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Tree hollows can affect epiphyte species composition

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Abstract Tree hollows often harbor animals and microorganisms, thereby storing nutritive resources derived from their biological activities. The outflows from tree hollows can create unique microenvironments, which may affect communities of epiphytic organisms on trunk surfaces below the hollows. In this study, we tested whether the species richness and composition of epiphytic bryophytes (liverworts and mosses) and lichens differ above and below tree hollows of *Aria japonica* and *Cercidiphyllum japonicum* in a Japanese temperate forest. The species richness of epiphytic bryophytes and lichens did not differ above and below hollows; however, the species composition of bryophytes differed significantly above and below hollows. Indicator species analyses showed that the moss species *Anomodon tristis* and the

liverwort species *Porella vernicosa* were significantly more common below than above hollows, while the liverwort species *Radula japonica* and four lichen species, including *Leptogium cyanescens*, occurred more frequently above than below hollows. Our results highlight that tree hollows can produce unique microenvironments on trunk surfaces that potentially contribute to the maintenance of epiphytic diversity on a local scale.

Keywords Biodiversity · Cryptogams · Bryophytes · Lichens · Tree cavities

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Introduction

Epiphytes contribute considerably to biodiversity and play important functions in many forest ecosystems (Ellis 2012; Ellis et al. 2015). For example, epiphytes serve as forage, habitat, and nesting materials for animals (Sillett 1994; Seaward 2008) and can alter the quality and quantity of stemflow (Van Stan and Pypker 2015). Covariance between the species compositions of epiphytes and of higher trophic groups (e.g., arthropods) has been previously reported (Lamit et al. 2015), suggesting that the loss of epiphytic diversity can have bottom-up cascading effects. Understanding the mechanisms underlying the maintenance of epiphytic diversity on a local scale could provide important insights into biodiversity and the functioning of forest ecosystems.

Trees, as living substrates, greatly impact epiphytic organisms. Epiphytic communities are strongly affected by host tree characteristics, such as species identities and ages (Barkman 1958; Johansson et al. 2007; Brunet et al. 2010; Thor et al. 2010; Mežaka et al. 2012), by the environments surrounding the host trees (e.g., forest interior/edge, patch size, and canopy cover; Oishi 2009; Quin et al. 2015), and by management practices that alter those environments (reviewed in Brunet et al. 2010). There is also a within-tree compositional turnover that is derived from a number of factors, such as tree height (de Oliveira and ter Steege 2015), substrate types

(e.g., stems and branches; Woods et al. 2015; Zhao et al. 2015), aspects (Barkman 1958), and exposure to rain-water (Ranius et al. 2008). Additionally, epiphytes can be affected by animals and fungi. For example, arboreal mammals can prune epiphytes on tree limbs (Perry 1978), and molds can affect them by altering bark pH levels (Fritz and Heilmann-Clausen 2010). Yet, in contrast to the direct influences of host trees as living substrates, limited studies have focused on the indirect effects of tree attributes on epiphytes mediated by other groups of organisms.

Tree hollows are one possible tree attribute that can exert indirect effects on epiphytic communities. Hollows of trees are hotspots of biological activities, such as animal breeding (Derraik and Heath 2010) and defecation (Voigt et al. 2015). Hollows also store plant litter and arboreal soils, which harbor a variety of organisms (Dickinson and Tanner 1978; Nadkarni and Matelson 1991). Nutrient-containing deposits are decomposed by microbes and exude from hollows. Such nutrient-dense outflows from tree hollows have been hypothesized to fertilize tree bases well enough to increase the trees' fitness (Janzen 1976). Here, we hypothesized that the epiphytic communities would differ above and below tree hollows through possible differences in microenvironments (e.g., nutrients and moisture levels). We tested this hypothesis by comparing the species richness and composition of epiphytic cryptogams between above and below the hollows of living trees (Fig. 1) in a Japanese temperate forest.

Materials and methods

Study site

This study was conducted in the Utsunomiya University Forest in Nikko, central Japan (36°48'31"–36°48'29"N, 139°28'05"–139°29'27"E; altitude 1500–1970 m; Tadakara et al. 2014). The study site is located inside the Nikko National Park. The site is mainly covered by temperate deciduous forests, which are dominated by broad-leaved species, such as *Quercus crispula* Blume and *Betula ermanii* Cham. The mean annual temperature and precipitation during 2002–2011 were 7.1 °C and 2,102 mm, respectively (Tadakara et al. 2014). The forest had not undergone harvesting for at least four decades prior to the survey.

Community data

In September and October 2015, we investigated epiphytic bryophytes (liverworts and mosses) and lichens on hollow-bearing individuals of two deciduous tree species, *Aria japonica* Decne. and *Cercidiphyllum japonicum* Siebold & Zucc. These tree species were suitable because some of them had hollows and were

inhabited by a wealth of epiphytes in our study site. Additionally, these tree species are native to Japan, which made it particularly interesting to study their epiphytic communities. Our study included 11 hollows from nine trees: six *A. japonica* trees, consisting of five individuals with one hollow each and one individual with two hollows, and three *C. japonicum* trees, consisting of two individuals with one hollow each and one individual with two hollows. The trees were ca. 12.4–22.0 m tall and the heights of the hollows from the ground were 0.7–11.1 m. The opening areas of the hollows were used as an index of the hollows' size. The lengths and widths of the hollows were measured to the nearest 0.5 cm, and then the area was calculated by approximating the shape of the opening using an ellipse (Fig. 1). Detailed data on the trees and hollows are listed in Table S1. When we conducted the survey, the tree hollows were inhabited by neither mammals nor birds; however, a remaining bird nest was found in one hollow (Hollow no. 10; Table S1). Insects, such as an unidentified species of click beetles (Coleoptera: Elateridae) and a tineid moth species (Lepidoptera: Tineidae), were found in the litter inside some of the hollows.

Three consecutive 10-cm-high and 20-cm-wide quadrates were vertically established on the tree trunk above and below the hollows (Fig. 1). Bryophyte and lichen samples in each quadrate were collected by removing small bark samples off the trunk surface using a knife. The samples were brought back to the laboratory and identified based on their morphologies. A total of 66 quadrats (11 hollows × 6 quadrats) were investigated, and a species assemblage within each quadrate was defined as a community. The nomenclatures for bryophytes and lichens followed those of Iwatsuki (2001) and Kurokawa and Kashiwadani (2006), respectively. The observed bryophytes and lichens are listed in Tables S2 and S3, respectively. Reference materials of the lichens were deposited in the Museum of Evolution Herbarium in Uppsala, Sweden, owing to the possible inclusion of species new to science or to Japan. Those of bryophytes were not deposited because they did not include species new to science or to Japan.

The single rope technique (Ter Steege and Cornelissen 1988; Coffey and Andersen 2012) was used to access and collect the bryophyte and lichen samples because most of the hollows, except one, were positioned high in the trees. This technique was determined to be the most adequate method in terms of minimizing tree damage. However, the method has practical difficulties, in terms of physical effort, and safety issues (Anderson et al. 2015). Thus, sample collectors were limited to investigators with climbing skills, but the collectors were not the investigators who conducted the species identifications. Because of this, the community data was collected on a presence/absence basis only, and some samples could not be identified at the species level.

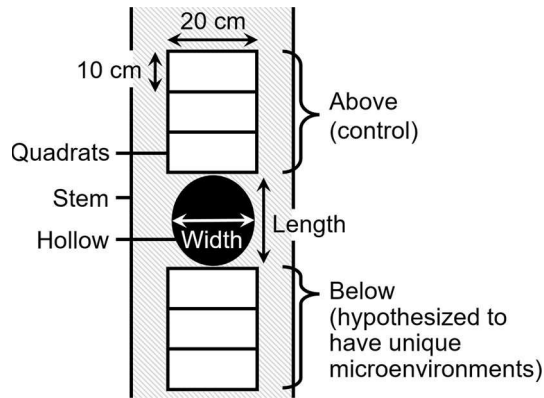


Fig. 1 Schematic representation of the sampling design

Statistical analyses

Generalized linear mixed models (GLMMs) were used to test the effects of the quadrats' position (either above or below the hollow) and the tree species on the species richness of epiphytes. Although our main interest was to test the difference between above and below the hollows, 'tree species' was included as a fixed effect in the models because it is known to affect epiphytic species richness and community composition in many cases (e.g., Thor et al. 2010; Ellis 2012). 'Hollow ID' was incorporated as a random effect to account for possible environmental variations driven by the location, height, and size of the tree (Table S1). We used a Poisson distribution with a log-link function because species richness (i.e., the number of species) is a count variable.

Sørensen and Raup–Crick indices (Chase et al. 2011), which are dissimilarity measures for presence/absence data, were used to quantify the compositional dissimilarity. We used two indices to confirm the robustness of our results. We selected the Sørensen index because it is among the most widely used dissimilarity measure (Anderson et al. 2011) and the Raup–Crick index to confirm that the dissimilarity was not driven simply by the variation in the alpha diversity among the quadrats (Chase et al. 2011). Two quadrats where bryophytes were absent were removed for the analyses of the bryophyte species composition. The communities were ordinated using non-metric multidimensional scaling (NMDS).

The effects of the quadrats' position (below or above hollows) and tree species on the epiphytic composition were tested using a two-way permutational multivariate analysis of variance (PERMANOVA). We conducted a PERMANOVA with and without 'hollow ID' being incorporated as a random effect. When the random effect was included, the statistical significance levels of the variables were estimated under the constraint that permutations occurred only among the six quadrats above and below each hollow. This allowed us to account for pseudoreplication in our hierarchical sampling design. The case without the random effect was tested as well because *hollow* was a subclass of *individual trees* and *tree*

species in our sampling design. Thus, including 'hollow ID' as a random effect had a possibility of masking the real influence of the tree species. We also tested the effects of hollow size, heights of the hollows from the ground, and distances of quadrats from the hollow (10, 20, and 30) on epiphytic composition by fitting the vectors onto the NMDS ordination.

Indicator species analyses were conducted to assess the strengths and statistical significances of the relationships between species and quadrats' positions. The analyses were conducted using data of bryophytes and lichens from the same quadrat treated both separately and together. We used R 3.2.2 (R Core Team 2015) for all of the analyses. The 'lme4' (Bates et al. 2015), 'vegan' (Oksanen et al. 2016), and 'indicpecies' (Cáceres and Legendre 2009) packages were used for the GLMM, the NMDS and PERMANOVA, and the indicator species analyses, respectively.

Results

A total of 25 bryophyte and 71 lichen species were observed in the 66 200-cm² quadrats (Fig. 2). The total numbers of observations were 286 for bryophytes and 550 for lichens. The mean numbers of bryophyte species per quadrat were 5.0 (± 1.3 SD) on *A. japonica* and 3.2 (± 2.1 SD) on *C. japonicum*. The mean numbers of lichen species per quadrat were 9.1 (± 3.2 SD) on *A. japonica* and 6.9 (± 2.6 SD) on *C. japonicum*. The species

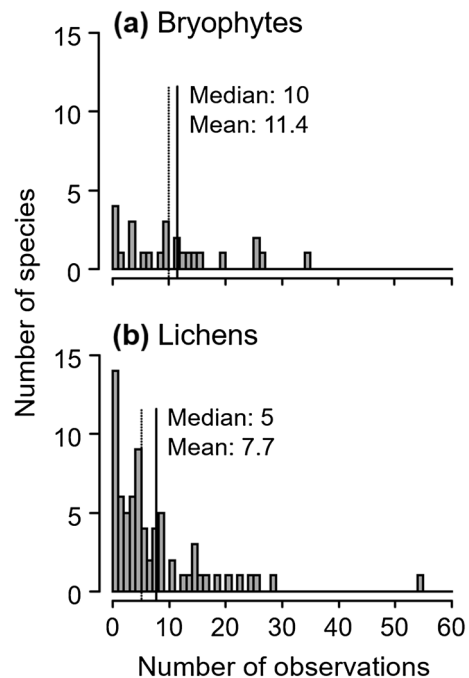


Fig. 2 Number of species for each of the numbers of observations, for **a** bryophytes and **b** lichens. The *x*-axis represents the number of quadrats in which a given species was observed out of 66 studied quadrats. The vertical dashed lines and solid lines indicate the medians and means of the distributions, respectively

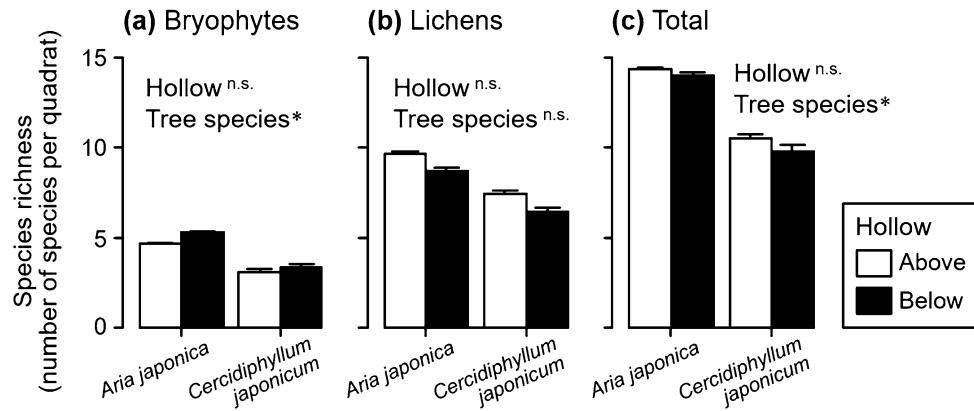


Fig. 3 Species richness of **a** bryophytes, **b** lichens, and **c** their totals. Generalized linear mixed models were used to test the effects of the quadrats' position (*above* or *below* hollows) and tree species on species richness. * $P < 0.05$; *n.s.* not significant

richness of epiphytes did not differ above and below hollows when bryophytes and lichens were analyzed separately nor when they were analyzed together (Fig. 3).

The PERMANOVA revealed that the species composition above and below hollows was significantly different for bryophytes but not for lichens, nor when bryophytes and lichens were analyzed together (Table 1). Because the two dissimilarity indices yielded similar results, those based on the Raup–Crick index are not shown. The species compositions of both bryophytes and lichens were significantly different between the two tree species when 'hollow ID' was incorporated as a random effect (Table 1). Differences were not detected when 'hollow ID' was included as a random effect (Table 1), likely because the permutation was constrained to occur only among the six quadrats above and below each hollow. The height of the hollow from the ground had a significant effect on species composition ($P < 0.001$, Fig. 4). The effects of hollow size and the distance of quadrats from the hollow were not significant ($P \geq 0.05$). The compositional dissimilarity levels above and below hollows, as well as between the two tree species, were mainly reflected along the first axis of the NMDS ordination (Fig. 4). The variation along the second axis roughly paralleled the difference in the heights of the hollows.

The indicator species analyses showed that the moss species *Anomodon tristis* (Ces.) Sull. and the liverwort

species *Porella vernicosa* Lindb. were more common below than above hollows, while the liverwort species *Radula japonica* Gottsche ex Steph. was less common below than above hollows (Table 2). Four lichen species, *Leptogium cyanescens* (Rabh.) Körb., *Melaspilea* sp., *Parmelia laevior* Nyl., and *Pertusaria* sp. 1, were less common below than above hollows (Table 2).

Discussion

The species composition of epiphytic bryophytes differed above and below tree hollows in our study site (Table 1). The compositional dissimilarities above and below hollows, as well as between the two tree species, were reflected mainly along the first axis of the NMDS ordination (Fig. 4). The variation along the second axis was mostly explained by the difference in the heights of the hollows. Both bryophytes (de Oliveira and ter Steege 2015) and lichens (Komposch and Hafellner 2000; Ranius et al. 2008) undergo vertical compositional turnover along tree heights. Such turnover is often explained by the gradient in microenvironments (e.g., light, temperature, and humidity; Sporn et al. 2010, de Oliveira and ter Steege 2015) and/or bark traits (e.g., bark crevice depth; Ranius et al. 2008). The variation along the second axis of our NMDS ordination may also be attributed to such changes in the environment that are associated with height.

Table 1 Effects of the quadrats' position (above or below hollows) and tree species on the dissimilarity of species composition (Sørensen index) of bryophytes and lichens tested by permutational multivariate analysis of variance

	Bryophytes				Lichens				Total			
	<i>F</i> static	<i>R</i> ²	<i>P</i> value ^a	<i>P</i> value ^b	<i>F</i> static	<i>R</i> ²	<i>P</i> value ^a	<i>P</i> value ^b	<i>F</i> static	<i>R</i> ²	<i>P</i> value ^a	<i>P</i> value ^b
Above/below hollows	2.335	0.028	0.003	0.045	0.223	0.003	0.874	0.989	0.979	0.012	0.057	0.433
Tree species	19.746	0.238	0.304	<0.001	18.567	0.227	0.874	<0.001	20.653	0.244	0.057	<0.001
Total		0.266			0.230				0.256			

Variables with $P < 0.05$ are indicated by boldface

^a*P* values when 'hollow ID' was included as a random effect

^b*P* values when 'hollow ID' was not included as a random effect

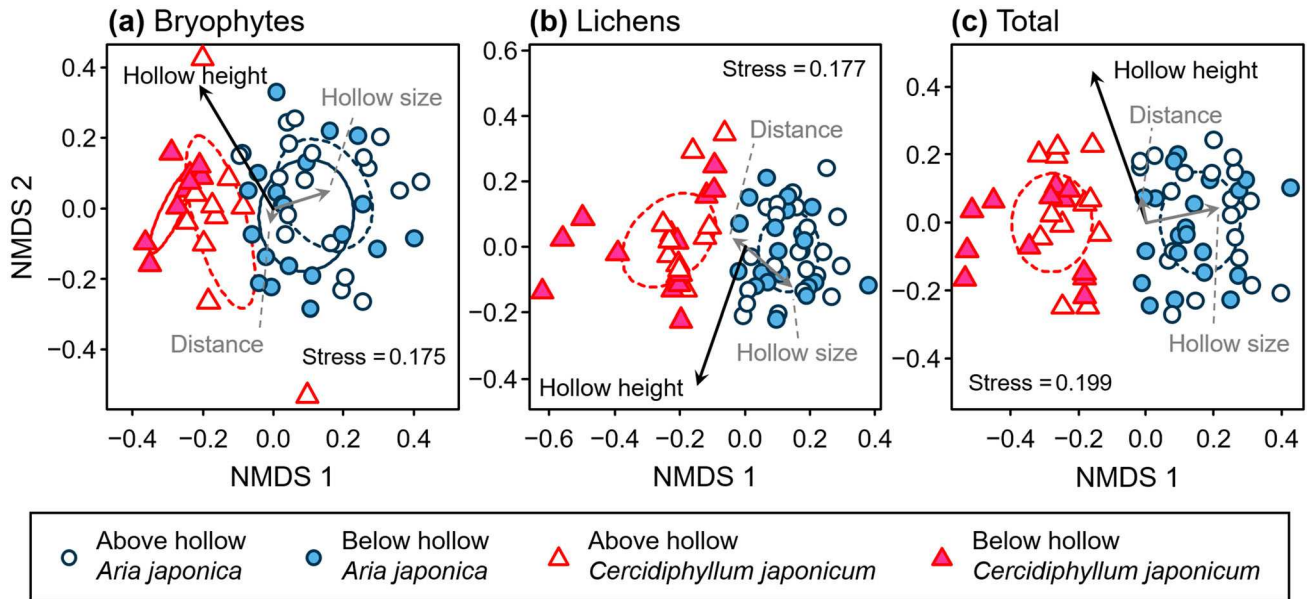


Fig. 4 Ordination of communities based on non-metric multidimensional scaling (NMDS) for **a** bryophytes, **b** lichens, and **c** their totals. The Sørensen index was used to quantify the dissimilarity of species composition. Dispersion ellipses were drawn using $1 \times \text{SD}$ of point scores. The ellipses were drawn for each set of communities with different explanatory variables that had statistically significant effects (see Table 1). For bryophytes, which were significantly affected by both 'position of quadrats' and 'tree species', ellipses were drawn with dashed and solid lines representing

above and below hollows, respectively, and with different colors representing different tree species. For lichens and combined cases, which were only significantly affected by 'tree species', ellipses were drawn with different colors representing different tree species. Arrows represent the effects of hollow size, height of the hollows from the ground ('Hollow height'), and distances of quadrats from the hollow ('Distance') on epiphytic composition. Black and grey arrows indicate significant and insignificant effects, respectively

Some bryophyte and lichen species occurred more frequently either above or below the hollows (Table 2), likely reflecting the species' preferences for microhabitats. For example, *A. tristis* is a moss species known to favor wet substrates (Wilson 1933). Thus, this species being selected as a below-hollow indicator (Table 2) may be attributed to the possible outflow from hollows and the resultant moist microenvironment (although further examination is needed because most cyanolichens, to which the above-hollow indicator lichen *L. cyanescens* belongs, need liquid water to activate photosynthesis and prefer dampness; Lange et al. 1993). Additionally, an experiment using *Radula flaccida* Lindenb. & Gottsche, a congeneric liverwort species of the above-hollow indicator liverwort *R. japonica* (Table 2), found that *R. flaccida* grows faster under lower inorganic mineral conditions than higher conditions (Olarinmoye

1975). Assuming that the two congeneric species have a similar niche, *R. japonica* may also prefer the above-hollow, nutrient-poor conditions. However, this is speculation, and a more detailed study on the associations between species distributions and hollow-driven microenvironments is required.

In this study, we illustrated part of the high level of epiphytic diversity, especially that of lichens, in the Nikko National Park. We observed 71 lichen species in a relatively small area ($66 \times 200\text{-cm}^2$ quadrats), indicating high species richness compared with nearby sites (e.g., 68 species in the whole Tsukuba Mountain range in the same Kanto region; Nakajima 1968). The mean numbers of lichen species (alpha diversity) in the 200-cm^2 quadrat on *A. japonica* and *C. japonicum* were 9.1 and 6.9 species, respectively. More than half, 40 out of the 71 species, only occurred in ≤ 5 quadrats, indicating that

Table 2 Bryophyte and lichen species that significantly preferred areas either above or below hollows on two tree species determined by Pearson's ϕ coefficient of association

	<i>Aria japonica</i>		<i>Cercidiphyllum japonicum</i>	
	Above	Below	Above	Below
Bryophytes	<i>Radula japonica</i> (0.39*)	<i>Anomodon tristis</i> (0.39*)	–	<i>Porella vernicosa</i> (0.36*)
Lichens	<i>Melaspilea</i> sp. (0.39*) <i>Parmelia laevior</i> (0.37*)	–	<i>Leptogium cyanescens</i> (0.60**) <i>Pertusaria</i> sp. 1 (0.43*)	–

The numbers in parentheses indicate the estimated values of the ϕ coefficient

* $P < 0.05$, ** $P < 0.01$

spatial turnover (beta diversity) was high as well (Fig. 2b). While the indicator species analyses revealed that some lichen species were indeed affected by hollows (Table 2), no significant sign of overall dissimilarity was detected between areas above and below hollows (Table 1; Fig. 4b). The high number of rare species and rapid spatial turnover, as well as the relatively small number of samples (11 hollows \times 6 quadrats), may have made it difficult to discern a dissimilarity pattern for lichens. We expect that the accumulation of further data will allow us to gain a better picture of epiphytic diversity in the Nikko National Park.

Our research serves as a pilot study, showing that tree hollows can affect epiphytic communities by creating unique microhabitats. There are several issues yet to be addressed before the findings from this study can be generalized. Notably, our study was based on observations of epiphytes alone. Additional studies measuring the chemical (e.g., bark pH and nutrient content), hydrological (e.g., water flow), and physical (e.g., bark density and roughness) environments are needed. Fritz and Heilmann-Clausen (2010) found that the bark pH levels below rot hollows tend to be high because of the downward influence of wood mold. For nutrients, their amounts and types may largely depend on the organisms that use the hollows. For example, many cavity nesters perform nest sanitation (e.g., Gow et al. 2015), indicating that the effects of nesting on epiphytes can be limited in some cases. Additionally, while we used the single rope technique in this study, the use of other canopy-access methods (e.g. tower crane; Komposch and Hafellner 2000) could increase the sampling efficiency. Careful measurements of environments and increases in the sample size may help us to further investigate the differences among species and between groups (i.e., bryophytes and lichens) in their responses to the hollow-derived microenvironments.

Conclusions

We found that the species composition of epiphytic bryophytes differs above and below tree hollows in our study site (Table 1; Fig. 4). Some bryophyte and lichen species occurred more frequently either above or below hollows (Table 2). Tree hollows are hotspots of biological activities, such as animal defecation, and the decomposition of organic matter deposited in the hollow (Nadkarni and Matelson 1991; Derraik and Heath 2010; Voigt et al. 2015). The possible outflow from hollows may have created unique microenvironments below them, which in turn led to the difference in the epiphytic composition above and below hollows. If such links are true, then trees with hollows and the organisms that use them could have considerable importance in maintaining epiphytic diversity on a local scale.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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