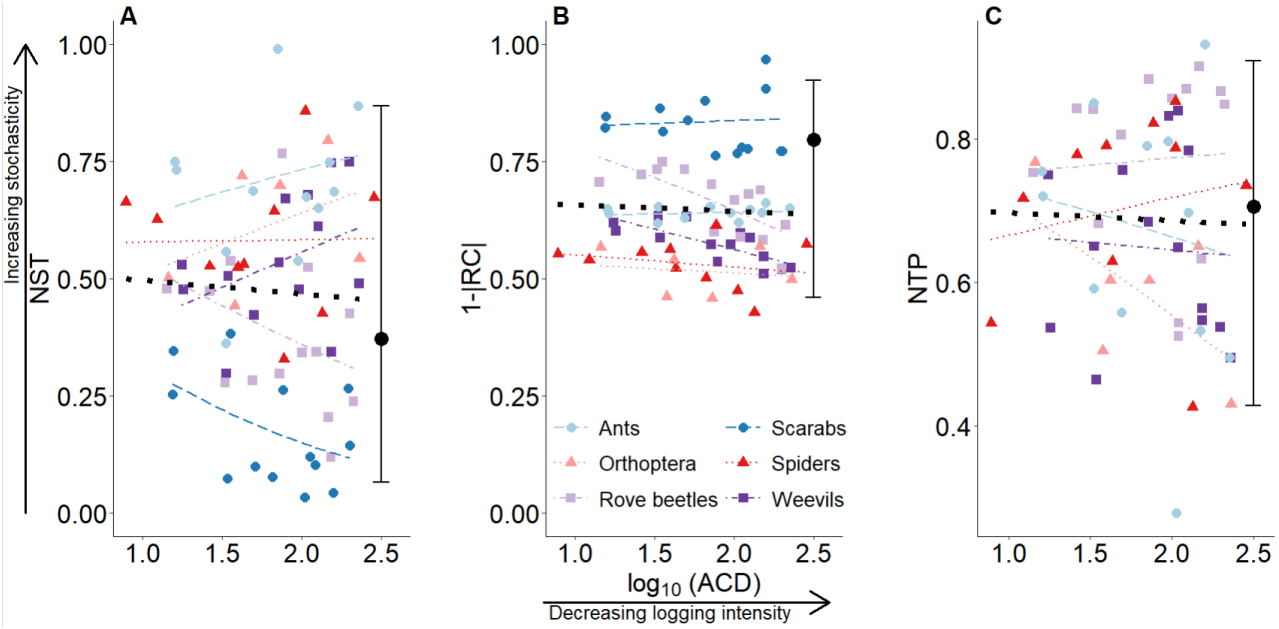
Across all datasets, our analysis included 25,847 individuals belonging to 1,002 species or morphospecies (Table S1). In general, community similarity between sampling blocks was low. Each of the three beetle taxa showed a decrease in community similarity compared to old growth forest as logging intensity increased, whereas the remaining three taxa did not (Figure S2).

Stochasticity metrics

The overall average NST across all taxa was 0.47 (95% CI = 0.42 – 0.53), which was not significantly different from 0.5 (one-sample *t*-test, *t* = -0.90, df = 68, *p* = 0.37). However, the remaining two metrics of stochasticity did identify a significant bias indicating that ecological stochasticity plays a significantly greater role in structuring invertebrate communities than deterministic processes (|RC|: mean = 0.64; 95 % CI = 0.62 – 0.67; *t* = 10.3, df = 69, *p* <0.0001; NTP: mean = 0.69; 95 % CI = 0.65 – 0.73; *t* = 9.6, df = 55, *p* < 0.0001). When the overall average NST was weighted by the variance of each taxon, it reduced to 0.37 (95 % CI = 0.07 – 0.87). By contrast, the weighted average |RC| (0.80, 95 % CI = 0.46 – 0.92) was higher than the unweighted average and the weighted average NTP was 0.71 (95 % CI = 0.43 – 0.91) (Figure 1).

267 There were significant differences in the role of stochasticity among taxa for NST and |RC| (ANOVA, NST:
268 $F_{63, 5}$ = 20.2, p <0.0001; |RC|: $F_{64, 5}$ = 55.7, p < 0.0001), but not for NTP ($F_{51, 4}$ = 2.4, p = 0.06). Ants had the
269 highest NST, whereas scarabs had the lowest NST. However, scarabs showed the highest stochasticity in
270 terms of |RC|. Weevils had the lowest stochasticity in terms of |RC|. Ants, which are mostly generalists,
271 had higher NST and |RC| than spiders which are mostly predators. However other generalist taxa like
272 Orthoptera had lower |RC| than spiders, and rove beetles also had lower NST than spiders (Table S3).

273 The relative importance of stochasticity was calculated within each sampling block then compared among
274 blocks. Each block had a different level of logging intensity. When all taxa were combined, there was no
275 significant effect of logging on stochasticity (Figure 1. NST: slope = -0.12, z = -0.40, p = 0.67. |RC|: slope = -
276 0.06, z = -0.34, p = 074. NTP: slope = -0.05, z = -0.23, p =0.82). The relationship between logging and
277 stochasticity varied among taxa (Figure 1), but the only significant relationship was a decrease in |RC| with
278 decreasing logging intensity for rove beetles (slope = -0.64, z = -2.65, p = 0.008). There was a weak
279 indication of a decrease in NST with decreasing logging intensity for scarabs (slope = -0.94, z = -1.90, p =
280 0.06) and rove beetles (slope = -0.70, z = -1.69, p = 0.09). However, all other slopes were not significant,
281 suggesting that these metrics of stochasticity are generally not affected by logging intensity for the taxa
282 investigated. Sloan's neutral model could not be fitted to the scarabs dataset, so scarabs were excluded
283 from the NTP analysis (Figure 1).



284 **Figure 1.** Variation in three different metrics of ecological stochasticity across a gradient of logging intensity
285 for six invertebrate taxa. Logging is quantified as $\log_{10}$-transformed above-ground carbon density (ACD),
286 where a higher ACD corresponds to a lower logging intensity. The thick black dotted regression lines
287 indicate that there was no significant effect of logging on stochasticity when all taxa were combined. The
288 black circles show the weighted average stochasticity metrics for across all taxa combined, and the error
289 bars represent bootstrapped 95 % quantiles of these averages. The three stochasticity metrics are: (A)

290 Normalised stochasticity ratio (Ning et al. 2019); (B) Absolute deviation of the Raup-Crick metric (Chase et
291 al. 2011); and (C) Abundance-weighted proportion of taxa with observed occurrence frequencies within
292 one confidence interval of that expected by Sloan's neutral model (Sloan et al. 2006, 2007, Burns et al.
293 2016).

294 Community assembly processes

295 Dispersal limitation appeared to be the dominant community assembly process across all taxa (Figure 2a,
296 Table S4). When all groups of taxa were combined, the weighted summary mean relative importance of
297 dispersal limitation was 78 % (95 % quantiles = 4 - 98). For four out of the six groups of taxa (ants, rove
298 beetles, scarabs and weevils), dispersal limitation was the dominant community assembly process with a
299 relative importance ranging from 94 to 98 % (95 % quantiles = 89 - 99). The exceptions were spiders and
300 Orthoptera, where drift was the dominant process; 92 % of spider community assembly (95 % quantiles =
301 86 - 94) was estimated to be underpinned by drift, while this was estimated to be 74 % for Orthoptera (95
302 % quantiles = 60 - 82).

303 When comparing the relative importance of community assembly processes among sampling blocks, each
304 of which had a different level of logging intensity, the relative importance of the five community assembly
305 processes was generally not significantly affected by logging intensity (Figure 2b, Table S5). When all groups
306 of taxa were combined, the weighted summary mean slopes for all processes were not significantly
307 different from zero. The strongest effects were an increase in the importance of dispersal limitation as
308 logging intensity increases (-0.19, 95 % CI = -1.51 – 1.14) and a decrease in heterogeneous selection with
309 increasing logging intensity (0.19, 95 % CI = -1.14 – 1.51), but these were not significantly different from
310 zero. The summary mean effects for homogeneous selection (0.05), homogenizing dispersal (-0.05) and
311 drift (0.11) were even weaker. All slopes for the individual groups of taxa were not statistically significant
312 (Figure 2b).

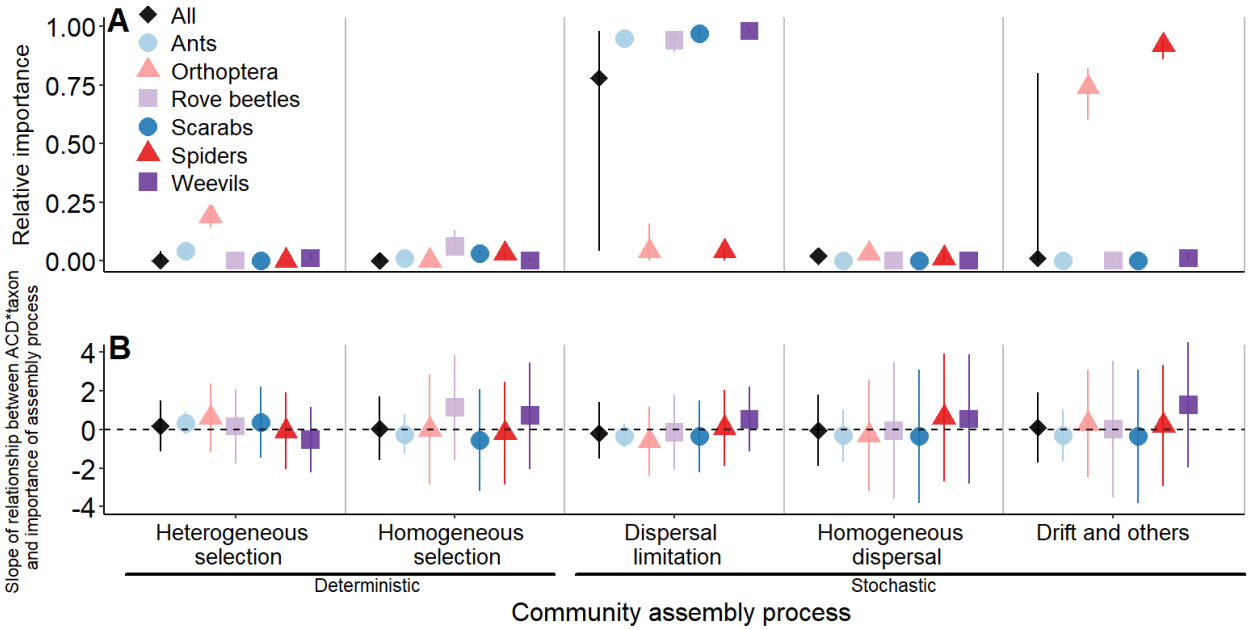


Figure 2. (A) Mean relative importance of five community assembly processes for generating the community structure of six invertebrate taxa and for all taxa combined. Error bars show bootstrapped 95 % quantiles. (B) The estimates for the slopes of the relationships between the relative importance of five community assembly processes and above-ground carbon density (ACD). Values are shown separately for each of six invertebrate taxa and for all groups of taxa combined. Positive slopes indicate processes that become less important as logging intensity increases.

Discussion

We found that ecological stochasticity was highly important in underpinning the assembly of all insect communities studied. At a finer resolution, dispersal limitation – one of the three stochastic processes we quantified – was the dominant community assembly process for most groups of taxa. In general, land use change had little impact on the relative importance of ecological stochasticity, nor on the relative importance of a suite of community assembly processes. Together, this suggests that stochastic community assembly processes, especially dispersal limitation, are the main drivers of invertebrate community assembly at our tropical rainforest site, regardless of the extent to which that habitat has been modified by logging. While logging has profoundly negative impacts on biodiversity, the balance between stochastic and deterministic processes is robust to changes in logging intensity for the invertebrate taxa studied.

Overall, there was at best a very weak effect of land use intensity on the role of ecological stochasticity in structuring insect communities. Different taxa showed different directions of the relationship between logging and the three stochasticity metrics, but these relationships were generally not significant. The relative importance of different community assembly mechanisms was also not significantly affected by logging intensity for most taxa (Figure 2b). We might expect to find little evidence of a change in the

community assembly processes governing invertebrate communities if those communities do not exhibit turnover in species composition across the logging gradient. For three of the taxa (ants, Orthoptera and spiders), this assumption holds true: we found no evidence of changing taxonomic identities across the logging gradient (Figure S2) which aligns well with a lack of change in the assembly processes governing those taxa (Figure 2b). However, all three beetle taxa (rove beetles, scarabs and weevils) did exhibit significant turnover in the identity of species as logging intensity increased (Figure S2), which is consistent with previous studies (Hamer et al. 2003, Cleary et al. 2007, Sharp et al. 2019). Yet two of those taxa (scarabs and weevils) appeared to have logging-related turnover in species identities where that turnover was generated by the same ecological processes, regardless of logging intensity. Even for the rove beetles, who did exhibit a small change from deterministic homogenous selection to stochastic dispersal limitation as logging intensity increased (Figure 2b), dispersal limitation remained the dominant process across the entire gradient (Figure 2a). This leads to the general conclusion that, regardless of whether or not species identities change, community assembly processes remain robust to changes in above-ground carbon density.

One possible explanation for why community assembly processes appear to be strongly conserved across the gradient of logging intensity is that our data were collected after logging had taken place. While our study landscape encompasses a very wide range of historic logging intensity, the time delay between the logging event itself and our description of the invertebrate communities means any transitory impacts of logging on community assembly processes would not have been detectable. Mahayani et al. (2020) showed that phylogenetic diversity and community structure of tree communities had recovered 10 years after a single logging cycle in Bornean tropical forest. Therefore, it could be possible, that the ecological communities we sampled might have recovered their basic, pre-logging structures so that the community assembly mechanisms in logged forests now resemble those of unlogged forests.

Dispersal limitation was the most important driver of community assembly when all groups of taxa were combined, and for four of the taxa individually. Spiders and Orthoptera were the exceptions, having a lower importance of dispersal limitation, and higher importance of drift, compared to the other taxa (Figure 2a). The sample sizes for spiders and Orthoptera were smaller than for the other taxa (Table S1, Figure S1). We cannot therefore definitively rule out the possibility that this result may represent a sampling effect. We do note, however, that the scarab community had a lower total number of individuals and a higher number of species than the Orthoptera, suggesting that an undersampling-driven effect should have exerted a greater impact on them than on the Orthoptera. Further, when we conducted a sensitivity analysis by grouping sites within the same, drift was still the dominant community assembly process for spiders and orthoptera (Text S1)

We have explicitly considered dispersal limitation to be a stochastic process, although we recognise in some cases it can be generated by deterministic processes, or a combination of both (Lowe & McPeek

2014, Zhou & Ning 2017). However, in neutral models and in empirical studies, dispersal is most often assumed to be stochastic, partly due to difficulties associated with studying dispersal traits (Lowe & McPeek 2014). Moreover, our results which demonstrate that invertebrate communities are both predominantly stochastically structured and that the main assembly process is dispersal limitation, is consistent with the idea that dispersal limitation is a stochastic process.

The overall importance of dispersal limitation as the dominant community assembly process highlights the importance of maintaining and, if necessary, restoring landscape connectivity in logged forests (Wearn et al. 2019). Dispersal limitation can result in high spatial turnover in community composition due to low levels of exchange of organisms among local communities (Stegen et al. 2013). The slight increase in dispersal limitation we detected as logging intensity increased, though not significant, is in a direction that is consistent with previous studies suggesting that animal communities in logged tropical forests may experience lower levels of dispersal compared to primary forests (Stratford & Robinson 2005, Laurance et al. 2009, Edwards et al. 2014). Therefore, local communities would be expected to exhibit more spatial turnover in community composition as logging intensity increases and could become more isolated from each other.

We found that invertebrate community assembly processes were robust to a gradient of logging intensity. Stochastic dispersal limitation remained the dominant driver of community assembly at all levels of habitat degradation in our tropical rainforest site. This therefore suggests that knowledge of primary community assembly can be useful in planning the restoration of modified communities as, when assembly was driven mainly by stochastic dispersal limitation, there were not significant changes in assembly processes despite changes in land use.

This study has quantified community assembly mechanisms across a gradient of logging intensity for six invertebrate taxa in Bornean rainforests. The effect of logging on stochasticity, and on different community assembly processes, varied only minimally among the different taxa and different metrics of stochasticity, and painted a picture in which the dominant community assembly mechanisms are not impacted by logging disturbance. Although logging did not alter the relative importance of stochastic and deterministic community assembly processes in our study, we emphasize that logging, and in particular severe logging, profoundly reduces species richness and changes community composition (Newbold et al. 2015). Stochastic community assembly, underpinned predominantly by dispersal limitation, appeared to be the dominant force structuring invertebrate communities. The dominance of dispersal limitation suggests that maintaining landscape connectivity is important for maintaining those invertebrate communities in Bornean forests.

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