Short Communication

Bark traits affect epiphytic bryophyte community assembly in a temperate forest

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Abstract

Bark traits of trees often serve as a key factor determining the community structure of epiphytes. However, the extent to which barks modulate the relative importance of abiotic and biotic assembly processes of epiphytes is poorly understood. Here, using a community phylogenetic approach, we aimed to infer the assembly processes of epiphytic mosses and liverworts on tree species with varying bark traits in a temperate forest of central Japan. We observed a total of 56 moss and 35 liverwort species on 150 trees. Moss communities showed decreasing species richness and a tendency toward phylogenetic overdispersion, that is, higher phylogenetic diversity than expected by chance, in relation to increasing bark roughness and acidity. Along the same bark gradients, liverwort communities became phylogenetically clustered. Species richness of both mosses and liverworts increased with the nitrogen content of barks. The results indicate non-random assembly processes such as abiotic filtering associated with environmental harshness and microhabitat variety determined by barks. Our findings imply that bark traits modulate community assembly processes through which epiphyte diversity is maintained.

Keywords: Biodiversity, Competition, Environmental filtering, Evolutionary history, Mosses, Phylogenetic diversity

Introduction

Epiphytes are essential components of forest biodiversity (Burns and Zotz 2010; Mendieta-Leiva and Zotz 2015; Tatsumi et al. 2017). Understanding the processes through which epiphyte species assemble on host trees provides a crucial step toward developing effective conservation strategies and preserving the functional roles epiphytes play in forest ecosystems (Ellis 2012). Notably, the characteristics of barks have been recognized as a key determinant of epiphyte community structure (Callaway et al. 2002; Wyse and Burns 2011; Mendieta-Leiva and Zotz 2015). However, despite extensive research describing the composition and distribution patterns of epiphytes on various barks, comparatively little is known about how bark traits modulate the relative importance of assembly processes (e.g., abiotic filtering or biotic interactions) driving such patterns (Spicer and Woods 2022).

Phylogenetic diversity has been widely employed to account for evolutionary and ecological relatedness among species within a community. In particular, the sign and magnitude of phylogenetic diversity deviating from null expectations have commonly served as proxies representing the relative strengths of different assembly processes (Webb et al. 2002; Cavender-Bares et al. 2004; Gerhold et al. 2015). Under evolutionary niche conservatism, phylogenetic diversity lower or higher than expected by chance, referred to as phylogenetic clustering and overdispersion, respectively, has been interpreted as indicative of abiotic and biotic assembly (Webb 2000; Webb et al. 2002). In combination with demonstrable environmental gradients, phylogenetic diversity can provide insights into ecological processes through which species assemble into communities (Cadotte and Tucker 2017; Cadotte et al. 2019; Tatsumi et al. 2019).

For example, the acidity of barks can serve as a gradient determining the environmental harshness for epiphytes (Mitchell et al. 2021). Abiotic filtering can thus become more pronounced on barks with lower pH, resulting in phylogenetic clustering of communities under niche conservatism and overdispersion under convergent evolution (Webb 2000; Webb et al. 2002). On the other hand, the significance of biotic interactions often increase with resource availability (Briones et al. 1998). Therefore, on barks that can retain resources such as water (Zamfir and Goldberg 2000), competitive exclusion among closely related species may become a dominant assembly process, leading to phylogenetic overdispersion under niche conservatism (Webb 2000; Cavender-Bares et al. 2004; Cadotte et al. 2019).

Here, we explore community assembly of epiphytic bryophytes on barks. Specifically, we analyze phylogenetic diversity of mosses and liverworts, which

constitute two major clades of bryophytes, on multiple tree species that represent gradients of bark traits in a temperate forest. Using null models, we test whether communities show tendency toward phylogenetic clustering or overdispersion along the gradients. Based on the phylogenetic community structure observed, we infer underlying assembly processes and their links to bark traits.

Methods

Study site and tree species

This study was conducted in the Ashiu Forest Research Station of the Kyoto University, western Japan (4186 ha; 35.3° N, 135.8° E; 355 to 959 m elevation) (Fig. S1). The study site is covered by primary forests and part of it is designated as a National Bryophyte Heritage Site of Japan for the rich bryophyte flora. The study site is located in a warm- and cool-temperate ecotone dominated by an evergreen conifer *Cryptomeria japonica* and deciduous broadleaves including *Aesculus turbinata*, *Fagus crenata*, and *Quercus crispula*. The mean monthly temperature ranges from −0.4°C in January to 24.0°C in August. The mean annual precipitation is 2568 mm.

We selected 10 tree species for our study: *Acer pictum* subsp. *mono*, *Acer sieboldianum*, *Aesculus turbinata*, *Betula grossa*, *Castanea crenata*, *Clethra barbinervis*, *Cryptomeria japonica*, *Fagus crenata*, *Quercus crispula*, and *Quercus serrata*. These species were selected to cover a large variety of bark traits as possible. For each tree species, we surveyed bryophyte communities on 15 trees, totalling 150 trees, in six plots distributed across the study area (Fig. S1). The surveyed trees were selected in such a way that most tree species had similar levels of variation in tree sizes (except for *A. sieboldianum* and *C. barbinervis* which are shrub species; Fig. S2) and among-individual geographical distances (Fig. S1). We selected trees in closed-canopy stands that were at least ~20 m away from the nearest forest edge to minimize the potential variation in light environment. We measured the diameters at breast height (DBH) of the trees using diameter tapes.

Bryophyte survey and diversity

In October 2016, we surveyed epiphytic bryophytes in four 10-cm wide, 200-cm high quadrats positioned at the cardinal directions of each tree, totalling 8000 cm^2 per tree. We recorded the presence or absence of bryophyte species on each tree. Species were identified in the field or in the laboratory under a microscope. To prevent epigeic species from being included, the quadrats were placed approximately 5–30 cm above the

ground surface, depending on the inclination of stems and slopes. We used quadrats with a fixed size so that bryophyte diversity would be comparable among trees of different sizes, without being affected by variation in the survey area *per se*. All trees were surveyed at their cardinal directions to keep the possible influences of aspect consistent.

A bryophyte phylogeny was reconstructed based on three chloroplast genes (*rbc*L, *rps*4, and *trn*L-F), which are commonly used in bryophyte phylogenetics (Stech and Quandt 2010). See Supplementary text 1 for details on phylogeny reconstruction.

We quantified phylogenetic diversity of bryophyte communities using mean pairwise distance (MPD) (Webb 2000). We calculated the standardized effect size of MPD, referred to as net relatedness index (NRI), based on null modelling (Webb et al. 2002). The NRI was defined as $-1 \cdot (x - \mu_{\text{null}})/\sigma_{\text{null}}$, where x is the observed MPD, μ_{null} is the mean MPD of a null distribution, and σ_{null} is the standard deviation of a null distribution (Webb et al. 2002). The null distributions were generated based on 999 iterations of presence-absence randomizations across 150 communities using the independent swap algorithm (Gotelli 2000). Randomizations were conducted separately for mosses and liverworts. To examine for possible effects of tree sizes on bryophyte community structure, we compared models with and without DBH as an explanatory variable.

Bark traits

For each of the 10 tree species, we measured bark roughness, water holding capacity, pH, and inorganic nitrogen content. These traits were selected based on previous research that has shown their associations with epiphyte community structure (Gustafsson and Eriksson, 1995; reviewed by Ellis, 2012). We measured each trait on three trees per species and used the mean value for statistical analyses. See Supplementary text 2 for details of the measurement methods and Table S1 for the observed bark trait values. To account for correlations between some pairs of traits (Table S2), we performed a principal component analysis to derive composite measures of bark traits.

Regression analyses

We tested the changes in bryophyte species richness along bark trait gradients using generalized linear mixed models with a Poisson error distribution and a log-link function. Changes in MPD were tested using log-normal linear mixed models. Changes in NRI were tested using linear mixed models. We included ‘plots’ as a random variable in all

models. We used R 4.3.0 (R Core Team 2023) for all statistical analyses.

Results and Discussion

We observed a total of 56 moss and 35 liverwort species on 150 trees, with 1016 occurrences of mosses and 515 occurrences of liverworts (Fig. 1). Regarding bark traits, more than half of the variation was captured by the first principal component (PC 1) (Fig. 2). Bark roughness and pH showed a negative correlation (Table S2), likely due to the tendency for rougher barks to capture more atmospheric materials, resulting in increased acidity (Oka et al. 2021). The PC 1 represented a composite gradient of bark roughness, pH, and water holding capacity (Fig. 2, Table S3), along which we found significant changes in species richness of mosses (Figs. 3a, S3). This result may reflect the impact of bark acidity (ranging from pH 4.16 to 6.18; Table S1), which often reduce germination and growth rates of mosses (Löbel and Rydin 2010), thereby leading to a decrease in species richness (Kaufmann et al. 2019; Mitchell et al. 2021).

The MPD and NRI of mosses increased and decreased along the PC 1 axis (Fig. 3e, 3i), respectively, suggesting changes in assembly processes. Specifically, moss communities became phylogenetically overdispersed (NRI < 0) on rough and acid barks (Figs. 3i, S3i, S3j); that is, communities became composed of species belonging to a larger variety of lineages than would be expected by chance. A possible reason for this pattern is that rough barks, which often have a greater heterogeneity of microhabitats than smooth barks (Wyse and Burns 2011; Lamit et al. 2015), allowed moss species from different lineages favouring different microhabitats to coexist. Alternatively, the observed pattern of overdispersion (Fig. 3i) may reflect independent adaptations among moss lineages to harsh environments. Convergent evolution of plants to harsh environments is a commonly observed phenomenon, including adaptations of alpine plants to high elevations (Bryant et al. 2008) and mangrove trees to salinity (Shi et al. 2005). In our study, we observed moss species from distant lineages (e.g., *Tetraphis pellucida* [order Tetraphidales], *Dicranum viride* var. *hakkodense* [Dicranales], *Brotherella complanata* [Hypnales]) on *C. japonica* trees (Fig. 1a) that have rough, acidic, and wet barks (Fig. 2). Among these bark traits, acidity (pH = 4.16 for *C. japonica*) may have acted as an environmental filter representing harshness, given the fact that many extant moss species favour neutral pH (Robinson et al. 1989).

Contrary to our expectation, we found no significant effect of water holding capacity on moss community assembly (Fig. S3k). Water often serves as key resource for which mosses compete (Zamfir and Goldberg 2000). We therefore expected biotic interactions

to intensify with increasing water availability on barks, leading to phylogenetic overdispersion (Webb 2000; Cavender-Bares et al. 2004; Cadotte et al. 2019). However, such competition-mediated assembly was not evident in our study site, possibly because it receives ample precipitation, making water a non-limiting resource regardless of bark traits. It is also worth noting that the water holding capacity only serves as a rough proxy for hydrological environment on barks. Future studies are thus needed to examine whether other hydrological variables, such as cortical runoff which quantifies stem flow in relation to tree-canopy morphology (González-Mancebo et al. 2003), can better explain the impacts of water availability on epiphytic bryophyte communities.

In contrast to mosses, liverwort communities showed decreasing MPD and a tendency toward phylogenetic clustering (NRI > 0) in relation to the increased roughness and acidity of barks (Figs. 3g, 3k, S4). According to Fiz-Palacios et al. (2011), liverworts experienced a relatively slow diversification process from the mid-Cretaceous to the early Cenozoic era, during which mosses and ferns rapidly diversified in habitats created by angiosperms (as proposed by the "shadow of angiosperms" hypothesis; Schneider et al. 2004). It is possible that liverwort species, due to this constrained niche evolution, have maintained their specific habitats over time, leading to phylogenetic niche conservatism. The combination of closely related species having similar habitat preferences and environmental filtering associated with rough and acidic barks could have contributed to the observed pattern of phylogenetic clustering (Figs. 3k, S4i, S4j). A logical next step of our study would be to test the assumption of niche conservatism based on relationships between functional traits, phylogeny, and community structure of bryophytes.

Ample evidence has shown that excess nitrogen owing to human activities (e.g., fertilization and atmospheric deposition) can reduce bryophyte richness (Oishi and Hiura 2017), both directly by posing toxic impacts and indirectly by enhancing the competitiveness of vascular plants (Turetsky 2003). In contrast, we found increasing species richness of both mosses and liverworts in response to inorganic nitrogen content (Figs. 3b, 3d, S3d, S4d). The observed pattern could be attributed to the fact that our study was conducted in a primary temperate forest where anthropogenic nitrogen inputs are kept minimal and epiphytic vascular plants are rare. In a nitrogen-limited environment with few competitors like our study site, barks with a high nitrogen content may serve as a hotspot for bryophytes. Nevertheless, it should be noted that we observed low levels of MPD on nitrogen-rich barks (Fig. 3f), indicating that only a restricted number of moss lineages could utilize such habitats.

While we identified significant relationships between bark traits and bryophyte community patterns (Fig. 3), there are still some uncertainties associated with our findings. Specifically, the absolute values of NRI that we observed were smaller than 1.96 (Fig. 3i, 3j, 3k, 3l), suggesting relatively weak signals of community assembly processes (Webb et al. 2002). Moreover, we were only able to measure bark traits at the species level, without accounting for the possible variations that derive from individual-tree characteristics (e.g., tree size) and environments (Burns and Zotz 2010; Lamit et al. 2015; Rosell 2019). In fact, some bark traits showed relatively large levels of variations among trees (Table S1). Nevertheless, we confirmed that the signs and statistical significance of the estimated relationships between bark traits and bryophyte communities remained consistent whether or not DBH was included as an explanatory variable (Table S4). Moving forward, future studies should verify the robustness of the relationships using a larger dataset than ours, while accounting for variations in barks and environmental conditions at individual-tree levels.

In this study, we found that epiphytic bryophyte communities assemble non-randomly along gradients of bark traits (Fig. 3). Our study provides an important step toward understanding how host trees, as living patches, determine epiphyte assembly processes. Trees with different bark traits respond differently to environments (Rosell and Olson 2014), implying that potential future changes in tree bark diversity under environmental change can have cascading effects on epiphytic bryophyte diversity. While our study was based on snapshot data, future research should incorporate long-term monitoring and investigate the dynamics of host trees and epiphytes over time. Doing so would provide a more comprehensive understanding of epiphyte community assembly, which is essential for informing effective strategies for their conservation in the face of changing environments.

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Authors contributions. ST conceived and led the study. All authors conducted the field survey. TO identified the bryophyte species. ST and WAA measured the bark traits. ST analyzed the data. ST wrote the manuscript with inputs from other authors.

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Data availability. The bryophyte community matrix (presence-absence of 91 bryophyte species on 150 trees), the reconstructed bryophyte phylogenetic tree (Newick format), and the bark trait data are available at FigShare (https://doi.org/10.6084/m9.figshare.23673258).

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Figures


a
Moss species
Number of occurrence
0
20
40
60
80
100
Tetraphis pellucida
Tortella japonica
Syrrhopodon japonicus
Fissidens teysmannianum
Fissidens gymnogynus
Leucobryum juniperoideum
Dicranum viride var. hakkodense
Dicranum japonicum
Dicranum hamulosum
Ulota crispa
Orthotrichum consobrinum
Pyrrhobryum spiniforme var. badakense
Trachycystis ussuriensis
Trachycystis microphylla
Rhizomnium striatulum
Mnium lycopodioides
Gemmabryum caespiticium
Plagiothecium nemorale
Plagiothecium euryphyllum
Pterigynandrum filiforme
Rhytidiastrum japonicum
Hylocomium brevistre var. cavifolium
Pylaisiadelpha tristoviridis
Pylaisiadelpha tenuirostris
Brotherella henonii
Brotherella complanata
Isothecium subdiversiforme
Homalothecium laevisetum
Myuroclada maximowiczii
Sciuro-hypnum plumosum
Sciuro-hypnum brotheri
Brachythecium buchananii
Taxiphyllum aomoriense
Gollania ruginosa
Ctenidium capillifolium
Platygyrium repens
Callicladium haldanianum
Schwetschkeopsis fabronia
Schwetschkea laxa
Neckera humilis
Thamnobryum subseriatum
Homalia trichomanoides
Okamuraea hakoniensis
Leucodon atrovirens
Forsstroemia japonica
Forsstroemia cryphaeoides
Dolichomitriopsis diversiformis
Dolichomitra cymbifolia
Fauriella tenuis
Thuidium cymbifolium
Boulaya mittenii
Anomodon thraustus
Anomodon pseudo-tristis
Anomodon tristis
Anomodon minor var. integerrimus
Anomodon giraldii
50 Myr
Tree species
Acer pictum
Acer sieboldianum
Aesculus turbinate
Quercus crispula
Quercus serrata
Fagus crenata
Castanea crenata
Betula grossa
Clethra barbinervis
Cryptomeria japonica
b
Liverwort species
Number of occurrence
0
20
40
60
80
100
Metzgeria temperata
Trichocoleopsis sacculata
Mylia verrucosa
Syzygiella autumnalis
Lophozia subulata
Scapania ciliata
Cephaloziella spinicaulis
Odontoschisma grosseverrucosum
Odontoschisma denudatum
Schiffneria hyalina
Cephalozia otaruensis
Calypogeia tosana
Blepharostoma minus
Plagiochila sciophila
Plagiochila porelloides
Heteroscyphus planus
Chiloscyphus profundus
Chiloscyphus minor
Bazzania tridens
Bazzania denudata
Porella vernicosa
Macvicaria ulophylla
Radula oyamensis
Radula japonica
Radula constricta
Frullania tamarisci subsp. obscura
Frullania valida
Frullania muscicola
Frullania usamiensis
Frullania davurica
Nipponolejeunea pilifera
Lejeunea ulicina
Lejeunea japonica
Cololejeunea spinosa
Acrolejeunea sandvicensis
100 Myr

Figure 1. Reconstructed phylogenies and the number of occurrences of (a) mosses and (b) liverworts. Three chloroplast genes (*rbc*L, *rps*4, and *trn*L-F) were used for reconstruction.

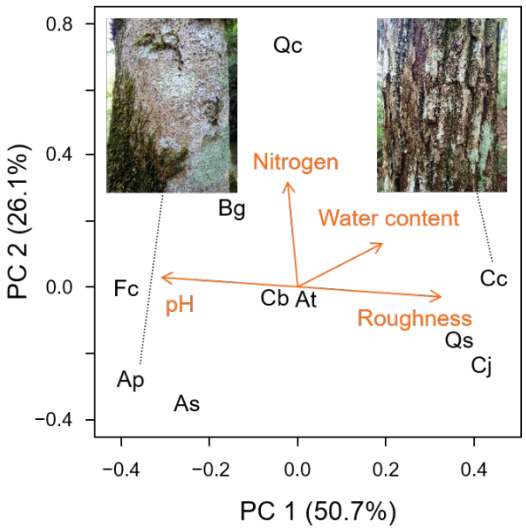

Figure 2. Ordination plot of tree bark traits. Values in parentheses indicate the proportion of variation explained by the first and second principal components (PC). Ap = *Acer pictum* subsp. *mono*, As = *Acer sieboldianum*, At = *Aesculus turbinata*, Bg = *Betula grossa*, Cc = *Castanea crenata*, Cb = *Clethra barbinervis*, Cj = *Cryptomeria japonica*, Fc = *Fagus crenata*, Qc = *Quercus crispula*, and Qs = *Quercus serrata*. The pictures show barks of Ap and Cc as examples with contrasting barks.

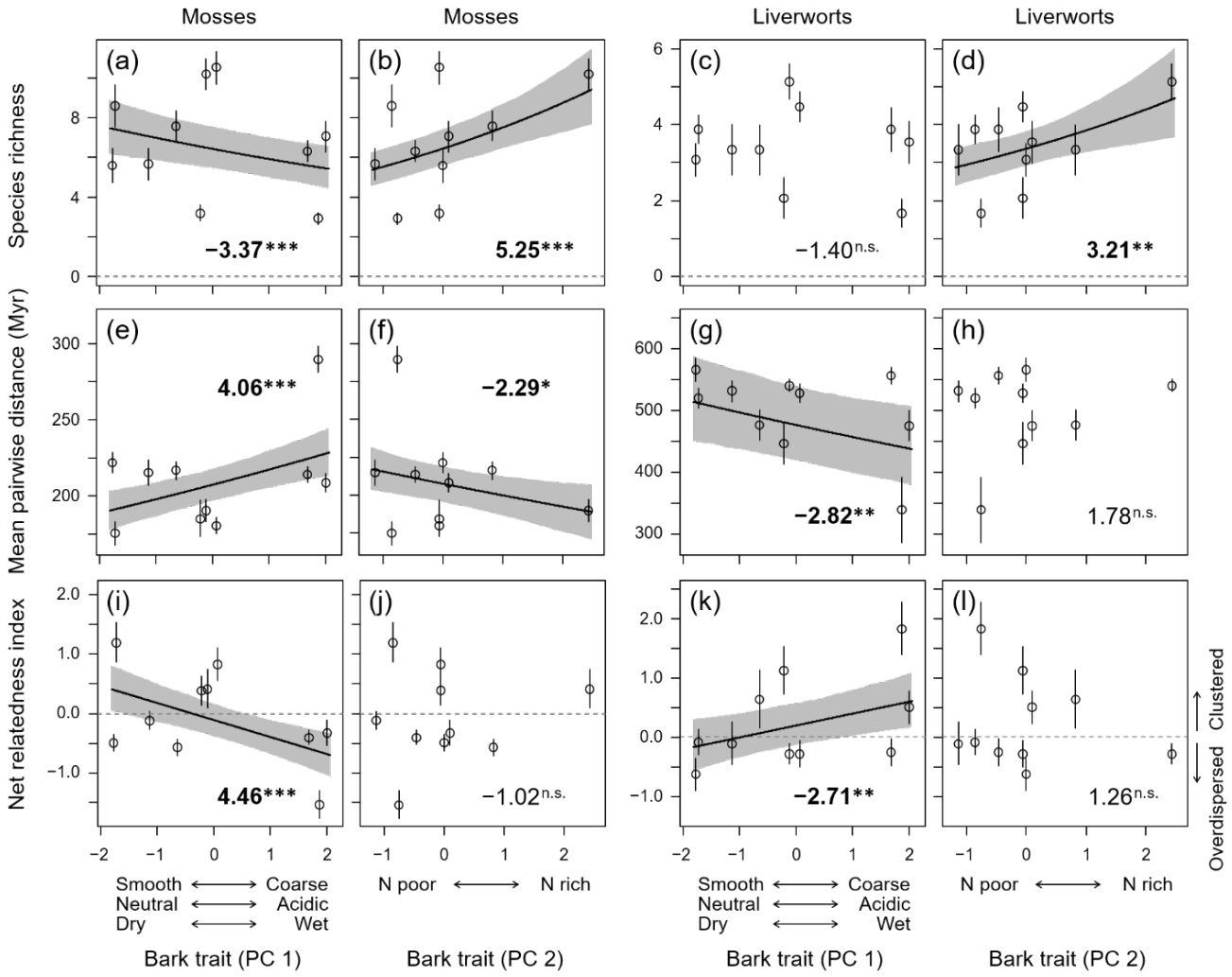

Figure 3. Changes in bryophyte diversity along bark trait gradients. (a, b, c, d) Species richness, **(e, f, g, h)** mean phylogenetic diversity, and **(i, j, k, l)** net relatedness indices of mosses and liverworts along the first and second principal components (PC 1 and PC 2) of bark traits. Circles and vertical bars represent the mean and standard errors for each tree species (n = 15 trees surveyed for each of 10 tree species, totalling n = 150). Lines show fitted models with significant slopes ($P < 0.05$). Grey areas represent 95% confidence intervals of the fitted models. The values in each panel indicate the z-statistics of the slope of the fitted model. Significance: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; not significant (n.s.), $P \geq 0.05$.