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Cryptic interactions revisited from ecological networks: Mosses as a key link between trees and hummingbirds

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Abstract

1. Ecological interactions are the glue of biodiversity, structuring communities and determining their functionality. However, our knowledge about ecological interactions is usually biased against cryptic interactions (i.e. overlooked interactions involving inconspicuous species). Mosses are a neglected component in community ecology despite being diverse and abundant in boreal and temperate forests. Therefore, the cryptic relationships of trees as hosts for epiphytic mosses, and vertebrates using mosses as nesting material, may have important consequences for community structuring.
2. We built species- and individual-based ecological networks to characterise tree–moss associations in 120 tree individuals representing 13 species, which hosted 19 moss species. We also used those ecological networks to simulate the effects of non-random extinctions due to selective logging, to assess the presence of moss species in hummingbird nests (30 nests), whether these mosses were a subset of those found on the trees if moss diversity varies with tree height and whether these moss–tree relationships are phylogenetically constrained.
3. We found a nested pattern in the tree–moss network. Taller trees were the most connected, with tree height positively related to number of moss species, network degree and centrality. Extinction simulations showed changes in network topology, with the strongest effect from the removal of the most connected tree species. However, tree and moss networks were not influenced by phylogenetic relatedness. The hummingbird *Sephanoides sephaniodes* selectively collected mosses; the moss species used as nesting material by hummingbirds were a subset of available species. These complex relationships among trees, birds and mosses underpin the importance of neglected components in the community.
4. We found that tree–moss associations were non-random, showing a positive relationship between tree height and moss diversity. Those associations are the reflection of preferences beyond relative abundances in the forest, and the removal of certain tree species (due to selective logging) may have cascade effects in the community. Furthermore, the lack of phylogenetic correspondence suggests that tree–moss associations are governed by ecological factors (host tree preferences). Moss–hummingbird associations are non-random, as hummingbirds (that pollinate

these trees) are actively selecting mosses for nest building, stressing the importance of cryptic interactions as a community-structuring process.

KEYWORDS
bryophytes, ecological networks, forest, interactions, nests, phylogeny

1 | INTRODUCTION

Ecological interactions are essential for community structure and functioning, being responsible for maintaining and generating biodiversity (Bascompte et al., 2003, 2006), as they act as the 'glue' that holds different species together (Bascompte & Jordano, 2007). However, our knowledge about ecological interactions is usually biased against cryptic interactions, involving inconspicuous species (Hunt, 2003; Philpott et al., 2012). Such cryptic interactions may have central effects on community structure and functioning (Kinnison et al., 2015; Philpott et al., 2012). However, our limited understanding of those interactions has led to partial and sometimes erroneous interpretations of community ecology dynamics (Kinnison et al., 2015). In this context, mosses are an excellent example of species involved in cryptic interactions. Interspecific interactions involving mosses are often ignored because they are inconspicuous, difficult to identify or inhabit remote places (Müller et al., 2016).

Mosses are diverse and abundant in temperate and boreal forests (Kuglerova et al., 2016). This group has high environmental plasticity, and some mosses can colonise many habitats as pioneer species, and others are important in late forest successional stages (Fritz et al., 2009; Odor et al., 2013). As epiphytes, they can constitute an important fraction of canopy biomass (Diaz et al., 2010) and perform different ecological functions, such as capturing moisture, enriching organic matter, facilitating plant establishment and providing favourable microhabitat conditions for animals (Hörnberg et al., 1997; Parker et al., 1997). However, the role of mosses as nesting material is a less studied ecological function (Deeming & Mainwaring, 2015). Cup nests are common in many bird groups and typically contain an important proportion of plant material, including mosses (Healy et al., 2015). Mosses present in bird nests may increase water retention (that prevents egg desiccation; Blem & Blem, 1994) and thermal isolation, and have also been associated with antimicrobial activity that may enhance fledgling survival (Fontúrbel, Osorio, Riffo et al., 2020). For example, in the Appalachian (USA), 12 passerine bird species used 65 bryophyte species as nesting material (Breil & Moyle, 1976). In temperate forests of South America, mosses constitute a high proportion of nesting material for the hummingbird species *Sephanoides sephaniodes* (Calvelo et al., 2006; Osorio-Zuñiga et al., 2014) and the endemic marsupial *Dromiciops gliroides* (Vazquez et al., 2020).

Some studies reported moss propagules being transported by birds (Lewis et al., 2014) and other animals (Boch et al., 2013; Parsons et al., 2007; Rudolphi, 2009) through endo- or ectozoochory. Nevertheless, mosses transported by animals to their nests give mosses a greater dispersal potential beneath the forest canopy (Osorio-Zuñiga et al., 2014; Warren et al., 2017). This relationship constitutes a mutualistic synzoochory: an intermediate dispersal type between endo and ectozoochory in which propagules are deliberately transported with no ingestion or gut passage (Osorio-Zuñiga et al., 2014). Synzoochory has been described for the hummingbird *Sephanoides sephaniodes* that builds its nest using different moss species and disperses their sporophytes at the same time (Osorio-Zuñiga et al., 2014). When synzoochory occurs, mosses in the nests remain reproductive for at least 1 year, and spores contained in those sporophytes reach greater distances than those dispersed only by wind (Osorio-Zuñiga et al., 2014).

Plant propagules dispersed from nests might explain the presence of mosses species beneath tree canopies (Clement et al., 2001; Diaz et al., 2010; Fritz et al., 2009; Odor et al., 2013). Bryophyte dispersal limitations (Lönnell et al., 2012; Sundberg, 2013) and selective use of nest material by birds (Dean et al., 1990; Deeming & Mainwaring, 2015; Dykstra et al., 2009; Osorio-Zuñiga et al., 2014) may lead to non-random moss distribution, both within trees (e.g. their vertical distribution) and among tree species in the forest. As other complex interactions, moss–tree relationships may be phylogenetically constrained (Rezende et al., 2007), in the sense that related tree species share more moss species than unrelated ones. This could lead to complex ecoevolutionary dynamics (Cameron et al., 2013). While exploring these kinds of relationships in the wild may be a challenging task, ecological networks provide a useful toolbox to understand the complexity of nature. Network analysis allows us to describe and quantify interactions patterns among interacting species based on mathematical calculations. Therefore, ecological networks can be used to assess the asymmetry, nestedness, robustness and dependence of ecological interactions (Bascompte & Jordano, 2007; Bascompte et al., 2003, 2006; Olesen et al., 2007).

The local removal of trees hosting several moss species (e.g. by selective logging or deforestation) may result in the co-extinction of the mosses that hummingbirds use as nesting materials. Using ecological networks, we examined network properties between trees and mosses, and between hummingbirds (nests) and mosses. Ecological networks also allow us to simulate hypothetical extinction scenarios to test community vulnerability (Bascompte & Jordano, 2007). Knowing the full network, we can predict changes in topology by non-randomly removing certain tree species (e.g. tallest or older individuals) and their cascade consequences in the community.

In this study, we characterised moss–tree interactions in the temperate Valdivian rainforests (southern Chile) using ecological networks.

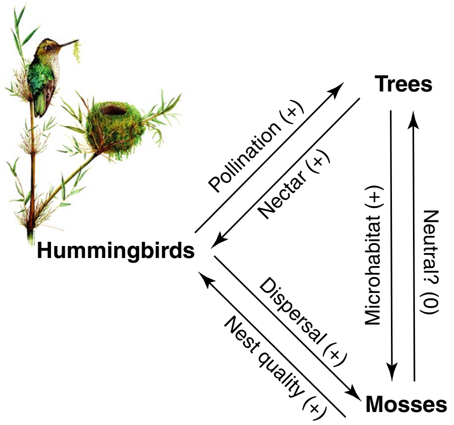


FIGURE 1 A conceptual model of the ecological relationships among trees, mosses and hummingbirds (using mosses for nest-building) in our study system. '+' denotes a positive interaction; '0' denotes a neutral interaction

Furthermore, we assessed the interactions between epiphytic mosses used by the hummingbird *Sephanoides sephaniodes* (the most important vertebrate pollinator of this ecosystem) as nest-building material (Figure 1). We ask the following questions: (a) Do moss diversity and biomass depend on host tree species and position on the tree? (b) Are moss–tree and moss–nest interaction networks randomly structured (i.e. depending on the abundance)? (c) Does the removal of the most and the least connected tree species affect network topology? (d) Are moss–tree networks phylogenetically constrained? (e) Are moss species in hummingbird nests a random subset of those available in the forest? We hypothesised that host preferences in mosses and preference for certain moss species by the hummingbird results in non-random moss–tree and moss–nests interactions; therefore, the extinction of the most and the least connected tree species (commonly logged to be used as firewood) may generate the loss of some moss species used as nesting material by hummingbirds. In this sense, network theory could contribute to understanding a complex cryptic relationship among trees, mosses and hummingbirds.

2 | MATERIALS AND METHODS

2.1 | Study site and species

We conducted this study at Parque Oncol (39°41′S 73°18′W, 715 m a.s.l.), a 750-ha private protected area located 28 km NE of Valdivia (southern Chile). Parque Oncol comprises 754 ha of coastal temperate rainforests, characterised by moist-evergreen mixed-species vegetation (Osorio-Zuñiga et al., 2014). The Green-backed Firecrown (*Sephanoides sephaniodes*, Trochilidae) is the only hummingbird in the region, and the only vertebrate pollinator (Aizen, 2003). This generalist hummingbird pollinates ~20% of the native flora of these forests, including several of the tree species assessed here (e.g. *Amomyrtus* spp. *Embothrium coccineum* and *Dasyphyllum diacanthoides*). *Sephanoides sephaniodes* makes cup nests with the fern *Lophosoria quadripinnata* and the mosses *Ancistrodes genuflexa*, *Weymouthia cochlearifolia* and *W. mollis* as the main components (Osorio-Zuñiga et al., 2014).

2.2 | Data collection

From March 2008 to June 2009, we sampled 30 nests of *S. sephaniodes* found in branches of the native bamboo *Chusquea quila*. Nest search at the Oncol park covered an extension of ~185 ha (area corresponding to the *Weinmannia trichosperma–Podocarpus salignus–Laureliopsis philippiana* forest type). These *S. sephaniodes* nests corresponded to the samples analysed in Osorio-Zuñiga et al. (2014), with species composition and biomass data for new (freshly made nests built <3 months ago) and 1-year-old nests (abandoned after the second breeding season; all sampled nests were found perched on bamboo). We searched for new and old nests from March 2008 to June 2009. Additionally, we selected the nearest trees to the north, south, east and west of each nest. We sampled moss composition on these trees. These trees ($N = 120$ individuals) belonged to 13 species (Table S1, available online as Supporting Information). The sampled trees hosted 19 moss species. The number of moss species found on a particular tree species was independent of the number of trees sampled of that species (linear regression: $R^2 = 0.001$; $p = 0.98$).

Of these 120 trees, 66 had epiphyte mosses, and the remaining 54 individuals did not. Mosses present on these 66 trees were sampled on each stem at 2-m height intervals, starting at 2 m until treetop, using tree climbing equipment. We measured total height (from the base to the treetop) and stem diameter at breast height for each sampled tree. We collected bryophytes in a 20-cm strip at each height. If there were branches at the sampling height, all mosses on the branches were also collected and summed to the stem sample. Once in the laboratory, all collected material was separated by species when possible, otherwise by genus. With this information we built a tree–moss interaction matrix (i.e. which indicates that moss species are present in each individual tree and tree species). Then, we measured moss biomass after drying the samples collected at 60°C for 24 hr. We assessed the completeness of our sampling effort using rarefaction curves (Gotelli & Colwell, 2001) for the number of moss species per tree (individual-based rarefaction) and the number of moss–tree interactions per tree species (sample-based rarefaction). Assessing sampling completeness is important as it can influence the outcome of the ecological network analysis (Falcão et al., 2016). We used the R package VEGAN (Oksanen et al., 2013) to perform rarefaction analyses.

2.3 | Data analysis

To assess if moss species were randonmly distributed among tree species and along the stem vertical profile, we performed a two-way Analysis of Similarity (ANOSIM), using tree height as a nested factor within tree species. ANOSIM is a nonparametric test based on permutations that calculate similarities within and between groups to assess differences in community composition (Clarke, 1993). We used a Bray–Curtis similarity index to perform the ANOSIM analysis and 9,999 permutations to estimate the significance. We conducted ANOSIM analyses using the R package VEGAN (Oksanen et al., 2013).

To assess how moss–tree interactions are arranged, we conducted a network analysis, using the commensalist network approach (Ceballos et al., 2016), which applies the same analyses used for bipartite mutualistic networks, but differs only in its interpretation; commensalist interactions are beneficial for one party (the mosses) and neutral for the other (the trees). We used two analysis levels on the moss–tree network: tree species and tree individuals. We used qualitative data (i.e. binary data expressed as interaction presence/absence) to build the networks, aiming to describe interaction distribution within the community (Miranda et al., 2019). We also tested a quantitative analysis using moss biomass as a proxy of abundance. However, the results were governed by the two dominant *Weymouthia* species (which together constituted ~94% of the moss biomass in the forest: Figure S1) and therefore difficult to interpret. For that reason, we decided to use qualitative networks. From those networks, we estimated the following descriptors: the number of links per species, connectance, nestedness, modularity and module identity. Connectance is the proportion of actual interactions among the total number of potential interactions (Montoya & Raffaelli, 2010). Nestedness is a network property that indicates a tendency of progressive generalisation across species (Bascompte et al., 2003). Therefore, a nested network occurs when the species interacting with specialists are a proper subset of the species interacting with generalists (Bascompte et al., 2003; Chamberlain et al., 2014). We estimated nestedness based on the NODF metric (Nested Overlap and Decreasing Fill; Almeida-Neto et al., 2008), which range between 0 (not nested) and 100 (perfectly nested). The NODF metric is a suitable nestedness descriptor when using qualitative data, as it is insensitive to network size and shape (Chamberlain et al., 2014). Complementarily, we examined the core-periphery structure of the networks, which goes beyond nestedness to characterise the species subset that is densely connected (i.e. the core) and the sparsely connected periphery (Martín-González et al., 2020). While nestedness measures the extent in which interactions of less connected nodes form subsets of interaction of more connected nodes, the core-periphery analysis estimates the 'core' (formed by densely connected species) and 'periphery' (formed by sparsely connected nodes connected to the core) subsets (Martín-González et al., 2020). Both approaches may be used complementarily to understand network structure. Modularity depicts the degree of compartmentalisation in a network (Olesen et al., 2007). We estimated modularity using the DIRTLPAwb+ algorithm (Beckett, 2016), which provides a robust module partition. To assess the statistical validity of each network descriptor, we built null models (using the shuffle.web method, which relocates the matrix maintaining its dimensionality; Fortuna & Bascompte, 2006) with 999 randomisations to determine if the observed connectance, nestedness and modularity differed from chance (Jordano, 2016). Randomised networks keep the number of interactions and connectance constant (Dormann et al., 2009). We then simulated extinction scenarios (by removing the entire row corresponding to a given species) and recalculated network parameters (using the species-based network) when the most (*Weinmannia trichosperma*) and the least connected (*Aextoxicon punctatum*) tree species were removed (which also corresponded to the species with the tallest and the shortest vertical profiles, respectively) and estimated changes in network topology due to their loss. Those non-random extinctions are likely to happen in nature, as those trees are commonly logged to be used as firewood.

Aiming to study the relationship between mosses and individual *S. sephaniodes* nests (assuming that each nest is built by a hummingbird individual that selectively collect mosses; Fontúrbel, Osorio, Riffo et al., 2020), we first elaborated qualitative interaction matrices (as described for tree–moss networks) with the moss species present at each nest (using data from Osorio-Zuñiga et al., 2014). We ran separate network analyses for new (freshly made) and 1-year-old nests, estimating the number of links, connectance and nestedness using the same procedures described above. Those parameters described network topology and allowed us to compare moss–tree and moss–nest networks.

Individual-based network depicts the relationship among trees based on mosses species that they share. We used qualitative data to calculate individual-based networks. From the individual-based network, we estimated the degree (i.e. number of links per node) and centrality for each vertex. Centrality is a measure of the importance of a given node that estimates how connected a given individual is to remaining individuals of the community, whereas degree can be used as a proxy of average node connection on the network (Gómez & Perfectti, 2012). To assess the relationship of network descriptors and environmental factors, we related degree and centrality (using the closeness centrality index as a proxy of the relative importance of each node within the network; Martín-González et al., 2010) with individual tree height and tree diameter. We estimated all network descriptors (for species- and individual-based networks) using the packages BIPARTITE (Dormann, Gruber, & Fruend, 2008, 2009), SNA (Butts, 2016) and ERGM (Handcock et al., 2018; Hunter et al., 2008), we conducted the core-periphery analysis using the package ECONETWORK (Dray et al., 2020) and we elaborated the figures using the packages GGPLOT2 (Wickham, 2016) and GGALLY (Schloerke et al., 2018) in R 3.6.0 (R Development Core Team, 2019).

To examine if there was a phylogenetic correspondence between trees and mosses in the species-based network, we tested how moss phylogenetic distance is related to different host trees (i.e. their ecological distance). We used the compositional dissimilarity of host trees as an ecological distance descriptor, which is measured as $1 - J$, using the Jaccard index $J = C/(A + B - C)$, where A and B are the number of mosses hosted by each pair of tree species (or the tree species used by each moss pair), and C is the number of species shared between A and B. We estimated phylogenetic distance matrices (for mosses and trees) as the evolutionary distance between each pair of terminal taxa, representing the amount of shared branch length (Swenson, 2014).

We standardised phylogenetic distances using the *decostand* function in R generating values that range from 0 to 1, going from more to less phylogenetically related species. Regarding the individual-based network, we assessed whether tree species within each module were phylogenetically related differentiating from random. To do this, we estimated the mean phylogenetic distance among taxa (Webb, 2000) within each module and compared the observed value against a random distribution obtained after 1,000 matrix iterations, using the R package PICANTE (Kembel et al., 2019).

We obtained the tree species phylogeny using PHYLOMATIC, a database and toolkit used for the assembly of phylogenies (Webb & Donoghue, 2005). We used backbone version R20120829, which is based on APG III (Bremer et al., 2009). The topology produced was age-calibrated with the BLADJ (branch length adjustment algorithm) implemented in PHYLOCOM (Webb et al., 2008) based on the divergence of angiosperms reported by Wikström et al. (2001). The resulting phylogeny of trees was fully resolved. The phylogeny for mosses was built using maximum likelihood method (1,000 bootstrap replicates) based on sequences of *rbcL* (ribulose bisphosphate carboxylase large chain subunit) and *rps4* genes (ribosomal plant S4 subunit) obtained from NCBI GenBank (Table S2). When mosses from our list were not available at GenBank, we used a sequence of species from the same genus (Table S2). Studied genes were independently aligned using multiple sequence alignment ClustalW (Chenna et al., 2003) and concatenated using MEGA7 (Kumar et al., 2016). The resulting matrix had 1,729 sites (1,178 sites from *rbcL* and 551 sites from *rps4*). We used the Tamura 3-parameter evolutionary model (Tamura, 1992) to build the moss phylogeny using DIVEIN web service (Deng et al., 2010). Branches corresponding to partitions reproduced in <50% bootstrap replicates were collapsed.

Conversely, for trees, we assessed how their phylogenetic proximity relates to the compositional dissimilarity of mosses they host. Phylogenetic distance and ecological dissimilarity matrices were correlated using a Mantel test (Rezende et al., 2007) with 999 iterations. A positive relationship between phylogenetic distance with ecological distance matrices suggested a phylogenetic signal on the interaction partners used by species pairs (Swenson, 2014). In our case, a Mantel test is a more accurate estimator of the phylogenetic signal compared to Blomberg's *K* or Pagel's lambda, since these estimators apply only to continuous data (Swenson, 2014).

3 | RESULTS

Moss biomass significantly varied among tree species (ANOSIM $R = 0.370$, $p < 0.001$) and along the vertical profile of tree stems ($R = 0.494$, $p < 0.001$), showing that vertical distribution is not random. Tall trees such as *Amomyrtus luma*, *Amomyrtus meli*, *Podocarpus nubigenus* and *Weinmannia trichosperma* had more moss biomass at higher heights (Figure 2). The number of moss species increased with maximum height of the tree species ($R^2 = 0.52$; $p = 0.006$; Figure S2a); the same pattern was also found on individual trees ($R^2 = 0.58$; $p < 0.001$; Figure S2b). The rarefaction curves show that our sampling effort was enough to sample moss species across tree individuals (92%, Figure S3a), and moss–tree interactions (88%, Figure S3b).

The tree–moss network showed the presence of highly and little connected species, with *Weinmannia trichosperma* and *Podocarpus nubigenus* as the most connected trees and *Weymouthia mollis* and *W. cochlearifolia* as the most connected mosses (Figure 3a). The tree *Aextoxicon punctatum* and the moss *Macromitrium krausei* were the least connected species, linked only to each other in a separate network module. The tree–moss network showed a nested pattern (Figure 4a), which is significantly different from random (NODF = 59.35, $p = 0.001$), and had a L-shaped core-periphery structure (Figure 4b; core-peripheriness = 0.695) with a densely connected 'core' formed by two tree species (*W. trichosperma* and *P. nubigenus*) and two moss species (*W. mollis* and *W. cochlearifolia*), and the remaining species constituted the 'periphery' subset of species sparsely connected to the 'core'. We observed a similar pattern from the individual-based network (Figure 5a), in which we observed a nested pattern (Figure 5b; NODF = 66.74, $p < 0.001$), but we found no core-periphery structure in this case. Also, we observed that degree and centrality increased with tree height (Figure S4) but not with tree diameter (Figure S5).

Then, we simulated extinction scenarios by removing the most and the least connected tree species to explore their effect in the network topology (Figure S6). When we removed the most connected species (*W. trichosperma*), we observed slight changes in the network topology, as the number of links per species decreased but connectance increased, while when we removed the least connected species (*A. punctatum*) both connectance and the number of links per species increased (Table 1). In both scenarios, we observed that nestedness and core-peripheriness values increased, the core-periphery analysis provides a better explanation of the structure changes than nestedness. When the most connected species is excluded, the number of tree species in the 'core' change from two to six due to the loss of *W. trichosperma*, whereas when the least connected species is removed, a third moss species (*Dicranoloma robustum*) is added to the 'core' (Figure S6b). The number of modules was reduced from six to five in both scenarios. When we removed the least connected species, the removal of *A. punctatum* results in the co-extinction of *M. krausei*.

Regarding the phylogenetic analysis of the species-based network, 61% of the internal nodes for the moss phylogeny were resolved. We obtained an ultrametric tree (i.e. a tree with all terminal nodes equal-distant from the root) with 19 tips and 11 internal nodes. We observed a phylogenetic distance of 0.63 ± 0.04 ($M \pm SE$, $N = 78$ pairs) for trees and 0.45 ± 0.02 ($N = 171$ pairs) for mosses. Among trees, the species with the highest mean phylogenetic distance for other tree species was *Saxegothaea conspicua* (Figure 3b), while *Caldcluvia paniculata* and *Eucryphia cordifolia* showed the lowest phylogenetic distances. Among mosses, we found the lowest mean phylogenetic distance for *Hypnum* sp. and the greatest was for *Dicranoloma* sp. (Figure 3b). The ecological distance ($1 - J$) for mosses was 0.73 ± 0.02

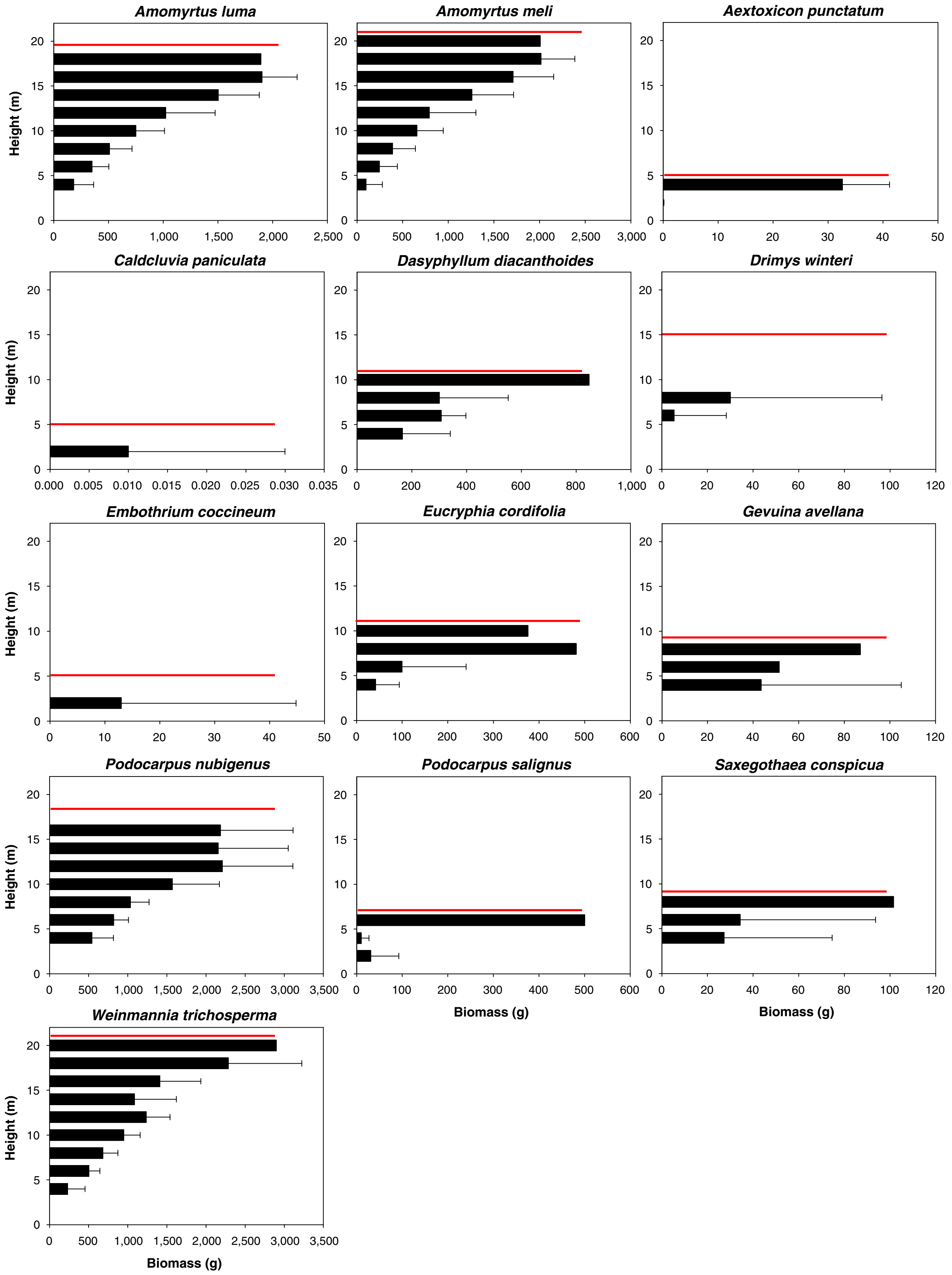
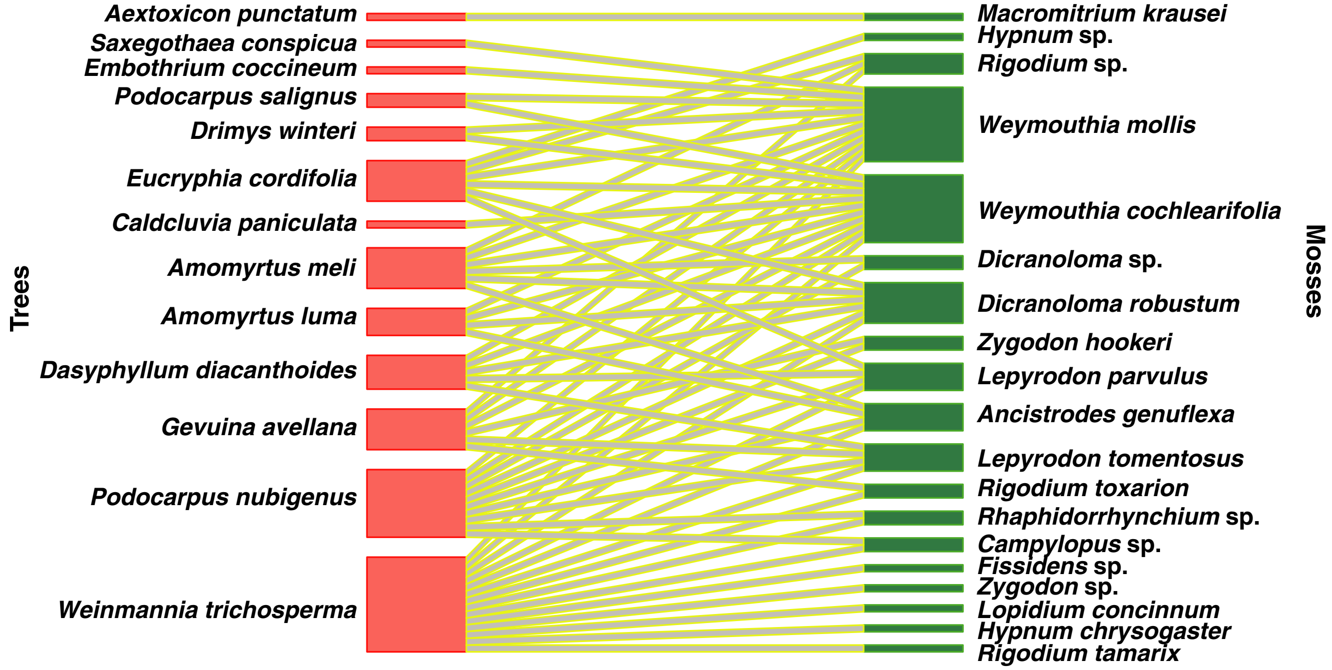


FIGURE 2 Bryophyte biomass along vertical tree profiles (from 2 to 20 m above the ground, measured in 2-m intervals) by tree species. Red lines indicate the maximum height of each tree species. Bars and error bars represent mean and *SE* respectively

(a) Ecological network



(b) Tanglegram

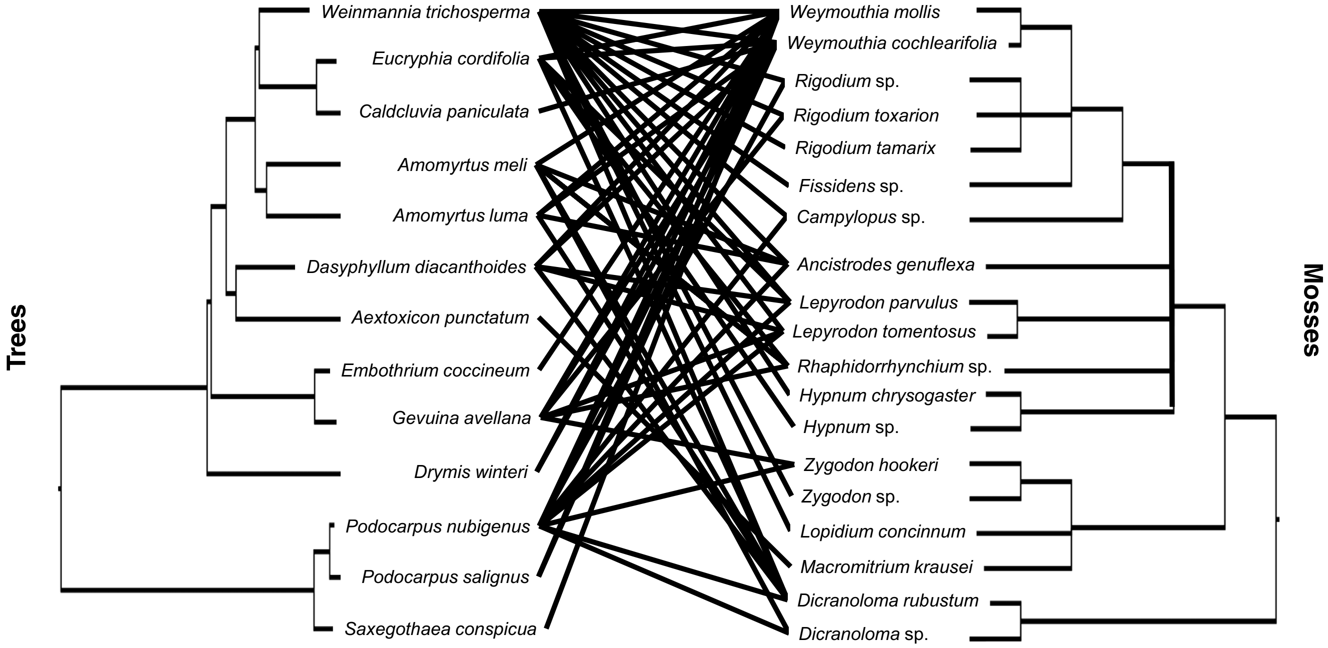


FIGURE 3 (a) Ecological network for tree and moss species. (b) Tanglegram of tree and moss relationships, based on phylogenies estimated using *rcbL* and *rsp4* genes

(N = 171 pairs) and for trees was 0.72 ± 0.02 (N = 78 pairs). Among trees, *Aextoxicon punctatum* showed the highest mean ecological distance when compared with the other trees, while *Drimys winteri* and *Podocarpus salignus* showed the lowest values. Among mosses, *Macromitrium krausei* showed the highest ecological distance compared to the other moss species, while *Campylopus* sp. and *Rigodium* sp. showed the lowest mean ecological distance to other species. The two species with the highest ecological distance in each group are specialists forming a highly specialised module: *A. punctatum* is the exclusive host of *M. krausei*. Mantel tests showed no statistical relationship among phylogenetic and ecological matrices, neither for trees ($r = -0.155$, $p = 0.851$) nor for mosses ($r = -0.049$, $p = 0.617$).

Regarding the individual-based network, we observed a mean phylogenetic distance within modules of 0.307 ± 0.089 (M ± 1 SE),

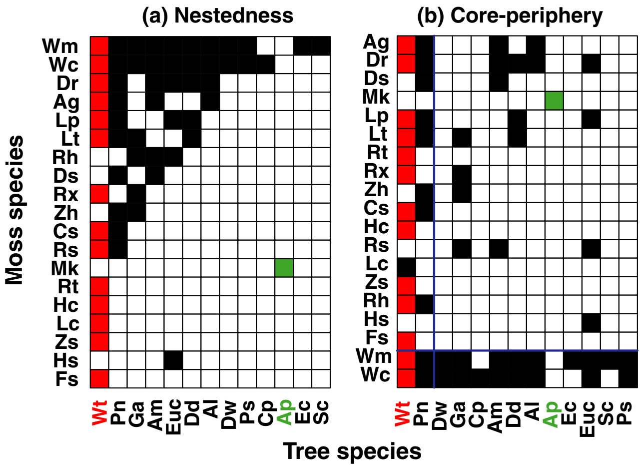


FIGURE 4 (a) Nestedness patterns and (b) core-periphery structure of the tree–moss network. The most connected tree species (*Weinmannia trichosperma*) is labelled in red and the least connected tree species (*Aextoxicon punctatum*) is labelled in green. Tree species abbreviations: Al = *Amomyrtus luma*, Am = *Amomyrtus meli*, Ap = *Aextoxicon punctatum*, Cp = *Caldcluvia paniculata*, Dd = *Dasyphyllum diacanthoides*, Dw = *Drimys winteri*, Ec = *Embothrium coccineum*, Euc = *Eucryphia cordifolia*, Ga = *Gevuina avellana*, Pn = *Podocarpus nubigenus*, Ps = *Podocarpus salignus*, Sc = *Saxegothaea conspicua*, Wt = *Weinmannia trichosperma*. Moss species abbreviations: Ag = *Ancistrodes genuflexa*, Cs = *Campylopus* sp., Dr = *Dicranoloma robustum*, Ds = *Dicranoloma* sp., Fs = *Fissidens* sp., Hc = *Hypnum chrysogaster*, Hs = *Hypnum* sp., Lc = *Lopidium concinnum*, Lp = *Lepyrodon parvulus*, Lt = *Lepyrodon tomentosus*, Mk = *Macromitrium krausei*, Rt = *Rigodium tamarix*, Rx = *Rigodium toxarion*, Rs = *Rigodium* sp., Rh = *Rhaphidorrhynchium* sp., Wc = *Weymouthia cochlearifolia*, Wm = *Weymouthia mollis*, Zh = *Zygodon hookeri*, Zs = *Zygodon* sp.

with this value not being different from those obtained in a null distribution ($Z = -0.981$, $p = 0.274$). Therefore, individual tree modules are not phylogenetically structured either.

For the moss–nest networks, we observed contrasting results for new and old nests. Both nest types had *Ancistrodes genuflexa* as the most abundant moss. However, new nests contained only three moss species, whereas old nests contained seven moss species (Figure S7). As more moss species are incorporated to the nest over time, the number of links per species and connectance values decrease. Furthermore, the network for new nests was not significantly nested, but old-nest network showed a significantly nested (Table 2). We did not find a core-periphery structure in any case. Examining tree–moss and moss–nest networks together (Figure 6), we obtain a tripartite network formed by two significantly nested networks, in which 26% (five out of 19) of the moss species found in the trees are used by the hummingbirds to build their nests, while those five moss species constitute 71% of the species found in the hummingbird nests.

4 | DISCUSSION

Our results show that moss species were non-randomly distributed among tree species in the forest and within hummingbird nests. To the best of our knowledge, this is the first report on community structuring in bryophytes, linking trees and bird behaviour. In this sense, our results suggest an important cryptic ecological interaction in the Valdivian rainforest, with mosses acting as a link between trees and hummingbirds.

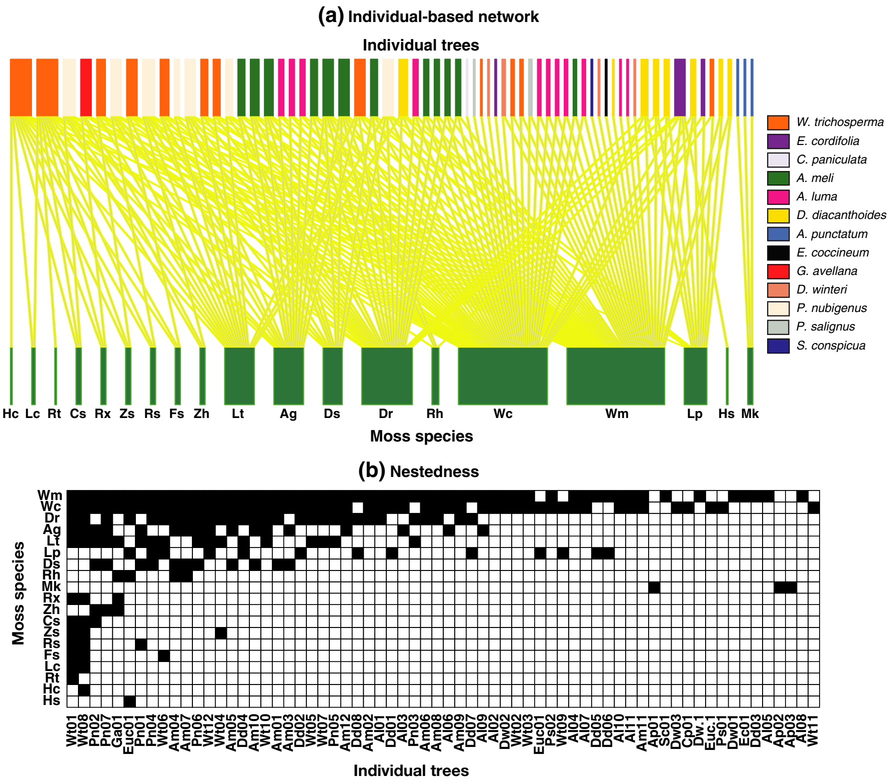


FIGURE 5 Individual-based network for trees and mosses: (a) bipartite network, and (b) nestedness pattern (species abbreviations as in Figure 4)

TABLE 1 Descriptors for the tree–moss networks built. Results presented correspond to the full network (all species included) and the resulting networks when the most connected (MC: *Weinmannia trichosperma*) or the least connected tree species (LC: *Aextoxicon punctatum*) were removed. *p*-Values correspond to the comparison of observed network with null models (significant values indicate results different from random)

	Complete network		MC excluded		LC excluded	
Metric	**Estimate**	***p*-Value**	**Estimate**	***p*-Value**	**Estimate**	***p*-Value**
Links per species	1.84	<0.001	1.73	<0.001	1.93	<0.001
Connectance	0.24	<0.001	0.27	<0.001	0.27	<0.001
Nestedness (NODF)	59.35	<0.001	61.08	<0.001	67.48	<0.001
Core-peripheriness	0.695	—	0.978	—	0.776	—
Modules	6	0.399	5	0.063	5	0.552

TABLE 2 Descriptors for the moss–nest networks built; nests correspond to new (i.e. freshly made) or old nests (1-year-old) built by the hummingbird *Sephanoides sephaniodes*. *p*-Values correspond to the comparison of observed networks with null models; significant values indicate results different from random

	New nests		Old nests	
Metric	**Estimate**	***p*-Value**	**Estimate**	***p*-Value**
Links per species	2.15	<0.001	1.90	<0.001
Connectance	0.61	<0.001	0.33	<0.001
Nestedness (NODF)	51.16	0.332	50.3	0.013
Core-peripheriness	0	—	0	—
Modules	2	—	3	0.827

Tree height was important not only for the number of moss species present along tree stems but also their vertical biomass distribution. Moss biomass was highly variable among tree species with four tree species (*Amomyrtus luma*, *Amomyrtus meli*, *Podocarpus nubigenus* and *Weinmannia trichosperma*) carrying most of the moss biomass. In tall trees (except *Drimys winteri*), moss biomass increased with height. Thus, tall trees will have more abundant biomass than smaller trees. Our results (based on *N* = 120 trees) are consistent with similar assessments that had smaller sample sizes (*N* = 7 in Clement et al., 2001; *N* = 3 in Diaz et al., 2010; *N* = 10 in Mellado-Mansilla et al., 2017).

Our tree–moss networks (both species- and individual-based) showed a nested pattern. Contrary to our initial expectations, we observed that tree–moss associations were not phylogenetically constrained, indicating that these associations are mainly determined by ecological rather than by evolutionary factors. Ecological factors potentially related to moss distribution in trees are moss dispersal (Löbel et al., 2009; Osorio-Zuñiga et al., 2014), vegetation cover (Pouliot et al., 2011) and bark roughness (Dislich et al., 2018). All these are non-mutually exclusive determinants of mosses distribution on trees, and complementary studies are required to assess the specific contribution of each for the moss–tree network structure.

Our extinction simulations suggest that the non-random removal of a tree species (which can commonly happen by selective logging) would have important consequences for network topology, altering network topology and causing the co-extinctions of specialist moss species. Such structural changes are evident when we examine the core-periphery plots (Figure S6b); removing the most connected species alters the tree species in the 'core' while removing the least connected species alters the moss species in the 'core'. In a particular case, removing the most connected tree species (*Weinmannia trichosperma*) altered network modularity and put five specialist moss species at risk. In our study system, taller trees were also the most connected and constituted more connected and central nodes than lower trees. Selective logging of taller trees, a common practice in the Chilean temperate rainforest, may cause impacts in tree–moss interactions as the number of moss species increases with maximum tree height. This will then indirectly affect the availability of nest material.

Conversely, removal of the least connected tree species (*Aextoxicon punctatum*, an endangered species) leads to the co-extinction of *M. krausei*. This finding stresses how cryptic interactions can be lost in changing landscapes, leading to the loss of rare species. Exemplified by these two extreme scenarios and due to the non-random nature of the moss–tree relationships, the removal of a single or a few tree species can have cascading effects on the mosses, and further on the animal species that use them for nesting. The pollinator hummingbird *S. sephaniodes* is a vulnerable species in this light.

We observed contrasting results regarding the moss species used for nest building by *S. sephaniodes* between new and old nests. Although freshly made nests are composed of only three moss species, old nests had up to six moss species in the same nest. The increase in moss diversity within nests may result either from the presence of spores that germinated in the second year or accumulation of new material collected by hummingbirds (Osorio-Zuñiga et al., 2014), also related to their proximity to taller trees (mainly *Amomyrtus meli* and *A. luma*) that hold a high moss diversity. The most abundant species in both new and old nests is *Ancistrodes genuflexa*, a hanging moss that is usually associated with the tree species *A. luma* and *A. meli* but also found on *Podocarpus nubigenus* and *Weinmannia trichosperma*. *Ancistrodes genuflexa* constitutes up to 97% of the dry nest biomass but represents only 0.1% of the total moss biomass in the sampled trees. A previous study attributed this finding to an active selection by *S. sephaniodes* (Osorio-Zuñiga et al., 2014), which was recently associated to unique antimicrobial properties that

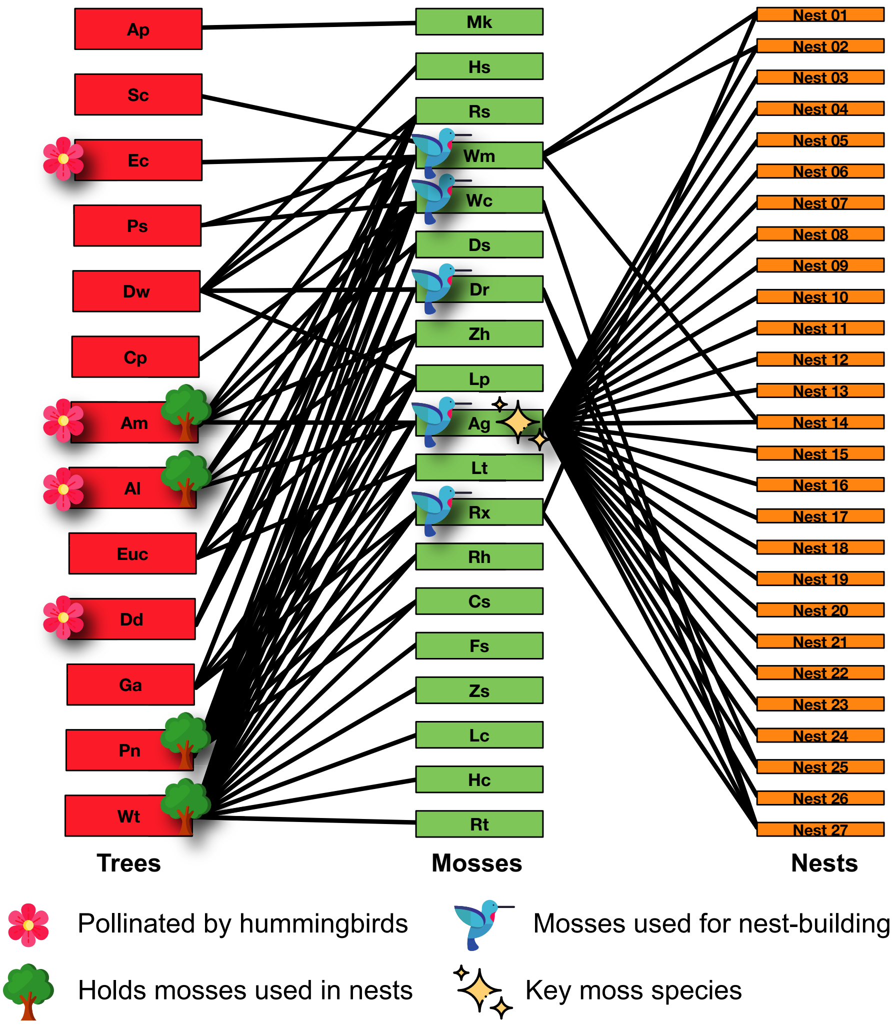


FIGURE 6 Direct and indirect relationships of the tree–moss–nest tripartite system, represented as a tripartite network showing the links between trees and mosses, and between mosses and hummingbird nests (species abbreviations as in Figure 4)

A. genuflexa has (Fontúrbel, Osorio, Riffo et al., 2020). Therefore, moss material used for nest building seems to have limited substitutability.

The tripartite system (trees–mosses–hummingbird nests) examined here provides a unique opportunity to use a tripartite ecological networks (Fontaine et al., 2011; Pilosof et al., 2017) to assess cryptic links in the community. In this tripartite network, 26% of the moss species (five species) found in the trees can be found in hummingbird nests (representing 71% of the moss species found in the nests; Figure 6). This tripartite network is formed by two nested bipartite networks, which provides robustness to the entire system (Fontaine et al., 2011). Considering that most moss biomass in the nests corresponds to *A. genuflexa* (Osorio-Zuñiga et al., 2014), this moss is an important link within the tripartite network. Four tree species (*A. meli*, *A. luma*, *P. nubigenus* and *W. trichosperma*) are indirectly important for nest building, as they contain all the mosses used for nest building. Therefore, the removal of those trees (which are commonly logged for firewood in southern Chile) can produce extinction cascades (Pilosof et al., 2017), possibly affecting nest material supply for hummingbirds and indirectly compromising the pollination of other tree species. Beyond our study system, the conceptual model proposed here (Figure 1) can be used to understand the direct and indirect effects of those interactions at the community level. We initially conceptualised tree–moss associations (Ceballos et al., 2016) as commensalism, without assuming harm or benefit for the trees (while mosses are benefited from microhabitat conditions), but trees hosting large moss biomass may have important costs, leaving this question open for future studies. On the other hand, nest–moss associations can be considered as mutualistic, given the synzoochoric relationship between *S. sephaniodes* and the mosses (Osorio-Zuñiga et al., 2014). Mosses may benefit by having their spores dispersed longer distances, while hummingbirds benefit by having a functional nest material for egg and chick survival (Fontúrbel, Osorio, Riffo et al., 2020).

In conclusion, we found that the links among mosses, trees and hummingbirds are non-random. On the one hand, the tree–moss relationship governed by host preferences among the mosses determines the nesting material available to hummingbirds. On the other hand, hummingbird moss selection and the location of their nests favour the dispersal of some moss species. While *S. sephaniodes* relies on particular moss species for nesting, these mosses are associated with specific tree species and present at specific heights. Natural or human disturbances on those trees may have repercussions on nesting material availability, indirectly affecting *S. sephaniodes* reproductive success.

Because *S. sephaniodes* is the most important vertebrate pollinator in the temperate rainforests of South America, this may, in turn, affect the demography of many species of flowering plants. Given that trees are also dependent on this pollinator, changes in hummingbird demography may also affect the moss epiphytes, completing the loop. These relationships among tree, bird and moss species display the importance of indirect interactions in this complex, but potentially sensitive ecosystem. Beyond our study system, the cryptic nature of interactions, including mosses, ubiquitous in many ecosystems suggests that their role in community processes still has many hidden surprises awaiting discovery.

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AUTHORS' CONTRIBUTIONS

F.E.F. and F.O. designed the study; F.O. collected field data; F.E.F., V.R.-D. and G.O.C. analysed data; G.O.C. conducted phylogenetic analyses; F.E.F. and H.R. lead the writing of the manuscript. All authors approved the final version for publication.

DATA AVAILABILITY STATEMENT

Original data and R code associated with this article are available from the figshare digital repository https://doi.org/10.6084/m9.figshare.7859864 (Fontúrbel, Osorio, Riffo-Donoso et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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