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RESEARCH ARTICLE

Composition patterns and network structure of epiphyte-host interactions in Chilean and New Zealand temperate forests

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ABSTRACT

Ecological networks are becoming increasingly used as a framework to study epiphyte-host interactions. However, efforts to quantify the properties of epiphyte-host networks have produced inconsistent results. Epiphyte-host interactions in New Zealand and Chilean temperate forests were quantified to test for non-random patterns in nestedness, negative co-occurrences, number of links, and network specialisation. Results showed that three out of five New Zealand networks were significantly more nested than null model expectations, compared with just one out of four Chilean networks. Epiphytes co-occurred more often than null model expectations in one New Zealand network and one in Chile. In all cases, the number of links maintained by each epiphyte and host species was consistent with null model expectations. Lastly, two New Zealand networks and one in southern Chile were significantly less specialised than null model expectations, with all remaining networks returning low specialisation scores. As such, aside from the tendency for greater nestedness in New Zealand networks, most epiphyte species were distributed on their host trees at random. We attribute the result of nestedness in New Zealand to the abundance of large nest epiphytes (Astelia spp. in particular), which may facilitate the sequential colonisation of epiphyte species on developing host trees. The lack of negative co-occurrences suggests that negative species interactions are not an important determinant of species assemblage structure. Low network specialisation scores suggest that epiphytes are selecting for specific host traits, rather than specific host species for colonisation.

RESUMEN

La aproximación de redes ecológicas como marco para estudiar las interacciones entre epifitas y hospederos ha ido en aumento. Sin embargo, los esfuerzos para cuantificar las propiedades de estas redes aún muestran resultados inconsistentes. Se cuantificaron las interacciones entre epifitas y hospederos en bosques templados Neozelandeses y Chilenos para determinar patrones no aleatorios de anidamiento, co-ocurrencias negativas, numero de vínculos yespecialización de estas redes. Tres de las cinco redes de Nueva

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Zelanda fueron significativamente más anidadas que lo esperado por el modelo nulo, comparado con solo una de las cuatro redes de Chile. En todos los casos el número de vínculos mantenido por cada especie de epifita y hospedero fue consistente con lo esperado por el modelo nulo. Dos redes de Nueva Zelanda y una de Chile fueron significativamente menos especializadas que lo esperado por el modelo nulo, con el resto de las redes mostrando bajos valores de especialización. Aparte de la tendencia general de anidamiento en las redes de Nueva Zelanda, la mayor parte de las especies de epifitas se distribuyen al azar entre los árboles hospederos. Atribuimos el resultado de anidamiento en Nueva Zelanda a la abundancia de grandes epifitas-nido (en particular Astelia spp.), las cuales pueden facilitar la colonización secuencial de epifitas en árboles en desarrollo. La ausencia de co-ocurrencias negativas sugiere que las interacciones interespecíficas no son un determinante importante de la estructura del ensamble. La baja especialización a una determinada red de las epifitas, sugiere que para su colonización estas seleccionan características específicas en los hospederos más que especies de hospederos en particular.

Introduction

Theoretical and empirical studies of species interaction networks have substantially improved our understanding of the general processes structuring species assemblages (Bascompte et al. 2003; Ulrich & Gotelli 2007; Vázquez et al. 2009; Blüthgen 2010). Antagonistic interactions between parasites and hosts, for example, are significantly influenced by host phylogeny (Bellay et al. 2011). Similarly, spatio-temporal species distributions may influence the mutually beneficial interactions between plants and pollinators (review in Vázquez et al. 2009). However, recent efforts to quantify the properties of commensalistic epiphyte–host interactions have produced inconsistent results, and the occurrence of general patterns in epiphyte–host networks remains poorly resolved.

Species interaction networks can be characterised by two properties; the number of links maintained by each higher and lower trophic level (i.e. number of species interactions), and the compositions of interacting species (Figure 1; Boccaletti et al. 2006). One common measure used to describe species composition patterns is the degree of nestedness. Nested species assemblages occur when specialist (i.e. rare) species interact with generalist (i.e. common) species, so producing a pattern of asymmetric specialisation (Darlington 1957). Nestedness is a pattern often associated with mutualistic networks (Bascompte et al. 2003); however, it is also postulated to commonly occur in epiphytehost networks (Piazzon et al. 2011). Burns (2007), for example, observed one of the highest levels of nestedness ever recorded for any type of species interaction in an epiphyte-host network in New Zealand. Similarly, Sáyago et al. (2013) observed a high degree of nestedness in an epiphyte-host network on the central western coast of Mexico. However, a distinct lack of nestedness was later observed in a similar analysis in Panama (Burns & Zotz 2010), and in British Columbia, Canada (Burns 2008), which suggests that nestedness may not be a general pattern in epiphyte–host networks.

Mutually exclusive to nestedness is the measure of negative species co-occurrence patterns, or 'checkerboard' distributions, which arise when particular species pairs never coexist (Diamond 1975). Competition for resources and niche differentiation are thought to



Figure 1. Schematic representation of three common measures of network structure used to describe epiphyte–host interactions: number of links, nestedness and network specialisation (negative species co-occurrences not shown). Lines drawn between each epiphyte (Epn) and host species (Hn) depicts an interaction or 'link'. Line thickness increases with the frequency at which each species pair interacts. If all species in a network frequently interact with one another, the degree of network specialisation will be considered low. Species that interact with a number of other species are considered 'generalists', and species that form few interactions are regarded as 'specialists'. Nestedness occurs when generalist species interact with specialist species, which is illustrated in the schematic. Negative species co-occurrences, which are not illustrated here, are derived by taking the average number of species pairs that never coexist.

exclude weaker competitors, so causing segregation among taxa (Silvertown 2004). Negative co-occurrence patterns in epiphyte-host networks may arise from preferential interactions by epiphyte species with different host species (Burns & Zotz 2010). However, similar to nestedness, negative species co-occurrences may not be a general characteristic of epiphyte-host networks. For example, positive species co-occurrences are also observed (e.g. Blick & Burns 2009), and are postulated to result from the sequential colonisation of epiphyte species (Burns 2007).

Arguably the most general pattern in epiphyte-host networks is the lack of strict host specificity (e.g. Sáyago et al. 2013). Although strict host specificity is rare, the observation that some epiphyte species occur non-randomly on particular host species is not uncommon (review in Wagner et al. 2015). The extent to which an epiphyte species is a generalist or specialist is typically quantified as the number of 'links' (i.e. species interactions) maintained by each epiphyte and host tree species (Burns 2007). At the network level, overall 'network specialisation' may be quantified by incorporating the frequency of species interactions (Blüthgen et al. 2007). Unlike computing the number of 'links', which is sensitive to sampling effort and network size (Martinez et al. 1999), 'network specialisation' does not underestimate a species' true level of specialisation (Blüthgen et al. 2008).

Deviations from general patterns in epiphyte-host interaction networks may be produced by two factors. First, in some cases analyses are restricted to select taxonomic groups or species. For example, Sáyago et al. (2013) only considered 18 epiphytic bromeliad species, despite the co-occurrence of 10 epiphytic orchids and one epiphytic cactus at their study site in Mexico. Similarly, Burns (2008) restricted analyses to epiphyte assemblages on one host tree species in British Columbia, Canada. Second, different metrics are

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used, some of which may overestimate the degree of nestedness in an interaction network (Almeida-Neto & Ulrich 2011). For one, Burns (2007) characterised nestedness using the nestedness temperature calculator, which is arguably the most common technique used to quantify nestedness in species interaction networks (Atmar & Patterson 1993). However, the nestedness temperature calculator is prone to type-I statistical errors and is sensitive to matrix size, owing to the way in which the matrix is reshuffled (Almeida-Neto & Ulrich 2011). Although Burns (2007) corrected for these errors, a comprehensive study by Almeida-Neto et al. (2008) suggests that an even more conservative metric should be used when characterising nestedness.

Nested Overlap and Decreasing Fill (NODF) is one such metric. It calculates deviations from perfect nestedness for each column and row separately. Unlike the calculation of matrix temperature, NODF is both robust to sampling effort and network size, so making it appropriate for comparisons of nestedness between sites (Almeida-Neto et al. 2008). Nevertheless, this metric is used in just half the published epiphyte–host network literature, with all others using variations of matrix temperature. Here, we use the conservative NODF metric to compare the degree of nestedness in epiphyte–host networks from New Zealand and southern Chile. In addition, we quantify the degree of negative species co-occurrences, number of links and network specialisation, in an attempt to elucidate general patterns in epiphyte–host network structure. We do not restrict sampling to specific taxonomic groups or species; rather, interactions among all sighted epiphyte and host tree species are included in the analyses.

Material and methods

Study areas

Our analyses relied upon inventories of epiphyte distributional data collected from five New Zealand forests and four from southern Chile (Figure 2). In all cases, epiphyte assemblages were sampled from the ground using binoculars, and only sections of mature forest were sampled. Details on the number of trees sampled, tree heights, tree diameters and climate of each site are provided in Table 1. To minimise difference in sampling effort, we pooled data collected from two pairs of adjacent sites on the upper North Island of New Zealand. The first pair, Hakarimata Scenic Reserve (37°39'S, 175°07'E) and Pukemokemoke Reserve (37°35'S, 175°22'E) is located in the Waikato region of New Zealand's North Island. These two sites (termed North Waikato) were pooled together based on similarities in tree assemblages and climate, although they differ in size. The canopy of the 1850 ha Hakarimata Scenic Reserve primarily consists of broadleaved evergreens, particularly Beilschmiedia tawa (Lauraceae), Dysoxylum spectabile (Meliaceae), Elaeocarpus dentatus var. dentatus (Elaeocarpaceae) and Litsea calicaris (Lauraceae). Canopy emergents such as Knightia excelsa (Proteaceae), Laurelia novae-zelandiae (Atherospermataceae) and Metrosideros robusta (Myrtaceae) are also common. Podocarps, mainly Dacrydium cupressinum, Prumnopitys ferruginea, Podocarpus laetus, Phyllocladus trichomanoides (Podocarpaceae) and Agathis australis (Araucariaceae), occur in pockets. Pukemokemoke Reserve, although smaller with only 38 ha, is one of the most ecologically diverse forest remnants in the Waikato region. Podocarpus totara var. totara, and Prumnopitys taxifolia (Podocarpaceae) are common canopy species at Pukemokemoke Reserve, in addition to those found at Hakarimata Reserve.



Figure 2. Map illustrating the location of each inventory of epiphyte–host distribution data collected from Chile and New Zealand.

The second pair of pooled sites, Maungatautari Ecological Island (38°02'S, 175°34'E) and Pirongia Forest Park (37°58'S, 175°01'E) is also located in the Waikato region of New Zealand's North Island (termed South Waikato). Maungatautari Ecological Island features 3363 ha of broadleaf/podocarp forest with a surrounding predator-proof fence. Common canopy tree species include *Beilschmiedia tawa*, *Dacrydium cupressinum*, *Prumnopitys ferruginea* and *Metrosideros robusta* (Myrtaceae). Pirongia Forest Park is the most extensive patch of forest remaining in the Waikato region, and consists of the same forest type and climate as Maungatautari Ecological Island. However, unlike Maungatautari, a predator-proof fence does not protect Pirongia Forest Park, although controls for introduced pests are in place.

The third New Zealand site, Otari Wilton's Bush reserve (41°14'S, 174°45'E), is the largest area of remaining native forest on the Wellington Peninsula, located in the

Site	n	Tree heights (m)	% <25 cm dbh	% 25-50 cm dbh	% 50-75 cm dbh	% >75 cm dbh	Rain (mm)	Temp (°C)				
North Waikato	100	15–35	14	65	15	6	1285	13.8				
South Waikato	100	20-35	13	54	18	15	1811	13.8				
North Wellington	371	15–35	9	44	30	17	1249	12.8				
South Wellington	269	15-50	41	39	12	7	1415	14.0				
Stewart Island	203	9–50	33	49	10	7	1700	9.3				
Hualpén	227	20-25	33	47	17	4	1107	12.7				
Contulmo	262	25-30	28	41	25	5	1961	12.7				
Anticura	244	35-40	30	31	24	15	2800	9.8				
ago Toro	202	20-25	31	34	25	10	2200	9.2				

Table 1. Details on the number of individual host trees sampled (*n*), maximum host tree heights (m), and host tree diameter (cm dbh) from each site.

Tree diameter is divided up into four size categories where the corresponding cells show the percentage (%) of trees in a particular diameter class. Annual average rainfall (mm), and average annual temperature (°C) of sampling sites in New Zealand and southern Chile are also shown. Climate data are averages of 20 years (CliFlo: NIWA's National Climate Database), and 38 years (Luebert & Pliscoff 2006), respectively.

lower North Island of New Zealand (termed North Wellington). The reserve encompasses 96 ha of mature and regenerating coastal broadleaf/podocarp forest. The higher strata of the forest are dominated by five broadleaved evergreen tree species, *Beilschmiedia tawa*, *Dysoxylum spectabile*, *Corynocarpus laevigatus* (Corynocarpaceae), *Elaeocarpus dentatus* var. *dentatus* and *Melicytus ramiflorus*. *Knightia excelsa* and *Laurelia novae-zelandiae* frequently emerge above the canopy, along with scattered remnants of *Dacrydium cupressinum* and *Prumnopitys ferruginea* (for a full site description see Taylor & Burns 2015).

East Harbour Regional Park (41°19'S, 174°45'E), another Wellington site (termed South Wellington), covers approximately 2000 ha split into four forest zones. Sampling occurred in the 'northern zone', which consists of mixed beech/broadleaf/podocarp forest. Two southern beeches, *Fuscospora solandri* and *Fuscospora truncata* commonly grow on the hill slopes while broadleaf/podocarp forest prevails in the valleys. Here, the canopy consists of mature *Dacrydium cupressinum*, *Prumnopitys ferruginea*, *Prumnopitys taxifolia*, *Weinmannia racemosa* (Cunoniaceae), *Melicytus ramiflorus*, *Elaeocarpus dentatus* var. *dentatus* and *Elaeocarpus hookerianus*. *Dacrycarpus dacrydioides* (Podocarpaceae) and *Laurelia novae-zelandiae* are common emergent trees. *Metrosideros robusta* is scattered throughout the forest. One conspicuous feature of the East Harbour Regional Park is the large number of podocarps at either the seedling or mature stages of growth, with comparatively few at intermediate stages of growth.

The southernmost forest sampled in this study, Rakiura National Park, Stewart Island (47°00'S, 167°50'E), is also the southernmost broadleaf/podocarp forest in New Zealand. After the North and South Islands, Stewart Island is the third largest island in the New Zealand archipelago. Rakiura National Park covers 85% of the island, and is the most undisturbed New Zealand forest sampled in this study. Dominant canopy species include *Dacry-dium cupressinum*, *Metrosideros umbellata*, *Dacrycarpus dacrydioides*, *Podocarpus laetus Prumnopitys ferruginea* and *Weinmannia racemosa*. New Zealand plant species nomenclature follows Allan (1961), Healy and Edgar (1980) and Connor and Edgar (1987). Nomenclature for *Prumnopitys* follows de Laubenfels (1978), Fuscospora follows Heenan and Smissen (2013), Podocarpus laetus follows Molloy (2015), and Astelia hastata follows Birch (2015).

The northernmost Chilean site, Hualpén Botanical Reserve, is located on the Hualpén Peninsula in close proximity to the Biobio River mouth, Concepción (36°47'S, 73°09'W). The 73 ha reserve is one of the largest remnants of Coastal Mediterranean sclerophyll forest, which is comprised exclusively of angiosperms. The canopy is dominated by four tree species *Lithrea caustica* (Anacardiaceae), *Cryptocarya alba* (Lauraceae), *Peumus boldus* (Monimiaceae) and *Aextoxicon punctatum* (Aextoxicaceae). Also occurring in the canopy to a lesser extent are *Citronella mucronata* (Cardiopteridaceae) and *Eucryphia cordifolia* (Eucryphiaceae). Regenerating individuals of *Gevuina avellana* (Proteaceae), *Myrceugenia planipes* (Myrtaceae) and *Luma apiculata* (Myrtaceae) occur in the understorey (Luebert & Pliscoff 2006).

Contulmo Reserve (38°00'S, 73°10'W) is a Valdivian rainforest located in the seaward foothills of the Cordillera Nahuelbuta (coastal range). This reserve is of considerable interest as the flora represents an outlier of the Valdivian rainforest, which is typical of more southerly latitudes (Baeza et al. 1999). The canopy of the 82 ha reserve is dominated by three evergreen tree species, *Persea lingue* (Lauraceae), *Laurelia sempervirens* (Lauraceae) and *Eucryphia cordifolia* (Eucryphiaceae), and one deciduous tree species *Lophozonia obliqua* (Nothofagaceae). *Podocarpus salignus* (Podocarpaceae) occurs to a lesser extent, while individuals of *Nothofagus dombeyi* (Nothofagaceae) frequently emerge above the canopy.

Anticura (40°39'57"S, 73°10'W) is an old-growth temperate rainforest comprised primarily of broadleaved evergreens within the Puyehue National Park. Dominant canopy species and understorey regrowth include *Eucryphia cordifolia* (Cunoniaceae), *Nothofagus dombeyi* (Nothofagaceae), *Laureliopsis philippiana* (Atherospermataceae) and *Aextoxicon punctatum* (Aextoxicaceae; Luebert & Pliscoff 2006). Also common in the understorey are regenerating individuals of *Amomyrtus luma* (Myrtaceae), *Azara lanceolata* (Salicaceae), *Caldcluvia paniculata* (Cunoniaceae), *Gevuina avellana* (Proteaceae), *Myrceugenia planipes* (Myrtaceae) and *Rhaphithamnus spinosus* (Verbenaceae; Saldaña & Lusk 2003).

The southernmost Chilean site, Lago Toro (40°46'S, 72°16'W), is a Valdivian rainforest located within the Puyehue National Park. Two co-occurring angiosperms, *Nothofagus nitida* and *Laureliopsis phillippiana* (Monimiaceae) are common in the canopy, as well as two podocarps *Saxegothaea conspicua* (Podocarpaceae) and *Podocarpus nubigenus* (Podocarpaceae). *Drimys winteri* (Winteraceae), *Weinmannia trichosperma* (Cunoniaceae) and *Embothrium coccineum* (Proteaceae) occur to a lesser extent (Muñoz-Schick 1980). Chilean plant species nomenclature follows Zuloaga et al. (2008). Nomenclature for *Lophozonia* follows Heenan and Smissen (2013).

Analyses

Rarefaction was used to determine if complete inventories of epiphyte species and their host trees were obtained from each forest, and that observed network properties were not an artefact of sampling effort (Gotelli & Colwell 2001; Zartman 2003). Rarefaction calculates the expected number of species interactions from a subset of species randomly drawn from the wider species pool (Simberloff 1978). A hyperbolic curve was fitted to the rarefaction analyses with subsamples of individual epiphyte occurrences, which were randomly drawn 1000 times from the total species pool.

We tested for non-random patterns in nestedness and negative species co-occurrences using two metrics, NODF and the checkerboard score (c-score), respectively. All NODF scores were weighted for easy comparison between sites. Perfectly nested assemblages were given a score of 100 and communities that assembled at random were given a score of zero. The c-score is simply the average number of species pairs that never coexist in a matrix (Stone & Roberts 1990). A c-score that is significantly larger than randomised expectations is indicative of segregation among taxa (i.e. species co-occur less often than expected by chance). Conversely, a c-score that is significantly less than randomised expectations suggests aggregation among taxa (i.e. species co-occur more often than expected by chance). Similar to the NODF metric, we normalised the c-score so that a value of zero indicated that all species pairs coexist and one indicated that all species pairs never coexist. The observed NODF and c-score values were then compared to 5000 simulated replicates using fixed marginal sums and a swap algorithm.

We quantified species specialisation by comparing the observed number of links (i.e. number of species interactions) maintained by each epiphyte and host species to the expected number of links. The expected number of links was calculated using a simple procedure following Burns (2007). First, epiphytes were randomly assigned to individual host trees to form a null interaction matrix with marginal totals identical to the observed

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values. This was replicated 5000 times for each site separately. The average number of links maintained by each epiphyte and host species in the null interaction matrix was considered the expected number of links. Overall network specialisation was determined using the specialisation index (H_2') . The H_2' index is a derivative of the Shannon entropy, and considers the frequency of species interactions. Networks composed of only specialist species were given an H_2' value of one, whereas networks composed of only generalist species were given an H_2' value of zero. The observed H_2' index was compared to 5000 simulated replicates using fixed marginal sums and a swap algorithm (Gotelli 2000). Lastly, we compared the degree of species and network specialisation, negative species co-occurrences, and nestedness between New Zealand and southern Chile using two-tailed *t*-tests. All statistical analyses were conducted in R version 3.1.2 (R Development Core Team, Vienna, Austria) with the add-on libraries bipartite version 2.04 (Dormann et al. 2009) and vegan version 2.0-10 (Dixon & Palmer 2003).

Results

A total of 4721 epiphyte occurrences were recorded on 1978 host individuals (see Appendix 1 for all epiphyte and host species names, including authorities). All hyperbolic curves reached an asymptote and provided a good fit to the rarefaction analyses for each site (mean $R^2 = 0.98$). Three out of five New Zealand networks were significantly more nested than expected by chance (Figure 3, Table 2). In addition, epiphyte assemblages were significantly more nested in New Zealand compared with Chile (t-test = 3.65, P = 0.02). Epiphyte species co-occurred more often than expected by chance at one New Zealand site (South Wellington: c-score = 0.07, ZS = 0.90, P = < 0.001) and one site in Chile (Anticura: c-score = 0.11, ZS = 0.84, P = < 0.001). However, the degree of species co-occurrence did not differ between the two regions (*t*-test = -1.17, *P* = 0.30, Figure 4). In all cases, the observed number of links between each host tree and epiphyte species was statistically indistinguishable from randomised expectations (Figure 5). However, the frequency-based H_2 ' index showed significantly less network specialisation at two sites in New Zealand (South Waikato: H_2 ' = 0.10, ZS = -1.77, P = < 0.001; Stewart Island: $H_2' = 0.11$, ZS = 3.18, P = 0.002) and one site in Chile (Anticura: $H_2' = 0.11$, ZS = -3.34, P = < 0.001), but no significant difference in specialisation between the two regions (t-test = -2.20, P = 0.11, Figure 6).

Discussion

The purpose of this paper was to elucidate general patterns in epiphyte assemblage structure by comparing epiphyte-host network properties across south-temperate forests in New Zealand and southern Chile. Deterministic structure was observed in five out of nine epiphyte-host networks; however, when considering each individual network against the four metrics tested (9×4), 27 out of 36 results were consistent with null model expectations. As such, the majority of epiphyte-host networks showed no deterministic structure when taking into account individual measures of network properties. Despite this, we found a general tendency for nestedness in New Zealand networks, which were significantly more nested relative to southern Chile (Figure 3). Nestedness in epiphyte-host networks is hypothesised to occur as a result of the sequential colonisation of epiphyte species on



Figure 3. Nestedness (weighted Nested Overlap and Decreasing Fill [NODF]) scores of nine south-temperate forests in New Zealand and Chile. Scores were generated by taking the average weighted NODF from 5000 randomised simulations using fixed marginal sums and a swap algorithm. Arrows indicate the observed NODF score. Observed values that differ significantly from null model expectations (P < 0.05) are depicted with an asterisk.

developing host trees (Burns 2007). Two large 'nest' epiphytes (Figure 7), *Astelia hastata* and *Astelia solandri* (Asteliaceae), facilitate this process by accumulating organic debris and water, which break down into a moisture-rich humus (Dawson & Sneddon 1969). A number of epiphytes with higher resource requirements are almost exclusively associated with these large nests, particularly woody shrubs and hemi-epiphytes. In support of Burn's (2007) interpretation, nest epiphytes were uncommon at the sites where nestedness did not deviate from null model expectations. For example, only one *Astelia* individual was recorded on Stewart Island, New Zealand. Additionally, the nest-like *Fascicularia bicolor* (Bromeliaceae) was only sparsely recorded in southern Chile.

However, factors other than the abundance of nest epiphytes may produce a nested result. For one, Burns (2007) suggested that specialist epiphyte species are only found on the largest host trees, so producing nested assemblages. Alternatively, nestedness may occur when epiphyte assemblages on small-diameter trees form perfect subsets of epiphyte

-	NODF		c-score		H ₂ '		No. of links	
Site	Statistic	z-score	Statistic	z-score	Statistic	z-score	Epiphytes	Hosts
North Waikato	62.84	-0.66	0.14	0.15	0.12	0.53	8.69	5.14
South Waikato	68.10 ⁺	0.17	0.22	-0.82	0.10 -	-1.77	6.20	5.05
North Wellington	76.88 ⁺	-3.45	0.08	-0.74	0.09	0.51	5.40	5.40
South Wellington	71.39 ⁺	2.50	0.07	0.90	0.11	1.15	9.64	5.40
Stewart Island	65.41	3.28	0.18	-0.41	0.11 -	3.18	5.00	8.00
Hualpén	32.17	0.70	0.20	0.19	0.35	1.18	5.07	5.07
Contulmo	48.56	-0.58	0.23	-0.06	0.17	-1.15	4.56	4.56
Anticura	60.15 ⁺	-0.54	0.11 -	0.84	0.11 -	-3.34	6.07	8.27
Lago Toro	41.59	-0.02	0.22	-0.42	0.25	-1.34	5.27	5.27

Table 2. Results of the network analyses; nestedness (NODF), species co-occurrences (c-score), network specialisation (H_2'), and the number of links (no. of links) conducted for nine epiphyte–host networks in New Zealand and southern Chile.

Observed values that differ significantly from randomised expectations (P < 0.05) are in bold. Plus and minus signs indicate if observed values were significantly more or less than randomised expectations.

NODF, Nested Overlap and Decreasing Fill.



Figure 4. Results from the species co-occurrence analyses testing for the number of checkerboard units (c-score) between all species pairs in nine epiphyte–host interaction matrices from New Zealand and southern Chile. The observed c-score was compared with the expected c-score, which was derived from 5000 randomised simulations using fixed marginal totals and a swap algorithm. The height of each bin represents the observed c-score and the dashed lines represents the expected c-score. Observed values that differ significantly from randomised expectations (P < 0.05) are indicated by a solid bold line and an asterisk.

assemblages on large-diameter trees (Zhao et al. 2015). In this study, there was no marked difference in host tree diameter distributions; however, sites with a higher percentage of larger diameter trees were on average significantly nested. For example, 17% of trees sampled in North Wellington, and 15% of trees sampled in South Waikato and Anticura were > 75 cm diameter, and were all significantly nested. In comparison, only 4%–10% of trees at other sites were in the same diameter range. Another factor that may influence



Figure 5. Relationship between the observed number of links (species degree) and expected number of links for **A**, New Zealand host trees; **B**, New Zealand epiphyte species; **C**, Chilean host trees; and **D**, Chilean epiphyte species. Expected values were generated by taking the average number of links from 5000 randomised simulations. The centred dotted line is the isocline. Points below the isocline indicate segregation among taxa and points above the isocline indicate aggregation among taxa.

nestedness is network size (i.e. number of interacting species). Nielsen and Bascompte (2007) demonstrated that network size, rather than sampling effort (i.e. number of sampling units), is more important in determining a nested structure in species interaction networks. In support of this, New Zealand networks were on average larger than those from Chile. Similarly, the largest network in Chile, Anticura, also showed a significant nested pattern.

Species co-occurrences were consistent with null model expectations in seven of the nine epiphyte-host networks, which suggests that negative species interactions (e.g. competition) are not important in structuring epiphyte assemblages (Figure 4). Randomised species co-occurrences are hypothesised to occur when species persistence is low relative to colonisation (Zalewski & Ulrich 2006). However, epiphyte colonisation is inherently slow, and depends on the availability of suitable microhabitats (Dickinson et al. 1993), bark characteristics (Mehltreter et al. 2005), and tree diameter (Hirata et al. 2008). Likewise, epiphyte persistence varies with patch connectivity (Johansson et al. 2012) and disturbance (Winkler et al. 2007). As such, we propose that slow rates of colonisation and variation in species persistence may randomise epiphyte assemblages. It is important to note, however, that in two epiphyte–host networks, species co-occurred significantly



Figure 6. Results from the network specialisation analyses (H_2') of nine south-temperate forests in New Zealand and Chile. The observed H_2' score was compared with the expected H_2' score, which was derived from 5000 randomised simulations using fixed marginal totals and a swap algorithm. The height of each bin represents the observed H_2' score and the dashed line represents the expected H_2' score. Observed values that differ significantly from randomised expectations (P < 0.05) are indicated by a solid bold line and an asterisk.

more than randomised expectations, which agrees with some previous results on the aggregated distributions of epiphytes on their host trees (Blick & Burns 2009).

The degree of species specialisation, quantified by the number of links maintained by each epiphyte and host species, was consistent with null model expectations (Figure 5). However, the specialisation (H_2) index, which accounts for species interaction



Figure 7. A common nest epiphyte endemic to New Zealand, Astelia hastata (Asteliaceae), perched on an Elaeocarpus dentatus var. dentatus (Elaeocarpaceae) host.

frequencies, found three epiphyte-host networks to be less specialised than expected by chance, with all remaining networks returning low specialisation (H_2') scores (Fig. 6). Generalised species interactions are commonly observed in plant-pollinator networks (Olesen et al. 2002). In commensalistic epiphyte-host networks, low specialisation scores may result from epiphytes selecting for specific host traits, rather than specific host species (Wagner et al. 2015). Moreover, as trees grow, host traits and microclimate conditions change in ways that can influence epiphyte species occupancy (Benzing 1990). A young tree in the understorey, for example, may lack suitable growing sites, but a larger individual of the same species may offer a number of habitats, which may facilitate the establishment of epiphytes (Zotz & Vollrath 2003).

These results illustrate some general patterns in epiphyte–host interaction networks, which may be built upon in comparisons between other sites. We stress the importance of consistency in terms of what metrics and null models to use in network analyses. Here, the most conservative metric to measure nestedness, NODF (Almeida-Neto et al. 2008), still suggests nestedness in New Zealand networks. Although this may be attributed to network size (Nielsen & Bascompte 2007), tree diameter distributions (Zhao et al. 2015), or branching architecture, we hypothesise that the abundance of nest epiphytes is the main determinant of nestedness in this study. However, further fine-grained analyses are needed to tease apart specific factors that produce a nested structure in epiphyte–host networks. For example, are assemblages on podocarps more nested than broadleaved evergreens? Similarly, what specific host traits affect epiphyte distributions most? By comparing the results of this study more broadly with future data sets, we may be able to elucidate the mechanisms structuring commensalistic epiphyte–host interactions.

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Appendix 1A

Species, genus, authorities and family names of vascular epiphytes and host trees recorded in New Zealand. Nomenclature for angiosperms follows Allan (1961) and Moore and Edgar (1976). Nomenclature for *Prumnopitys* follows de Laubenfels (1978). Fern and allies nomenclature follows Brownsey and Smith-Dodsworth (2000).

Epiphytes

- 1. Asplenium flaccidum G.Forst. (Aspleniaceae)
- 2. Asplenium polyodon G.Forst. (Aspleniaceae)
- 3. Asplenium oblongifolium Colenso (Aspleniaceae)
- 4. Astelia hastata (Col.) Skottsb. (Asteliaceae)
- 5. Astelia solandri A.Cunn. (Asteliaceae)
- 6. Bulbophyllum pygmaeum (Sm.) Lindl. (Orchidaceae)
- 7. Cardiomanes reniforme (G.Forst.) C.Presl. (Hymenophyllaceae)
- 8. Dendrobium cunninghamii Lindl. (Orchidaceae)
- 9. Drymoanthus adversus (Hook.f.) Dockrill (Orchidaceae)
- 10. Earina autumnalis (G.Forst.) Hook.f. (Orchidaceae)
- 11. Earina mucronata Lindl. (Orchidaceae)
- 12. Griselinia lucida G.Forst. (Griseliniaceae)
- 13. Griselinia littoralis Raoul. (Griseliniaceae)
- 14. Hymenophyllum bivalve (G.Forst.) Sw. (Hymenophyllaceae)
- 15. Hymenophyllum demissum (G.Forst.) Sw. (Hymenophyllaceae)
- 16. Hymenophyllum dilatatum (G.Forst.) Sw. (Hymenophyllaceae)
- 17. Hymenophyllum flabellatum Labill. (Hymenophyllaceae)
- 18. Hymenophyllum multifidum (G.Forst.) Sw. (Hymenophyllaceae)
- 19. Luzuriaga parviflora (Hook.f.) Kunth (Luzuriagaceae)
- 20. Metrosideros robusta A.Cunn. (Myrtaceae)
- 21. *Metrosideros umbellata* Cav. (Myrtaceae)
- 22. Notogrammitis billardierei (Willd.) Parris (Polypodiaceae)
- 23. Notogrammitis heterophylla (Labill.) Parris (Polypodiaceae)
- 24. Phlegmariurus varius (R.Br.) A.R. Field et Bostock (Lycopodiaceae)
- 25. Pittosporum cornifolium A.Cunn. (Pittosporaceae)
- 26. Pyrrosia eleagnifolia (Bory.) Hovenkamp. (Polypodiaceae)
- 27. Rumohra adiantiformis (G.Forst.) Ching. (Dryopteridaceae)
- 28. Tmesipteris elongata P.A. Dang. (Psilotaceae)

Host trees

- 1. Agathis australis (D.Don) Lindl. (Araucariaceae)
- 2. Alectryon excelsus Gaertn. subsp. excelsus (Sapindaceae)

- 3. Beilschmiedia tawa (A. Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae)
- 4. Brachyglottis rotundifolia var. rotundifolia (J.R.Forst. et G.Forst.) B.Nord. var. rotundifolia (Asteraceae)
- 5. Carpodetus serratus J.R.Forst. et G.Forst. (Rousseaceae)
- 6. Coprosma arborea Kirk (Rubiaceae)
- 7. Coprosma foetidissima J.R.Forst. et G.Forst. (Rubiaceae)
- 8. Cordyline australis (Forst.f.) Endl. (Asparagaceae)
- 9. Corynocarpus laevigatus J.R.Forst. et G.Forst. (Corynocarpaceae)
- 10. Dacrycarpus dacrydioides (A.Rich.) de Laub. (Podocarpaceae)
- 11. Dacrydium cupressinum (Lamb.) (Podocarpaceae)
- 12. Dysoxylum spectabile (G.Forst.) Hook.f. (Meliaceae)
- 13. *Elaeocarpus dentatus* var. *dentatus* (J.R. Forst et G. Forst) Vahl var. dentatus (Elaeocarpaceae)
- 14. Fuscospora solandri (Hook.f.) Heenan et Smissen (Nothofagaceae)
- 15. Fuscospora truncata (Colenso) Heenan et Smissen (Nothofagaceae)
- 16. Griselinia littoralis Raoul. (Griseliniaceae)
- 17. Hedycarya arborea J.R.Forst. et G.Forst. (Monimiaceae)
- 18. Knightia excelsa R. Br. (Proteaceae)
- 19. Kunzea ericoides (A.Rich) Joy Thomps. (Myrtaceae)
- 20. Laurelia novae-zelandiae A.Cunn. (Atherospermataceae)
- 21. *Leptecophylla juniperina* subsp. *juniperina* (J.R.Forst. et G.Forst.) C.M.Weiller subsp. *juniperina* (Ericaceae)
- 22. Litsea calicaris (A.Cunn.) Benth. et Hook.f. ex Kirk (Lauraceae)
- 23. Lophomyrtus bullata Burret (Myrtaceae)
- 24. Melicytus ramiflorus J.R.Forst. et G.Forst (Violaceae)
- 25. Metrosideros robusta A.Cunn. (Myrtaceae)
- 26. Metrosideros umbellata Cav. (Myrtaceae)
- 27. Myrsine australis (A.Rich.) Allan (Primulaceae)
- 28. Neomyrtus pedunculata (Hook.f.) Allan (Myrtaceae)
- 29. Nestegis cunninghamii (Hook.f.) L.A.S.Johnson (Oleaceae)
- 30. Olearia rani var. colorata (Colenso) Kirk (Asteraceae)
- 31. Pennantia corymbosa J.R.Forst. et G.Forst (Pennantiaceae)
- 32. Phyllocladus trichomanoides D.Don (Podocarpaceae)
- 33. Pinus radiata D.Don (Pinaceae)
- 34. Pittosporum eugenioides A.Cunn. (Pittosporaceae)
- 35. Podocarpus laetus Hooibr. Ex Endl. (Podocarpaceae)
- 36. Podocarpus totara G.Benn. ex D.Don var. totara (Podocarpaceae)
- 37. Prumnopitys ferruginea (D.Don) Laubenf. (Podocarpaceae)
- 38. Prumnopitys taxifolia (DDon) de Laub. (Podocarpaceae)
- 39. Pseudopanax arboreus (L.f.) Allan (Araliaceae)
- 40. Pseudopanax crassifolius (Sol. Ex A.Cunn.) C.Koch (Araliaceae)
- 41. Rhopalostylis sapida H.Wendl. et Drude (Arecaceae)
- 42. Schefflera digitata J.R.Forst. et G.Forst (Araliaceae)
- 43. Weinmannia racemosa L.f. (Cunoniaceae)

Appendix 1B

Species, genus, authorities, and family names of vascular epiphytes and host trees recorded in Chile. Nomenclature for angiosperms, gymnosperms and pteridophytes follow Zuloaga et al. (2008).

Epiphytes

- 1. Asplenium dareoides Desv. (Aspleniaceae)
- 2. Asplenium trilobum Cav. (Aspleniaceae)
- 3. Fascicularia bicolor (Ruiz & Pav.) Mez ssp. bicolor (Bromeliaceae)
- 4. Grammitis magellanica Desv. (Polypodiaceae)
- 5. Hymenophyllum caudiculatum Mart. var. caudiculatum (Hymenophyllaceae)
- 6. Hymenoglossum cruentum (Cav.) C. Presl (Hymenophyllaceae)
- 7. Hymenophyllum dentatum Cav. (Hymenophyllaceae)
- 8. Hymenophyllum dicranotrichum (C.Presl) Hook. ex Sadeb. (Hymenophyllaceae)
- 9. Hymenophyllum krauseanum Phil. (Hymenophyllaceae)
- 10. Hymenophyllum pectinatum Cav. (Hymenophyllaceae)
- 11. Hymenophyllum peltatum (Poir.) Desv. (Hymenophyllaceae)
- 12. *Hymenophyllum plicatum* Kaulf. (Hymenophyllaceae)
- 13. Luzuriaga radicans Ruiz & Pav. (Luzuriagaceae)
- 14. Luzuriaga polyphylla (Hook.) J.F.Macbr. (Luzuriagaceae)
- 15. Pleopeltis macrocarpa (Bory ex Willd.) Kaulf. (Polypodiaceae)
- 16. Raukaua laetevirens (Gay) Frodin (Araliaceae)
- 17. Synammia feuillei (Bertero) Copel. var. feuillei (Polypodiaceae)
- 18. Sarmienta scandens (J.D.Brandis ex Molina) Pers. (Gesneriaceae)
- 19. Tillandsia usneoides (L.) L. (Bromeliaceae)

Host trees

- 1. Aextoxicon punctatum Ruiz & Pav. (Aextoxicaceae)
- 2. Caldcluvia paniculata (Cav.) D.Don (Cunoniaceae)
- 3. Citronella mucronata (Ruiz & Pav.) D.Don (Cardiopteridaceae)
- 4. Cryptocarya alba (Molina) Looser (Lauraceae)
- 5. Dasyphyllum diacanthoides (Less.) Cabrera (Asteraceae)
- 6. Drimys winteri J.R. Forst. & G.Forst. var. winteri (Winteraceae)
- 7. Embothrium coccineum J.R.Forst. & G.Forst. (Proteaceae)
- 8. Eucryphia cordifolia Cav. (Eucryphiaceae)
- 9. Gevuina avellana Molina (Proteaceae)
- 10. Laurelia sempervirens (Ruiz & Pav.) Tul. (Monimiaceae)
- 11. Laureliopsis phillippiana (Looser) Schodde (Monimiaceae)
- 12. Lithraea caustica (Molina) Hook. & Arn. (Anacardiaceae)
- 13. Lophozonia alpina (Poepp. & Endl.) Heenan & Smissen (Nothofagaceae)
- 14. Lophozonia obliqua (Mirb.) Heenan & Smissen subsp. obliqua (Nothofagaceae)
- 15. Luma apiculata (DC.) Burret (Myrtaceae)
- 16. Myrceugenia planipes (Hook. & Arn.) O.Berg (Myrtaceae)
- 17. Nothofagus dombeyi (Mirb.) Oerst. (Nothofagaceae)
- 18. Nothofagus nitida (Phil.) Krasser (Nothofagaceae)

- 19. Persea lingue Nees (Lauraceae)
- 20. Peumus boldus Molina (Monimiaceae)
- 21. Podocarpus nubigenus Lindl. (Podocarpaceae)
- 22. Saxegothaea conspicua Lindl. (Podocarpaceae)
- 23. Weinmannia trichosperma Cav. (Cunoniaceae)