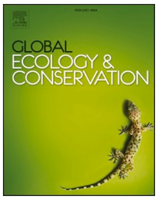
Global Ecology and Conservation 59 (2025) e03561

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco



Original research article

Impact of landscape disturbance on butterfly communities: Diversity, distance dependence, and neutral model predictions

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ARTICLE INFO

Keywords:
Borneo
Community composition
Indonesia
Neutral model

ABSTRACT

Recent theoretical work suggests that rainforest biotas are not primarily structured by environmental determinism but rather by stochastic processes. We sampled butterflies from primary and disturbed (logged, and burnt) forest landscapes and compared diversity, examined geographic distance and dissimilarity relationships, and tested for deviations from neutral model predictions. Significant distance dependence was observed in all landscapes except one. All primary forest landscapes deviated significantly from neutral model predictions; in contrast, only one of the disturbed landscapes deviated significantly. Deviation from neutrality in primary forest suggests potentially important contributions of niche specialisation and/or competitive exclusion in structuring butterfly communities. Disturbances like logging or fires, which open up the forest, seem to push these communities toward neutrality with greater species richness and evenness than proximate primary forest. Multiple disturbance events, however, appear to lead to a loss of species while maintaining relatively high evenness and communities consistent with neutral model predictions. Furthermore, the butterfly communities of once- and twice-burnt landscapes appeared to consist of species with greater tolerances to disturbance or able to rebound following disturbance in addition to species, which entered from surrounding severely degraded habitat. Interestingly, a frequently-burnt landscape, now largely devoid of forest, aligned with neutral model predictions. This landscape contained a low-richness, highly impoverished fauna consisting of widespread generalists, but with relatively high evenness. We suggest that differentially disturbed habitats act as environmental filters to butterfly species, but that neutral processes dominate after environmental filtering.

1. Introduction

There is considerable debate on the relative importance of deterministic versus stochastic processes in explaining beta diversity, which is the variation in species composition among sampling units (Bell, 2001; Condit et al., 2002; Duivenvoorden et al., 2002; Tuomisto et al., 2003; Wright, 2002; Whitfield, 2002). Whereas niche based theories have a long history in ecological research

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https://doi.org/10.1016/j.gecco.2025.e03561
Received 1 November 2024; Received in revised form 8 February 2025; Accepted 21 March 2025

(Grinnell, 1917; Levin, 1970; MacArthur, 1970; Diamond, 1975) and are implicit in the work of Darwin, neutral theories that focus on the random nature of communities are of more recent origin (Caswell, 1976; Harte et al., 1999; Hubbell, 2001). An important stimulus in this debate is the work of Hubbell (2001) in which he described a 'unified theory of biodiversity and biogeography'. Under Hubbell's neutral theory, all organisms within a trophic level are considered to function as ecologically indistinguishable units. Species in any given habitat at any point in time are assumed to be an amalgamation of individuals thrown together from a much larger and biogeographically-constrained metacommunity.

One of the most critical factors in describing communities/assemblages with neutral models is dispersal limitation. Under very low rates of dispersal a single species is expected to dominate each local community. As dispersal increases, immigrants are able to reach neighbouring communities thereby changing the local species abundance distributions (Bell, 2001). The idea of dispersal limitation is somewhat older than the general neutral theories, and points to an early perception that random processes could play a role in structuring communities. Gleason (1923) and Palmgren (1926), for example, suggested that dispersal limitation and passive propagule dispersal were major factors in structuring communities of plants and animals.

In a study that compared predictions of neutral theory with observations of lowland tree communities in central and South America, Condit et al. (2002) found that patterns of beta diversity reflected those predicted by neutral theory at intermediate spatial scales, but broke down at small and large scales. At the smaller spatial scales they noted that similarity declined rapidly with distances up to 3–5 km in all three areas they surveyed. They concluded that species are more aggregated than predicted by theory at small spatial scales and at large spatial scales low species turnover rates may be bounded by as yet unexplained processes.

Their study was, however, criticised by Ruokolainen and Tuomisto (2002). First of all Ruokolainen and Tuomisto (2002) claimed that Condit et al. (2002) had sampled relatively few plots over large spatial scales; 34 plots in Central America up to 50 km apart, and 16 and 14 plots in two areas of South America at even greater spatial scales. This means that their rapid decline in similarity at small spatial scales was based on relatively poor sampling. Moreover the Central American study consisted of plots in old growth and new growth habitat without explicitly addressing this in the analyses, while the South American studies only consisted of plots in old growth habitat.

Previous studies that confirmed neutral model predictions include studies of nearctic snake communities (Burbrink et al., 2015), root-associated fungi (Beck et al., 2015), chicken, swine and bovine gut microbiota (Sala et al., 2016), waterborne bacterial communities in tree-holes (Woodcock et al., 2007), phytoplankton communities (Chust et al., 2013), riverine fish communities (Muneepeerakul et al., 2008), microbial communities in a wastewater treatment plant (Ofiţeru et al., 2010) and certain tropical tree communities (Jabot and Chave, 2011) whereas neutral model predictions were rejected in communities of soil-associated fungi, (Beck et al., 2015), Indo-Pacific coral communities (Dornelas et al., 2006) and other tropical tree communities (Jabot and Chave, 2011). In a study of fruit-feeding butterflies, the neutral model provided a good fit with empirical data, but Aduse-Poku et al. (2018) noted that they also found evidence of deterministic processes playing a role in structuring community composition.

The question arises as to how disturbance will affect community structure and neutral model predictions. Caswell (1976) showed that communities in more stable pristine environments tend to be less diverse and exhibit greater degrees of dominance than early or mid-succession communities or communities in disturbed habitats. Various mechanisms can be used to explain the increased dominance of pristine environments. In climax situations, dominant species, for example, may be able to competitively exclude rare species that were able to survive previously due to past disturbances. Alternatively the climax community may alter the environment, creating new niches, and further facilitate immigration of rare species to occupy these niches. These rare species would then increase the dominance exhibited by the species present in the climax community (Caswell, 1976). This suggests that communities in pristine habitat may exhibit a greater deviation from neutral model predictions. Alternatively, severe disturbances may shorten the time a drifting species takes to go extinct in the local community. Forest fires in particular can fragment patches of unburnt forest in a highly inhospitable burnt forest matrix thereby isolating surviving populations in the unburnt fragment and leading to reduced gene flow. These remnant fragmented communities will be more susceptible to local extinction under reduced immigration rates and greater isolation leading to species loss and increased dominance (Hubbell, 2001).

Disturbances, furthermore, tend to favour species with specific traits, such as high intrinsic growth rates (Haddad et al., 2008), high dispersal abilities (Ribera et al., 2001; Moretti and Legg, 2009; Cunillera-Montcusí et al., 2021; Piano et al., 2023), the ability to survive a disturbance (Moretti and Legg, 2009; Seifan et al., 2013), resilience, or the ability to recover following a disturbance (Moretti and Legg, 2009) and long-term seed dormancy in the specific case of plants (Seifan et al., 2013). This selective pressure on species traits leads to non-neutral processes, such as niche filtering, driving community assembly, especially in fragmented habitats (Püttker et al., 2015). For tropical insect communities, this can mean that habitat specialists and species with limited geographical distributions decline, while more adaptable generalists and widely-distributed species become dominant (Cleary and Mooers, 2006; Ibarra and Martin, 2015; Lehosmaa et al., 2017).

Disturbances also alter colonisation dynamics, which are critical to neutral model predictions, by for example enabling an influx of strongly dispersing pioneers into recently disturbed forest. Multiple disturbance events can, furthermore, change this dynamic. In the case of trees, for example, multiple disturbance events allow the establishment of a seed bank of pioneers allowing for rapid recolonisation of recently disturbed habitat such that pioneer density can differ dramatically between previously undisturbed and disturbed forests (Slik and Eichhorn, 2003; Cleary and Eichhorn unpublished data). In tropical forests, habitat fragmentation and other forms of disturbance can create barriers to dispersal, reducing gene flow and altering metacommunity structure. Studies have found that post-disturbance communities often exhibit reduced immigration and increased extinction rates, which drive further deviations from neutral model predictions (Alonso et al., 2015; Tatsumi et al., 2020).

In the present study, butterfly communities were compared in differentially disturbed (burnt, logged, and primary) tropical rainforest landscapes in Borneo. Borneo has long been renowned for its remarkable diversity (Wallace, 1869) and is located in one of the worlds most threatened hotspots (Myers et al., 2000). Logging and forest fires are both considered major threats to the forests of Borneo and other biodiversity hotspots such as the Amazon (Cleary and Mooers, 2006; Curran et al., 2004; Jamhuri et al., 2018; Langner and Siegert, 2009). Borneo is home to around 1000 butterfly species (Hamer et al., 2003); most of these depend on tropical rainforest habitats including lowland dipterocarp forests and montane ecosystems. However, habitat loss due to deforestation and land conversion for agriculture pose significant threats to butterfly populations, highlighting the need for conservation efforts to preserve these ecologically important pollinators (Koh, 2007).

The following hypotheses were examined in the present study: 1. We hypothesised that landscapes subjected to a single disturbance event would exhibit higher species richness, 2. We hypothesised that landscapes subjected to multiple disturbance events would exhibit reduced species richness. 3. We anticipated a correlation between geographic distance and the dissimilarity of butterfly species in landscapes that have been disturbed by logging and burning. 4. We predicted that in landscapes disturbed by logging and burning, there would be significant deviations from the biodiversity patterns predicted by Hubbell's neutral model (Hubbell, 2001), indicating that these disturbances alter the natural ecological dynamics proposed by the model.

2. Material and methods

2.1. Study area

Sampling took place from 1998 to 2000 in the Indonesian provinces of Central and East Kalimantan, Indonesia. Nine forest landscapes, including three primary, three logged and three burnt, were sampled. All landscapes are situated between zero and two degrees latitude and 112 and 118 degrees longitude in Indonesian Borneo. See Supplementary data 1 for the location of all plots. Supplementary data 2 contains the raw data for all butterflies recorded during the study. Supplementary data 3 contains information about the landscapes and plots.

The original vegetation of all landscapes was predominantly moist lowland dipterocarp forest in generally hilly terrain located less than 500 m above sea level. The landscapes were sampled in three areas including an area in Central Kalimantan located within the Kayu Mas forest concession that was unaffected by ENSO-induced burning, a 138 000 ha large unburnt isolate in East Kalimantan and a small 3 500 ha unburnt isolate in the Sungai Wain nature reserve and surrounding burnt forest in East Kalimantan (Cleary, 2003). In the small unburnt isolate, we sampled one primary forest landscape (P1S) and three burnt forest landscapes surrounding this isolate. This included adjacent once-burnt forest in the burnt part of the Sungai Wain nature reserve (B1S), twice-burnt forest in the proximate Wanariset research forest (B2S) and a frequently-burnt predominantly grassland area located at Km 30 along the Balikpapan to

Fig. 1. Photographs of selected butterfly species: a. *Tanaecia iapis*, b. *Ragadia makuta*, c. *Elymnias hypermnestra*, d. *Eooxylides tharis*, e. *Ionolyce helicon*, f. *Jamides celeno*, g. *Junonia atlites*, h. *Orsotriaena medus*, and i. *Notocrypta curvifascia*.

Samarinda highway that has been subjected to shifting cultivation (B3S; Cleary, 2016). In the large unburnt isolate, we sampled primary forest in the Gunung Meratus protected forest (P2L) and adjacent logged forest (L1L) (Cleary, 2017). In the Central Kalimantan area, we sampled primary forest (P3C) and surrounding logged forest (L2C and L3C). L1L was logged in 1993/94, L2C in 1993/94 and L3C logged in 1989/90. Logging was selective, extracting mainly dipterocarp species with a cutting cycle of 35 years. Landscapes P3C, L2C and L3C were sampled from July to October 1998, while landscapes P1S, P2L, L1L, B1S, B2S and B3S were sampled from January to November 2000 and are all located within a 5.2 million ha area of East Kalimantan that was predominantly undisturbed forest prior to the severe 1982/1983 and 1997/1998 ENSO events. After these events the area was turned into a mosaic of burnt and regenerating forest with smaller and larger unburnt patches (Siegert et al., 2001). Landscape B1S burnt for the first time during the 1997/98 ENSO event while landscape B2S burnt during the 1982/83 and 1997/98 ENSO events. Detailed maps and spatial analyses of the impact of the 1997/98 ENSO event in eastern Borneo can be found in Siegert et al. (2001).

The burnt forests in B1S and B2S were not uniformly burnt but had networks of remnant unburnt forest in the burnt forest matrix. These networks made up an estimated 10.6 % (B1S) and 8.1 % (B2S) respectively of the total area in each landscape (Eichhorn, 2006) and were primarily found along the flood plain. Vegetation in these remnants was visually similar to unburnt forest (pers obs. DFRC).

2.2. *Sampling*

Sampling took place along 300-m transects demarcated with ironwood poles; 16 transects were randomly allocated and sampled in each landscape. Transects were located in the field with compass and clinometer and georeferenced with a handheld GPS device (Garmin 12XL). In each plot, elevation was recorded and inclination measured using a clinometer from a base position. Butterflies were sampled when encountered along the 300-m transect. Selected butterfly species are shown in Fig. 1. The transect was traversed repeatedly on foot from one end to the other at a steady pace, which was only halted to collect specimens. This procedure was repeated until 200 butterflies were caught per transect and was followed during all sampling events. The goal was to avoid small samples, which may yield unreliable similarity indices when comparing transects (Wolda, 1981). It is very difficult, if not impossible to identify most Bornean butterflies on the wing (Walpole and Sheldon, 1999). Individuals were, therefore, hand-netted and subsequently identified in the field. These individuals were marked with an edding 3000 permanent marker to avoid counting the same individual more than once. Because of the minimum sample size, sometimes-adverse weather conditions, and local variations in abundance, the number of days spent at each plot varied (for example, the mean and standard deviation spent sampling plots of P2L and L1L was 6.4 ± 0.7 days). Sampling took place between 9:00 and 16:00 hours, except during rain, using nets and with two people catching per plot. The date of capture and location were noted for each individual. All butterflies were identified to species following Maruyama and Otsuka (1991), Otsuka (1988), and Seki et al. (1991). All individuals encountered in the superfamilies Papilionoidea and Hesperioidea were collected. Specimens from all butterfly species were preserved (using silica gel) and later rechecked in the Netherlands. Voucher specimens of all species have been deposited at Naturalis Biodiversity Center, Leiden.

2.3. *Statistical analyses*

2.3.1. *Composition*

Butterfly and geographic distance data matrices were imported into R (R Core Team, 2022). For the butterfly data, a distance matrix was constructed using the Bray-Curtis index with the vegdist function in the vegan package in R (Oksanen et al., 2022). For geographic distance, a distance matrix was obtained using the earth.dist function from the fossil package. This creates a distance matrix of pairwise distances in kms between all sample plots. Variation in butterfly species composition among plots was visually assessed for each landscape with plots of pairwise dissimilarity as a function of the distance between plots. The MRM function from the ecodist library in R was used with 1000 permutations to carry out regressions on distance matrices with the Bray-Curtis dissimilarity matrix as response variable and geographic distance as predictor variable. Species accumulation curves showing the number of species versus plots and the number of individuals were obtained for each landscape using the specaccum function from the vegan package with the method argument set to "random" and "rarefaction", respectively. Evenness (Pielou's J) was calculated for each plot and mean values calculated using the diversity function in vegan. Note that values of species richness and evenness were presented in a previous study (Cleary, 2003) in the context of isolate size and burning. Here, we reanalyse the data and focus on the disturbance type (primary, logged, and burnt forest landscapes).

2.4. *Neutral model*

Our research used a method developed by Harris et al. (2017) to test for deviations from neutral model predictions. This approach uses Bayesian inference to analyse data and test for neutral community assemblage. Unlike other neutral approaches, it models the unified neutral theory of biodiversity as a hierarchical Dirichlet process and provides estimates of the fundamental biodiversity number θ and immigration rates (I). The parameter θ can be considered as the rate at which new species enter the metacommunity due to speciation (Harris et al., 2017). With higher values of θ, the more species accumulate in the metacommunity and the distribution becomes skewed towards species with lower abundances. The method of Harris et al. (2017) provided more reliable estimates of θ and immigration rates than previous methods, e.g. Etienne (2009). To obtain data for the Harris et al. (2017) method, we first downloaded the NMGS-master folder, which can be obtained from https://github.com/microbiome/NMGS (last checked: 2024 09 05). For each landscape, comma-delimited species (rows) by sites (columns) tables were generated in R. These were used as input for NMGS. The output files consisted of simulated estimates of θ for the metacommunity of each landscape and immigration estimates for each plot.

These were imported into R and mean, median, and standard deviation values were calculated for θ and the immigration values. The output files also consisted of '_m' and '_s' files. We tested for deviations from neutral model predictions at metacommunity and local scales for each landscape using the Sig.pl script from the Scripts folder in the C folder of the NMGS-master folder with./Scripts/Sig.pl 1 3 and./Scripts/Sig.pl 2 3, respectively, with the _m files as input.

In addition to the method of Harris et al. (2017), we followed the approach of Maaß et al. ((2014) where they developed a general neutral model to predict beta diversity and to test for deviations thereof. In the present study, 999 simulated communities were generated following Maaß et al. (2014). Beta diversity was assessed following Legendre and De Cáceres (2013) and Maaß et al. (2014). If the observed beta diversity of a landscape fell outside the range of the simulated data sets, it was considered to have a higher (more dissimilar) or lower (more similar) beta diversity than expected by chance. Observed communities within the simulated range were considered to be consistent with neutral dynamics. The results of these analyses are interpreted in the context of expected assembly processes resulting from the observed disturbance regimes. Mean beta diversities were calculated for each landscape and the histogram of these values plotted against observed beta diversity following Maaß et al. (2014).

3. Results

Landscape scale species richness was higher in landscapes unaffected by ENSO-induced burning (P3C, L2C and L3C) than all other landscapes and higher in logged landscapes than proximate primary landscapes (Fig. 2). Species richness was also higher in once-burnt forest (B1S) than adjacent primary forest (P1S). Richness was, however, lower in the twice-burnt landscape and lowest in the frequently-burnt forest landscape (B3S). There was significant distance dependence in all landscapes with the exception of one logged landscape (L3C; Fig. 3) (Table 1). The variance in dissimilarity values between pairs of plots was, furthermore, much greater in burnt than unburnt forest landscapes, particularly in B2S and B3S.

The distribution of the 50 most abundant butterfly species is presented in Fig. 4. Of note are the absences of otherwise abundant *Arhopala* species in the twice-burnt and frequently-burnt landscapes and of *Arhopala democritus* and *Drupadia ravindra* from the once-burnt forest landscape. Certain other species such as the hesperids *Ancistroides gemmifer* and *Koruthaialos rubecula*, and the nymphalids

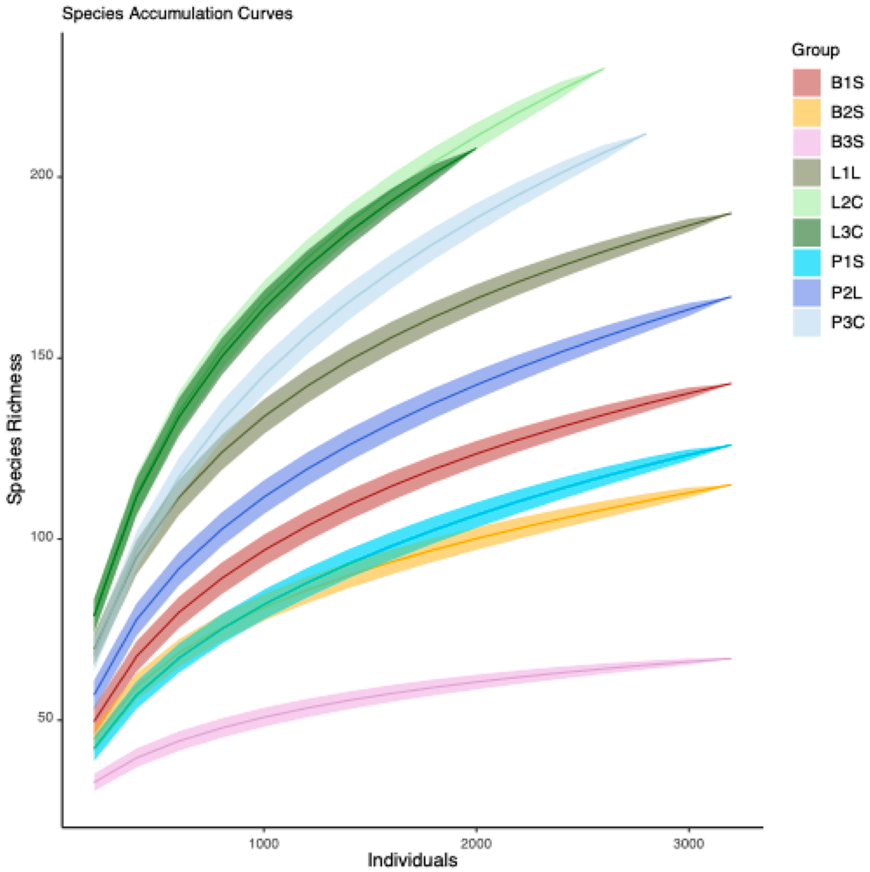

Fig. 2. Butterfly species accumulation curves as a function of increasing numbers of individuals sampled. The curves represent once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in the Meratus logging concession (P2L), logged forest in the Kayu Mas logging concession, L2C, and L3C, primary forest in Sungai Wain nature reserve (P1S), primary forest in Meratus logging concession (P2L), and primary forest in Kayu Mas logging concession (P3C).

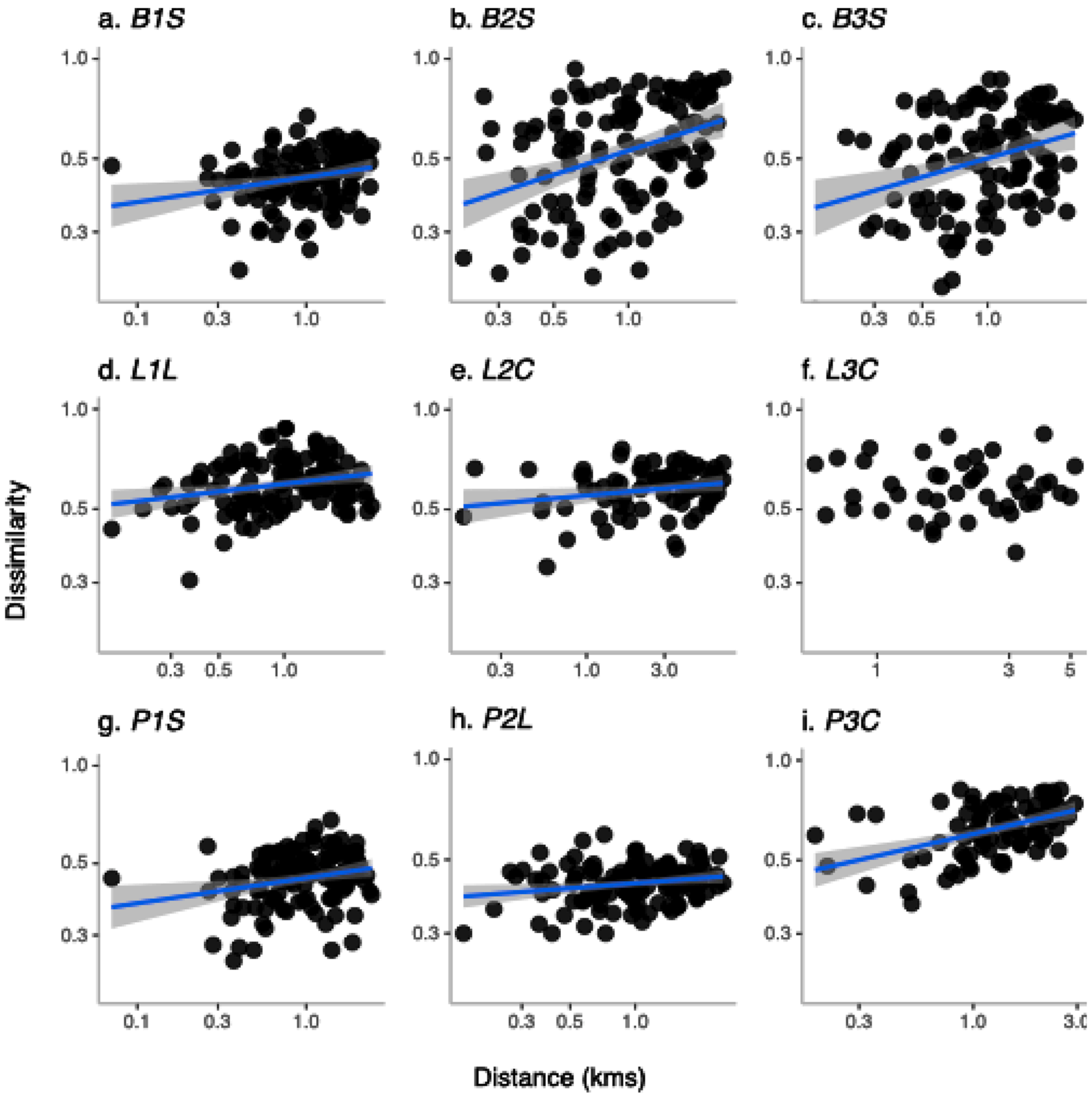

Fig. 3. Variation in dissimilarity as a function of distance between sample plots for a. once-burnt forest (B1S), b. twice-burnt forest forest (B2S), c. frequently-burnt forest (B3S), d. logged forest in the Meratus logging concession (P2L), logged forest in the Kayu Mas logging concession, e. L2C, and f. L3C, g. primary forest in the Sungai Wain nature reserve (P1S), h. primary forest in the Meratus logging concession (P2L), and i. primary forest in the Kayu Mas logging concession (P3C).

Tanaecia iapis and *Mycalesis patiana* were observed in all unburnt forest landscapes, but were not observed in any of the burnt forest landscapes. All forest landscapes had similar levels of evenness ranging from 0.75 ± 0.07 in B2S to 0.84 ± 0.07 in L2C. Evenness was even slightly higher in the once-burnt forest (B1S) than adjacent primary forest (P1S; Table 1).

Butterfly communities in all primary forest landscapes and the once-burnt landscape deviated significantly ($p_N < 0.05$) from neutral model predictions at the metacommunity scale (Table 1). None of the landscapes differed significantly from neutral model expectations at the local scale ($p_L > 0.05$). θ values ranged from 15.2 ± 2.1 in B3S to 75.0 ± 6.0 in L2C. (Table 1). θ was higher in the once-burnt forest landscape (B1S: 35.7 ± 3.5) than the adjacent primary forest landscape (P1S: 31.9 ± 3.3), but was lower in the twice- (B2S: 30.5 ± 3.3) and frequently-burnt forest landscapes (Table 1). Mean immigration values ranged from 52.2 ± 35.1 in B3S to 174.1 ± 50.7 in P2L (Fig. 5). Mean immigration rates were also higher in the once-burnt forest landscape than the adjacent primary forest landscape, but were much lower in the twice-burnt and frequently-burnt forest landscapes.

Mean beta diversity values ranged from 0.237 in B1S to 0.441 in P3C (Table 1). Values were relatively high in all three logged

Table 1

Summary statistics of the number of species, stems, plots, species density, evenness, beta diversity, results of the MRM analyses, estimates of θ, immigration (I), and tests for significant deviations from neutral model expectations at metacommunity and local scales for once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in the Meratus logging concession (P2L), logged forest in the Kayu Mas logging concession, L2C, and L3C, primary forest in the Sungai Wain nature reserve (P1S), primary forest in the Meratus logging concession (P2L), and primary forest in the Kayu Mas logging concession (P3C).

	Variable	B1S	B2S	B3S	L1L	L2C	L3C	P1S	P2L	P3C
Total	Species richness	123.6	100.1	60.5	166.5	211.3	208.0	106.6	142.6	188.7
sd		3.6	3.1	2.1	3.9	3.8	0.0	3.6	4.0	4.1
Total	Individuals	3200	3200	3200	3200	2600	2000	3200	3200	2800
Total	Plots	16	16	16	16	10	13	16	16	14
Mean	Species richness	44.0	35.8	27.2	57.9	62.9	64.3	36.8	50.6	50.5
sd		6.0	5.9	5.0	10.7	10.6	13.6	5.183	6.365	8.065
Mean	Evenness	0.81	0.75	0.79	0.84	0.84	0.84	0.78	0.82	0.794
sd	Evenness	0.04	0.07	0.09	0.06	0.07	0.09	0.05	0.04	0.067
	Beta diversity	0.237	0.346	0.306	0.408	0.406	0.415	0.245	0.244	0.441
	MRM – F	**7.10**	**19.07**	**13.12**	**8.55**	**4.19**	0.02	**7.16**	**5.84**	**25.39**
	MRM – p	**0.008**	**0.005**	**0.004**	**0.014**	**0.020**	0.920	**0.012**	**0.018**	**0.001**
	MRM – R^2	**0.057**	**0.139**	**0.100**	**0.068**	**0.052**	0.001	**0.057**	**0.047**	**0.222**
Mean	θ	35.7	30.5	15.2	54.6	75.0	73.1	31.9	42.43	72.67
sd	θ	3.5	3.3	2.1	4.7	6.0	6.3	3.3	3.818	6.153
Mean	Immigration ‘I’	136.9	56.4	52.2	113.6	143.3	136.1	88.2	174.1	71.7
sd	Immigration ‘I’	64.6	35.9	35.1	79.0	86.8	56.5	42.9	50.67	44.82
median	Immigration ‘I’	114.6	50.4	38.9	94.0	106.5	140.1	69.2	174	62.83
min	Immigration ‘I’	52.3	21.0	4.2	21.9	41.5	16.5	29.6	91.77	26.51
max	Immigration ‘I’	262.5	150.3	121.1	328.9	290.2	220.6	175.4	255.6	196
	Metacommunity p_N	**0.043**	0.162	0.525	0.413	0.111	0.248	**0.023**	**0.034**	**0.041**
	Local p_L	0.506	0.558	0.601	0.474	0.604	0.634	0.390	0.467	0.488

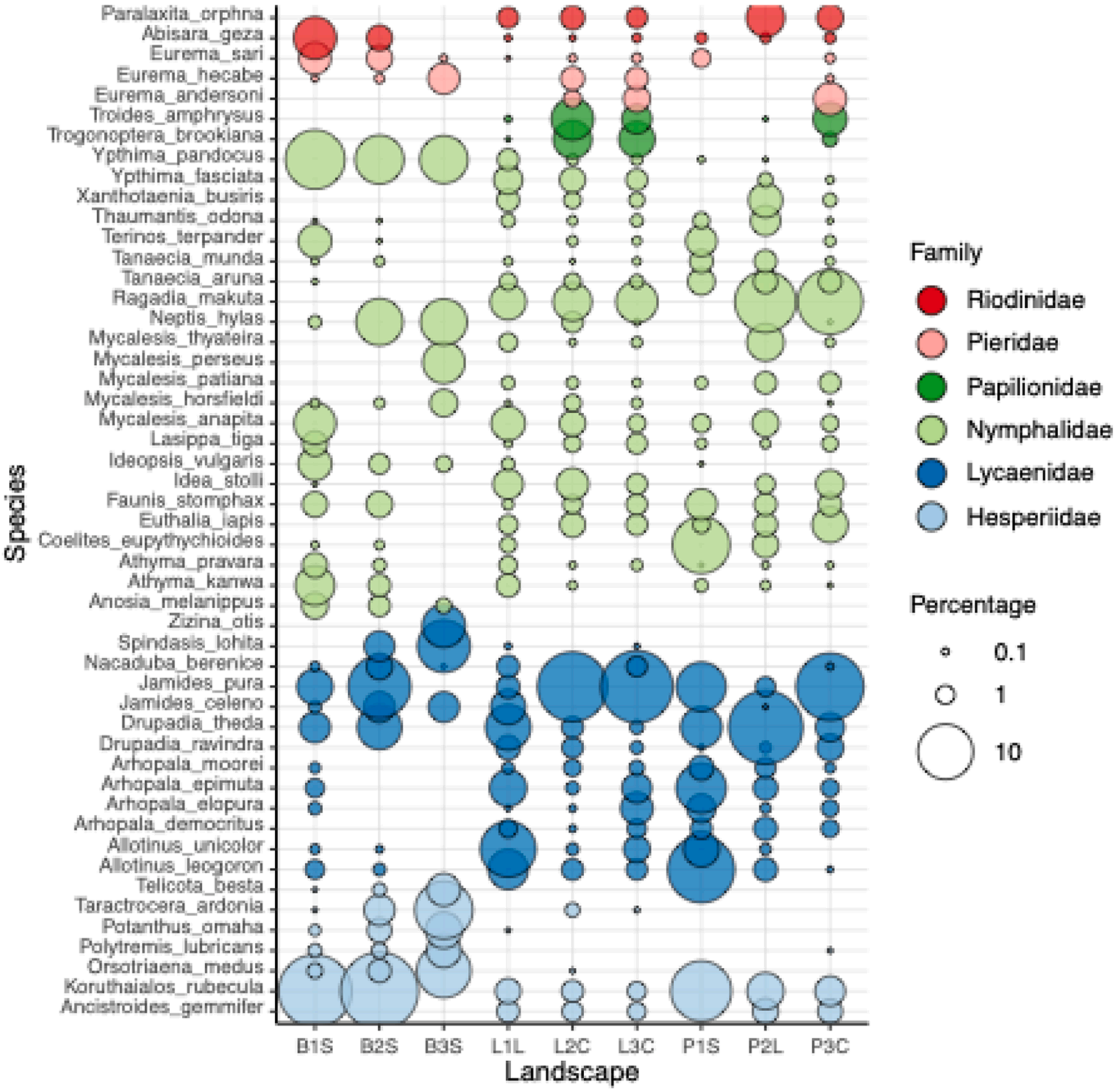

Fig. 4. Percentages of the 50 most abundant butterfly species (shown along the y-axis) recorded in burnt, logged and primary forest landscapes. The symbols are colour-coded according to butterfly family classification. The circle size of the symbol is proportional to the mean percentage of individuals per landscape as indicated by the symbol legend in the upper right corner of the figure. The x-axis codes refer to once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in the Meratus logging concession (P2L), logged forest in the Kayu Mas logging concession, L2C, and L3C, primary forest in the Sungai Wain nature reserve (P1S), primary forest in the Meratus logging concession (P2L), and primary forest in the Kayu Mas logging concession (P3C).

landscapes, but lower in burnt and primary forest (with the exception of P3C). Observed beta diversity was at the lower end of expected beta diversity in all landscapes (Fig. 6). The difference between observed and expected was, however, greatest in the once-burnt and primary landscapes in line with the results of the Harris test.

4. Discussion

Concerning our hypotheses, we confirmed Hypothesis 1, which posited higher butterfly landscape-scale richness in landscapes affected by a single disturbance event. We also confirmed Hypothesis 2, which posited lower landscape-scale butterfly richness in landscapes affected by multiple disturbance events. For Hypothesis 3, we confirm the general association between geographic distance and butterfly dissimilarity although a single landscape deviated from this expectation. In contrast to our hypothesis, the association

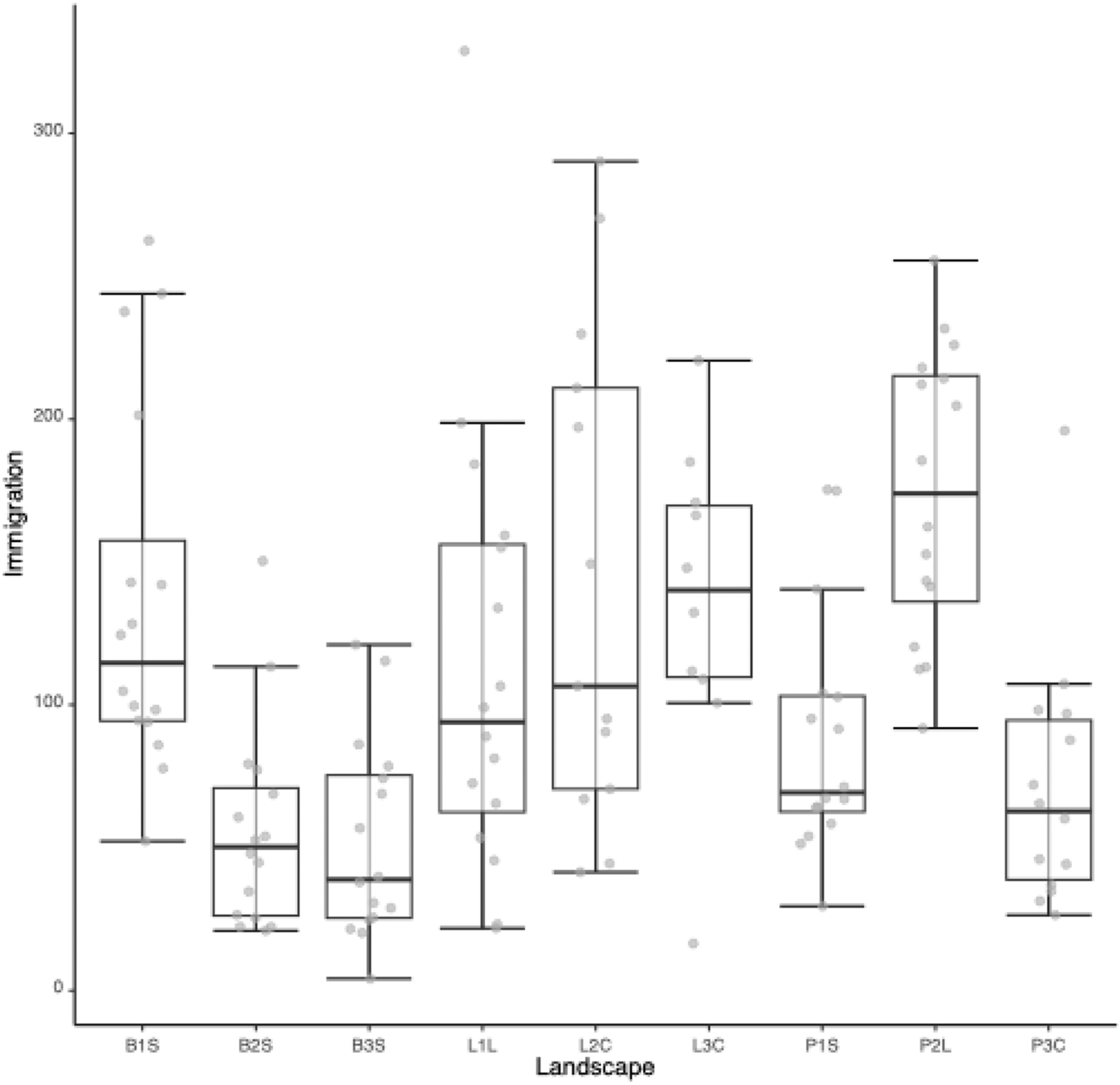

Fig. 5. Variation in immigration rates (I) for once-burnt forest (B1S), twice-burnt forest forest (B2S), frequently-burnt forest (B3S), logged forest in the Meratus logging concession (P2L), logged forest in the Kayu Mas logging concession, L2C, and L3C, primary forest in the Sungai Wain nature reserve (P1S), primary forest in the Meratus logging concession (P2L), and primary forest in the Kayu Mas logging concession (P3C). Grey dots represent immigration values calculated with the model of Harris et al. (2017).

between geographic distance and dissimilarity also applied to primary forest landscapes. Hypothesis 4 was rejected as only one of the six disturbed landscapes significantly deviated from Hubbell's neutral model predictions. All of the primary forest landscapes, however, deviated from neutral model predictions.

4.1. Diversity

The lower species richness in the primary forest of the large and small unburnt fragments suggest that the 1997/98 ENSO event had a very large scale and adverse effect on richness as reported previously (Cleary et al., 2006). Richness was also higher in logged and once-burnt forest than adjacent primary unburnt forest. Repeated burning though appears to have had a detrimental impact on butterfly species richness with landscape-scale richness lower in the twice- and frequently-burnt forest landscapes. Previous studies have generally found that logging has either no or a positive effect on species richness of a variety of rainforest communities although results can be scale-dependent (Johns, 1996; Willott, 1999; Vasconcelos et al., 2000; Lewis, 2001; Hamer et al., 2003). Evenness was relatively similar across landscapes ranging from 0.78 ± 0.5–0.84 ± 0.7. Mean evenness was, however, slightly higher in logged than

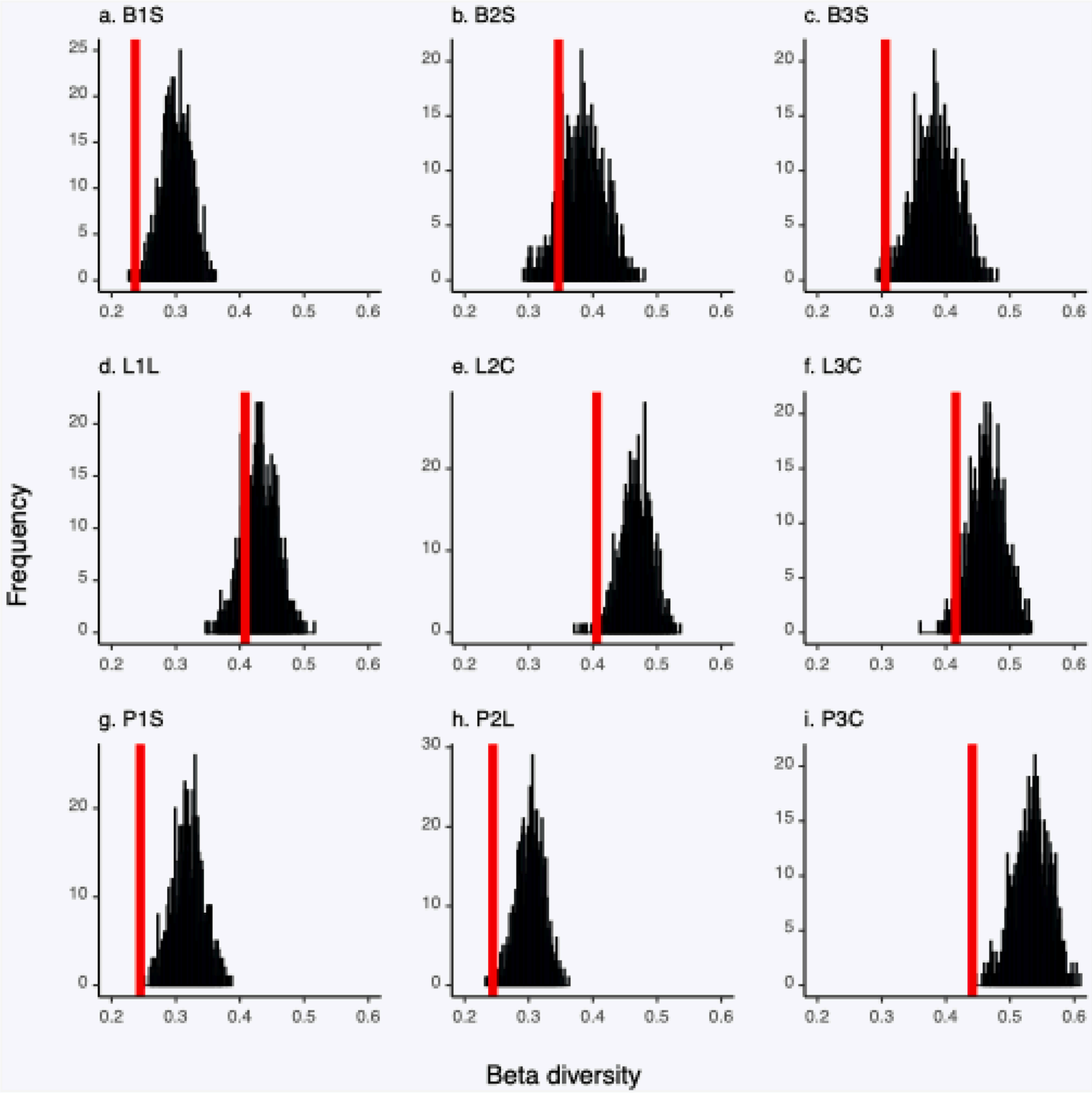

Fig. 6. Observed (red line) and simulated (histograms) beta diversity values for a. once-burnt forest (B1S), b. twice-burnt forest forest (B2S), c. frequently-burnt forest (B3S), d. logged forest in the Meratus logging concession (P2L), logged forest in the Kayu Mas logging concession, e. L2C, and f. L3C, g. primary forest in the Sungai Wain nature reserve (P1S), h. primary forest in the Meratus logging concession (P2L), and i. primary forest in the Kayu Mas logging concession (P3C).

in burnt and primary landscapes. Evenness was also higher in the once-burnt (B1S: 0.81 ± 0.4) and frequently-burnt (B3S: 0.79 ± 0.9) landscapes than in proximate primary forest (P1S: 0.78 ± 0.5).

4.2. Distance dependence

Distance dependence was significant in all landscapes with the exception of a single logged landscape. Distance dependence was greatest in the primary landscape P3C. However, it should be noted that this landscape encompassed a greater elevational range (220 −400 m above sea level) than all other landscapes and was sampled over a slightly larger spatial scale. In contrast, to lowland forest, Novotny and Weiblen (2005) observed high beta diversity of insect herbivores along altitudinal gradients. Novotny and Weiblen (2005) suggested that this was driven by a combination of factors including shifting plant diversity, abiotic factors, and natural enemy abundance. Our results confirm previous studies highlighting the prevalence of distance dependence across a range of plant, animal and microbial communities (Nekola and White, 1999; Cleary et al., 2004, 2022; Soininen et al., 2007; Clark et al., 2021). An interesting observation in the present study was the markedly greater variance in dissimilarity in burnt landscapes. This observation aligns with a similar study of plant communities in the same region (Cleary and Eichhorn unpublished data). In that study, the variance was attributed to the highly patchy distribution of several pioneer tree species including *Macaranga trichocarpa*, *M. gigantea* and *Vernonia arborea* in burnt forest. These species were absent from the majority of plots but highly abundant in others. This effect was less pronounced with butterflies although certain species were more patchily distributed. For example, a total of 93 specimens of *J. celeno* were observed in BS3, but 43 of these were observed in a single plot. In 4 of 16 plots in B3S, no specimens of *J. celeno* were observed. Despite this, the butterfly community of B3S did not deviate significantly from neutral model predictions in contrast to plant commmunities in burnt forest (Cleary and Eichhorn unpublished data).

4.3. Neutral model

Butterfly communities of logged forest landscapes did not differ from neutral model predictions. As mentioned previously, logged forest was also more diverse in terms of richness and evenness than proximate primary forest. In terms of species composition, abundant species in primary forest were also observed in logged forest. These results indicate that logged forest is a suitable habitat for forest butterfly species. The increase in species richness in logged forest, furthermore, aligns with the intermediate disturbance hypothesis (Connell, 1978; Swart et al., 2019) and with several previous studies of the impact of logging on animal communities (Willott et al., 1999; Lewis, 2001; Hamer et al., 2003; Cleary et al., 2005, 2007). Disturbance can create opportunities for new species to colonise by opening up space in the existing community (Foster et al., 2004).

Burning, in contrast, to logging appeared to have a more detrimental effect on butterfly communities, particularly in forests subjected to multiple burn events. Once-burnt forest had higher richness than adjacent primary forest and also deviated significantly from neutral model expectations. Several butterfly species (*A. democritus, D. ravindra, T. iapis and M. patiana*), which were observed in all unburnt forest landscapes were, however, not observed in the once-burnt forest landscape. In contrast, several hesperids, including *Orsotriaena medus*, *Polytremis lubricans*, *Potanthus omaha*, and *Telicota besta*, were observed in all three burnt forest landscapes, but were not observed in proximate unburnt forest suggesting an influx of disturbance-adapted species into the burnt forest from surrounding degraded habitat.

Burnt forest was, thus, characterised by a mixed community consisting of butterfly species associated with unburnt forests such as *J. pura*, *D. theda* and *K. rubecula*, which had apparently survived the fires in addition to butterfly species associated with highly perturbed environments. In addition to those previously mentioned, this would also include species such as such as *J. celeno*, *Y. pandocus* and *N. hylas*. One of the first species to return to twice-burnt forest following the fires was *J. celeno*, which increased in abundance from 3 % of the pre-ENSO community (1997) to 58 % of the post-ENSO (1998) community (Cleary and Grill, 2004). This species was recorded feeding on resprouts of *Fordia splendidissima*, which was one of the few available resources in the severely burnt forest (Cleary and Grill, 2004). *Ypthima pandocus* is a delicate satyrid often found along forest edges and in perturbed habitat. The species has been recorded feeding on monocots including *Bambusa* spp., *Imperata cylindrica*, *Miscanthus sinensis* and *Paspalum conjugatum* (Gramineae; Robinson et al., 2010). *Neptis hylas* is a wide-ranging species often seen flying in short bursts or basking with wings open on taller understory plants along forest edges. The species has been recorded on a wide range of herbs, lianas and trees in various plant families including Bombacaceae, Euphorbiaceae, Fabaceae, Icacinaceae and Moraceae among others (Suguru and Haruo, 1997, 2000; Robinson et al., 2010)

Disturbed habitats appear to act as a filters to butterfly species analagous to to how host organisms appear to filter specific subsets of microorganisms (Douglas, 2019). For example, butterfly species such as *J. pura*, *D. theda* and *K. rubecula* appear to be resilient to disturbance. This resilience appears to be beneficial allowing them to be a dominant component of primary, logged and burnt forest landscapes. All three, however, were completely absent from the frequently-burnt landscape (B3S) despite the presence of remnant, degraded forest patches along small streams in the grassland-dominated habitat.

In contrast to the above, other dominant and sub-dominant species consisting of taxa such as *Ragadia makuta*, *Arhopala epimuta* and *Paralaxita orphna* were often abundant in primary and logged forest and were present in the Wanariset Research forest before the 1997/98 fires. They all, however, disappeared following the fires and had not returned as of 2004 (Cleary and Genner, 2006). *Ragadia makuta* and *P. orphna* were also not recorded in the primary Sungai Wain forest landscape (P1S) following the fires suggesting that even a relatively large unburnt fragment (~ 3500 ha) was not large enough to prevent their demise (Cleary and Genner, 2006).

As noted previously, the butterfly community in the once-burnt landscape (B1S) was more diverse in terms of species richness and evenness than in the adjacent primary forest landscape (P1S). Butterfly communities of both landscapes also differed from neutral model predictions and had similar mean beta diversity levels. They were, however, compositionally distinct with the once-burnt forest landscape housing a mixture of remnant butterflies, which had presumably survived the fires and butterflies derived from proximate degraded habitat. This result is reminiscent of a study of ground vegetation communities where Tatsumi et al. (2020) found that fire and harvesting had no overall effect on beta diversity two years after the treatments. When examining the extinction and colonisation components of beta diversity separately, however, both measures were significantly lower in burnt sites compared to unburnt sites. The diminished extinction beta diversity (the set of species, which went extinct during the study) component implied that fire and harvesting eliminated similar sets of species across the plots within each stand. These species were initially prevalent across plots such that their loss increased heterogeneity with differing sets of remnant species occupying different plots. In the present study, this would entail species such as *A. democritus, D. ravindra, T. iapis and M. patiana.* in addition to *R. makuta*, *A. epimuta* and *P. orphna*, which probably disappeared from both primary and burnt forest due to prolonged drought. Fire and harvesting also lowered colonisation beta diversity, which indicated spatially uniform colonisation, leading to homogenisation (Tatsumi et al., 2020). Both processes (extinction and colonisation), thus, canceled one another out with respect to beta diversity. Species turnover also remained high in the burnt sites over the course of the experiment. Importantly, the relative importance of extinction and colonisation changed over time, with a synergistic negative impact on extinction beta diversity after ten years (Tatsumi et al., 2020).

In contrast to the logged and burnt landscapes, the butterfly communities of all primary forest landscapes deviated significantly from neutral model predictions. Butterfly communities can deviate from neutral theory predictions due to the influence of species-specific traits and environmental factors. For example, traits like habitat specialisation, feeding preferences, and dispersal abilities can create competitive imbalances, favouring certain species over others. Studies show that niche differentiation, such as varying host plant availability and microhabitat preferences, plays a significant role in shaping butterfly communities (Pavoine et al., 2014; Nakadai et al., 2018). Butterfly species with different resource specialisations may also occupy different ecological niches, leading to more structured communities than a neutral model would suggest.

Although environmental disturbances, such as forest fires, can influence species richness and distribution in ways that deviate from purely neutral predictions (Maaß et al., 2014; Cleary and Eichhorn unpublished data), habitat disturbance in the present study appeared to drive butterfly communities towards neutral dynamics. This suggests that competitive exclusion in undisturbed habitat may cause the butterfly communities to deviate from neutral model predictions. By opening up the forest, logging and forest fires create habitat suitable to certain butterflies and their host-plants. Interestingly, the response in terms of community structure is the opposite to that observed in plant communities which did not differ from neutral model expectations in primary forest, but did differ substantially in burnt forest (Cleary and Eichhorn unpubished data). The effect was also much more pronounced in plant communities from the same forests than with butterflies. Although all primary forest landscapes deviated from neutral predictions, the effect was modest and only applied at the metacommunity scale.

Interestingly, despite severe disturbance, the impoverished grassland butterfly community of the frequently-burnt landscape (B3S) did not deviate from neutral model predictions. Even the most abundant and apparently resilient of forest butterfly species such as *J. pura*, *D. theda* and *K. rubecula* were, however, completely absent from this chronically disturbed environment. This begs the question as to why this community appeared to follow neutral model dynamics. Although impoverished, the resident butterfly community had relatively high evenness when compared to the butterfly communities of other unburnt and burnt landscapes. Many of the species were also widespread generalists or species that feed on the dominant grass species, *Imperata cylindrica* and other monocots (Cleary, 2016). Of those species that were able to survive in B3S, it would thus appear that life history differences are relatively unimportant in structuring the community such that community assembly followed neutral model predictions.

Research on tropical butterflies and other insect groups, furthermore, showed that after disturbances, community structures tend to become more homogenised, with fewer species exhibiting high local abundance while many rare species go extinct (Knop, 2016; Parreira de Castro et al., 2018; Gossner et al., 2023). Despite being a relatively well-studied group, there is still much to learn about the life histories of tropical forest butterflies including physiological responses to drought and other forms of disturbance and why restricted range species appear to be more susceptible to forest fire and drought (Charrette et al., 2006; Cleary and Mooers, 2006).

One explanation for the lack of deviations from neutral model predictions in disturbed landscapes may be that these habitats act as filters allowing certain species to thrive while inhibiting other species from entering or surviving. Importantly, neutral processes can operate at various scales. For instance, distinct habitats or biotopes, may only be successfully colonised by a limited subset of plant or animal species from the surrounding environment. This colonisation can occur through passive dispersal, such as wind or water, or active dispersal, which differs among different species. Once inside a newly established or recently perturbed habitat, these ’filtered’ species establish a local community. In this community, neutral dynamics may or may not be at play. When neutral dynamics are in effect, shifts in species populations determining which thrive and which die may happen by chance. Additionally, new organisms capable of passing through the habitat ‘filter’ can enter the local community from the larger metacommunity, contributing to overall diversity. However, the neutral model does not account how given habitats may restrict (e.g., certain plant and animal species are intolerant of specific light, temperature, salinity or pH thresholds) which species can colonise them or how they influence the resident species (Sieber et al., 2019).

Our results with respect to beta diversity showed relatively low levels within landscapes. Beta diversity was, furthermore, lower in burnt and primary forest (with the exception of one landscape) than logged forest. Our simulation study also showed that butterfly communities had lower beta diversities than predicted based on estimated values of θ and immigration using the model of Harris et al. (2017). This was most pronounced in primary landscapes in line with the significant deviations from neutral model predictions in these landscapes. Novotny and Weiblen (2005) and Novotny et al. (2007) showed that insect herbivores in tropical rainforests exhibited high alpha, but low beta diversity. One reason for this is the prevalence of species that feed on multiple host plants. Lewinsohn and Roslin (2008) also identified host plant richness as the dominant determinant of tropical herbivore megadiversity. The relatively low levels of beta diversity of butterfly communities in the present study may be related to several factors including environmental homogeneity, high dispersal abilities, broad niche breadths, habitat connectivity, neutral dynamics, and in the case of burning to homogenisation.

In comparison to logged forest, primary forest may also be relatively homogeneous over large areas in terms of soil type, climate, humidity, temperature, and canopy continuity (Blonder et al., 2018). Butterflies are also relatively strong dispersers although there can be considerable variation among species (Stevens et al., 2010). Many butterfly species are also able to consume a wide range of plants, which limits niche specialisation and ecological filtering. Primary forest landscapes are also often continuous with few barriers to dispersal. Ongoing degradation of forest habitat, however, is altering this situation leaving forest fragments surrounded by a largely inhospitable matrix of degraded habitat (Taubert et al., 2018). As with primary forest, burnt forest may be relatively homogeneous consisting of remnant patches of unburnt forest embedded within a matrix of burnt forest. The remnant unburnt fragments may also lose species due to edge effects although still supporting distinct sets of species from those found in the burnt forest (Harrison and Banks-Leite, 2020). Selective logging, in contrast, opens up the forest while leaving the forest matrix largely intact thereby increasing alpha and beta diversity. Logging, however, increases susceptibility to burning highlighting the importance of protecting previously logged forests (Siegert et al., 2001). Understanding the specific drivers of beta diversity requires detailed ecological studies of both the landscape and the butterfly species involved, taking into account how environmental factors, species traits, and human activities interact to shape community composition.

4.4. Conclusion

In conclusion, our study revealed higher levels of species richness in landscapes subjected to a single disturbance event, but lower levels in landscapes subjected to multiple disturbance events. Evenness levels, in contrast, were similar across all landscapes, with even slightly higher evenness in once- and frequently-burnt forest compared to proximate unburnt primary forest. Distance dependence was significant in all landscapes except one logged landscape. We did, however, observe greater variance in dissimilarity in burnt landscapes. Finally, butterfly communities in all of the primary landscapes, but only one of the disturbed landscapes deviated from neutral model predictions at the metacommunity scale.

The results from our study on butterfly communities in differentially disturbed landscapes carry several ecological and conservation implications. For example, the finding that species richness is higher in landscapes subjected to a single disturbance event but decreases with multiple disturbances implies that there is an optimal level of disturbance for biodiversity. A single disturbance might create a mosaic of habitats, promoting species that thrive in early successional stages. However, repeated disturbances might degrade habitats beyond the point where they can support a diverse butterfly community, leading to a loss of species. This suggests a need for careful management of disturbance regimes in conservation practices to maintain or enhance biodiversity. In the particular setting of Borneo, however, it is imperative to optimally protect pristine areas from further disturbance and protect logged areas from burning.

The observation that evenness levels do not vary much across different disturbance regimes, and might even increase slightly in disturbed areas, indicates that while the number of species might decrease with multiple disturbances, the distribution of individuals among species remains relatively stable. This could be beneficial for maintaining ecosystem functions where evenness plays a role in promoting community resilience (Wilcox et al., 2020), although it might also suggest a shift towards generalist species that can tolerate or capitalise on disturbed conditions.

The deviation from neutral model predictions in primary but not in most disturbed landscapes indicates that in undisturbed ecosystems, species interactions or local environmental filters play a more significant role in community assembly than in disturbed ones. This suggests that in natural, unaltered landscapes, ecological processes like competition or niche differentiation are important drivers of community structure. In contrast, disturbed landscapes might be more influenced by stochastic (random) events or generalist species.

Declaration of Competing Interest

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

Acknowledgements

This study was supported by grant 895.100.005 of the Dutch Science Foundation (NWO), within the Priority Programme 'Biodiversity in Disturbed Ecosystems'. We acknowledge financial support to CESAM from FCT/MCTES (UIDP/50017/2020 + UIDB/50017/2020 + LA/P/0094/2020), through national funds. We acknowledge financial support to CESAM from FCT/MCTES (UIDP/50017/2020 + UIDB/50017/2020 + LA/P/0094/2020), through national funds. The Indonesian Institute of Sciences (PPO-LIPI) and the Indonesian State Ministry of Research and Technology (RISTEK) provided the research permits in Indonesia. All field assistants in Kalimantan are thanked for their help. KAO Eichhorn provided valuable help with fieldwork in Indonesia. The raw data of this project have been deposited in the Predicts database (http://www.predicts.org.uk/; last checked 2017 01 05).

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03561.

Data availability

Data will be made available on request.

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