

Research Article

Topographic patterns in the phylogenetic structure of temperate forests on steep mountainous terrain

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Abstract. In rugged terrain subject to active geomorphological processes, the species composition of forest communities changes along topographic gradients over short distances. However, the phylogenetic structure of forests on rugged terrain has rarely been examined. Understanding such structures provides insight into community assembly rules dependent on local environmental conditions. To this end, we tested the topographic trends of measurements of phylogenetic community structure [net relatedness index (NRI) and nearest taxon index] in a catchment covered by temperate forests with complex relief in Japan. We found that phylogenetic structure changed from over-dispersion to clustering with increasing slope inclination, change of slope aspect from south to north and decreasing soil depth. This result suggested that environmental filtering tended to restrict community composition at relatively stressful sites, whereas species interaction functioned more strongly at relatively stress-free sites. Relatively stressful sites were characterized by early-successional species that tended to assemble in certain phylogenetic clades, whereas highly competitive late-successional species associated with lower NRI at relatively stress-free sites. However, despite this significant topographic tendency, phylogenetic community structures were not statistically different from random assumptions in most plots. This obscuration of the phylogenetic structures at the plot level could be interpreted as species adapting to disturbances because they were abundant in this catchment. Accordingly, we suggest that a stochastic process was also important for this community at the plot level, although biotic and abiotic environmental filtering controlled the vegetation structure in the catchment, where disturbances occur frequently because of geomorphological mountain denudation processes owing to active crustal movements and abundant rainfall.

Keywords: Community assembly rule; heterogeneous environmental condition; phylogenetic diversity; temperate forest in East Asia; topographic gradients.

Introduction

Understanding the causal factors of fine-grained spatial variations in species diversity and composition within a forest is one of traditional tasks of ecology (Clark *et al.* 1998). Theory suggests that both deterministic and stochastic processes explain spatial variation in community patterns

(e.g. Kraft *et al.* 2008; Chase 2010). The deterministic process is based on the classical niche theory, i.e. each species distributes to its own niche, and thus, the members of a community should be determined depending on local biotic and abiotic environment conditions (Hutchinson 1959). On the other hand, the stochastic process has

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been emphasized in recent studies, involving increases in the randomness of species composition (e.g. Chase 2003). Namely, the occurrence of a species adapting to a local condition at a given site is not assured but is with a certain level of probability caused by factors such as dispersal limitation and/or differential dynamics between colonization and local extinction (Hubbell 2001). Many studies have tried to determine whether deterministic or stochastic processes predominate. Moreover, if a deterministic process is noticeable, the interests of community ecology moves on to reveal the causal factors of the non-random community structure, such as biotic or abiotic environmental factors. Many studies suggest that recent trait-based and phylogenetic approaches are effective for disentangling these questions relating to forest community structure (HilleRisLambers *et al.* 2012). In particular, even in the absence of trait data, a phylogenetic approach could provide insight into the forest community assembly of local habitats (e.g. Kembel and Hubbell 2006; Swenson and Enquist 2009; Kraft and Ackerly 2010; Duarte 2011, Pei *et al.* 2011).

The phylogenetic approach to validate the community assembly has basically evolved from the traditional theory of niche evolution; closely related species can be considered to have similar niches (Harvey and Pagel 1991). Under this assumption, phylogenetic relatedness can be regarded as an index of the differences in niche-related traits, which have come about through evolution. Here, there are two patterns of non-random phylogenetic community structures that are detected by comparison with a random expectation, interpreted as the consequences of two different assembly rules (Webb 2000; Webb *et al.* 2002). Firstly, ‘phylogenetic clustering’, i.e. closely related species co-occur within a community more frequently than expected from a random assumption [lower phylogenetic diversity (PD) than expected], which is interpreted to result from constraints on community members caused by abiotic environmental conditions. Some studies have shown that phylogenetic clustering appears in stressful conditions such as highly disturbed sites (González-Caro *et al.* 2014), and nutrient-poor and arid habitats (Kembel and Hubbell 2006; Spasojevic and Suding 2012). Secondly, if distantly related species tend to co-occur more than expected by chance, this is termed ‘phylogenetic over-dispersion’. This pattern is explained by the rule of limiting similarity, where competitive exclusion acts more strongly between closely related species (Cavender-Bares *et al.* 2004), and/or with facilitation (Verdú *et al.* 2009), which is more probable between distantly related species. Phylogenetic over-dispersion has been detected at sites with relatively mild conditions, e.g. nutrient- and water-rich habitats (Cavender-Bares *et al.* 2004; Spasojevic and Suding 2012), less-disturbed

sites (González-Caro *et al.* 2014), and at lower elevations and warm-temperate sites (Qian *et al.* 2014). If neither pattern is detected, the community is interpreted as a phylogenetically random assembly from the species pool (Webb *et al.* 2002; Mouquet *et al.* 2012), or birth filtering and competition are acting in concert. Although the cause-and-effect relationship between these patterns in phylogenetic structure and assembly rule is still under debate, and various interpretations are argued (for example Mayfield and Levine 2010 suggested ‘competition drives phylogenetic clustering’), this conceptual idea is recognized as the basic framework of phylogenetic community ecology.

Therefore, a phylogenetic approach is useful to understand the driving force of spatial variation of species diversity and composition (e.g. Kembel and Hubbell 2006; Spasojevic and Suding 2012; De Oliveira *et al.* 2014; Qian *et al.* 2014). These studies have focussed on habitat heterogeneity, and the phylogenetic structures of local wood communities were examined in relation to environmental conditions, for example as represented by topography. Except for a few studies, this approach has been adopted for tropical and subtropical forests, where there are regarded as being too many species to estimate the assembly rule by detecting niche-related traits of respective species. However, other ecosystems, including temperate forests, have rarely been examined.

East Asian temperate forests show high regional and local plant species richness owing to geological and climatic conditions (Qian and Ricklefs 2000; Qian *et al.* 2005), i.e. complex relief is common because of rapid uplift and abundant rainfall, providing high niche diversity over various spatial scales. In such regions, large variations in species distribution pattern in terms of topography have been reported (Masaki *et al.* 1992; Sakai and Ohsawa 1994; Nagamatsu and Miura 1997; Kitagawa *et al.* 2014). However, local community assembly rules have not yet been investigated in such regions.

Kitagawa *et al.* (2014) analysed the spatial pattern of forest structure for a 306-ha water catchment in a Japanese mountainous area, and they pointed out that local above-ground biomass could be explained through the topographical features of the site. Above-ground biomass was larger around ridges but smaller near valleys, coinciding with an assumable gradient of disturbance intensity from weak on ridges to strong in valleys, which is a pattern that has been reported previously in East Asia (e.g. Sakai and Ohsawa 1994; Enoki 2003; Chang *et al.* 2012). Relating to previous topography–forest structure studies, a hypothesis for community assembly on a topographic gradient can be formulated; if the biomass reflects environmental stress, phylogenetic community structure may change from over-dispersion to clustering with gradient from

ridges to valley. However, other topographical variables such as slope aspect, slope inclination and soil depth may also be crucial. Moreover, the function of community assembly in areas with frequent ground-surface disturbance is unclear. Relating to this uncertainty, we assumed that the community assembly rule may be rather stochastic in such highly disturbed conditions (Fukami and Nakajima 2011), whereas it might act as an environmental filter producing more phylogenetic clustering, given the existence of unique disturbance-tolerant species on lower slopes in East Asia (Sakai et al. 1995; Qian et al. 2005). Verification of these predictions can increase the certainty of the hypothesis for community assembly rules described above and contribute to understand the mechanisms relating to topographical variation of species composition within forests.

Although the above predictions are basically testable by phylogenetic approaches with our inventory data, we should not ignore the uncertainties for the general framework of the phylogenetic approach that were suggested in recent studies (e.g. Godoy et al. 2014), in addition to the pattern of phylogenetic niche lability (Losos 2008). In particular, recent studies suggested scepticism about the interpretation of phylogenetic over-dispersion in the existing framework, because they found that competitive interaction was not necessary to limit the phylogenetic similarity within a community. Consequently, we paid attention to species characteristics that contribute to each phylogenetic structure (over-dispersion and clustering). Fortunately, there are many descriptive works on the distribution and ecological characteristics of woody species that are related to local topography in temperate forests in East Asia (e.g. Masaki et al. 1992; Sakai and Ohsawa 1994; Nagamatsu and Miura 1997), including our previous study (Kitagawa et al. 2014). Accumulation of such information may empirically support the interpretation of

phylogenetic community structure, and may complement the concern about the existing framework.

This study aims to understand the community assembly rule along local topographical gradients in a heterogeneous mountain landscape. To this end, we examined the topographic trends of phylogenetic structure of 99 study plots within a 306-ha water catchment using the same inventory data as Kitagawa et al. (2014), and discuss the distribution pattern of key species groups that affected the phylogenetic structure.

Methods

Study area

The study catchment (306 ha) is located in the western Mt Tanzawa region, Kanagawa prefecture, central Japan ($35^{\circ}28'00''\text{N}$ – $35^{\circ}29'10''\text{N}$, $139^{\circ}01'55''\text{E}$ – $139^{\circ}03'50''\text{E}$) (Fig. 1). In this study, we targeted one catchment that is a unit of a watershed ecosystem to reveal the overall trends in the community assembly that may depend on the hydrogeological cycle through disturbances relating to mass movements. Mean annual temperature is 12.8°C (mean temperature in the coldest and warmest months of the year are 2.5 and 23.7°C , respectively) and the mean annual precipitation is 2819.1 mm, which were all measured at Gotenba ($35^{\circ}18'18''\text{N}$, $138^{\circ}55'37.2''\text{E}$), 472 m above sea level, near the study catchment (AMeDAS by Japan Metrological Agency). The highest point of the catchment is the summit of Mt Azegamaru (1200 m), and the lowest point is the outlet of the main stream, Nishizawa river (560 m). The upper part of the catchment, approximately over 800 m, is covered by cool-temperate forests dominated by deciduous trees, and the lower part is warm-temperate forest dominated by evergreen and deciduous broadleaved trees. The complex terrain of this region

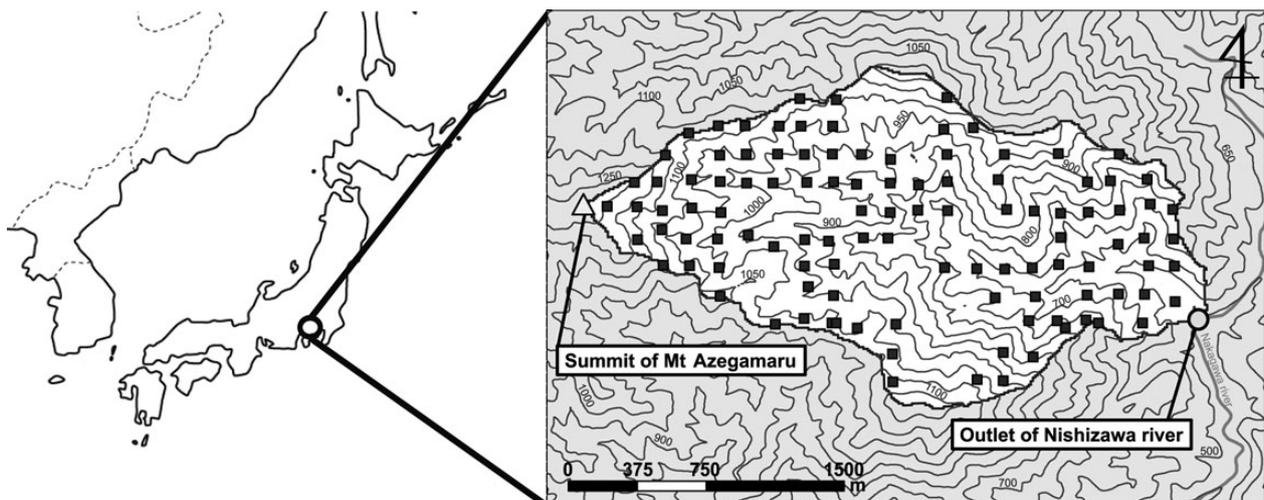


Figure 1. Location of the study catchment and sampling plots, denoted by black squares.

consists of steep slopes, which are caused by abundant rainfall, erodible substratum rocks and active crustal movements (Ishikawa et al. 2006).

Inventory data and topographical variables

Ninety-nine plots out of the original 105 plots were used in this study; six plots were excluded because tree species were absent or soil depth data were lacking. To detect the whole trends in community structure in the catchment, these plots were essentially set at the intersection points of every 5 s of latitude and longitude, excluding inaccessible steep slopes and conifer plantations but with the addition of plots on main ridges of the catchment boundary (Fig. 1). To detect geomorphological responses in vegetation, we adopted relatively small plot sizes (10 × 10 m), and slightly moved some locations, because species composition and habitat conditions changed dramatically over short distances in this steep terrain. Species records were for all plant stems that were 5 cm or greater in diameter at breast height (DBH). With the exception of climbing plants, data for all 75 species were used in this study. Mean soil depth was calculated from three recordings in each plot. An iron rod of 50 cm length was used to measure the soil depth, and if the depth was > 50 cm, 60 cm was used for analyses.

Slope inclination, laplacian, i.e. an index of concavity and convexity of the ground, elevation and slope aspect were obtained from a 20 × 20 m digital elevation model using Arc GIS (version 9.3, Esri Inc.). Laplacian was calculated using:

$$\frac{nx - \sum_{i=1}^n y}{n}$$

where x , y and n are the elevation of the target cell, the elevation of a surrounding cell and the number of surrounding cells, respectively. Positive and negative values show a convex site, such as ridge top, and a concave site, respectively. Each cell was a square of 20 × 20 m. We considered two kinds of laplacian in this study: laplacian using eight surrounding cells (lap8_3; total area 60 × 60 m), which indicated small-scale convexity or concavity of the terrain, and laplacian using 360 surrounding cells (lap8_19; 380 × 380 m), indicating a large ridge or valley that roughly reflected main ridges and valleys of the catchment. Tangent transformation was applied for slope inclination ($\tan(\text{slope})$), and sine transformation was applied for slope aspect ($\sin(\text{aspect})$), ranging from -1 (south facing) to 1 (north facing).

Phylogenetic structure

To measure phylogenetic distances between species, we constructed a phylogenetic tree: the phylogenies of all species examined in this study were constructed based

on the R20120829 megatree in Phylomatic v3 (<http://phylodiversity.net/phylomatic/>). Branch lengths of angiosperms were assigned based on divergence times estimated by Wikström et al. (2001) using the *bladj* algorithm in PYLOCOM 4.2 (Webb et al. 2008). For the calibration of the branches of gymnosperms, we used four calibration points estimated with molecular data and fossil constraints by Magallón et al. (2013), including the branching point of angiosperms and gymnosperms [312 million years ago (mya)], the crown age of Pinales (278 mya), the branching point of Taxaceae and Cupressaceae (175 mya) and the crown age of Pinaceae (153 mya).

To evaluate the phylogenetic structure of each plot, we calculated Faith's PD (Faith 1992), the net relatedness index (NRI; Webb 2000; Webb et al. 2002) and the nearest taxon index (NTI; Webb et al. 2002) using the *picante* libraries (Kembel et al. 2010) in R (<http://www.R-project.org>; R Development Core Team). Net relatedness index and NTI were defined as:

$$\text{NRI} = - \frac{\text{MPD} - \text{MEAN}(\text{MPDnull})}{\text{SD}(\text{MPDnull})}$$

$$\text{NTI} = - \frac{\text{MNTD} - \text{MEAN}(\text{MNTDnull})}{\text{SD}(\text{MNTDnull})}$$

where MPD is the mean of pairwise phylogenetic distance between all species in a plot, MNTD is the mean for all species within the plot in relation to the phylogenetic distance from another closest species in the plot, MEAN(MPDnull) and MEAN(MNTDnull) are the means of MPD and MNTD calculated from 999 null communities and SD(MPDnull) and SD(MNTDnull) are their standard deviations. An independent swap approach (Gotelli and Entsminger 2003) was used to generate the 999 null communities, i.e. for each plot, the same number of species as in the plot was chosen at random from the whole species inventory, where the probability of choice for a species was adjusted to the frequency of species occurrence across all plots. Net relatedness index reflects the more general structure, whereas NTI is a more sensitive indicator of phylogenetic extendability or segregation among components.

Positive NRI and NTI values indicated a trend that the community consisted of more-closely related species than expected at random, known as 'phylogenetic clustering'. On the other hand, negative NRI and NTI values indicated that the community composition was more phylogenetically divergent than expected at random, i.e. 'phylogenetic over-dispersion'. Here, if the regional flora involves species belonging to much older clades than the majority, the local trends in these indices may be largely affected by the distribution pattern of such

older species. Specifically, because the five conifer species might have strong effect on our results, a data set with conifers removed was also used for the calculation of the NRI and NTI. To detect whether a non-random or a random structure was dominant, the numbers of plots that deviated significantly from the random assumption were identified.

Analyses of topographical trends in phylogenetic structure

To assess the topographic variables meaningful for phylogenetic community structure, linear models were constructed:

$$y \sim \text{elevation} + \tan(\text{slope}) + \sin(\text{aspect}) + \text{soil depth} \\ + \text{lap8_3} + \text{lap8_19}$$

as the full model. Response variable (y) was any of four indices of the phylogenetic structure (NRI and NTI for all species and the same for only angiosperms), Gaussian distribution was assumed for response variables and linear regressions were fitted. For each response variable, after constructing models for all combinations of the topographical variables, i.e. 144 patterns, we identified the model with the smallest Akaike information criterion (AIC) as the best model, and also detected the other top three models. For these models, r^2 values were calculated to confirm the predictive ability. Spatial autocorrelation for all response variables was not detected by Moran's I (NRI for all species: -0.040 ; NTI for all species: -0.043 ; NRI for angiosperms: -0.043 and NTI for angiosperms: -0.039). We confirmed that multicollinearity was not detected using variance inflation factors (Fox and Monette 1992) between any explanatory variables except for between two laplacians. Two laplacians did not appear simultaneously in the best model or the other selected models. Each single relationship for the response variables against topographical variables that was selected in the best models of NRI and NTI for all species was tested using linear regression. Because the analysis without conifers was applied to confirm the effect of much older clades for whole trends, single correlations for the selected variables in the best models for NRI and NTI without conifers were not tested.

To understand the contribution of respective species to the observed phylogenetic structures, for each of the 28 species that occurred in 10 or more plots, the frequency of occurrence was calculated for three NRI groups by plot, using NRI for all species, i.e. 33 plots with lower, middle and higher values of NRI, respectively; these NRI ranges were -3.42 to -0.38 for the lower NRI group, -0.29 to 0.66 for the middle group and 0.73 – 1.81 for the higher group.

All statistical tests were performed in R version 3.1.1 (<http://www.R-project.org>; R Development Core Team).

Results

The 75 woody species that were non-climbing and had $\text{DBH} \geq 5$ cm in the 306 ha watershed included 8 evergreen angiosperms, 62 deciduous angiosperms and 5 evergreen gymnosperms. These belonged to five monophyletic clades, eurosides (42 species), asteroids (20), magnoliids (4), austrobaileyales (1), conifers (5) and other eudicots (3) (Fig. 2). Three *Carpinus* species, *Carpinus japonica*, *C. tschonoskii* and *C. laxiflora*, and *Acer amoenum* were frequent species in this catchment (they occurred in more than half of the 99 plots), whereas 21 species appeared in only one plot. The average number of species and individuals \pm SD in a plot were 8.818 ± 3.102 and 17.263 ± 7.591 , respectively.

The mean (\pm SD) per plot for NRI for all species, NTI for all species, NRI for angiosperms and NTI for angiosperms were 0.064 ± 1.108 , 0.061 ± 1.108 , 0.061 ± 1.018 and 0.031 ± 0.994 , respectively. These variables varied with a unimodal distribution. They showed a significant negative correlation with Faith's PD; NRI for all species: $r^2 = 0.505$, $P < 0.001$; NTI for all species: $r^2 = 0.498$, $P < 0.001$; NRI for angiosperms: $r^2 = 0.198$, $P < 0.001$ and NTI for angiosperms: $r^2 = 0.214$, $P < 0.001$. However, they did not correlate with species richness; NRI for all species: $r^2 = 0.004$, $P = 0.947$; NTI for all species: $r^2 = 0$, $P = 0.881$; NRI for angiosperms: $r^2 = 0.016$, $P = 0.218$ and NTI for all angiosperms: $r^2 = 0.016$, $P = 0.211$. The number of plots that showed a significantly positive or negative deviation from a random assumption with a 95 % confidence level were as follows: five plots were positive and four plots were negative for NRI for all species, five plots each were positive and negative for NTI for all species, four plots were positive and two plots were negative for NRI for all angiosperms and three plots each were positive and negative for NTI for all angiosperms.

In the best models for all-species NRI and NTI, slope aspect, soil depth and slope inclination were selected (Table 1). These topographic variables were also selected in the other models with lower AIC values. Accordingly, NRI and NTI tended to be lower in plots with a gentle slope, a south-facing slope and with deep soil, and the values increased significantly for plots with a steep slope, a north-facing slope and with thin soil (Fig. 3). In addition to a similar topographical trend, elevation and lap8_3 were selected in the best model for NRI for all angiosperms, meaning that it was also higher at lower elevation and at more convex sites over small scales. For models of the NTI for all angiosperms, the AIC

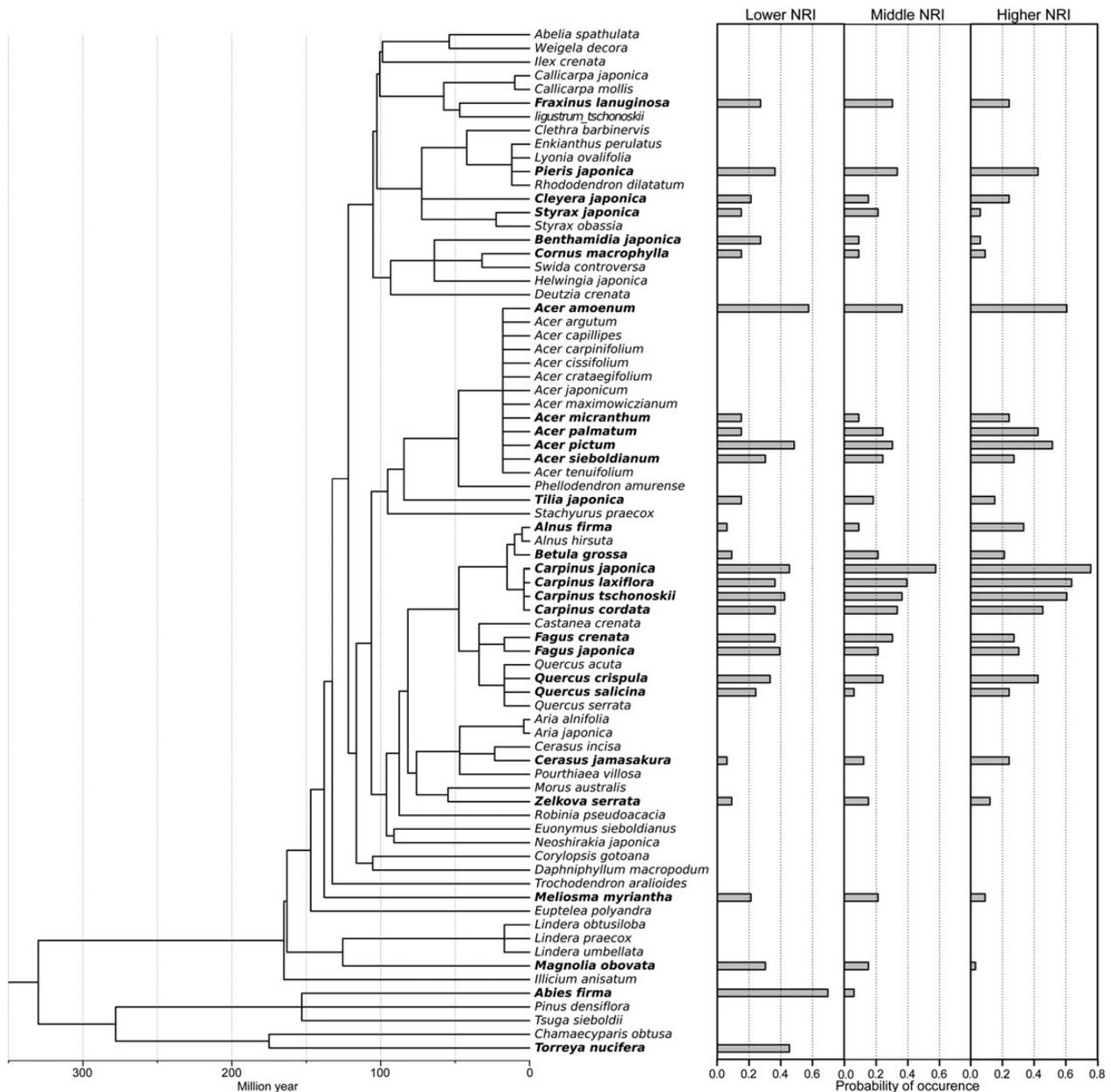


Figure 2. Phylogenetic tree for 75 woody plant species occurring in the 99 sampling plots. Bar charts on the right side show the occurrence ratio of 28 species that occurred in 10 or more plots. Plots are classified into three groups based on NRI for all species (see text). Each group includes 33 plots.

difference between the best and null model was small, and lower r^2 values compared with other response variables were indicated. Although the phylogenetic trend was more non-explicit than the other three response variables, and soil depth was not selected, slope aspect and slope inclination as well as elevation and lap8_3 were selected for the best model.

For the NRI for all species, Betulaceae including *Carpinus*, *Alnus* and *Betula*, *Acer palmatum*, *Acer micranthum* and *Cerasus jamasakura* tended to occur more frequently in plots with higher NRI (Fig. 2). In plots with significantly higher

NRI, *C. tschonoskii* occurred in all five plots, *C. japonica* occurred in four plots and *C. laxiflora* occurred in three plots. The opposite tendency was observed for old-clade species, such as *Torreya nucifera*, *Abies firma* (conifers), *Magnolia obovata* and *Meliosma myriantha*. In addition, *Fagus* species, *Fagus crenata* and *F. japonica*, and *Benthamidia japonica* frequently occurred in the lower NRI plots compared with higher NRI plots (Fig. 2). For the significantly lower NRI plots, *T. nucifera* and *A. firma* occurred in all four plots, and *Tilia japonica* occurred in three plots. Moreover, it was noted that the species that tended to occur more

Table 1. Top three significant and null generalized linear models for four response variables (NRI for all species, NTI for all species, NRI for angiosperm only and NTI for angiosperm only) of local wood communities in a temperate forest in a 306-ha water catchment, Mt Tanzawa, Japan. AIC, Akaike information criterion; tan(slope), tangent transformed slope inclination; lap8_3, lap8_19, convex/concavity in each spatial scale (see text).

Response variables	Models	Intercept	Standard multiple regression coefficients for selected explanatory variables					AIC	Δ AIC	r^2
			Elevation	sin(aspect)	Soil depth	tan(slope)	lap8_3			
NRI for all species	1	0.064		0.396	-0.286	0.204		278.999	0.000	0.274
	2	0.064	-0.099	0.388	-0.280	0.182		279.980	0.981	0.282
	3	0.064		0.392	-0.286	0.208	0.050	280.723	1.723	0.276
	Null	0.064						304.293	25.294	-
NTI for all species	1	0.061		0.357	-0.265	0.206		283.732	0.000	0.237
	2	0.061	-0.123	0.347	-0.259	0.180		284.228	0.496	0.249
	3	0.061	-0.168	0.324	-0.251	0.197	0.144	284.314	0.583	0.264
	Null	0.061						304.206	20.474	-
NRI for angiosperms	1	0.061	-0.180	0.170	-0.176	0.236	0.145	273.857	0.000	0.212
	2	0.061	-0.171	0.182	-0.174	0.225		274.332	0.475	0.192
	3	0.061	-0.195		-0.193	0.233	0.159	275.231	1.374	0.186
	Null	0.061						287.477	13.620	-
NTI for angiosperms	1	0.031	-0.174	0.150		0.190	0.136	277.614	0.000	0.125
	2	0.031	-0.165	0.161		0.180		277.670	0.056	0.107
	3	0.031	-0.207	0.139		0.194	0.133	277.947	0.333	0.122
	Null	0.031						282.813	5.200	-

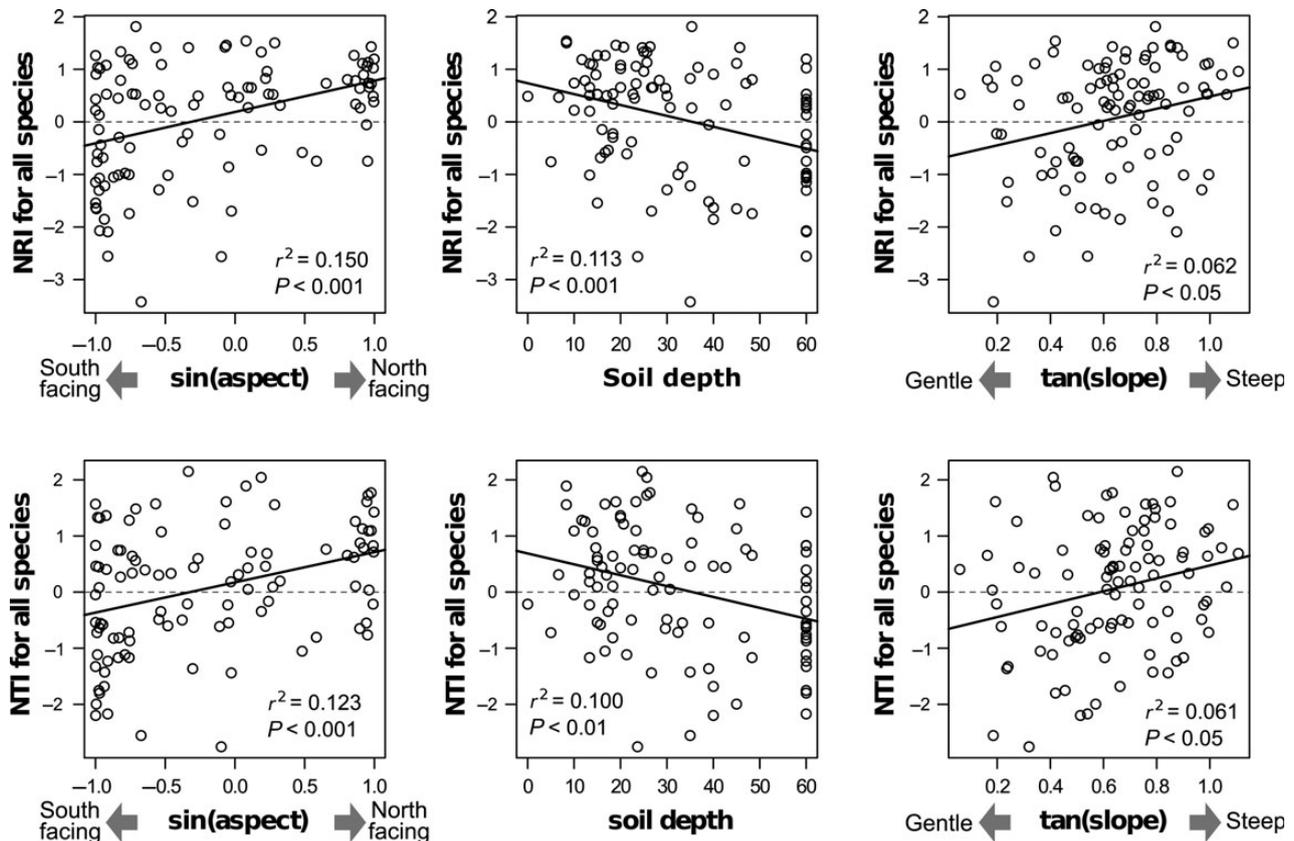


Figure 3. Single relationships between topographic variables selected in the best model and NRI and NTI for all species.

frequently in plots with higher NRI also appeared in the lower NRI plots, although their occurrence ratio was different between lower and higher NRI plots.

Discussion

Deterministic processes in forest community structure on rugged terrain

We found that the phylogenetic community structure changed significantly along the topographic gradients. Namely, phylogenetically clustering was observed in plots on steep and north-facing slopes with thin soils, and a shift to phylogenetic over-dispersion towards gentle and south-facing slopes with deep soils. Even if conifers were removed, the NRI showed almost the same trend, although other topographic variables (elevation and lap8_3) were also effective. For the NTI without conifers, the phylogenetic trend along the topographic gradient was relatively non-explicit, and soil depth was not selected, unlike the best models for other response variables. This may depend on the effect of particular clades such as Betulaceae, Fagaceae and Acer (Aceraceae in the previous classification system before APGIII), which were frequent in this catchment. The NTI is more sensitive to ‘phylogenetic closeness’ within a community than the

NRI. Some frequent clades often occurred simultaneously in the same plot in our data set. Thus, phylogenetic closeness within the community may be emphasized by species belonging to the same clades when conifers were removed. Then, the statistical power was reduced by the equalization of NTI values among communities. Although the NTI for all species showed almost the same trend as the NRI in this study, this should be interpreted carefully for the NTI calculated from low resolution trees such as in our study (Swenson 2009). Thus, discussion of this study was mainly based on the topographic trends of the NRI.

Although the effect of gymnosperms could not be ignored, we suggest that the phylogenetic trends along with topographic variables were obvious, and these phylogenetic trends were seemingly derived from the stress gradient that was related to the topography. A similar spectrum, i.e. a change in phylogenetic community structure coinciding with the intensity of abiotic stress, was reported in previous studies (Kembel and Hubbell 2006; Verdú and Pausas 2007; Ding et al. 2012; Spasojevic and Suding 2012); for example, Kembel and Hubbell (2006) reported phylogenetic clustering on plateaus suffering from seasonal drought and over-dispersion at sites with moist conditions on Barro Colorado Island in

Panama. In addition, [Spasojevic and Suding \(2012\)](#) found the same phylogenetic trend along the abiotic stress gradient on alpine tundra.

There were steep and north-facing slopes with thin soils in the plots with relatively higher NRI for all species. Environmental conditions at these locations included not only insufficient light and poor nutrient levels but also ground instability. Landslide scars are frequently observed in this catchment, especially on steep slopes, where soils are easily eroded. Phylogenetic clustering in such highly disturbed sites was also reported ([González-Caro et al. 2014](#)). *Carpinus*, an abundant genus in this catchment ([Kitagawa et al. 2014](#)), was a characteristic clade for plots with relatively high NRI for all species. Such species are known to show a pioneer-like strategy that aims to enhance the chance of arrival and survival after or during frequent disturbances ([Geritz et al. 1984](#)). Their seedlings are predominantly shade intolerant, and they can dominate in gaps via abundant wind-dispersed seeds ([Shibata and Nakashizuka 1995](#)), namely a seed rain strategy ([Alvarez-Buylla and Martínez-Ramos 1990](#)). Among 28 major species analysed by [Kitagawa et al. \(2014\)](#), statistically significant habitat preferences for harsh sites were shown mainly for *Carpinus* species; biased distribution on steeper slopes was detected for *C. japonica* and *C. cordata* and also another Betulaceae, *Alnus firma*, a typical pioneer tree in this region. Biased distribution to plots with thinner soils was detected for *C. japonica* and *C. laxiflora*. Moreover, individuals of *C. japonica* tended to grow to a large size on north-facing slopes ([Kitagawa et al. 2014](#)). Thus, we suggest that adaptive traits for the harsh topographic conditions may be conserved phylogenetically in the *Carpinus* clade, as well as their invasive ability as pioneers ([Letcher 2010; Norden et al. 2012](#)). As described in the Introduction, we expected that phylogenetically unique clades, such as *Euptelea polyandra*, would be distributed on such harsh sites disturbed frequently by active geomorphological processes ([Sakai et al. 1995](#)); however, such a trend was not detected. This was partly because minor species or species with limited distribution could not be identified sufficiently in analyses using this method. Nevertheless, it was interesting that a rather modern clade dominating the regional flora, *Carpinus*, can be considered to pass through abiotic environmental filters, bringing phylogenetic clustering to the community at the stressful end of the topographical gradient.

On the other hand, lower NRI values indicated that distantly related species tended to co-occur, i.e. phylogenetic over-dispersion at the opposite end of the topographic gradients. Environmental conditions in this location can be regarded as relatively mild. Such phylogenetic over-dispersion observed in relatively mild abiotic environmental conditions was often interpreted as a consequence of

competition in previous studies ([Kembel and Hubbell 2006; Spasojevic and Suding 2012](#)). These studies suggested that many species establish owing to lower abiotic stress, but high competitive pressure among closely related species limited the phylogenetic similarity within the community and led to the coexistence of distantly related species. We considered that a similar mechanism also drives the lower values of NRI for all species in relatively mild conditions on the topographical gradients in this study. [Kitagawa et al. \(2014\)](#) analysed topographical trends in tree biomass in the same catchment and showed that total basal area of trees (Total BA) in a plot was higher on more gentle slopes. Here, the first causal factor of biomass, basal area of the maximum tree (MAX BA), showed the same trend, but the second factor, number of trees, did not. Although the NRI for all species was not significantly correlated with the number of trees, it was significantly negatively correlated with Total BA ($r^2 = 0.067$, $P < 0.01$), MAX BA ($r^2 = 0.093$, $P < 0.01$) and with mean basal area in a plot ($r^2 = 0.103$, $P < 0.01$). This meant that the over-dispersion tendency observed in the relatively stress-free sites did not coincide with the abundance of competitors, but the existence of stronger competitors was effective. In addition, our previous study suggested that the spatial tendency of Total BA was largely contributed to by *F. crenata* and *A. firma* ([Kitagawa et al. 2014](#)), which were typical late-successional species in this region ([Nozaki and Okutomi 1990](#)). The occurrence ratios of two such species were relatively high in plots with lower NRI for all species (Fig. 2). Competition among trees is rather one sided; thus, late-successionals that could become larger trees are disproportionately much stronger ([Kohyama and Takada 2009](#)), and plots with lower NRI are considered to have higher competitive pressure. Therefore, we suggest that competitive exclusion may be the underlying mechanism for phylogenetic over-dispersion on the topographical gradients.

In addition to competitive exclusion, we also mention two other possible explanations for the phylogenetic over-dispersion, although the three explanations are not exclusive of each other. Firstly, we could not neglect the distribution of old-clade plants, because conifers obviously contributed to the lower NRI and higher PD. In fact, the significant negative correlation of the NRI for all species with Faith's PD suggested that the distribution pattern of old-clade species, such as conifers, affected the overall trend in PD, although the phylogenetic trend was sustained even if conifers were removed. Secondly, we suggest that lower NRI is associated with the late-successional stage. Studies in tropical forests found that changes in phylogenetic community structure from clustering to over-dispersion with the way of succession ([Letcher 2010; Norden et al. 2012](#)). They suggested that phylogenetic conservatism for pioneer-like strategies

yielded phylogenetic clustering in early-successional communities, whereas phylogenetic over-dispersion was caused by a rise in species interaction in late-successional communities. This explanation can be adopted with our results. Thus, it can be said that topography governs PD via controlling the distribution of each species, successional status and thus the strength of competition in this rugged terrain. It is difficult to distinguish between the two explanations, successional stage or competition, because late-successional species were often stronger competitors within the forest community. However, we noted that local communities with different NRI values in this catchment could not be regarded as being in the same successional sequence. In other words, topographic gradient is not completely in accordance with successional gradient. Instead, there are rather specialized communities established in different environmental conditions depending on their topographic position (Sakai and Ohsawa 1994). Furthermore, the distribution pattern was different between the typical late-successional species (Kitagawa et al. 2014): *F. crenata* preferred stable ground with a small inclination, but *A. firma* had a biased distribution to south-facing slopes with deep soils. Thus, the late-successional communities were also a combination of different topocommunities. Although negative evidence for the implication of phylogenetic over-dispersion in the existing framework was alleged (e.g. Godoy et al. 2014), we suggest that biotic filtering may work as a dominant rule to achieve ‘phylogenetic over-dispersion’ in topographic conditions with lower abiotic stress in our study area.

Stochastic processes in forest community structure on rugged terrain

Irrespective of the significant changes in phylogenetic community structure with topographical variables, as mentioned above, we found that the PD in most plots did not deviate statistically from the random expectation. This was in accordance with the fact that the species composition was not clearly differentiated among groups of plots with different values of NRI for all species. Notably, *Carpinus* was also a main group in high NRI plots, and *Fagus* appeared also in low NRI plots. In this rugged terrain with fine texture of steep relief, mutual stochastic invasions of early- and late-successional species may be enhanced because of the short distances required for conspicuous changes in environmental conditions. However, for *F. crenata*, which can grow to a large stature on deep soils (Kitagawa et al. 2014), invasion into areas with thin soils may be an opportunistic event and may not contribute its fitness. Such inconsistency between sites of occurrence and sites where species can grow to a large size was observed for all species that could be analysed in Kitagawa et al. (2014). Thus, if we could examine only

mature individuals, a more deterministic pattern might be detected.

Nevertheless, disturbance is thought to be a major causal factor for stochastic processes. Because this region generally has highly erodible terrain, even plots that were in the most stress-free locations on the topographical gradients, the ground may be disturbed sometimes. Otherwise, even if the location is undisturbed, light may reach the forest floor from adjacent disturbed sites. Such conditions may enable early-successional species to immigrate and remain with late-successional competitors. Accordingly, we agree with general arguments that disturbances increase the chance of immigration by species with various niches from the regional species pool (Sousa 1984; Myers and Harms 2011), and stochastic immigration history could obscure the explicit community assembly rules (Chase 2010). However, we also noted that a stochastic process was not equal to random processes but was more or less regulated by the rules of the disturbance regime resulting from natural processes, such as geomorphological processes resulting in mountain denudation, as in the present case.

Conclusions

In a mountainous forest area with steep and complex topography in Japan, we determined the assembly rules for the heterogeneous community structure of tree species. Community structure on the topographical gradient was basically controlled by deterministic processes including abiotic and biotic filtering. However, frequent surface disturbance due to unstable ground conditions increased the stochasticity and obscured the environment–community structure relations. These results were provided using the species characteristics reported by previous studies, and information on phylogenetic community structure. Thus, we suggest that the existing framework of the phylogenetic community approach is useful to understand the community assembly rules at a fine-grained vegetation structure level, at least in the present study area.

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Contributions by the Authors

R.K. and A.S. originally formulated the idea; R.K., M.M. and A.S. developed original idea; R.K. conducted fieldwork; M.M., A.S.M. and A.S. jointed fieldwork; R.K., M.M. and

A.S.M. performed statistical analyses and R.K., M.M., A.S.M. and A.S. wrote the manuscript.

Conflict of Interest Statement

None declared.

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