

# Epiphyte community development throughout tree ontogeny: an island ontogeny framework

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#### Keywords

Darwin: New Zealand; Epiphyte community development; Island ontogeny; Tree ontogeny

#### Nomenclature

Allan (1961), Moore & Edgar (1976), de Laubenfels (1978)

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## Abstract

**Aim:** Epiphytes are a conspicuous feature of numerous forests, yet they are poorly understood compared with terrestrial plants. Theoretical frameworks have helped bridge this gap; however, important questions relating to epiphyte community development have yet to be answered. For example, at what point in tree ontogeny do epiphytes first establish? Do epiphyte communities develop uniformly, or is there variation among host trees?

**Methods:** In this study, we build upon Darwin's geological theory of island ontogeny to explore changes in epiphyte species richness throughout the life span of their respective host trees. Based on the general features of island ontogeny, we predict that there are three stages of epiphyte community development: (i) an initial stage where host trees are devoid of epiphytes because they lack sufficient architectural and physiological characteristics suitable for epiphyte establishment, (ii) a second stage where trees acquire epiphytes as adults and continue to do so into maturity, and (iii) a final stage where epiphyte communities progress through a period of species decline following host tree mortality. To test our model predictions, we censused epiphyte communities on 371 host trees from six New Zealand tree species. We first assessed the relationship between epiphyte species richness and host tree diameter. We then tested whether relationships between epiphyte species.

**Results and conclusion:** Results were consistent with model predictions. Our investigation found variation in the ontogenetic stage at which host trees become favourable for epiphyte establishment. Moreover, the rate at which epiphyte species richness increased with host tree diameter varied among host species. Our findings indicate that an island ontogeny framework is useful for guiding investigations on epiphyte community development.

## Introduction

Approximately 10% of the world's vascular flora live nonparasitically on other plants, typically trees (Benzing 1990). These epiphytic plants contribute significantly to local species diversity, and can represent up to 35% (Gentry & Dodson 1987) or even 50% (Kelly et al. 2004) of all vascular flora. Despite being a conspicuous feature of numerous forests, patterns of epiphyte species richness are still poorly understood compared with terrestrial plants. Theoretical frameworks have helped bridge this gap; however, none have been implemented to guide investigations on epiphyte community development throughout tree ontogeny. As trees grow, their morphological and physiological characteristics change in ways that can influence epiphyte community development (Benzing 1990). These may include changes in tree architecture (Bennett 1987), bark characteristics (López-Villalobos et al. 2008), canopy soil chemistry (Gustafsson & Eriksson 1995), microclimate conditions (Sporn et al. 2010) and host tree size (Flores-Palacios & Garcia-Franco 2006). During early tree ontogeny, the simple branching architecture precludes the development of epiphyte communities (Benzing 1990). However, as trees age, epiphytes become established and undergo primary succession. Consequently, positive linear relationships between tree size and epiphyte species richness are regularly documented (Hietz-Seifert et al. 1996;

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Burns & Dawson 2005; Flores-Palacios & Garcia-Franco 2006; Hirata et al. 2008), and are analogous to the species– area relationships commonly observed between oceanic islands of varying size.

MacArthur & Wilson's (1967) theory of island biogeography (ToIB) has supported epiphyte investigations on colonization and extinction dynamics (Yeaton & Gladstone 1982; Snäll et al. 2003; Löbel et al. 2006; Laube & Zotz 2007; Burns 2008), dispersal limitations (Buckley 2011), habitat complexity (McMullin et al. 2010) and the effect of tree size (Flores-Palacios & Garcia-Franco 2006). However, the underlying assumptions of the ToIB make it less applicable to exploring changes in epiphyte species richness throughout the life span of a host tree. Trees, like oceanic islands, vary in size throughout ontogeny. Therefore, species richness is not a linear or curvilinear function of area, as predicted by the ToIB. Most importantly, the ToIB makes the implicit assumption that the area and isolation of habitat patches remains constant throughout the life span of the species they support.

Darwin's geological theory of oceanic island ontogeny, where islands are born, and islands die, may be a more appropriate guide to investigate epiphyte community development. Although Darwin is best known for his theory of evolution via natural selection, he also made significant contributions to geology. Undoubtedly, the most significant contribution is the observation that different types of islands represent a particular developmental stage ranging from very young islands, to submerged coral reefs. This geological theory of island ontogeny predicts that as islands age, inhabitable area decreases through the processes of subsidence and erosion (Darwin 1859; Fig. 1A). During this time, an island becomes colonized by dispersing species that radiate and fill all available niche space (Whittaker et al. 2008). As island area decreases, species are lost. The island life cycle is complete when an island submerges back into the ocean, leaving only a coralline ring (Darwin 1859). Thus, very young islands have no species. As islands age, species richness steadily increases. Mature islands are species-rich. Dead islands are devoid of species because they are fully submerged. This is not unlike what we would expect to occur with epiphyte species richness throughout host tree ontogeny. However, contrary to islands, inhabitable area increases with the continual expansion of the trunk and branches (Benzing 1990). Additionally, interspecific differences in host tree characteristics may cause variation in epiphyte community development.

Despite many similarilties in the dynamic and transient nature of trees and islands, there are some obvious differences to consider. While island ontogeny operates on an evolutionary time scale, trees are much shorter lived. Therefore, the adaptive radiations common on isolated islands do not occur with epiphytes on their host trees. An isolated archipelago may be thousands of miles away from the nearest population source. Consequently, the establishment of a new species may take several years. For example, a new species would only establish on the Hawiian archipelago once every 35 000 yr, prior to the arrival of humans (Loope 1998). An epiphyte, however, may establish on a host tree within 2–20 yr (Zotz & Vollrath 2003; Werner & Gradstein 2008). Additionally, the nearest population source may be just meters away. Despite these differences, trees and islands are both discrete ecological units, and both share characteristics that may explain their species–area relationships.

For example, habitat heterogeneity strongly influences species occurrence patterns on islands, and often correlates with island size (Williams 1964). The complex topography of young to middle-aged oceanic islands allows diversification of species, thus increasing species richness (Paulay 1994). As islands age and subside, area decreases synchronously with habitat heterogeneity and species richness. Conversely, as trees age habitat heterogeneity increases with the addition of new microclimates and niche space (Kernan & Fowler 1995). Microclimatic conditions are recognized as significant drivers of within-tree epiphyte distributions (Sporn et al. 2010). During tree ontogeny, microclimatic conditions change and may favour different epiphyte species through successional processes. Therefore, habitat heterogeneity of host trees, at least at a within-tree scale, may cause variation in epiphyte species richness.

In this study, we make predictions on how epiphyte communities might change during the growth, maturation and eventual death of host trees using the general principles of island ontogeny. Specifically, we predict that there are three stages of epiphyte community development: (i) an initial stage where host trees are devoid of epiphytes because they lack sufficient architectural and physiological characteristics suitable for epiphyte establishment, (ii) a second stage where trees acquire epiphytes as adults and continue to do so into maturity, and (iii) a final stage where epiphyte communities progress through a period of species decline following host tree mortality (Fig. 1B). We tested our model predictions on populations of six host tree species that are endemic to New Zealand. We first assessed the relationship between epiphyte species richness and host tree diameter. We then tested whether the relationship between epiphyte species richness and host tree diameter differs between host species. Lastly, we attempt to determine why epiphyte community development may vary between host species. We used tree diameter as an independent variable, with the assumption that larger diameters are indicative of older trees. The scaling laws of tree allometry correlate tree diameter with other characteristics, including tree height and age (Thomas



**Fig. 1.** Schematic illustrating the island ontogeny framework (**A**) with respect to epiphyte community development throughout tree ontogeny (**B**). The theory of island ontogeny predicts that as islands age, inhabitable area decreases through the processes of subsidence and erosion. Young islands initially lack species, however, species eventually become established and undergo adaptive radiation (a). Islands are at their peak species richness at maturity (b). Islands subside and inhabitable area decreases concurrently with species richness (c). The island life cycle is complete when an island submerges back into the ocean, leaving only a coralline ring (d). Our model (**B**), predicts that there are three stages of epiphyte community development: (a) an initial stage where host trees are devoid of epiphytes because they lack sufficient morphological and physiological characteristics suitable for epiphyte establishment, (b) a second stage where trees acquire epiphytes as adults and continue to do so into maturity, (c) a final stage where epiphyte communities progress through a period of species decline following host tree mortality. The dotted line represents the rate of epiphyte species decline. This line may vary depending on a number of factors (e.g. tree fall vs standing dead tree) and therefore we have kept this prediction hypothetical. The slope (*z*) represents the rate of species colonisation.

1996; Van Pelt & Nadkarni 2004; Nascimbene et al. 2008). The relationship between tree diameter and tree height is asymptotic; while tree height reaches its maximum, tree diameter may still be increasing (Niklas 1995). Tree diameter is also correlated with other tree characteristics such as bark structure, habitat complexity and tree architecture (Benzing 1981; Balfour & Bond 1993; Campbell & Newbery 1993; Lyons et al. 2000; Malizia 2003; Male & Roberts 2005).

#### Methods

#### Study site

The study was conducted in Otari-Wilton's Bush Reserve (41°14′ S, 174°45′ E), the largest area of remaining native forest on the Wellington Peninsula, located in the lower North Island of New Zealand. The reserve encompasses 96 ha of mature and regenerating coastal conifer-broadleaf forest at an altitude of 70-280 m a.s.l. Topography consists of very steep hill slopes with a Greywacke soil parent material. Soil is shallow, and ranges from stony colluvium on ridges and hill slopes to silt loam over colluvium in alleys and hollows. Rainfall normally does not exceed an average of 1240 mm per annum, and average daily temperatures range from 7 °C in winter (Jun-Aug) to 20 °C in summer (Dec-Feb) (Anonymous 1996). Approximately 150 species of flowering plants, conifers and ferns, including epiphytes and lianas, occur in this complex structured forest, similar to that of many tropical forests (Burns & Dawson 2005). The higher strata of the forest are dominated by five tree species, Beilschmiedia tawa

(Lauraceae), Dysoxylum spectabile (Meliaceae), Corynocarpus laevigatus (Corynocarpaceae), Elaeocarpus dentatus var. dentatus (Elaeocarpaceae) and Melicytus ramiflorus (Violaceae). Knightia excelsa (Proteaceae) and Laurelia novae-zelandiae (Atherospermataceae) frequently emerge above the canopy, along with scattered remnants of Dacrydium cupressinum and Prumnopitys ferruginea (Podocarpaceae; nomenclature for angiosperms and conifers follows Allan (1961); Moore & Edgar (1976); de Laubenfels (1978) for Prumnopitys; see Appendix S1 for species authorities). Twenty-two species of vascular epiphytes are commonly found in the area. The most common epiphyte, Pyrrosia eleagnifolia (Polypodiaceae), grows laterally around the trunk and branches of their hosts. Also common in the region are three additional ferns, Asplenium flaccidum, A. oblongifolium and A. polyodon, (Aspleniaceae; fern and allies nomenclature follows Brownsey & Smith-Dodsworth (2000)), four orchids Earina autumnalis, E. mucronata, Dendrobium cunninghamii and Drymoanthus adversus (Orchidaceae), and three shrub epiphytes. Pittosporum cornifolium (Pittosporaceae), Griselinia lucida (Griseliniaceae) and Metrosideros robusta (Myrtaceae) are shrub epiphytes that grow in already well-established epiphyte communities. The latter two are primary hemi-epiphytes that germinate in the canopy, eventually sending roots down to connect with the forest floor. Metrosideros robusta eventually becomes a free-standing tree once the host has died, similar to species from the genus Ficus. These shrub epiphytes frequently germinate in two nest epiphytes, Astelia solandri and Collospermum hastatum (Asteliaceae). A hanging club moss, Phlegmariurus varius (Lycopodiaceae) also germinates

in these large nests. Eight flowering shrubs in the region regularly occur as accidental epiphytes. These are Coprosma lucida, C. grandifolia (Rubiaceae), Leucopogon fasciculatus (Ericaceae), Melicytus ramiflorus (Violaceae), Myrsine australis (Primulaceae), Piper excelsum subsp. excelsum (Piperaceae), Pseudopanax arboreus (Araliaceae) and Rumohra adiantiformis (Dryopteridaceae). Filmy ferns (Hymenophyllaceae) are typically found in tropical montane forests of high humidity but also extend into temperate latitudes in areas with high rainfall (Proctor 2012). Otari Wilton's Bush Reserve has a drier climate and, as such, filmy ferns are not a conspicuous feature, although they do occur. When they occur epiphytically, they are often intertwined with liverworts and mosses or in a shrivelled, desiccated state that make them difficult to confidently identify from the ground. Because of this, we decided to omit filmy ferns from this study.

## Data collection

Sampling took place within 10 m on either side of a 0.6 km trail in the reserve. By sampling along a trail, we were able to better visually access the canopy than would be possible in off-trail plots. The total area sampled was 1.2 ha. We restricted sampling to the six most common host tree species, *B. tawa, D. cupressinum, E. dentatus, K. excelsa, M. ramiflorus* and *P. ferruginea*. We measured the DBH at 1.3 m of all target host tree species, including those without epiphytes, in order to obtain a complete size inventory of potential hosts.

The study of epiphyte communities is fraught with logistical difficulties in accessing the canopy. Consequently, either few trees are sampled (Pupulin et al. 1995; Freiberg 1996) or only the lower trunk is sampled (Tewari et al. 1985; Mehltreter et al. 2005). Burns & Dawson (2005) critically evaluated ground-based sampling and correctly identified 91.1% of all epiphyte and vine species from the ground. We employed similar, strict sampling criteria to ensure accurate inventories of vascular epiphytes from ground-based surveying. First, all trees within the study area were examined for vascular epiphytes by two people using high-powered binoculars. Only host trees that could be accurately viewed from the ground were considered. Six host trees were omitted from the study as visual access into their crowns was unsatisfactory. Host trees were extensively searched by each person at four different locations making sure each branch and area of the trunk was surveyed. Each location around each host tree was repeatedly visited until we could both traverse around the host tree without locating another epiphyte. An additional, unimpeded view of 30 host trees was obtained from two raised viewing platforms in the reserve and a 60-m canopy walkway.

Our third prediction of epiphyte community development states that epiphyte species richness should decline following host tree mortality. However, this rate of decline is likely to vary. For example, a tree fall may wipe out an entire epiphyte community (Snäll et al. 2003). Conversely, epiphyte communities that remain on an upright deceased or diseased tree, may persist for a lengthy period of time. As such, we did not sample epiphyte communities on dead or dying host trees, and kept this prediction hypothetical.

#### Analysis

We tested model predictions by first comparing linear with breakpoint regression models. The simple linear regression model, in the log-linear form is:

$$\log S_i = \log C + z \log A_i + e_i$$

where *S* is the number of species, *A* is island area, *C* and *z* are fitted constants and *e* is the normally-distributed additive error. The breakpoint regression model, where there is only one breakpoint, can be written as:

 $\log S_i = \log C + z_1 \log A_i + e_i \quad \text{for } \log A_i \le \alpha$  $\log S_i = \log C + z_1 \log A_i + z_2 (\log A_i - \alpha) + e_i \quad \text{for } \log A_i > \alpha$ 

where  $\alpha$  is the breakpoint, and the regression slopes are  $z_1$ and  $z_1 + z_2$ . We compared the relative fit of each model using Akaike's information criterion corrected for finite sample sizes (AIC<sub>c</sub>). This second-order information criterion was used because the *n*/*K* ratio was small (<40) where *n* is the sample size and *K* is the number of fitted parameters including the intercept (Burnham & Anderson 2002). Following Burnham & Anderson (2002), we calculated DAIC<sub>c</sub> which represents the differences in AIC<sub>c</sub> from the model with the minimum AIC<sub>c</sub> value:

$$\Delta AIC_{ci} = AIC_{ci} - AIC_{min}$$

The models considered to have the most support have a  $\Delta AIC_c$  value of zero.  $AIC_c$  weights ( $\omega AIC_c$ ) were also calculated to provide probabilities of model support that range from 0 (no support) to 1 (whole support). All statistical analyses were conducted in R v 3.0.3 (R Foundation for Statistical Computing, Vienna, AT), with the add-on libraries Segmented v 0.3-0.0 (Muggeo 2003) and MuMln v 1.9.13 (Barton 2015).

#### Results

A total of 695 vascular epiphyte occurrences were recorded on 371 host trees. Breakpoint regression with an ln (x + 1 to avoid undefined values) transformation best described our model predictions, when AIC<sub>c</sub> values were compared between candidate models (Table 1). This was true in all cases except for *M. ramiflorus*, which was best described by linear regression. The 'breakpoint' is the mean diameter at which epiphytes established on host trees. However, epiphytes could establish at any stage within the 95% confidence limits (Fig. 2, Table 2). Before the breakpoint, there was no relationship between epiphyte species richness and host tree diameter (z = 0). Host trees acquired epiphytes at diameters ranging from 5.58 cm (M. ramiflorus) to 43.38 cm (D. cupressinum). After the breakpoint, epiphyte species richness consistently scaled positively with host tree diameter. However, the rate at which epiphyte species richness increased with host tree diameter varied between hosts. Beilschmiedia tawa had the lowest regression slope (z = 0.66), indicating epiphyte species richness increased with tree diameter more slowly than all other host species. This was followed consecutively by M. ramiflorus (z = 0.71), E. dentatus (z = 1.01), P. ferruginea (z = 1.02)and K. excelsa (z = 1.47). Dacrydium cupressinum had the

**Table 1.** Model selection using the second-order Akaike information criterion (AIC<sub>c</sub>).  $\Delta$ AIC<sub>c</sub> values were calculated to determine which model best described our model predictions. The models considered to have the most support have a  $\Delta$ AIC<sub>c</sub> value of 0. Additionally, AIC<sub>c</sub> weights ( $\omega$ AIC<sub>c</sub>) were also calculated to provide probabilities of model support that range from 0 (no support) to 1 (whole support). The candidate models included a simple linear regression (A), breakpoint regression (B), log-transformed linear regression (C) and log-transformed breakpoint regression (D). All models considered to have the most support are highlighted in bold

Host tree	Model	AICc	$\Delta \text{AIC}_{\text{c}}$	$\omega \text{AIC}_{\text{c}}$
Beilschmiedia tawa	А	202.54	152.18	1.41E-34
	В	200.45	150.08	4.01E-34
	С	53.98	3.61	0.03
	D	50.36	0	0.16
Dacrydium cupressinum	А	88.45	80.58	4.97E-19
	В	61.26	53.38	3.99E-13
	С	51.14	43.27	6.28E-11
	D	7.87	0	0.16
Elaeocarpus dentatus	А	379.12	269.85	3.96E-60
	В	378.26	268.98	6.11E-60
	С	119.8	10.52	8.10E-04
	D	109.28	0	0.16
Knightia excelsa	А	101.82	67.79	2.98E-16
	В	86.98	52.94	4.98E-13
	С	50.07	16.04	5.14E-05
	D	-34.03	0	0.16
Melicytus ramiflorus	А	255.62	175.29	1.35E-39
	В	255	174.68	1.83E-39
	С	80.32	0	0.16
	D	83.31	2.99	0.04
Prumnopitys ferruginea	А	57.01	54.913	1.86E-13
	В	46.36	44.26	3.84E-11
	С	13.59	11.49	5.00E-04
	D	2.1	0	0.16

steepest regression slope of z = 2.05. The percentage variation in epiphyte species richness explained by host tree diameter was highest for *K. excelsa* ( $R_{adj}^2 = 0.94$ ) and lowest for *M. ramiflorus* ( $R_{adj}^2 = 0.52$ ; Table 2). The size ranges of trees measured are included in Table 2.

# Discussion

Our findings indicate that Darwin's theory of island ontogeny, is useful for investigating epiphyte community development throughout tree ontogeny. We found variation in the ontogenetic stage at which host trees become favourable for epiphyte establishment. Moreover, the rate at which epiphyte species richness increased with host tree diameter varied between host species.

Epiphytes rely heavily on robust structures to colonize during tree ontogeny (Benzing 1990). Horizontal branches, in particular, support epiphyte communities because they allow canopy soil, a critical water source, to accumulate (ter Steege & Cornelissen 1989; Enloe et al. 2006). Interspecific differences in the development of branches and crotches may explain variation in epiphyte community development between host trees. Dispersing epiphyte propagules, particularly larger-seeded species, are less likely to establish on vertical compared with horizontal surfaces (Gaxiola et al. 2008). Three canopy emergent trees, D. cupressinum, P. ferruginea and K. excelsa, acquired epiphytes at larger diameters. Perhaps the vertical growth form of these trees inhibits epiphyte establishment until sufficient branches have formed. Moreover, larger diameter trees accumulated epiphyte species faster than smaller hosts, once the first epiphyte had established. This suggests that at some point in ontogeny, branches become ideal, horizontal growing platforms, which may withstand large epiphyte communities. The early development of suitable growing platforms may be why M. ramiflorus, a sub-canopy tree, acquired epiphytes prior to any other host. Despite this, epiphyte communities remained depauperate even on larger individuals. MacArthur & Wilson (1967) hypothesized that smaller islands are more vulnerable to stochastic events such as storms and tidal surges that may keep them below equilibrium. Sub-canopy trees do not produce structures capable of withstanding large epiphyte loads. Therefore, stochastic events such as branch falls may be more common in smaller tree species. Even so, smaller trees remain important habitat for epiphytes (Sporn et al. 2010). Small trees may be valuable 'stepping stones' for epiphyte dispersal between host trees. These stepping stones may increase the rate of colonization, and reduce extinctions on trees that have experienced a disturbance (Ruchty et al. 2001). Similarly, many species become established on isolated islands by using nearby islands as agents of dispersal (Gilpin 1979).



**Fig. 2.** Breakpoint regression analysis of epiphyte species richness as a function of host tree diameter (DBH) on *B. tawa*, *D. cupressinum*, *E. dentatus*, *K. excelsa*, *M. ramiflorus* and *P. ferruginea*. The breakpoint is the mean diameter at which epiphytes become established on their respective host tree. Below each breakpoint, the 95% CI is shown. Epiphytes could establish at any stage within the 95% CI. Both variables are  $\ln (x + 1)$  transformed to avoid undefined values.

**Table 2.** Results of the breakpoint regression analyses of epiphyte species richness-host tree diameter data on 371 host trees. The breakpoint is the mean diameter at which epiphytes established on host trees. The number of host trees sampled (n), coefficient of variation ( $R^2$ ), diameter range and 95% confidence interval (CI) are also shown.

Host tree	n	Breakpoint (cm DBH)	Range (cm DBH)	$R_{\rm adj}^2$	95% CI
B. tawa	92	11.70 ± 1.28	2.7–106	0.53	(7.10, 19.11)
D. cupressinum	25	43.38 ± 1.11	2.4–177.8	0.93	(34.81, 53.52)
E. dentatus	95	13.74 ± 1.51	2.6–97.8	0.59	(6.11, 31.19)
K. excelsa	53	17.64 ± 1.06	1.8–69.2	0.94	(15.64, 19.89)
M. ramiflorus	88	5.58 ± 1.51	1.9-53.4	0.52	(2.46, 12.68)
P. ferruginea	28	$14.59 \pm 1.19$	3–83.5	0.87	(10.18, 21.12)

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The role of dispersal limitation on structuring insular communities has been widely recognized (e.g. MacArthur 1972; Holyoak et al. 2005; Buckley 2011). Dispersal decreases with increasing isolation from the species pool, resulting in fewer species on isolated islands (MacArthur & Wilson 1967). For epiphytes, it is difficult to disentangle dispersal limitations from establishment limitations (Werth et al. 2006). The clumped distributions, often noted for epiphytes, may be a result of dispersal limitation (Burns & Zotz 2010). However, establishment depends on a range of other factors (e.g. site conditions, competition) that determine species persistence. Establishment success may explain the regime shift from colonizing species such as P. eleagnifolia to more competitively advanced species such as M. robusta as tree diameter increases. This is because changes in bark structure, pH, water-holding capacities, rugosity and branch architecture increase habitat heterogeneity (Bergey et al. 1995; Zotz et al. 1999; Belinchón et al. 2009; Jueriado et al. 2012). Habitat heterogeneity may cause variability in epiphyte species richness as each species is adapted to different habitats, some that may not become available until later in tree ontogeny or through facilitation cascades.

At a whole-tree scale, habitat heterogeneity may vary depending on the distribution of individual host trees. For example, trees distributed at low densities have higher light interception (Hietz 2005). Subsequently, epiphytes able to withstand exposed conditions may be more persistent than those heavily restricted by humidity. Conversely, trees distributed at high densities may produce a shaded understorey; therefore, epiphytes adapted to low-light environments may be more common than light-demanding species. Perhaps host trees that offer a wider variety of habitats are able to acquire more epiphyte species. Elaeocarpus dentatus, for example, had the second highest epiphyte species richness despite rarely growing above 15 m in height or 1.0 m in diameter (Allan 1961). The rough bark and highly branched architecture may produce a heterogeneous environment that supports different epiphyte species.

On oceanic islands, the presence of a freshwater lens is essential for species dependent on freshwater habitats (Sfenthourakis & Triantis 2009). Resource pressures are therefore increased on habitat specialists that require freshwater resources to persist. Similarly, epiphyte species adapted to specialize in higher water and soil nutrient environments have increased resource pressures (Angelini & Silliman 2014). Facilitation by other epiphytes may allow these specialists to survive in the arid canopy by providing water reservoirs. For example, the two endemic nest epiphytes, *C. hastatum* and *A. solandri*, facilitate the establishment of epiphytes with higher resource requirements. These Astelias have specific leaf structures that guide water down into a catchment area, similar to that of bromeliads (Dawson & Lucas 2005). Organic debris is intercepted by these leaf structures and eventually forms a rich canopy soil (Wardle et al. 2003). This may facilitate the establishment of epiphytes that are more vulnerable to desiccation stress. Consequently, facilitation cascades may increase the rate at which epiphyte species richness increases with host tree diameter by providing high quality and diverse habitats to support more species.

Finally, the rate at which epiphyte communities developed may be a result of the target area effect. Larger tree species are more likely to intercept dispersing epiphyte propagules simply by chance. This is true on islands where the larger islands provide a better target for colonizing species (Ricklefs & Lovette 1999). Interestingly, the diameter at which epiphytes established on host trees varied between tree species. This suggests that factors other than target area are more important for the initial development of epiphyte communities, such as establishment success. Studies on epiphyte population dynamics have shown that dispersal and establishment are important in structuring epiphyte communities because of the highly stochastic environment in which they live (Bennett 1987, 1991; Strong 1977).

In summary, we explored how epiphyte communities might change during the growth, maturation and eventual death of host trees using the general principles of Darwin's geological theory of island ontogeny. Our investigation found variation in the ontogenetic stage at which host trees become favourable for epiphyte establishment. Moreover, the rate at which epiphyte species richness increased with host tree diameter varied between host species. Whether or not the same comparison could be made in tropical forests is unknown. We suggest mechanisms driving variation in epiphyte community development; however, further quantitative analyses are needed to confirm such mechanisms.

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# **Supporting Information**

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Species, genus, authorities and family names of vascular epiphytes and host trees.