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AUTHOR(S):

Yano, Sakiko; Aoyagi, Ryota; Shogoro, Fujiki; Sugau, John B.; Pereira, Joan T.; Kitayama, Kanehiro

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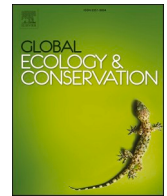
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## Effects of logging on landscape-level tree diversity across an elevational gradient in Bornean tropical forests

Sakiko Yano<sup>a</sup>, Ryota Aoyagi<sup>a,b,\*</sup>, Fujiki Shogoro<sup>a</sup>, John B. Sugau<sup>c</sup>, Joan T. Pereira<sup>c</sup>,  
Kanehiro Kitayama<sup>a</sup><sup>a</sup> Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwake-cho, Kyoto 606-8502, Japan<sup>b</sup> Forestry and Forest Products Research Institute (FFPRI), Forest Research and Management Organization, 1 Matsunosato, Tsukuba, Ibaraki 305-8687, Japan<sup>c</sup> Forest Research Centre, Sabah Forestry Department, 90715 Sandakan, Sabah, Malaysia

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## ABSTRACT

Logging has caused a substantial loss of biodiversity and associated ecosystem services. Therefore, it is important to examine how logging affects biodiversity on a landscape scale to plan responsible management of a tropical forest. Although a number of plot-based studies have shown the effect of logging on local tree species richness (alpha diversity), the effect on species turnover along environmental gradients (beta diversity) remains largely unknown. In this study, we evaluated how logging disturbance affects alpha and beta diversity along an elevational gradient on the eastern slope of Mount Trus Madi in Borneo. We further investigated how pioneer and late-successional tree species differed in the habitat range to clarify the mechanism underlying the beta diversity pattern. We selected 90 plots, each with a radius of 20 m, with a range of disturbance intensity (five classes from highly degraded forests to pristine forests) in lower (285–600 m asl) and higher elevation areas (600–1105 m asl). The remaining above-ground biomass, which is an indicator of past disturbance intensity, strongly varied across the plots (5.4–570.6 and 3.1–771.6 Mg ha<sup>-1</sup> in lower and higher elevation areas, respectively). Diameter at breast height (DBH) and species name were recorded for all trees with a DBH larger than 10 cm. We calculated the species number per 20 individual trees for each plot to represent alpha diversity. Beta diversity along the elevational gradient was calculated as the slope of the relationship between standardized compositional dissimilarity (beta deviation) and the elevational difference. Alpha diversity decreased in higher (17.3–12.3 species per 20 trees) and lower areas (16.8–11.3 species per 20 trees) with increasing logging intensity. Beta diversity along the elevational gradient also decreased to almost zero in highly disturbed areas. Pioneer tree species had a wider elevational range than late-successional species. These results suggest that the shift in dominant tree species after logging (from late-successional to pioneer species) was the main driver of the decline in beta diversity along the elevational gradient. We conclude that preserving and restoring beta diversity are important to sustain tropical production forests.

\* Corresponding author at: Laboratory of Forest Ecology, Graduate School of Agriculture, Kyoto University, Kitashirakawa Oiwake-cho, Kyoto 606-8502, Japan.

E-mail address: [aoyagi.ryota@gmail.com](mailto:aoyagi.ryota@gmail.com) (R. Aoyagi).

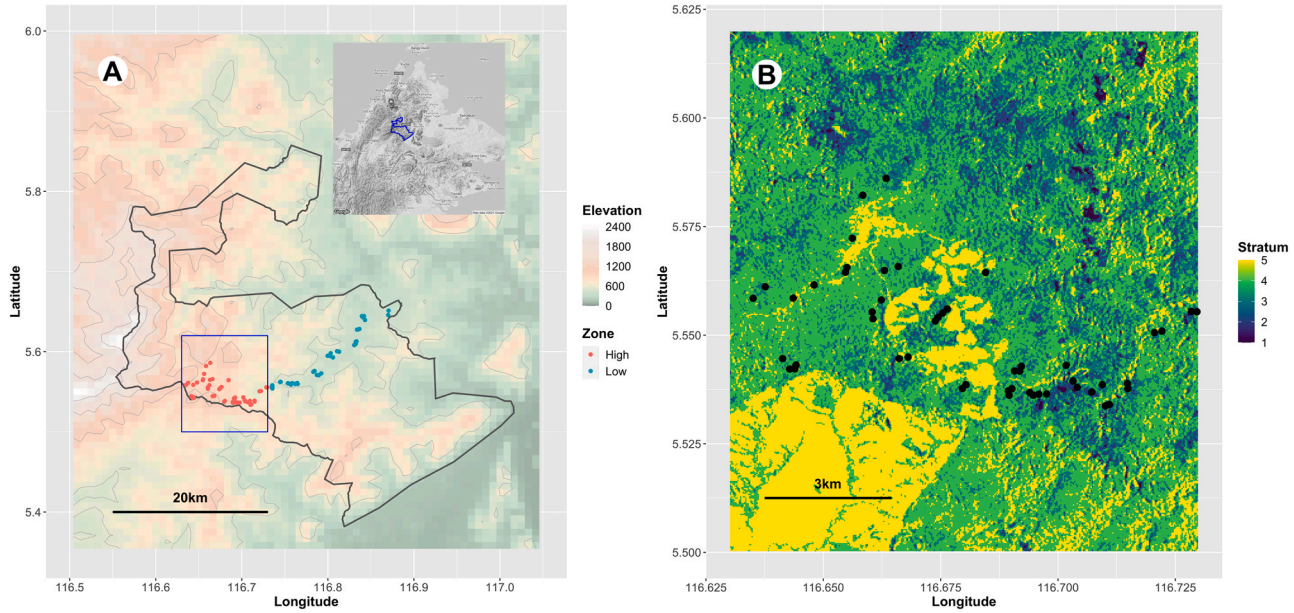
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**Fig. 1.** Location of the study sites, FMU05, Sabah, Malaysia, and plot distribution (A), and a stratum map of the higher elevational area (stratum 1, old-growth forests; stratum 5, highly disturbed forests) (B).

## 1. Introduction

Logging in the tropics has been a major cause of a substantial loss of biodiversity (Barlow et al., 2016; Edwards, 2016; Hosonuma et al., 2012; Wilcove et al., 2013) and associated ecosystem services (Foley et al., 2005). Synergizing timber production with biodiversity conservation in tropical rain forests is a long-standing concern (Bawa and Seidler, 1998; Fredericksen and Putz, 2003; Putz et al., 2008; Verissimo et al., 1992), and the importance of landscape design is often emphasized for effective conservation and rehabilitation of biodiversity (Bengtsson et al., 2000; Griscom and Ashton, 2011; Sayer et al., 2013; Runting et al., 2015). To achieve this goal, it is essential to clarify how logging affects biodiversity at the landscape level, which is largely unknown, particularly in the tropics (Karp et al., 2012).

Species diversity at the landscape level is composed of species richness within a plot and species turnover among plots (alpha and beta diversity, respectively; *sensu* Whittaker, 1972). The effects of logging on tree species diversity have been reported largely at the plot level (alpha diversity, reviewed by Edwards et al., 2014; Putz et al., 2012), and the results have been inconsistent among studies. Some studies have reported an increase in alpha diversity after logging (Sahu et al., 2008; Verschuyt et al., 2011), whereas others have reported either negative effects (Gibson et al., 2011; Paillet et al., 2010) or no significant effect (Hayward et al., 2021 except for saplings; Vellend et al., 2013). These inconsistent results can be partly explained by the intermediate disturbance hypothesis (Connell et al., 1978), suggesting that logging has a nonlinear effect on alpha diversity; the highest alpha diversity occurs at an intermediate level of disturbance (e.g., Bongers et al., 2009; Imai et al., 2014; Molino and Sabatier, 2001; Nzunda, 2011). According to this hypothesis, logging creates habitats for light-demanding pioneer tree species, which are competitively excluded by late-successional species in primary forests, leading to an increase in alpha diversity (Molino and Sabatier, 2001; Nzunda, 2011; Slik et al., 2008). However, when the disturbance is too strong or frequent, a few pioneer tree species become hyper-dominant and alpha diversity decreases (Paillet et al., 2010).

In contrast to alpha diversity, few studies have explored how logging affects beta diversity. Some previous studies have focused on beta diversity in less-disturbed forests (Cáceres et al., 2012; Guimara et al., 2014; Kraft et al., 2011; Mori et al., 2013; Myers et al., 2013; Paoli et al., 2006; Tello et al., 2015). Dispersal limitations and environmental gradients are major sources of beta diversity (López-Martínez et al., 2013a, 2013b). Pioneer species tend to have smaller seeds associated with higher dispersal ability (Holthulzen and Boerboom, 1982; Denslow and Gomez Diaz, 1990), and therefore beta diversity is presumed to decrease when pioneer species become dominant after logging. Additionally, some evidence suggests that pioneer species tend to have a wider habitat range in relation to resource gradients other than light, which may also suggest lower beta diversity in pioneer-prevalent tree communities. For example, a meta-analysis of 234 tree species in North America and Europe revealed that pioneer species had wider habitat ranges along a latitudinal gradient than late-successional tree species (Morin and Chuine, 2006). Wider habitat ranges of pioneer tree species have also been observed for other environmental gradients, such as temperature and water availability (Bazzaz, 1979). Among the various environmental axes supporting beta diversity and climate, elevation is one of the most important factors in the tropics (Aiba and Kitayama, 1999; Grubb et al., 1963; Kitayama, 1992; Lieberman et al., 1996; Slik et al., 2009; Willis and Whittaker, 2002). In Mexican tropical forests, turnover in tree community composition along an elevational gradient is approximately six times over the equivalent distance of elevation and horizontal distance (Vazquez and Givnish, 1998). To date, no studies have examined the effects of logging on beta diversity along elevational gradients in a tropical forest.

In this study, we conducted a systematic vegetation survey across elevational and disturbance gradients in a Bornean production forest and investigated the effects of logging on alpha and beta diversity. We also determined the habitat ranges of pioneer and late-successional tree species in relation to the elevational gradient to explore a possible mechanism underlying the beta diversity pattern. Specifically, we tested the following hypotheses: (1) alpha and beta diversity along the elevational gradient decrease with increasing disturbance intensity; and (2) pioneer tree species have wider habitat ranges along an elevational gradient than late-successional tree species, resulting in lower beta diversity in disturbed forests.

## 2. Materials and methods

### 2.1. Study area

This study was conducted at Forest Management Unit 5 (FMU5), in Sabah. FMU5 is located on the Trus Madi Range in central Sabah, Malaysia (Fig. 1). FMU5 is predominantly hilly to mountainous (43.6% of the area, 15–25° slopes; 48.3%, slopes > 25°). The highest point in FMU5 is Mt. Kaingaran at approximately 2560 m. FMU5 consists of four types of soil associations: the Crocker type (approximately 30% of FMU5), the Mentapok type (25%), the Trusmadi type (20%), and the Lokan and Delit type (the remaining area) (WWF Sabah, unpublished data). These soil associations are highly erodible and low in nutrients. The climate of the region is humid equatorial (2000–2500 mm annual rainfall; WorldClim, <http://www.worldclim.org>).

FMU5 is a long-lease forest concession formed in agreement with the Sabah Forestry Department, and it is part of the Trus Madi Forest Reserve. The Trus Madi Forest Reserve was gazetted as a commercial forest in 1961 and then licensed for short-term logging two times or more. In 1997, under the Sustainable Forest Management policy, Trus Madi Forest Reserve (175,897 ha) was split into two management units: the FMU5 (101,161 ha) was licensed under the FMU system for 100 years; and FMU10 (74,736 ha) was left for conservation. From 1997 to 2006, Anika Desiran, a registered company in Sabah, harvested a limited area of FMU5 for timber. All logging activities ceased in 2006. FMU5 was originally covered by lowland and hill mixed dipterocarp forest, and nearly all original forests were selectively logged for timber. Now, 80% of the area is logged-over forests and the remaining 20% is undisturbed.

## 2.2. Vegetation survey

A field survey was conducted in FMU5 from September 2015 to June 2016. We selected 90 plots, each with a radius of 20 m (11.3 ha total area), between 285 m and 1105 m asl. We used a stratified, fixed-area sampling method to select representative vegetation plots from heterogeneous forests with a varying magnitude of forest degradation to avoid localized sampling or the effects of artificial roads (Gibbs et al., 2007; Imai et al., 2014). The details of the sampling method are described in Imai et al. (2014). Briefly, the FMU5 area was classified into five strata based on the reflectance of Landsat imagery representing the extent of forest degradation, from old-growth forest (stratum 1) to highly disturbed forest with an open canopy (stratum 5) (Imai et al., 2014). The vegetation classification was conducted separately for land < and  $\geq$  600 m asl (285–588 and 601–1105 m asl, respectively). We a priori adopted this criterion (600 m asl) because the two zones are demarcated from each other at 600 m asl on Mount Kinabalu, which is close to the study area (Aiba and Kitayama, 1999; Kitayama, 1992). Here, we used the magnitude of forest degradation (i.e., disturbance intensity) as the remaining aboveground biomass (AGB) as defined by the Intergovernmental Panel on Climate Change: direct human-induced loss of forest property (particularly carbon) (Penman et al., 2003). The method used to compute AGB is explained below. AGB is an indicator of the intensity of past logging disturbances in tropical production forests (Aoyagi et al., 2017; Fujiki et al., 2016; Imai et al., 2014) because AGB decreases as the intensity of past logging disturbances increases (Imai et al., 2012). The difference in AGB among the strata was tested in the following analysis (see Table 1). We selected 10 circular plots, each with a radius of 20 m (1257 m<sup>2</sup> in area), per stratum for each of the two elevational ranges (< and  $\geq$  600 m asl). There were no undisturbed sites adequate for stratum 1 in the lower area; therefore, plots for stratum 1 were established only in the higher area from 651 m to 971 m asl.

Diameter at breast height (DBH) and species name were recorded for all trees with a DBH larger than 10 cm. We excluded woody vines from the inventory. All trees were identified to species by a local botanical expert. If a tree could not be identified in situ, voucher specimens were collected and identified in the herbarium of the Forest Research Centre, Sabah. Specimens that could not be identified to species were distinguished as morphospecies (123 species, 180 individuals). In total, 152 individuals for which we could not obtain a specimen or identify in the field were recorded as unknown species and excluded from analyses. Overall, 6782 stems with 241 genera and 909 species were recorded in the 90 plots.

## 2.3. Data analysis

The AGB of each plot was calculated as the sum of AGB of all individuals observed within the plot. Tree-level AGB was estimated using the allometric equation provided by Chave et al. (2014):

$$AGB(kg) = \exp[-1.803 - 0.976 E + 0.976 \ln(\rho) + 2.673 \ln(D) - 0.0299 \ln(D)^2]$$

$$E = 0.178 \times TS - 0.938 \times CWD - 6.61 \times PS \times 10^{-3}$$

where  $E$ ,  $\rho$ , and  $D$  are measures of environmental stress, wood specific gravity ( $\text{g cm}^{-3}$ ), and DBH (cm), respectively. Data on wood specific gravity were obtained from the global wood density database (Chave et al., 2009; Zanne et al., 2009). When wood specific

**Table 1**

Characteristics of each stratum (mean  $\pm$  standard deviation). Stratum number indicates disturbance intensity (stratum 1, primary forest; stratum 5, highly disturbed forest). DBH, AGB, and St. indicate diameter at breast height, above-ground biomass, and stratum, respectively. Plots with  $\leq$  20 trees (4 and 5 plots for high and low elevational areas, respectively) were excluded from the analysis of species numbers. Differences among strata were analyzed with ANOVA. F and P-values are shown. Groups sharing the same letters do not differ significantly from each other at  $P = 0.05$  (Tukey's HSD). Moran's I test was conducted for each model residual, and the observed Moran I is shown with the degree of significance (Moran I): The degree of significance is indicated as \*, < 0.05; \*\*, < 0.01; \*\*\*, < 0.001.

	Number of species (20 trees <sup>-1</sup> )	Maximum DBH (cm)	Basal area (m <sup>2</sup> )	AGB (Mg ha <sup>-1</sup> )	Tree density $\geq$ 10 cm DBH (plot <sup>-1</sup> )	Tree density $\geq$ 40 cm DBH (plot <sup>-1</sup> )
$\geq$ 600 m asl.						
St. 1	17.3 $\pm$ 0.9 a	93.3 $\pm$ 23.7 a	6.7 $\pm$ 1.2 a	591.9 $\pm$ 125.9 a	108.6 $\pm$ 14.2 a	13.3 $\pm$ 3.7 a
St. 2	17.4 $\pm$ 1.2 a	70.7 $\pm$ 13.6 b	5.5 $\pm$ 0.9 b	442.4 $\pm$ 91.7 b	108.5 $\pm$ 24.1 a	11.1 $\pm$ 4.2 a
St. 3	16.8 $\pm$ 1.0 a	67.7 $\pm$ 15.4 b	4.3 $\pm$ 0.8 c	325.6 $\pm$ 79.1 c	93.9 $\pm$ 29.7 a	6.6 $\pm$ 2.9 b
St. 4	12.3 $\pm$ 2.1 b	58.5 $\pm$ 12.7 bc	3.3 $\pm$ 0.7 c	214.7 $\pm$ 53.0 d	98.1 $\pm$ 29.1 a	3.8 $\pm$ 1.9 bc
St. 5	13.4 $\pm$ 3.5 b	36.5 $\pm$ 13.1 c	0.7 $\pm$ 0.4 d	46.1 $\pm$ 21.3 e	22.9 $\pm$ 13.7 b	0.6 $\pm$ 0.8 c
F	12.1	14.4	69.6	60.4	21.2	28.6
p	***	***	***	***	***	***
Moran I	0.07	0.11*	-0.07	-0.03	0.16**	0.06**
< 600 m asl						
St. 2	16.8 $\pm$ 1.2 a	85.6 $\pm$ 24.5 a	4.5 $\pm$ 0.9 a	390.2 $\pm$ 92.5 a	78.1 $\pm$ 15.8 a	8.9 $\pm$ 2.5 a
St. 3	16.3 $\pm$ 1.5 a	78.0 $\pm$ 21.5 a	3.9 $\pm$ 0.9 a	323.5 $\pm$ 85.6 a	79.5 $\pm$ 18.8 a	6.4 $\pm$ 2.6 a
St. 4	11.2 $\pm$ 2.9 b	44.3 $\pm$ 13.0 b	2.0 $\pm$ 0.5 b	117.2 $\pm$ 34.4 b	64.1 $\pm$ 14.1 a	1.5 $\pm$ 1.7 b
St. 5	11.3 $\pm$ 4.1 b	33.5 $\pm$ 11.0 b	0.6 $\pm$ 0.4 b	40.0 $\pm$ 21.4 b	21.1 $\pm$ 13.3 b	0.1 $\pm$ 0.3 b
F	13.8	16.1	53.7	53.8	31.4	36.5
p	***	***	***	***	***	***
Moran I	-0.07	0.05	0.01	0.02	-0.11	0.01**



gravity could not be found in the database, we used 0.58 as a common value, which is the average wood density in the tropics. A measure of environmental stress, explained by temperature seasonality, the climate water deficit, and precipitation seasonality, was obtained from a global gridded layer of  $E$  at 2.5" available online ([http://chave.ups-tlse.fr/pantropical\\_allometry.htm](http://chave.ups-tlse.fr/pantropical_allometry.htm)).

Differences in mean AGB, maximum DBH, basal area, and tree density among strata were analyzed by analysis of variance (ANOVA), followed by the Tukey's post-hoc test at  $p = 0.05$ . To check the spatial independence of the model residuals, we performed the Moran's  $I$  test using the `lm.morantest` function in the "spdep" package (Bivand and DWS, 2018). This analysis was conducted separately for each elevation zone (above and below 600 m asl.). Mean AGB values were different among the five strata and the strata well represented the AGB (Table 1). Therefore, the strata were considered to represent the extent of the logging disturbance and used in later analyses.

#### 2.4. Alpha and beta diversity

We investigated how species number per 20 individuals in each plot differed among the different strata for each elevational range to investigate the effects of logging on species richness (alpha diversity). The rarefy function in the "vegan" package of R was used for the calculation (Oksanen et al., 2017). Plots with fewer than 20 individuals (9 plots in stratum 5) were excluded from this analysis. Differences in mean species number among strata were analyzed by ANOVA. Pairwise differences among the strata were tested with Tukey's post-hoc test at  $P = 0.05$ .

Beta diversity is defined as the tree compositional dissimilarity between a given pair of vegetation plots (Anderson et al., 2011; Itow, 1991; Kitayama, 1996); thus, it is strongly affected by the regional species pool and tree number in each plot, which can vary after disturbance. A null-model approach was used to examine the effects of logging disturbance on beta diversity (Kraft et al., 2011; Myers et al., 2013). The species pool was defined for each disturbance regime (stratum) as the total number of species and the total abundance of each species occurring across the plots in each stratum (i.e., species in the two elevation zones were pooled). We simulated the species assemblage in each plot by randomly sampling trees from the species pool with a persistent relative abundance of each species across the plots in each stratum. Based on a simulation with 1000 iterations, a standardized effect size ( $\beta$ -deviation) was calculated as the observed beta diversity (Chao dissimilarity) minus the mean predicted beta diversity, divided by the standard deviation of the predicted beta diversity. We used the Chao index (Chao et al., 2005) based on abundance to calculate dissimilarity. The Chao index is suitable to assess compositional dissimilarity between plots (communities) containing numerous rare species, such as tropical tree communities (Chao et al., 2005). Zero beta deviation indicates that there is no difference between observed beta diversity and beta diversity expected by the null simulation, and positive beta deviation indicates that the observed beta diversity is higher than the value expected by the null simulation. A dissimilarity matrix based on the beta deviation was used for the following analyses.

We examined the effects of logging disturbance on beta diversity along the elevational gradient using a linear regression approach. Beta diversity along the elevational gradient was defined as the slope of the fitted relationship between tree compositional dissimilarity (beta deviation) and the elevation difference following the definition of previous studies (Anderson et al., 2011; Itow, 1991; Kitayama, 1996). We determined the beta diversity and its relationship with logging disturbance based on a method used in previous research, which consisted of three steps. The standardized compositional dissimilarity (i.e., beta deviation) between two given plots was calculated for every combination within each level of logging intensity (stratum). Tree-community dissimilarity was regressed as a function of the elevational difference for the pairwise plots in each level of logging intensity (stratum) to determine beta diversity along the elevational gradient. The slopes of the linear models were defined as beta diversity. The test of the null hypothesis of no relationship between compositional dissimilarity and elevation was conducted with the Mantel randomization test and 10,000 randomizations in each stratum. We also conducted a similar analysis using the Jaccard dissimilarity based on the presence/absence data. The difference in beta diversity among the strata (logging intensity) was tested using linear regression analysis. The model equation was as follows:

Tree compositional dissimilarity.

~ Elevational difference + Strata (1–5, from pristine to highly disturbed forest) + Interaction

The model was selected with a step function, and the model with the lowest Akaike information criterion was considered the best-fit model. The significance of the difference in the slope among strata was analyzed using the `lm` function in R.

#### 2.5. Habitat ranges of the two functional groups

We tested the hypothesis that pioneer trees species have a wider elevational range than late-successional tree species. Pioneer and late-successional species were statistically identified by an indicator species analysis following the method of Aoyagi et al. (2017) and Dufréne and Legendre (1997). This analysis was conducted separately for each elevational zone (above and below 600 m asl.). A cluster analysis was performed using the `hclust` function in the `vegan` package of R (Oksanen et al., 2017). The vegetation plots in each elevational zone were grouped into two clusters using the distance matrix based on Chao's dissimilarity and the UPGMA algorithm. Then, the indicator value (IV) for each species was calculated in each cluster (Dufréne and Legendre, 1997) by the `Indval` function in the "labdsv" package of R (Roberts, 2016). The IV of each species was calculated from relative mean abundance ( $A_{ij}$ ) and relative frequency ( $B_{ij}$ ) as follows:

$$IV_{ij} = A_{ij} * B_{ij} * 100$$

$$A_{ij} = N_{\text{individuals } ij} / N_{\text{individuals } i}$$

$$B_{ij} = N_{\text{plots } ij} / N_{\text{plots } j}$$

where  $N_{\text{individuals } ij}$  and  $N_{\text{individuals } i}$  are the mean number of individuals of species  $i$  in cluster  $j$  and the mean number of individuals of species  $i$  in all clusters, respectively, and  $N_{\text{plots } ij}$  and  $N_{\text{plots } j}$  are the number of plots in cluster  $j$  where species  $i$  occurred and the total number of plots in cluster  $j$ , respectively. Observed IVs were compared with randomly generated IVs (generated with the random allocation of plots to clusters) with 1000 iterations to test whether the observed IV was higher than the expected IV by the random distribution. Species with P-values < 0.05 were considered indicator species.

The characteristics of the two clusters for each elevational zone were examined by AGB and the nMDS axis-1 scores were calculated with Chao's dissimilarity index (Chao et al., 2005) based on the number of trees of each species. As shown in the following results, two groups derived from the cluster analysis corresponded to a mature (with a higher AGB) and a disturbed forest-type (with a lower AGB), in the higher and lower elevational zones. We defined the indicator species of the disturbed forest-type as 'pioneer species' and those of the mature forest-type as 'late-successional species' (Aoyagi et al., 2017).

We used two different definitions to describe the elevational range of a given species (species A):

- (1) Elevational range of appearance (m) = The highest elevation (m) at which species A appears – the lowest elevation (m) at which species A appears.
- (2) Elevational range of dominance (m) = The highest elevation (m) at which species A dominates – the lowest elevation (m) at which species A dominates.

The dominant species in each plot was defined as the three most abundant species based on the number of individuals.

We compared the elevational ranges of the pioneer species with those of the late-successional species using the Welch two-sample *t*-test, which is suitable for non-normally distributed datasets. Species that appeared in or dominated in only one plot were excluded from the analysis to avoid underestimating the elevational ranges. We also compared the habitat ranges between the two functional groups with the dataset excluding stratum 1 because plots in stratum 1 were established only in the higher elevational area from 651 m to 971 m asl. All statistical analyses were performed with R ver. 3.3.1 (R Core Team, 2021).

### 3. Results

#### 3.1. Alpha and beta diversity

The average number of species per 20 individuals (alpha diversity) was higher in less-disturbed forests (strata 1–3) than in highly disturbed forests (strata 4 and 5) in both the higher and lower areas (Table 1). Moran's *I* test revealed that the difference in species richness among strata was not explained by spatial autocorrelation (Table 1). Beta diversity along the elevational gradient (i.e., the slope of the relationship between tree compositional dissimilarity and elevational difference) was greater in strata 2–4 than in stratum 5 (Table 2). The Mantel test revealed that tree compositional dissimilarity tended to increase with increasing elevational difference in less-disturbed forests ( $P = 0.16$ , stratum 1;  $P < 0.05$ , strata 2–4) while it did not vary in relation to the elevational difference in highly disturbed forests ( $P = 0.56$ , stratum 5) (Fig. 2, Table S1). The analysis based on presence/absence data (Jaccard dissimilarity index) yielded results similar to those of the analysis based on Chao dissimilarity (Table S2).

#### 3.2. Habitat ranges of the two functional groups

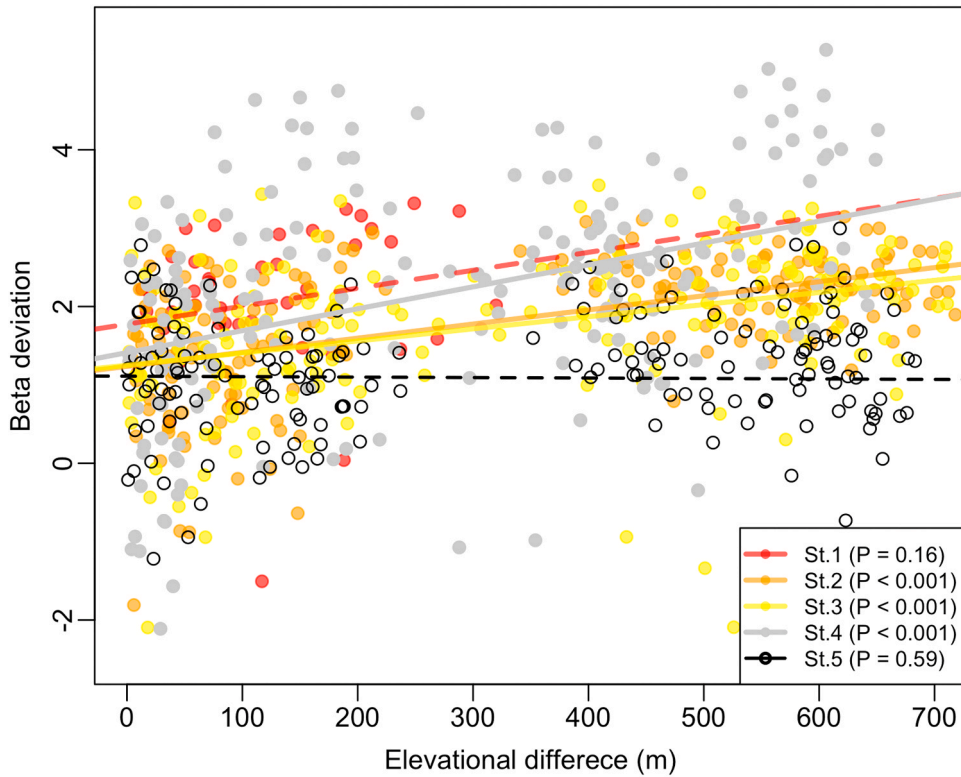
The vegetation plots in each elevational area were categorized into two main vegetation clusters, which were characterized by AGB and the nMDS axis-1 score (Fig. 3a, b). As AGB represents the extent of the logging disturbance (see Section 2), these two vegetation types were considered mature and disturbed forests.

In total, 93 and 18 species were classified as mature-forest and disturbed-forest indicators, respectively (Table S3). Overall, 4.3% (4 of the 93 species) and 34% (6 of the 18 species) of all species were shared in the two zones for the mature-forest and disturbed-forest indicators, respectively. Hereafter, mature-forest indicators are defined as 'late-successional species', and disturbed-forest indicators are defined as 'pioneer species'.

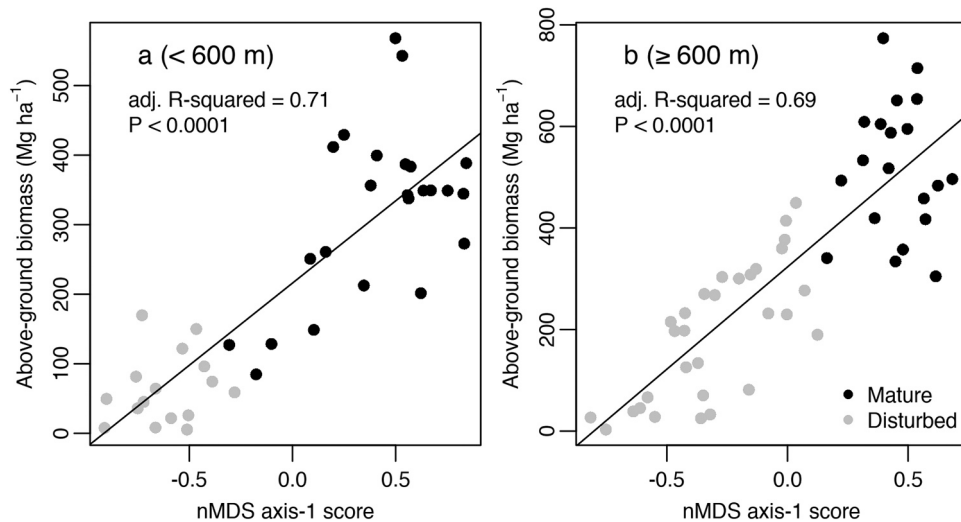
**Table 2**

Results of the linear regression analysis for the relationship between disturbance intensity (stratum 1, primary forests; stratum 5, disturbed forests) and elevational difference (m) between the two plots (i.e., beta diversity). Estimate, standard error (SE), and the *t* and *P*-values are shown for each variable. The model equation was tree community dissimilarity = Elevational difference + Stratum + Interaction.

	Estimate	SE	<i>t</i>	<i>P</i>
(Intercept)	1.56	0.17	9.15	< 0.001
Elevational distance	$2.28 \times 10^{-3}$	$0.46 \times 10^{-3}$	6.04	< 0.001
Stratum	$-5.63 \times 10^{-2}$	$4.84 \times 10^{-2}$	-1.16	0.24
Elevational distance × Stratum	$-4.60 \times 10^{-4}$	$1.27 \times 10^{-4}$	-3.62	< 0.001



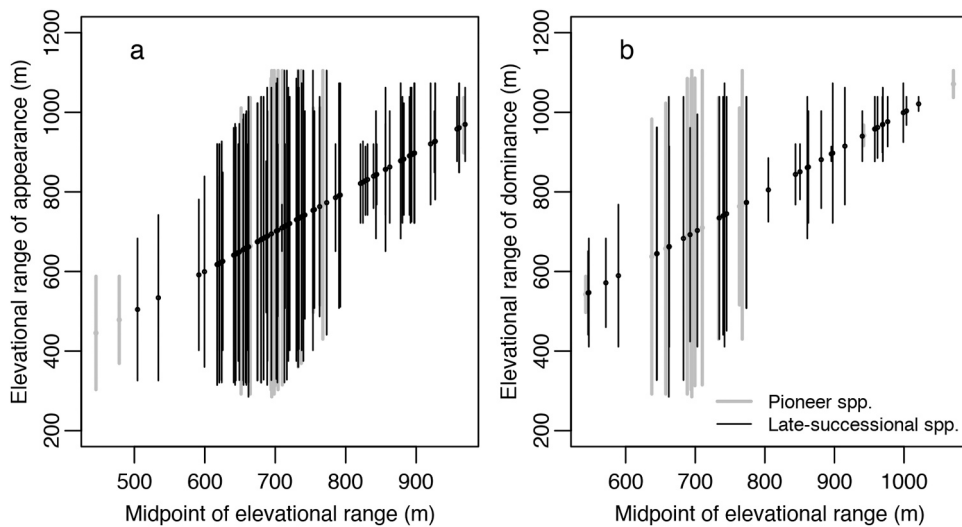
**Fig. 2.** Relationship between tree compositional dissimilarity expressed as the beta deviation and elevational difference (m) between the two plots. Different symbols represent different strata (St.: stratum 1, primary forests; stratum 5, highly disturbed forests). The slope of each line indicates the beta diversity along the elevational gradient (lines with no significant slope are shown as dashed lines). The P-values were derived from a Mantel randomization test with 10,000 randomizations (Table S1).



**Fig. 3.** Relationships between nMDS axis-1 score and aboveground biomass for the plots below 600 m asl. (a) and above 600 m asl. (b). Gray and black points indicate disturbed-forest and mature-forest clusters, respectively. Adjusted  $R^2$  values (ad. R-squared) and P-values derived from linear regression analysis are also shown.

Most of the pioneer species and some of the late-successional species appeared widely across the elevational gradient (Fig. 4a, b). The mean elevational range of dominance was 542.6 m and 191.3 m for the pioneer and late-successional species, respectively, whereas the mean elevational ranges of appearance were 635.9 m and 487.3 m, respectively. Both mean elevational ranges of





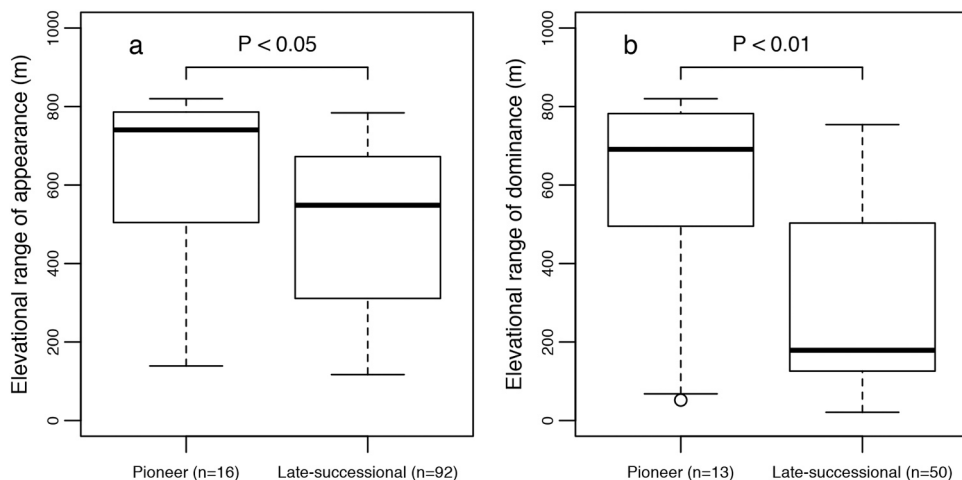
**Fig. 4.** Elevational ranges of appearance (a) and dominance (b) of pioneer and late-successional tree species derived from the indicator species analysis. Each gray and black line represents a pioneer and late-successional species, respectively. Species were sorted by the midpoint of the species elevational range.

appearance and dominance were wider in the pioneer species than in late-successional species (Welch two-sample *t*-test,  $P < 0.05$  and  $< 0.001$ , respectively), and the difference in habitat range between the two functional groups was more prominent when it was compared with the elevational range of dominance (Fig. 5a, b). Similarly, the mean elevational ranges of appearance and dominance were wider in pioneer species than in late-successional species when stratum 1 was excluded (Welch two-sample *t*-test,  $P < 0.05$  and  $< 0.005$ , respectively; Figs. S1 and S2).

#### 4. Discussion

##### 4.1. Logging affects alpha and beta diversity along the elevational gradient

We demonstrated that alpha diversity decreased in higher (17.3–12.3 species per 20 trees) and lower areas (16.8–11.3 species per 20 trees) with increasing logging intensity (Table 1). Beta diversity along the elevational gradient was also much lower in highly disturbed forests than in less-disturbed forests (Fig. 2). Although the slope of the relationship between tree compositional dissimilarity and the elevational difference (i.e., beta diversity along the elevational gradient) was not significant for primary forests, this might reflect the smaller sample size and narrow elevational range. Pioneer tree species had a wider elevational range than the late-



**Fig. 5.** Box plots for elevational ranges of appearance (a) and dominance (b) in pioneer and late-successional tree species. Horizontal bold lines represent median values. Upper and lower ends of the boxes indicate upper and lower quartiles, respectively. Extreme lines show the highest and lowest values excluding outliers. Circles represent outliers. P-values derived from a Welch two-sample *t*-test are also shown.

successional species, suggesting that a shift in dominant tree species after logging (from late-successional to pioneer species) was the main driver of the decline in beta diversity along the elevational gradient. Because logging has been performed in tropical landscapes with wide elevational ranges, these findings provide important implications for the effects of logging on biodiversity as well as possible measures toward effective forest management in Bornean tropical production forests, which is elaborated in a later section.

The effects of elevation and disturbance on alpha and beta diversity have been demonstrated in other studies. The decline in alpha diversity (species number per 20 individuals) in logged-over forests has been widely demonstrated in other tropical lowland forests (e.g., Imai et al., 2016; Slik et al., 2008). Alpha diversity was not higher in intermediately disturbed forests at our study site, indicating that there was no clear trend supporting the intermediate disturbance hypothesis. Imai et al. (2016) suggested that the applicability of the intermediate disturbance hypothesis varies with climate and that the hypothesis is weakly supported in humid climates. This idea or statistical errors related to the small size of plots and the extreme heterogeneity of the forest might explain why alpha diversity was not higher in the intermediately disturbed forests. We found a significant effect of elevational difference on tree community dissimilarity (Table 2), although our study plots were distributed within a relatively narrow range of elevation (285–1105 m asl). Consistent with this finding, Kitayama (1996) demonstrated that the elevation required for a given community to be reduced by 50% in compositional similarity (half change) is merely 237 m on nearby Mount Kinabalu using a 3000-m long elevational gradient. Significant effects of elevation with a narrow range are also observed in neotropical forests (Myers et al., 2013). In the lowland forests of the Brazilian Amazon, communities of tree species in logged-over forests have as high a beta diversity (compositional dissimilarity among plots) as old-growth forests; however, the authors of that study did not examine beta diversity associated with an environmental gradient, which is a major source of beta diversity (Solar et al., 2015). A decline in beta diversity under intensive anthropogenic disturbance (forest vs. non-forested agricultural landscape) has been observed in plants (Vellend et al., 2007) and arthropods (Hendrickx et al., 2007; Kuussaari et al., 2010) in temperate to cool-temperate regions, as well as in tropical birds (Karp et al., 2012).

#### 4.2. Habitat range of pioneer and late-successional tree species

The mean elevational range of the pioneer species was much wider than that of the late-successional species for both indices (i.e., mean elevational ranges of appearance and dominance) (Fig. 5a, b), and this likely explains the decreased beta diversity along the elevational gradient in disturbed forest (i.e., stratum 5, Fig. 2). This result indicates that a few pioneer species intensively dominated the highly disturbed forest across the elevational range on Mount Trus Madi. However, the elevational range of unlogged forest (i.e., stratum 1, 651–971 m asl) was narrower than those of logged forest (i.e., strata 2–5, 300–1100 m asl). Therefore, it is possible that biased sampling affected the results of the elevational range for the late-successional species. However, previous studies have demonstrated that species turnover occurs along the elevational gradient in undisturbed forests within a relatively narrow elevational range (Itow, 1991; Kitayama, 1996; Lieberman et al., 1985). For example, most of the species in an undisturbed tropical forest in Costa Rica had less than a 600-m habitat range in elevation (Lieberman et al., 1996). We found that pioneer species tend to have wider elevational ranges than these records, and this finding was not affected by biased sampling. However, some pioneer species had narrow habitat ranges (e.g., *Camposperma auriculatom*, *Adinandra lenticellata*, and *Alstonia spatulata*), although their abundance was too small to affect beta diversity.

One possible mechanism for the wider elevational range of appearance in pioneer species is higher seed dispersal ability. Seed dispersal capacity often contributes to the extent of a plant species distribution, i.e., species with smaller seeds tend to have wider geographical ranges (e.g., Clarke et al., 2011; Edwards and Westoby, 1996; Oakwood et al., 1993; Thompson et al., 1999). Pioneers tend to have smaller seeds, which is probably related to higher dispersal ability (Fenner and Thompson, 2005). However, this mechanism does not fully explain why few pioneer species had wider niche widths and became dominant across the elevational gradient. This may be partly explained by mechanisms similar to the energy availability hypothesis, which was originally proposed to explain the latitudinal gradient of species habitat width (Rapoport's rule; Stevens, 1989). Morin and Chuine (2006) demonstrated that pioneer tree species have a wider latitudinal range than late-successional species in temperate and boreal regions (see also Lane, 2007 and Stevens, 1989), and suggested that shorter tree height and faster life cycle in pioneer tree species could lead to greater tolerance for stressors related to high latitudes. Similarly, if pioneer species tend to be tolerant to the stressors related to high elevation areas, these species should have wider elevational ranges as demonstrated in this study. Pioneer species are generally recruited to open areas created by logging or natural disturbances. Because seedlings growing in open areas must survive large fluctuations in water and temperature, pioneer species are hypothesized to have eco-physiological adaptations to these variable environmental factors (Bazzaz, 1979). Additionally, some pioneer tree species, e.g., *Macaranga* spp., grow rapidly on skid trails where nutrient-rich surface soils were removed by bulldozers (Aoyagi et al., 2013), suggesting that those species are tolerant to infertile environments. The stronger irradiation and lower temperature associated with lower soil nutrient availability are also important factors limiting forest structure (Lieberman et al., 1996) and possibly species distribution in higher elevational areas. Therefore, these eco-physiological mechanisms might explain why the pioneer species had a wider habitat range along the elevational gradient.

#### 4.3. Implications for effective species conservation and rehabilitation

Our finding of homogenization of tree community composition in highly disturbed forests along an elevational gradient has important implications for species conservation and rehabilitation in Bornean production forests. Our results suggest that the homogenized vegetation in highly disturbed forests does not mean that natural vegetation before logging is similar across the elevational gradient. We emphasize the importance of seed source conservation at lower and higher elevations to rehabilitate beta diversity along elevation gradients. It is widely known that the seed supply of late-successional species is an important determinant of forest

regeneration (Cubiña and Aide, 2001). Dipterocarp species, a late-successional family in Southeast Asia, tend to have an aggregated distribution (Bunyavejchewin et al., 2003; Condit et al., 2000). Such a distribution pattern of late-successional species, which is often observed in tropical forests (Ashton, 1969; He et al., 1997; Smith et al., 2015), suggests that seed supply is considerably suppressed when disturbed forests are isolated from their seed sources (Markl et al., 2012). Protected areas are often located in regions that are inconvenient to access (e.g., higher elevation area). Therefore, mature forests should be preserved in a mosaic structure to maintain original species pools at each elevational zone and to facilitate the recruitment of late-successional species into disturbed forests. Forest managers and researchers should determine whether beta diversity is recovering in highly disturbed areas with homogenous vegetation. Furthermore, when the elevational gradient or the river system spans several production forests, land should be managed at a landscape scale so that the forest is preserved across important environmental gradients.

## 5. Conclusions

In conclusion, logging decreased beta diversity along the elevational gradient, and this was likely due to a shift in dominant species from late-successional to pioneer tree species that had a wider habitat range. These results suggest that intensive logging disturbances could have stronger effects on biodiversity at the landscape level. We emphasize that management plans must be effectively designed to maintain and restore biodiversity at the landscape level in tropical production forests.

## 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.

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## Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2021.e01739](https://doi.org/10.1016/j.gecco.2021.e01739).

## References

- Aiba, S., Kitayama, K., 1999. Structure, composition and species diversity in an altitude-substrate matrix of rainforest tree communities on Mount Kinabalu, Borneo. *Plant Ecol.* 140, 139–157. <https://doi.org/10.1023/A:1009710618040>.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of  $\beta$  diversity: a roadmap for the practicing ecologist. *Ecol. Lett.* 14, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>.
- Aoyagi, R., Imai, N., Kitayama, K., 2013. Ecological significance of the patches dominated by pioneer trees for the regeneration of dipterocarps in a Bornean logged-over secondary forest. *For. Ecol. Manag.* 289, 378–384. <https://doi.org/10.1016/j.foreco.2012.10.037>.
- Aoyagi, R., Imai, N., Fujiki, S., Sugau, J.B., Pereira, J.T., Kitayama, K., 2017. The mixing ratio of tree functional groups as a new index for biodiversity monitoring in Bornean production forests. *For. Ecol. Manag.* 403, 27–43. <https://doi.org/10.1016/j.foreco.2017.07.026>.
- Ashton, P.S., 1969. Speciation among tropical forest trees: some deductions in the Light of Recent Evidence. *Biol. J. Linn. Soc.* 1, 155–196.
- Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Nally, R., Mac, Thomson, J.R., Ferraz, S.F. de B., Louzada, J., Oliveira, V.H.F., Parry, L., Ribeiro de Castro Solar, R., Vieira, I.C.G., Aragão, L.E.O.C., Begotti, R.A., Braga, R.F., Cardoso, T.M., Jr, R.C. de O., Souza Jr, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A., Gardner, T.A., 2016. Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature* 535, 144–147. <https://doi.org/10.1038/nature18326>.
- Bawa, K.S., Seidler, R., 1998. Natural forest management and conservation of biodiversity in tropical forests. *Conserv. Biol.* 12, 46–55. <https://doi.org/10.1046/j.1523-1739.1998.96480.x>.
- Bazzaz, F., 1979. The physiological ecology of plant succession. *Annu. Rev. Ecol. Syst.* 10, 351–371. <https://doi.org/10.1146/annurev.es.10.110179.002031>.
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manag.* 132, 39–50. [https://doi.org/10.1016/S0378-1127\(00\)00378-9](https://doi.org/10.1016/S0378-1127(00)00378-9).
- Bivand, R., DWS, W., 2018. Comparing implementations of global and local indicators of spatial association. *Test* 27, 716–748. <https://doi.org/10.1007/s11749-018-0599-x>.
- Bongers, F., Poorter, L., Hawthorne, W.D., Sheil, D., 2009. The intermediate disturbance hypothesis applies to tropical forests, but disturbance contributes little to tree diversity. *Ecol. Lett.* 12, 798–805. <https://doi.org/10.1111/j.1461-0248.2009.01329.x>.
- Bunyavejchewin, S., Lafrankie, J.V., Baker, P.J., Kanzaki, M., Ashton, P.S., Yamakura, T., 2003. Spatial distribution patterns of the dominant canopy dipterocarp species in a seasonal dry evergreen forest in western Thailand. *For. Ecol. Manag.* 175, 87–101. [https://doi.org/10.1016/S0378-1127\(02\)00126-3](https://doi.org/10.1016/S0378-1127(02)00126-3).
- Cáceres, M. De, Legendre, P., Valencia, R., Cao, M., Chang, L., Chuyong, G., Condit, R., Hao, Z., 2012. The variation of tree beta diversity across a global network of forest plots. *Glob. Ecol. Biogeogr.* 21, 1191–1202. <https://doi.org/10.1111/j.1466-8238.2012.00770.x>.
- Chao, A., Chazdon, R.L., Colwell, R.K., Shen, T.J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecol. Lett.* 8, 148–159. <https://doi.org/10.1111/j.1461-0248.2004.00707.x>.
- Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. *Ecol. Lett.* 12, 351–366. <https://doi.org/10.1111/j.1461-0248.2009.01285.x>.

- Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrizar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. *Glob. Chang. Biol.* 20, 3177–3190. <https://doi.org/10.1111/gcb.12629>.
- Clarke, P.J., Knox, K.J.E., Butler, D., 2011. Fire intensity, serotiny and seed release in 19 woody species: evidence for risk spreading among wind-dispersed and resprouting syndromes. *Aust. J. Bot.* 58, 629–636. <https://doi.org/10.1071/BT10193>.
- Condit, R., Ashton, P., Baker, P., Bunyavejehwin, S., 2000. Spatial patterns in the distribution of tropical tree species. *Science* 288, 1414–1418. <https://doi.org/10.1126/science.288.5470.1414>.
- Connell, J.H., Series, N., Mar, N., 1978. Diversity in Tropical Rain Forests and Coral Reefs High diversity of trees and corals is maintained. *Science* 199, 1302–1310. <https://doi.org/10.2307/1745369>.
- Cubiña, A., Aide, T.M., 2001. The effect of distance from forest edge on seed rain and soil seed bank in a tropical pasture. *Biotropica* 33, 260–267. [https://doi.org/10.1646/0006-3606\(2001\)033](https://doi.org/10.1646/0006-3606(2001)033).
- Denslow, Julie Sloan, Gomez Diaz, A.E., 1990. Seed rain to tree-fall gaps in a neotropical rain forest. *Can. J. For. Res.* 20, 642–648. <https://doi.org/10.1139/x90-086>.
- Dufréne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366. <https://doi.org/10.2307/2963459>.
- Edwards, D.P., 2016. Conservation: the rainforest's “do not disturb” signs. *Nature* 535, 44–45. <https://doi.org/10.1038/nature18901>.
- Edwards, D.P., Tobias, J.A., Sheil, D., Meijaard, E., Laurance, W.F., 2014. Maintaining ecosystem function and services in logged tropical forests. *Trends Ecol. Evol.* 29, 1–10. <https://doi.org/10.1016/j.tree.2014.07.003>.
- Edwards, W., Westoby, M., 1996. Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. *J. Biogeogr.* 23, 329–338. <https://doi.org/10.1046/j.1365-2699.1996.00034.x>.
- Fenner, M., Thompson, K., 2005. *The Ecology of Seeds*. Cambridge University Press, Cambridge, UK. <https://doi.org/10.1017/CBO9780511614101>.
- Foley, J.A., Defries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E. A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Review global consequences of land use. *Science* 8, 570–574. <https://doi.org/10.1126/science.1111772>.
- Fredericksen, T.S., Putz, F.E., 2003. Silvicultural intensification for tropical forest conservation. *Biodivers. Conserv.* 12, 1445–1453. <https://doi.org/10.1023/A:1023673625940>.
- Fujiki, S., Aoyagi, R., Tanaka, A., Imai, N., Kusma, A.D., Kurniawan, Y., Lee, Y.F., Sugau, J.B., Pereira, J.T., Samejima, H., Kitayama, K., 2016. Large-scale mapping of tree-community composition as a surrogate of forest degradation in Bornean tropical rain forests. *Land* 5, 45. <https://doi.org/10.3390/land5040045>.
- Gibbs, H.K., Brown, S., Niles, J.O., Foley, J.A., 2007. Monitoring and estimating tropical forest carbon stocks: making REDD a reality. *Environ. Res. Lett.* 2, 045023. <https://doi.org/10.1088/1748-9326/2/4/045023>.
- Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., et al., 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature* 478, 378–381. <https://doi.org/10.1038/nature10425>.
- Griscom, H.P., Ashton, M.S., 2011. Restoration of dry tropical forests in Central America: a review of pattern and process. *For. Ecol. Manag.* 261, 1564–1579. <https://doi.org/10.1016/j.foreco.2010.08.027>.
- Grubb, P.J., Lloyd, J.R., Pennington, T.D., 1963. A comparison of montane and lowland rain forest in Ecuador I. The forest structure, physiognomy, and floristics. *J. Ecol.* 51, 567–601.
- Guimara, D.M., Gualberto, D., Pereira, S., Cristina, G., Menino, D.O., Yue, D., Tng, P., Pires, G.G., Aure, M., 2014. Beta-diversity in seasonally dry tropical forests (SDTF) in the Caatinga Biogeographic Domain, Brazil, and its implications for conservation. *Biodivers. Conserv.* 23, 217–232. <https://doi.org/10.1007/s10531-013-0599-9>.
- Hayward, R.M., Banin, L.F., Burslem, D.F.R.P., Chapman, D.S., Philipson, C.D., Cutler, M.E.J., Reynolds, G., Nilus, R., Dent, D.H., 2021. Three decades of post-logging tree community recovery in naturally regenerating and actively restored dipterocarp forest in Borneo. *For. Ecol. Manag.* 488, 119036. <https://doi.org/10.1016/j.foreco.2021.119036>.
- He, F., Legendre, P., LaFrankie, J., 1997. Distribution patterns of tree species in a Malaysian tropical rain forest. *J. Veg. Sci.* 8, 105–114. <https://doi.org/10.2307/3237248>.
- Hendrickx, F., Maelfait, J., Wingerden, W.V.A.N., Schweiger, O., Speelmans, M., Aviron, S., Augenstein, I., Billeter, R., Bailey, D., Bukacek, R., Burel, F., Diekötter, T.I. M., Dirksen, J., Herzog, F., Liira, J., Roubalova, M., Vandomme, V., Bugter, R.O.B., 2007. How landscape structure, land-use intensity and habitat diversity affect components of total arthropod diversity in agricultural landscapes, 340–351. doi:10.1111/j.1365-2664.2006.01270.x.
- Holthuljzen, A.M.A., Boerboom, J.H.A., 1982. *The Cecropia seedbank in the Surinam lowland rain forest*. *Biotropica* 14, 62–68.
- Hosonuma, N., Herold, M., De Sy, V., De Fries, R.S., Brockhaus, M., Verchot, L., Angelsen, A., Romijn, E., 2012. An assessment of deforestation and forest degradation drivers in developing countries. *Environ. Res. Lett.* 7, 4009. <https://doi.org/10.1088/1748-9326/7/4/044009>.
- Imai, N., Seino, T., Aiba, S., Takyu, M., Titin, J., Kitayama, K., 2012. Effects of selective logging on tree species diversity and composition of Bornean tropical rain forests at different spatial scales. *Plant Ecol.* 213, 1413–1424. <https://doi.org/10.1007/s11258-012-0100-y>.
- Imai, N., Tanaka, A., Samejima, H., Sugau, J.B., Pereira, J.T., Titin, J., Kurniawan, Y., Kitayama, K., 2014. Tree community composition as an indicator in biodiversity monitoring of REDD+. *For. Ecol. Manag.* 313, 169–179. <https://doi.org/10.1016/j.foreco.2013.10.041>.
- Imai, N., Samejima, H., Demies, M., Tanaka, A., Sugau, J.B., Pereira, J.T., Kitayama, K., 2016. Response of tree species diversity to disturbance in humid tropical forests of Borneo. *J. Veg. Sci.* 27, 739–748. <https://doi.org/10.1111/jvs.12401>.
- Ito, S., 1991. Species turnover and diversity patterns along an evergreen broad-leaved forest coenocline. *J. Veg. Sci.* 2, 477–484. <https://doi.org/10.2307/3236029>.
- Karp, D.S., Andrew, J., Zook, J., Ranganathan, J., Ehrlich, P.R., Daily, G.C., 2012. Intensive agriculture erodes  $\beta$ -diversity at large scales. *Ecol. Lett.* 15, 963–970. <https://doi.org/10.1111/j.1461-0248.2012.01815.x>.
- Kitayama, K., 1992. An altitudinal transect study of the vegetation on Mount Kinabalu, Borneo. *Vegetatio* 102, 149–171. <https://doi.org/10.1007/BF00044731>.
- Kitayama, K., 1996. Patterns of species diversity on an oceanic versus a continental island mountain: a hypothesis on species diversification. *J. Veg. Sci.* 7, 879–888. <https://doi.org/10.2307/3236463>.
- Kraft, N.J.B., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J., Cornell, H.V., Davies, K.F., Freestone, A.L., Inouye, B.D., Harrison, S.P., Myers, J.A., 2011. Disentangling the drivers of  $\beta$  diversity along latitudinal and elevational gradients. *Science* 333, 1755–1758. <https://doi.org/10.1126/science.1208584>.
- Kuussaari, M., Eklöf, J., Helio, J., 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes, 459–467. doi:10.1111/j.1365-2664.2009.01767.x.
- Lane, C.S., 2007. Latitudinal range variation of trees in the United States: a reanalysis of the applicability of Rapoport's rule. *Prof. Geogr.* 59, 115–130. <https://doi.org/10.1111/j.1467-9272.2007.00595.x>.
- Lieberman, D., Lieberman, M., Peralta, R., Hartshorn, G.S., 1996. Tropical forest structure and composition on a large-scale altitudinal gradient in Costa Rica. *J. Ecol.* 84, 137–152. (<https://www.jstor.org/stable/2261350>).
- Lieberman, Diana, Lieberman, Milton, Hartshorn, G.S., Peralta, R., 1985. Small-scale altitudinal variation in lowland wet tropical forest vegetation. *J. Ecol.* 73, 505–516. <https://doi.org/10.2307/2260490>.
- López-Martínez, J.O., Hernández-Stefanoni, J.L., Dupuy, J.M., Meave, J.A., 2013a. Partitioning the variation of woody plant  $\beta$ -diversity in a landscape of secondary tropical dry forests across spatial scales. *J. Veg. Sci.* 24, 33–45. <https://doi.org/10.1111/j.1654-1103.2012.01446.x>.
- López-Martínez, Jorge Omar, Sanaphre-Villanueva, L., Dupuy, J.M., Hernández-Stefanoni, J.L., Meave, J.A., Gallardo-Cruz, J.A., 2013b.  $\beta$ -Diversity of functional groups of woody plants in a tropical dry forest in Yucatan. *PLoS One* 8, e73660. <https://doi.org/10.1371/journal.pone.0073660>.
- Markl, J.S., Schleuning, M., Forget, P.M., Jordano, P., Lambert, J.E., Traveset, A., Wright, S.J., Bohning-Gaese, K., 2012. Meta-analysis of the effects of human disturbance on seed dispersal by animals. *Conserv. Biol.* 26, 1072–1081. <https://doi.org/10.1111/j.1523-1739.2012.01927.x>.



- Molino, J.-F., Sabatier, D., 2001. Tree diversity in tropical rain forests: a validation of the intermediate disturbance hypothesis. *Science* 294, 1702–1704. <https://doi.org/10.1126/science.1060284>.
- Mori, A.S., Shiono, T., Koide, D., Kitagawa, R., Ota, A.T., 2013. Community assembly processes shape an altitudinal gradient of forest biodiversity. *Glob. Ecol. Biogeogr.* 22, 878–888. <https://doi.org/10.1111/geb.12058>.
- Morin, X., Chuine, I., 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecol. Lett.* 9, 185–195. <https://doi.org/10.1111/j.1461-0248.2005.00864.x>.
- Myers, J.A., Chase, J.M., Jiménez, I., Jørgensen, P.M., Araujo-Murakami, A., Paniagua-Zambrana, N., Seidel, R., 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecol. Lett.* 16, 151–157. <https://doi.org/10.1111/ele.12021>.
- Nzunda, E.F., 2011. Sprouting, succession and tree species diversity in a South African coastal dune forest. *J. Trop. Ecol.* 27, 195–203. <https://doi.org/10.1017/S0266467410000659>.
- Oakwood, M., Jurado, E., Leishman, M., Westoby, M., 1993. Geographic ranges of plant species in relation to dispersal morphology, growth form and diaspore weight. *J. Biogeogr.* 20, 563–572. <https://doi.org/10.2307/2845727>.
- Oksanen, J., Guillaume Blanchet, F., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymus, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. Community Ecology Package, Package 'vegan'. R package version 2.4-5. 0-291. doi:ISBN 0-387-95457-0.
- Paillet, Y., Bergès, L., Hjaltn, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastián, M.T., Schmidt, W., Standovář, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>.
- Paoli, G.D., Curran, L.M., Zak, D.R., 2006. Soil nutrients and beta diversity in the Bornean Dipterocarpaceae: evidence for niche partitioning by tropical rain forest trees. *J. Ecol.* 94, 157–170. <https://doi.org/10.1111/j.1365-2745.2005.01077.x>.
- Penman, J., Gytarsky, M., Hiraishi, T., Krug, T., Kruger, D., Pipatti, R., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., 2003. Definitions and Methodological Options to Inventory Emissions from Direct Human-induced Degradation of Forests and Vegetation of Other Vegetation Types, The Institute for Global Environmental Strategies (IGES). doi:10.1016/B978-0-12-375067-9.00128-5.
- Putz, F.E., Sist, P., Fredericksen, T., Dykstra, D., 2008. Reduced-impact logging: challenges and opportunities. *For. Ecol. Manag.* 256, 1427–1433. <https://doi.org/10.1016/j.foreco.2008.03.036>.
- Putz, F.E., Zuidema, P.A., Synnott, T., Pe, M., Pinard, M.A., Sheil, D., Vanclay, J.K., Sist, P., Gourlet-fléury, S., Griscom, B., Palmer, J., Zagt, R., 2012. Sustaining conservation values in selectively logged tropical forests: the attained and the attainable. *Conserv. Lett.* 5, 296–303. <https://doi.org/10.1111/j.1755-263X.2012.00242.x>.
- Roberts, D.W., 2016. Ordination and Multivariate Analysis for Ecology. R package Version 1.8-0 <http://eco.R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria>.
- Runting, R.K., Meijaard, E., Abram, N.K., Wells, J.A., Gaveau, D.L.A., Ancrenaz, M., Possingham, H.P., Wich, S.A., Ardiansyah, F., Gumal, M.T., Ambu, L.N., Wilson, K.A., 2015. Alternative futures for Borneo show the value of integrating economic and conservation targets across borders. *Nat. Commun.* 6, 6819. <https://doi.org/10.1038/ncomms7819>.
- Sahu, P.K., Sagar, R., Singh, J.S., 2008. Tropical forest structure and diversity in relation to altitude and disturbance in a Biosphere Reserve in central India. *Appl. Veg. Sci.* 11, 461–470. <https://doi.org/10.3170/2008-7-18537>.
- Sayer, J., Sunderland, T., Ghazoul, J., Pfund, J., Sheil, D., Meijaard, E., Venter, M., Boedhihartono, A.K., Day, M., Garcia, C., Oosten, C., Buck, L.E., 2013. Ten principles for a landscape approach to reconciling agriculture, conservation, and other competing land uses. *Proc. Natl. Acad. Sci. USA* 110, 8349–8356. <https://doi.org/10.1073/pnas.1210595110>.
- Slik, J.W.F., Bernard, C.S., Breman, F.C., Van Beek, M., Salim, A., Sheil, D., 2008. Wood density as a conservation tool: quantification of disturbance and identification of conservation-priority areas in tropical forests. *Conserv. Biol.* 22, 1299–1308. <https://doi.org/10.1111/j.1523-1739.2008.00986.x>.
- Slik, J.W.F., Raes, N., Aiba, S.-I., Brearley, F.Q., Cannon, C.H., Meijaard, E., Nagamasu, H., Nilus, R., Paoli, G., Poulsen, A.D., Sheil, D., Suzuki, E., van Valkenburg, J.L.C.H., Webb, C.O., Wilkie, P., Wulffraat, S., 2009. Environmental correlates for tropical tree diversity and distribution patterns in Borneo. *Divers. Distrib.* 15, 523–532. <https://doi.org/10.1111/j.1472-4642.2009.00557.x>.
- Smith, J.R., Bagchi, R., Ellens, J., Kettle, C.J., Burslem, D.F.R.P., Colin, R., Khoo, E., Ghazoul, J., 2015. Predicting dispersal of auto-gyrating fruit in tropical trees: a case study from the Dipterocarpaceae. *Ecol. Evol.* 5, 1794–1801. <https://doi.org/10.1002/ece3.1469>.
- Solar, R., Ri, de, C., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., Julio, L., Maués, M., Moura, N.G., Oliveira, V.H.F., Chau, J.C.M., Schoederer, J. H., Vieira, I.C.G., Nally, R., Mac, Gardner, T.A., 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecol. Lett.* 18, 1108–1118. <https://doi.org/10.1111/ele.12494>.
- Stevens, G.C., 1989. The latitudinal gradient in geographical range: how so many species coexist in the tropics. *Am. Nat.* 133, 240–256. (<https://www.jstor.org/stable/2462300>).
- Tello, J.S., Myers, J.A., Macía, M.J., Fuentes, A.F., Cayola, L., Arellano, G., Loza, M.I., Torrez, V., Cornejo, M., Miranda, T.B., Peter, M.J., 2015. Elevational gradients in  $\beta$ -diversity reflect variation in the strength of local community assembly mechanisms across spatial scales. *PLoS One* 10, e0121458. <https://doi.org/10.1371/journal.pone.0121458>.
- Thompson, K., Gaston, K.J., Band, S.R., 1999. Range size, dispersal and niche breadth in the herbaceous flora of central England. *J. Ecology* 87, 150–155. <https://doi.org/10.1046/j.1365-2745.1999.00334.x>.
- Vazquez, J.A., Givnish, T.J., 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. *J. Ecol.* 86, 999–1020. <https://doi.org/10.1046/j.1365-2745.1998.00325.x>.
- Vellend, M., Verheyen, K., Flinn, K.M., Jacquemyn, H., Kolb, A., Calster, H.V.A.N., Peterken, G., Graae, B.J., Bellemare, J., Honnay, O., Brunet, J., Wulf, M., Gerhardt, F., Hermy, M., 2007. Homogenization of forest plant communities and weakening of species–environment relationships via agricultural land use, 565–573. doi:10.1111/j.1365-2745.2007.01233.x.
- Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beausejour, R., Brown, C.D., De Frenne, P., Verheyen, K., Wipf, S., 2013. Global meta-analysis reveals no net change in local-scale plant biodiversity over time. *Proc. Natl. Acad. Sci. USA* 110, 19456–19459. <https://doi.org/10.1073/pnas.1312779110>.
- Verissimo, A., Barreto, P., Mattos, M., Tarifa, R., Uhl, C., 1992. Logging impacts and prospects for sustainable forest management in an old Amazonian frontier: the case of Paragominas. *For. Ecol. Manag.* 55, 169–199. [https://doi.org/10.1016/0378-1127\(92\)90099-U](https://doi.org/10.1016/0378-1127(92)90099-U).
- Verschuyf, J., Riffell, S., Miller, D., Wigley, T.B., 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests - a meta-analysis. *For. Ecol. Manag.* 261, 221–232. <https://doi.org/10.1016/j.foreco.2010.10.010>.
- Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251. (<https://www.jstor.org/stable/1218190>).
- Wilcove, D.S., Giam, X., Edwards, D.P., Fisher, B., Koh, L.P., 2013. Navjot's nightmare revisited: logging, agriculture, and biodiversity in Southeast Asia. *Trends Ecol. Evol.* 28, 531–540. <https://doi.org/10.1016/j.tree.2013.04.005>.
- Willis, K.J., Whittaker, R.J., 2002. Species diversity - scale matters. *Science* 295, 1245–1248. <https://doi.org/10.1126/science.1067335>.
- Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., 2009. Data from: towards a worldwide wood economics spectrum. Dryad Digital Repository. <https://doi.org/10.5061/dryad.234>.