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

Natasha R. Granville[1]; Maxwell V. L. Barclay[2]; Michael J. W. Boyle[1,3,4]; Arthur Y. C. Chung[5]; Tom M. Fayle[6,7]; Huai En Hah[8]; Jane L. Hardwick[9]; Lois Kinneen[10]; Roger L. Kitching[11]; Sarah C. Maunsell[9]; Jeremy A. Miller[12]; Adam C. Sharp[1]; Nigel E. Stork[11]; Leona Wai[8]; Kalsum M. Yusah[13]; Robert M. Ewers[1]

[1] Georgina Mace Centre for the Living Planet, Imperial College London, Ascot SL5 7PY, UK

[2] Natural History Museum, London SW7 5BD

[3] School of Biological Sciences, University of Hong Kong, Hong Kong

[4] Department of Biological Sciences, National University of Singapore, Singapore

[5] Forest Research Centre, Sabah Forestry Department, Sandakan, Sabah, Malaysia

[6] School of Biological and Behavioural Sciences, Queen Mary University of London, United Kingdom.

[7] Biology Centre of the Czech Academy of Sciences, Institute of Entomology, Ceske Budejovice, Czech Republic

[8] Universiti Malaysia Sabah, Institute for Tropical Biology and Conservation, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia

[9] Griffith University, 170 Kessels Rd, Nathan, Queensland 4111, Australia

[10] Centre for Agri-Environmental Research, School of Agriculture, Policy and Development, University of Reading

[11] Centre for Planetary Health and Food Security, Griffith University, 170 Kessels Rd, Nathan, Queensland 4111, Australia

[12] Understanding Evolution Research Group, Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands

[13] Royal Botanic Gardens, Kew, Richmond, UK TW9 3AE

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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. Few 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 1,645 arthropod species across seven taxonomic groups in Malaysian Borneo, we quantified the importance of stochastic and deterministic assembly processes across a gradient of logging intensity. Dispersal limitation was the dominant process for most taxa 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 [1], but it is much less well-known that they can also affect community assembly mechanisms [2]. Currently, therefore, we have a strong awareness of the patterns of biodiversity change that are generated by land use change [1], 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 [3], meaning studies examining land use impacts on the assembly processes of mammals (e.g.[2]) 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 [4,5]. 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 [6], with the two sets of processes sitting at opposite ends of a continuum. Real-world communities exist somewhere between these two extremes [7,8]. 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 [7,9,10]. Neutral theory makes the extreme assumption that all individuals within a particular feeding guild 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 [11]. By contrast, determinism can be defined as non-random changes in community composition that can be predicted based on species' identities and niches [12], and is broadly described as niche theory which assumes that deterministic processes, such as selection, play a fundamental role in driving community assembly [13].

There has been long-standing debate over the relative influence of stochastic and deterministic processes on community assembly [14]. Numerous studies have investigated the relative importance of stochasticity and determinism in different environments [e.g. 9,15–18]. 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 [19,20]. 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 [21]. 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 [22]. Logging often results in a heterogeneous landscape, with habitat patches connected spatially but affected by different logging intensities [23]. This can result in gradients of disturbance intensity, which are a frequent consequence of land use change in the tropics [2].

There is uncertainty over how logging might affect stochastic and deterministic community assembly processes, with little in the way of direct evidence. In primary forests, stochastic turnover in plant species can drive deterministic changes in the niche dimensions available for moths, leading to a distance-turnover relationship. However, such distance-turnover relationships have been shown to be absent in moth assemblages in logged forests [24]. 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 [2,26–31].

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 within groups of animals, fungi and protists in the soil eukaryome, which could be due to differences in body size or niche breadth [32]. 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 [33]. However, other studies have explained higher percentages of variance in spider communities [34–36], 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 [37,38]. 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 [39,40]. 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 [3]. 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 seven 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 community assembly mechanisms for a range of invertebrate taxa including three groups of Coleoptera (beetles), along with Formicidae (ants), Lepidoptera (moths), Orthoptera and Araneae (spiders). Together, these taxonomic groups encompass a range of feeding guilds and are of immense ecological importance [41–45]. 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 [46]. We used data from 14 out of the 17 experimental sampling blocks at SAFE [46], 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 = 19). 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 [47,48]: 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 seven invertebrate taxa: three groups of beetles, plus ants, moths, 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) [49,50]. Because of differences in their feeding guilds, 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 [51]. Moths were sampled in 2014 using UV light traps which were run overnight in 8 sampling blocks. Moths were identified where possible and separated into morphospecies using morphology [52]. 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 [53]. 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 [54].

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 [12]. 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) [55]. 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 [55]. NST compares the observed dissimilarity of the real community with the null expected dissimilarity for 1,000 randomised communities [55]. 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 [55].

Second, we used the Raup-Crick metric (RC) [56,57]. 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 [56]. 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) [58]. NTP is the proportion of species with occurrence frequencies that could be predicted by Sloan's neutral model [59,60], which quantifies the relationship between the occurrence frequencies of taxa in a set of local communities and their abundances across the metacommunity [58]. '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 [58].

All three stochasticity metrics were calculated from a separate community composition (site × species) matrix for each of the seven 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 assembly processes. We examined three stochastic processes (dispersal limitation, homogenising dispersal and drift) and two deterministic processes (homogeneous selection and heterogeneous selection) [61,62]. Heterogeneous selection is selection under heterogeneous abiotic and biotic conditions in space and time that leads to high phylogenetic compositional variation among local communities. 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. Homogenising 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 [61,62].

The proportional contribution of each of these five community assembly mechanisms was inferred through phylogenetic bin-based null model analysis (iCAMP) [61,62]. For each of the seven 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 taxonomy trees as proxies for phylogenies. 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 [61]. 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 homogenising 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 [61,62].

Statistical analysis

All data analysis was conducted using R version 4.1.0 [63]. NST and RC stochasticity metrics were calculated using the NST package [55], while NTP and iCAMP metrics were calculated using iCAMP [61].

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 [64], and used beta regression [65] 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, homogenising 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. We also used ANOVA to test for significant differences in NST, |RC| and NTP among taxa.

To test the hypothesis that generalists (ants and rove beetles) would be more stochastic than specialists (moths, Orthoptera, spiders, scarabs and weevils), we used beta regression with a single categorical predictor variable that describes whether the taxon is considered generalist or specialist. We fitted three separate beta regression models, each with a stochasticity metric as the response variable. We broadly categorised each taxonomic group into generalists or specialists based on their feeding habits Ants were considered generalists because their diets can range from almost herbivorous to omnivorous and fully predatory [66]. Many rove beetles are generalist predators, though some can belong to other feeding guilds [67], so we also classified rove beetles as generalists. The Orthoptera and weevils included in our data were mainly herbivorous [50,54], so we classified them as specialists. Spiders were all predatory [68], scarabs were primarily coprophagous [49] and moths were herbivorous as larvae and nectarivorous as adults [69], so we classified these groups as specialists for our analysis.

To investigate the effect of logging on the importance of each stochasticity metric we used beta regression, with the mean ACD of each block as the predictor. 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 [70].

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 [71]. 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 [71]:

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 32,294 individuals belonging to 1,645 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 0.49 (95 % CI = 0.44 – 0.54), which was not significantly different from 0.5 (one-sample *t*-test, *t* = -0.30, df = 76, *p* = 0.76). 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 = 0.62; 95 % CI = 0.59 – 0.65; *t* = 7.52, df = 77, *p* <0.0001; NTP: mean = 0.68; 95 % CI = 0.64 – 0.71; *t* = 10.1, df = 63, *p* < 0.0001). When the overall average NST was weighted by the variance of each taxon, it reduced to 0.39 (95 % CI = 0.07 – 0.83). By contrast, the weighted average |RC| (0.73, 95 % CI = 0.37 – 0.91) was higher than the unweighted average. The unweighted average NTP was not different to the weighted average NTP was (0.69, 95 % CI = 0.43 – 0.89) (Figure 1).

There were significant differences in the role of stochasticity among taxa (ANOVA, NST: $F_{70, 6} = 19.7$, $p < 0.0001$; |RC|: $F_{71, 6} = 68.7$, $p < 0.0001$; NTP: $F_{58, 5} = 2.6$, $p = 0.04$). On average, ants had the highest NST, whereas scarabs had the lowest NST. However, scarabs showed the highest stochasticity in terms of |RC| and NTP (Table S3). Moths had the lowest stochasticity in terms of |RC| and Orthoptera had the lowest NTP. Generalist taxa had higher NTP than specialists (beta regression, coefficient = -0.39, $z = -2.56$, $p = 0.02$), however there was no significant difference in NST or |RC| between generalists and specialists (NST: coefficient = -0.22, $z = -1.02$, $p = 0.31$. |RC|: coefficient = -0.14, $z = -0.96$, $p = 0.34$).

The relative importance of stochasticity was calculated within each sampling block then compared among blocks. Each block had a different level of logging intensity. When all taxa were combined, there was no significant effect of logging on stochasticity (Figure 1. NST: slope = -0.07, $z = -0.28$, $p = 0.78$. |RC|: slope = 0.13, $z = 0.73$, $p = 0.47$. NTP: slope = -0.04, $z = -0.22$, $p = 0.83$). The relationship between logging and stochasticity varied among taxa (Figure 1), but the only significant relationships were an increase in 1-|RC| with decreasing logging intensity for moths (slope = 0.48, $z = 3.35$, $p = 0.0008$) and a decrease in 1-|RC| with decreasing logging intensity for rove beetles (slope = -0.64, $z = -3.93$, $p = 0.008$). There was a weak indication of an increase in NST with decreasing logging intensity for moths (slope = 0.63, $z = 1.97$, $p = 0.05$) and a decrease in NST with decreasing logging intensity for scarabs (slope = -0.94, $z = -1.92$, $p = 0.06$). However, all other slopes were not significant, suggesting that these metrics of stochasticity are generally not affected by logging for the taxa investigated. Sloan's neutral model could not be fitted to the scarabs dataset, so scarabs were excluded from the NTP analysis (Figure 1C).

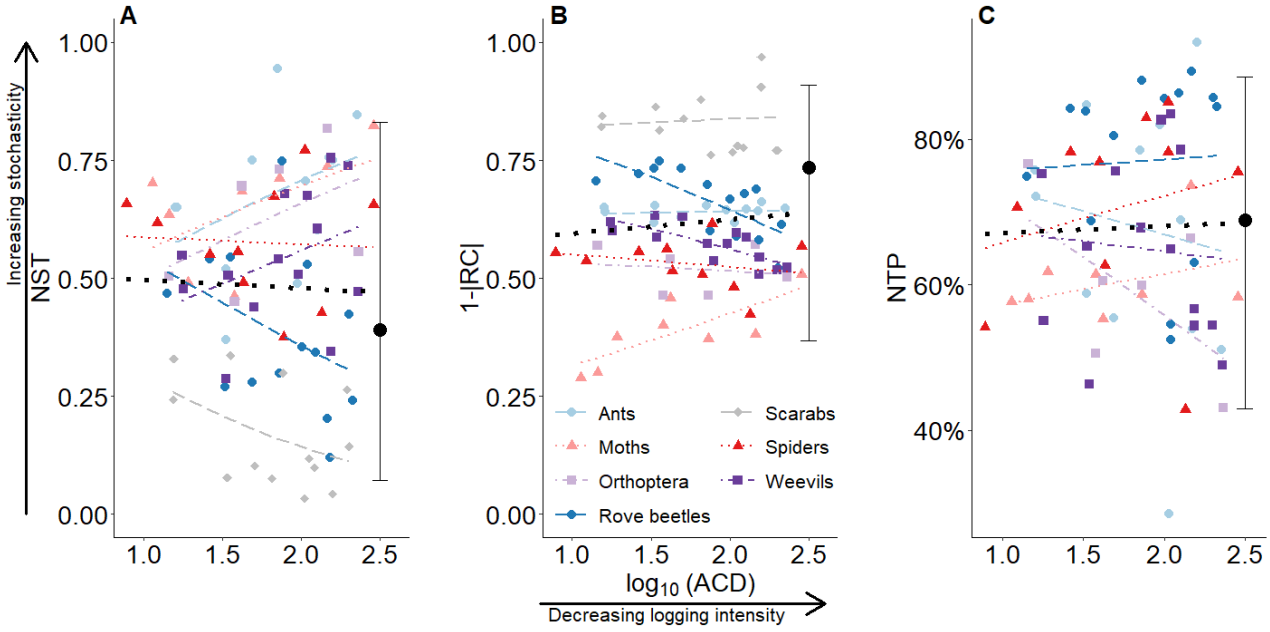

Figure 1. Variation in three different metrics of ecological stochasticity across a gradient of logging intensity for seven invertebrate taxa. Logging is quantified as $\log_{10}$-transformed above-ground carbon density (ACD), where a higher ACD corresponds to a lower logging intensity. The thick black dotted regression lines

indicate that there was no significant effect of logging on stochasticity when all taxa were combined. The black circles show the weighted average stochasticity metrics for all taxa combined, and the error bars represent bootstrapped 95 % quantiles of these averages. The three stochasticity metrics are: (A) Normalised stochasticity ratio [55]; (B) Absolute deviation of the Raup-Crick metric [56]; and (C) Abundance-weighted proportion of taxa with observed occurrence frequencies within one confidence interval of that expected by Sloan's neutral model [58–60].

Community assembly processes

Dispersal limitation was the dominant community assembly process when all taxa were combined and weighted by sample size (overall relative importance = 64 %, 95 % CI = 26 – 97). Dispersal limitation was the dominant process for four out of the seven taxonomic groups (rove beetles, scarabs, weevils and ants), with a relative importance ranging from 94 to 98 % (95 % quantiles = 89 - 99). Drift was the dominant process for spiders, Orthoptera and moths; 92 % of spider community assembly (95 % quantiles = 86 - 94) was estimated to be underpinned by drift, while this was estimated to be 74 % for Orthoptera (95 % quantiles = 60 - 82) and 67 % for moths (95 % quantiles = 62 - 75) (Figure 2A; Table S4).

When comparing the relative importance of community assembly processes among sampling blocks, each of which had a different level of logging intensity, the relative importance of the five community assembly processes was not significantly affected by logging intensity for most taxa (Figure 2b, Table S5). When all groups of taxa were combined, the weighted summary mean slopes for all processes were not significantly different from zero. The strongest effects were a decrease in the importance of dispersal limitation as logging intensity decreases (-0.85, 95 % CI = -2.01 – 0.32) and an increase in heterogeneous selection with decreasing logging intensity (0.85, 95 % CI = -0.32 – 2.01), but these were not significantly different from zero. The summary mean effects for homogeneous selection (-0.55), homogenising dispersal (-0.65) and drift (-0.61) were even weaker. The only significant slopes for individual groups of taxa were for moths, which showed a decrease in the importance of all three stochastic assembly processes with decreasing logging intensity (Dispersal limitation: slope = -2.45, 95 % CI = -3.11 – -1 .79. Homogenising dispersal: -2.49, 95 % CI = -3.34 – -1.64. Drift: -1.53, 95 % CI = -1.97 – -1.08) (Figure 2B; Table S5).

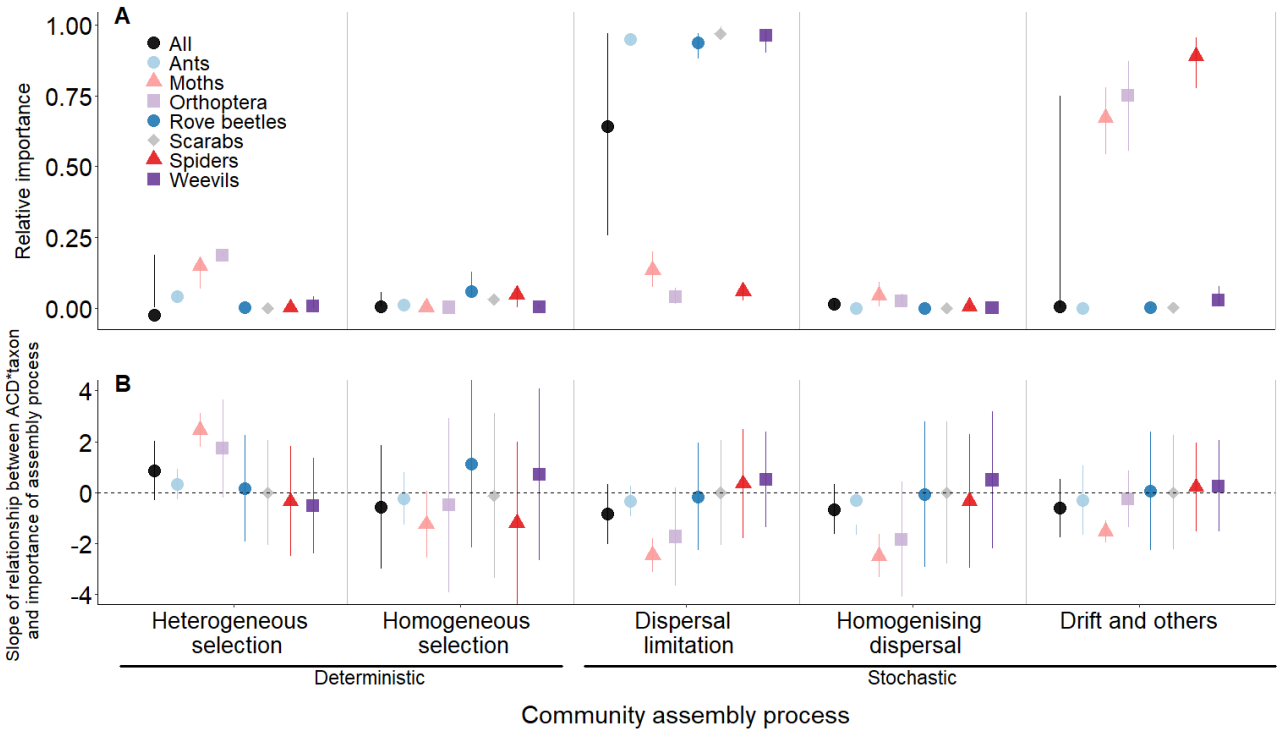

Figure 2. (A) Mean relative importance of five community assembly processes for generating the community structure of seven invertebrate taxa, and weighted averages for all taxa combined. Error bars show bootstrapped 95 % quantiles. (B) The estimates for the slopes of the relationships between the relative importance of five community assembly processes and above-ground carbon density (ACD). Values are shown separately for each of seven invertebrate taxa, and the black circles show weighted averages 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 was the dominant community assembly process overall. 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 dispersal assembly is the main driver 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 appears 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 six out of seven taxonomic groups (Figure 2b). Moths, however, were the exception, showing changes in community assembly processes (Figure 1; 2b) and turnover in species composition (Figure S2) with logging. For the six taxa that show no change in community assembly with logging, 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 [50,72,73]. 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.

Two out of the three stochasticity metrics (NST and |RC|) were not significantly different between generalists and specialists. Only the NTP metric supported our hypothesis that generalist taxa would be more stochastic than specialists. When comparing taxa at a finer resolution, our results show that dispersal limitation was the most important driver of community assembly for ants and beetles, whereas drift was the main driver of assembly for spiders, Orthoptera and moths (Figure 2a). Spiders, moths and Orthoptera were sampled at fewer sites than ants and beetles (Table S1), so we cannot 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 block, drift was still the dominant community assembly process for spiders, and orthoptera, and the importance of drift was even slightly increased for moths (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 [10,75]. 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 [75]. 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, especially for ants and beetles highlights the importance of maintaining and, if necessary, restoring landscape connectivity in logged forests [2]. Dispersal limitation can result in high spatial turnover in community composition due to low levels of exchange of organisms among local communities [62]. 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 [76–78]. 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, for six out of seven taxonomic groups, 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 seven groups of 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 [1]. Stochastic community assembly, underpinned predominantly by dispersal limitation, appeared to be the dominant force structuring all beetle and ant communities. The dominance of dispersal limitation suggests that

maintaining landscape connectivity is important for maintaining invertebrate communities in Bornean forests.

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Data accessibility statement

The data that support the findings of this study are openly available on Zenodo at:

https://doi.org/10.5281/zenodo.1323504 (beetles)

https://doi.org/10.5281/zenodo.7011354 (Orthoptera)

https://doi.org/10.5281/zenodo.4247169 (moths)

https://doi.org/10.5281/zenodo.3876227 (ants)

https://doi.org/10.5281/zenodo.4020697 (above-ground carbon density)

The R scripts used for all analyses in this study are openly available on GitHub at:

https://github.com/natashagranville/invertebrate-community-assembly

A pre-print of this manuscript was uploaded to BioRxiv:

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