



Interaction network of vascular epiphytes and trees in a subtropical forest



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ABSTRACT

The commensalistic interaction between vascular epiphytes and host trees is a type of biotic interaction that has been recently analysed with a network approach. This approach is useful to describe the network structure with metrics such as nestedness, specialization and interaction evenness, which can be compared with other vascular epiphyte-host tree networks from different forests of the world. However, in several cases these comparisons showed different and inconsistent patterns between these networks, and their possible ecological and evolutionary determinants have been scarcely studied. In this study, the interactions between vascular epiphytes and host trees of a subtropical forest of sierra de San Javier (Tucuman, Argentina) were analysed with a network approach. We calculated metrics to characterize the network and we analysed factors such as the abundance of species, tree size, tree bark texture, and tree wood density in order to predict interaction frequencies and network structure. The interaction network analysed exhibited a nested structure, an even distribution of interactions, and low specialization, properties shared with other obligated vascular epiphyte-host tree networks with a different assemblage structure. Interaction frequencies were predicted by the abundance of species, tree size and tree bark texture. Species abundance and tree size also predicted nestedness. Abundance indicated that abundant species interact more frequently; and tree size was an important predictor, since larger-diameter trees hosted more vascular epiphyte species than small-diameter trees. This is one of the first studies analyzing interactions between vascular epiphytes and host trees using a network approach in a subtropical forest, and taking the whole vascular epiphyte assemblage of the sampled community into account.

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1. Introduction

Vascular epiphytes are plants that germinate and grow on other plants without contact with the soil, and, in contrast to mistletoes, without parasitizing their hosts (Zotz, 2013). They are found in the canopy and exhibit a highest richness and abundance in largest and oldest trees (Benzing, 1990; Hietz and Hietz-Seifert, 1995; Ter Steege and Cornelissen, 1989). Vascular epiphytes are common in subtropical, tropical and temperate forests, reaching up to 10% of the world's total flora, and in some places they constitute one third of all plant species (Gentry and Dodson, 1987; Kress, 1986). They are an important component of the Neotropics biodiversity, not only in terms of the number of species they represent, but also due to the biomass they accumulate (Benzing, 1990; Gentry and Dodson, 1987;

Nadkarni, 1984). Despite their importance, ecological studies about vascular epiphytes are scarce in comparison to soil-rooted plants for which major insights have been gained in the last decades (Mendieta-Leiva and Zotz, 2015).

Vascular epiphytes depend on host trees for establishment and support, and the interaction among these plants includes a complex array of potential interactive mechanisms (Callaway et al., 2002). Host trees provide substrate for vascular epiphytes, and therefore, the success of the establishment may be determined by certain host tree traits (Wagner et al., 2015). These traits include trees size (i.e. larger trees are bigger and older and thus provide different microhabitats), architectural characteristics (e.g. shape and branching patterns), chemical composition, and bark morphology (e.g. bark roughness), which in turn might be related to substrate moisture conditions, phenological patterns, bark stability, canopy structure, and others (Benzing, 1990; Hietz and Hietz-Seifert, 1995; Hirata et al., 2009; Laube and Zotz, 2006; Wagner et al., 2015; Woods et al., 2015). All these factors are likely to vary

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among hosts (Callaway et al., 2002) and therefore, trees may offer different conditions according to their own subset of traits.

Vascular epiphyte-host tree interactions are commensal because epiphytes rely entirely on host trees for support, and rarely harm them (Blick and Burns, 2009). The interaction networks among these plants are composed by three main parts: vascular epiphytes, host trees, and links (interactions) between species. As other types of species interactions (Bascompte et al., 2003; Thébault and Fontaine, 2010; Verdú and Valiente-Banuet, 2008), commensalistic interactions between vascular epiphytes and host trees have recently been described and analysed with network approaches (Blick and Burns, 2009; Burns, 2007; Piazzon et al., 2011; Sáyago et al., 2013; Silva et al., 2010; Taylor et al., 2016; Zhao et al., 2015). One benefit of conceiving these species interactions as networks is that several metrics can be used to describe their structure, such as nestedness, interaction evenness, and specialization (Blick and Burns, 2009). In certain forests, vascular epiphyte-host tree interaction networks show a nested structure (i.e. the tendency of specialists to interact with subsets of the species interacting with generalists; Piazzon et al., 2011), high interaction evenness (Sáyago et al., 2013; Zhao et al., 2015; i.e. the absence of dominance of few interactions) and low levels of specialization (Sáyago et al., 2013; Zhao et al., 2015). Other patterns were reported for vascular epiphyte-host tree interaction networks in other regions (Burns, 2008; Burns and Zotz, 2010). For instance, Burns (2008) found that facultative vascular epiphytes in coastal conifer forests of Canada are compartmentalized, owing to five similar shrub species that tended to co-occur. Also, in a Panamanian rain forest, Burns and Zotz (2010) observed that the vascular epiphyte-host tree network showed evidence of a checkerboard pattern (i.e. species pairs replacing one another among communities; Diamond, 1975).

Studies on vascular epiphyte-host tree networks pointed out that species interact according to their abundance (Burns, 2007; Sáyago et al., 2013); meaning that abundant species interact more frequently and with more species than rare species (Vázquez et al., 2009). Studies of mutualistic networks found out that other factors in addition to abundance could influence the network structure (e.g. Olito and Fox, 2014; Vázquez et al., 2009). To our knowledge, only one study analysed different factors influencing the structure of a vascular epiphyte-host tree network. Sáyago et al. (2013) tested different factors which might explain or predict interactions frequencies and several network metrics in a bromeliad-host tree network from a tropical dry forest of Mexico. The most important factors in this study were species abundance, species spatial overlap and host traits such as size, wood density, and bark texture (Sáyago et al., 2013). This study, however, was restricted to one family of epiphytes (Bromeliaceae). Thus more studies are necessary to improve our knowledge of the factors that explain the structure of vascular epiphyte-host tree networks taking the whole assemblage of epiphyte communities into account.

By using a dataset of vascular epiphytes and host trees from a subtropical forest of sierra de San Javier (Tucuman, Argentina), we addressed the following questions: 1. What are the characteristics of the structure of the vascular epiphyte-host tree interaction network? 2. Are abundance and certain tree traits (dbh, bark texture and wood density) important to predict interaction frequencies in this network? 3. Are these factors important to predict certain network metrics (nestedness, interaction evenness and connectance)? We hypothesize that the vascular epiphyte-host tree network presents a nested structure, such as the majority of the interaction networks involving obligate vascular epiphytes. Also, we expect abundance and host tree traits to predict interaction frequencies and metrics of the vascular epiphyte-host tree network.

2. Material and methods

2.1. Study area

We studied the vascular epiphyte assemblage in a subtropical forest of Parque sierra de San Javier (−26.761957 S, −65.332857 W), a protected area in Tucuman province, Argentina. The area represents the southern-most extension of the Neotropical Andean montane forests, also known as “Yungas” (Cabrera, 1976). Yungas forests extend along discontinuous mountain ranges in north-western Argentina, from the border with Bolivia (22°S), down to Catamarca province (29°S), representing a forest belt of 700 km length and 50 km width, with an altitudinal range of 400–3000 m a.s.l. Annual rainfall in the study area ranges from 1300 to 1600 mm and the region presents a seasonal monsoonal regime with dry winters and wet summer seasons (Bianchi, 1981). Mean annual temperature is 18.8 °C.

The study area is located at 1000 m in elevation in a subtropical semi deciduous old-growth forest with an average of 23 tree species ha^{−1} (Malizia and Grau, 2006). Canopy vegetation (>20 m) is dominated by *Blepharocalyx salicifolius* (Myrtaceae), *Ocotea porphyria* (Lauraceae) and *Pisonia ambigua* (Nyctaginaceae); while understorey vegetation (5–12 m) is dominated by *Eugenia uniflora* (Myrtaceae), *Piper tucumanum* (Piperaceae) and *Allophylus edulis* (Sapindaceae) (Malizia and Grau, 2006). This forest has been selectively logged c. 50 y ago, probably for the species *Cedrela angustifolia* (Meliaceae) and *Juglans australis* (Juglandaceae), of which only two cut stumps were found in the plot (Grau, 2002; Grau and Brown, 1998).

Vascular epiphytes are very common in these subtropical forests, and they are distributed mainly on larger trees, such as *Ocotea porphyria*, *Blepharocalyx salicifolius*, *Parapiptadenia excelsa* (Fabaceae) and *Juglans australis* (Ayarde, 1995; Brown, 1990; Meyer, 1963). However, diversity of vascular epiphytes in these forests is low compared to that of other tropical forests (Brown, 1990). A previous study found 13 vascular epiphytes species distributed on 12 host tree species in a subtropical forest of sierra de San Javier (Roldán, 1995). The most common families of vascular epiphytes are Polypodiaceae, Aspleniaceae, Piperaceae, Cactaceae and Bromeliaceae and the most common species are *Pleopeltis tweediana* (Polypodiaceae) and *Peperomia* sp. (Piperaceae) (Ayarde, 1995; Brown, 1986; Roldán, 1995).

2.2. Sampling data

Data sampling consisted of vascular epiphytes surveys in randomly selected 20 × 20 m quadrants at three permanent plots located along the study area. We sampled 10 quadrats in each plot, resulting in 30 sampled quadrants (a total of 1.2 ha). These permanent plots belong to a forest monitoring system of the *Instituto de Ecología Regional* (IER) established in 1991–1992, in which every tree with a diameter at breast height (dbh) ≥ 10 cm was marked with an aluminium tag and re-measured every 5 years. For the purposes of this paper, the information used (species identity, dbh and tree abundance) corresponds to the last re-measurement, conducted between 2011 and 2012.

Observational surveys of vascular epiphytes were performed on trees with dbh ≥ 10 cm. Trees <10 cm dbh usually lacked of vascular epiphytes and were thus not considered (Burns, 2007). Surveys consisted on the observation of the entire tree surface, since vascular epiphytes in this forest grow from the basal part of the trunk to the outer part of branches. Observations were performed with binoculars from the ground. We selected this data sampling method due to its feasibility (a large number of hosts can be recorded in a short time), ability to replicate (each tree species was

represented by several individuals), height of the forest canopy (relatively accessible to observation of vascular epiphytes in comparison with other forests; mean average = 8.85 m, considering all trees with dbh ≥ 10 cm) and the relatively low richness of vascular epiphytes (16 spp. ha⁻¹; Ayarde, 1995). Vascular epiphyte occurrence was recorded in the five zones of trees, from the base to the crown, following the methodology proposed by Johansson (1974). However, we could not identify individuals, because most vascular epiphytes in the study area are rhizomatous ferns and angiosperms with clonal growth and asexual reproduction (Brown, 1990). For this reason, we considered the number of zones occupied by each vascular epiphyte species as a proxy of abundance. While this measure does not represent abundance itself, this method resulted adequate, since, according to our observations, species that were present in more zones were also the most abundant. Hereafter, we refer to abundance of each vascular epiphyte species as the absolute number of occupied zones in all sampled trees. Data was collected during summer and autumn of 2015 (from March to July).

2.3. Analysis of the structure of the vascular epiphyte-host tree network

We developed a presence-absence matrix between vascular epiphyte species (in columns) and host tree species (in rows). Based on the same distribution of species in rows and columns, we constructed a quantitative matrix with cell values containing the number of observed interactions between vascular epiphytes and tree species.

To characterize the structural parameters of the vascular epiphyte-host tree network (Objective 1) we calculated the following metrics: connectance, interaction evenness, H2, generality and vulnerability, and nestedness. Interaction evenness, H2, generality and vulnerability were calculated with the quantitative matrix, while connectance and nestedness were calculated with the presence-absence matrix.

Connectance: number of observed interactions divided by the total possible interactions (Dunne et al., 2002).

Interaction evenness: metric for detecting potential interaction dominance in an ecological network (Dormann et al., 2009); with higher values implying similar abundance among interactions, and lower values implying that few interactions are dominant.

H2: a quantitative measure of specialization (Blüthgen et al., 2006). If specialised or generalised species prevail, the network will be more specialised or generalised, respectively (Sfair et al., 2015). This metric runs from 0, for no specialization, to 1 for perfect specialization (Blüthgen et al., 2006).

Generality and vulnerability: weighted mean number of tree species per vascular epiphyte species, and vascular epiphyte species per tree species, respectively (Bersier et al., 2002; Sáyago et al., 2013).

Nestedness: the degree of nestedness of the given binary matrix was estimated with two different metrics: NODF (nestedness metric based on overlap and decreasing fill; Almeida-Neto et al., 2008), and nestedness temperature (Atmar and Patterson, 1993). We then assessed nestedness significance with different null models, by repeating random sampling to generate patterns that were then compared with the observed nestedness pattern (Bascompte et al., 2003). NODF varies from 0 to 100 (lower to higher values of nestedness, respectively), while nestedness temperature runs from 0 to 100 (with 0 implying maximum nestedness).

All metrics were obtained in R (R Development Core Team., 2015) using bipartite package (Dormann et al., 2009), except for NODF metric, which was calculated with ANINHADO 3.0 program (Guimaraes and Guimaraes, 2006).

2.4. Evaluating models to predict interactions frequencies

In order to predict the interaction frequencies of the vascular epiphyte-host tree network (Objective 2), we evaluated species abundance and host traits (size, bark texture and wood density) as predictors, which were selected based on the following reasons:

Abundance: included to assess whether abundant species interact more frequently. We considered the abundance of both trees and vascular epiphytes species in the matrix.

Size: tree diameter at breast height (dbh) was considered as a proxy of tree size and was obtained from the permanent plot database of IER (Table 1). This variable was selected because large diameter trees provide better traits for vascular epiphytes (e.g. more surface and microhabitats; Burns, 2008; Woods et al., 2015).

Bark texture: by definition, it is the roughness of the bark, an important factor associated to vascular epiphytes presence. Information on bark texture was derived from field observations, using the following scores: 1 (smooth: a very slight texture), 2 (little rough: coarse with a micro relief) and 3 (rough: a coarse texture with fissures, Table 1). Higher scores were assigned to rough bark trees since they provide more appropriate conditions for vascular epiphytes.

Wood density: defined as wood mass per unit volume; it was selected as a proxy of host traits influencing epiphyte presence, such as growth, longevity, and structural strength of trees (Easdale, 2006; Hirata et al., 2009; Pérez-Harguindeguy et al., 2013; Sáyago et al., 2013). Wood density (expressed in g/cm³) information was obtained from Easdale et al. (2007), Easdale (2006) and INTI-CITEMA database (Table 1).

Vascular epiphyte and tree species abundance (A), tree size (S), tree bark texture (B), and tree wood density (W) represent factors that were used to build models. By combining the factors, we created a total of six two-constraints models (AS: abundance + size, AB: abundance + bark texture, AW: abundance + wood density, SW: size + wood density, BW: bark texture + wood density, SB: size + bark texture), four three-constraints models (ASB: abundance + size + bark texture, ASW: abundance + size + wood density, ABW: abundance + bark texture + wood density, BSW: bark texture + size + wood density) and one four-constraint model (ASBW: abundance + size + bark texture + wood density). We also developed a null model in which all interactions have the same probability to occur. The ability of the models to explain interaction frequencies of the observed matrix was analysed following the methodology of Vázquez et al. (2009), using Akaike's information criterion (AIC, Bolker, 2008). AIC values are lower in better models (see Supplementary material).

2.5. Evaluating models to predict network metrics

To evaluate the performance of the models for predicting nestedness, interaction evenness and connectance (Objective 3) we implemented the methodology proposed by Vázquez et al. (2009). The method assigns the total observed number of interactions to create new matrices using the information provided by the models. For each model, we generated 1000 networks and obtained network metrics for each of them. With all these values, we defined confidence intervals (95%) for each model and evaluated whether they overlapped with the metric value of the observed network.

3. Results

The interaction network presented 128 links between 20 vascular epiphyte species (Table 2) and 24 tree species (Table 1). Vascular epiphyte species interacting with a higher number of tree species were: *Pleopeltis tweediana* (21 tree species), *Peperomia*

Table 1

List of the tree species at the sample plots in a subtropical forest of Argentina. Bark texture: 1 (smooth), 2 (slightly rough) and 3 (rough). Dbh: dbh average of tree individuals found in all sample plots.

Tree species	Family	Code	Abundance	Epiphyte richness	Wood density (g/cm ³)	Bark texture	Mean dbh
<i>Allophylus edulis</i> (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl.	Sapindaceae	Aed	52	9	0.622	2	16.24
<i>Aralia soratensis</i> Marchal	Araliaceae	Aso	2	4	0.415	3	23.96
<i>Blepharocalyx salicifolius</i> (Kunth) O. Berg	Myrtaceae	Bsa	9	4	0.685	3	18.38
<i>Cedrela angustifolia</i> DC.	Meliaceae	Cag	3	4	0.404	3	39.41
<i>Citrus aurantium</i> L.	Rutaceae	Cau	1	3	0.730	1	12.63
<i>Cupania vernalis</i> Cambess.	Sapindaceae	Cve	6	2	0.675	1	12.35
<i>Duranta serratifolia</i> (Griseb.) Kuntze	Verbenaceae	Dse	6	2	0.547	3	13.73
<i>Eugenia uniflora</i> L.	Myrtaceae	Eun	96	6	0.865	1	12.99
<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	Bigoniaceae	Him	2	4	0.965	3	29.14
<i>Heliocarpus popayanensis</i> Kunth	Tiliaceae	Hpo	1	2	0.275	1	29.62
<i>Myrcianthes pungens</i> (O. Berg) D. Legrand	Myrtaceae	Mpu	49	7	0.911	1	30.91
<i>Myrsine laetevirens</i> (Mez) Arechav.	Myrsinaceae	Mla	11	5	0.558	2	22.48
<i>Ocotea porphyria</i> (Griseb.) van der Werff	Lauraceae	Opo	35	16	0.453	3	59.98
<i>Parapiptadenia excelsa</i> (Griseb.) Burkart	Fabaceae	Pex	16	10	0.653	2	55.34
<i>Piper tucumanum</i> C. DC.	Piperaceae	Ptu	81	5	0.457	1	13.08
<i>Pisonia zapallo</i> Griseb.	Nyctaginaceae	Pza	41	10	0.357	2	34.96
<i>Ruprechtia apetala</i> Wedd.	Polygonaceae	Rap	2	3	0.710	2	18.79
<i>Ruprechtia laxiflora</i> Meisn.	Polygonaceae	Rla	12	8	0.653	3	23.76
<i>Solanum riparium</i> Pers.	Solanaceae	Sri	11	2	0.494	2	19.51
<i>Terminalia triflora</i> (Griseb.) Lillo	Combretaceae	Ter	45	12	0.710	2	38.36
<i>Tipuana tipu</i> (Benth.) Kuntze	Fabaceae	Tti	2	5	0.607	3	63.38
<i>Urera baccifera</i> (L.) Gaudich.	Urticaceae	Uba	4	2	0.165	2	12.42
<i>Urera caracasana</i> (Jacq.) Gaudich. ex Griseb.	Urticaceae	Uca	2	1	0.277	2	13.06
<i>Zanthoxylum coco</i> Gillies ex Hook. f. & Arn.	Rutaceae	Zco	2	2	0.472	2	24.12

Table 2

List of vascular epiphyte species found at the sample plots in a subtropical forest of Argentina. The abundance of each vascular epiphyte species was recorded as the total number of zones where it was present, considering all trees in all quadrats.

Vascular epiphytes species	Family	Code	Abundance
<i>Aechmea distichantha</i> Lem.	Bromeliaceae	Adi	127
<i>Asplenium praemorsum</i> Sw.	Aspleniaceae	Apr	12
<i>Campyloneurum aglaolepis</i> (Alston) de la Sota	Polypodiaceae	Cag	15
<i>Microgramma squamulosa</i> (Kaulf.) de la Sota	Polypodiaceae	Msq	224
<i>Gomesa viperina</i> (Lindl.) M.W. Chase & N.H. Williams	Orchidaceae	Gvi	7
<i>Peperomia hispiduliformis</i> Trel.	Piperaceae	Phi	1
<i>Peperomia tetraphylla</i> Hook. & Arn.	Piperaceae	Pte	462
<i>Peperomia</i> sp.	Piperaceae	Psp	62
<i>Phlebodium areolatum</i> (Humb. & Bonpl. ex Willd.) J. Sm.	Polypodiaceae	Par	14
<i>Pleopeltis minima</i> (Bory) J. Prado & R.Y. Hirai	Polypodiaceae	Pmi	1
<i>Pleopeltis tweediana</i> (Hook.) A.R. Sm.	Polypodiaceae	Ptw	379
<i>Rhipsalis aculeata</i> F.A.C. Weber	Cactaceae	Rac	1
<i>Rhipsalis floccosa</i> Pfeiff.	Cactaceae	Rfl	61
<i>Tillandsia didisticha</i> (E. Morren) Baker	Bromeliaceae	Tdi	5
<i>Tillandsia tenuifolia</i> L.	Bromeliaceae	Tte	32
<i>Vriesea friburgensis</i> Mez	Bromeliaceae	Vfr	14
<i>Urera baccifera</i> (L.) Gaudich.	Urticaceae	Uba	1
<i>Rhipsalis lorentziana</i> Griseb.	Cactaceae	Rlo	5
<i>Tillandsia</i> sp	Bromeliaceae	Tsp	1
<i>Tillandsia tricholepis</i> Baker	Bromeliaceae	Ttr	1

tetraphylla (Piperaceae, 20 species), *Peperomia* sp. (14 species), *Aechmea distichantha* (Bromeliaceae, 12 species) and *Microgramma squamulosa* (Polypodiaceae, 11 species) (Fig. 1). Tree species interacting with a higher number of vascular epiphyte species were: *Ocotea porphyria* (16 species), *Terminalia triflora* (Combretaceae, 12 species), *Parapiptadenia excelsa* and *Pisonia zapallo* (10 species each) (Fig. 2). The most frequent interactions were *Peperomia tetraphylla* in *Terminalia triflora* (31 times) and *Ocotea porphyria* (28 times), *Microgramma squamulosa* in *Terminalia triflora* (28 times), *Pleopeltis tweediana* in *Terminalia triflora* (26 times) and *Ocotea porphyria* (24 times), and *Aechmea distichantha* in *Ocotea porphyria* (24 times).

The vascular epiphyte-host tree network showed a low level of connectance (0.26), an even distribution of interactions (Interaction evenness = 0.64, max = 1) and very low levels of specialization

($H_2 = 0.084$, 0 = no specialization, 1 = perfect specialization). Vascular epiphyte species interacted on average with 8.47 tree species (generality) while tree species interacted with 5.7 vascular epiphyte species (vulnerability). The network showed a nested structure, independently of the metric used (Fig. 3). The nested temperature of the network was $T = 6.9$ (min = 0, max = 100) and was lower than the null model (T mean for 3-type null model = 28, $p < 0.001$). The $NODF_{total}$ metric had a value of 37.6 ($N_{rows} = 37.02$, $N_{columns} = 38.43$; min = 0, max = 100), which was also significantly higher than that of the null models Er ($NODF_{Er} = 14.18$, $p < 0.001$) and Ce ($NODF_{Ce} = 21.57$, $p < 0.001$).

AIC values showed that all the determinants tested to predict observed frequencies of the vascular epiphyte-host tree interaction matrix had a better performance than the null matrix, but far from the better fitting probability model (Fig. 4). Wood density was the

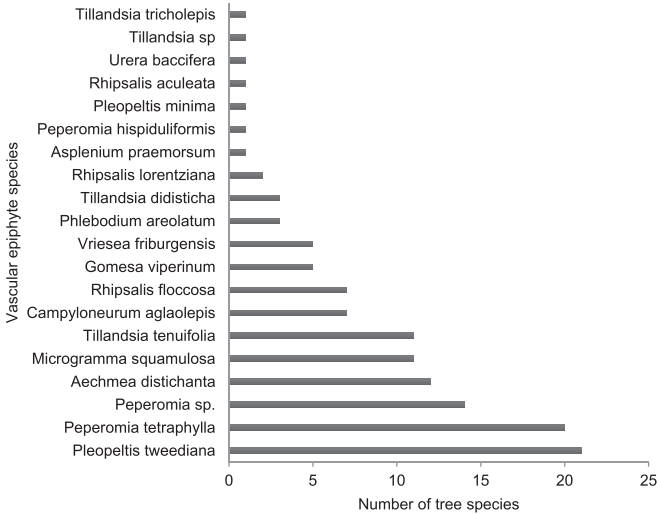


Fig. 1. Number of tree species interacting with each vascular epiphyte species in a subtropical forest of Argentina.

only exception, with higher values than the null model and less contribution to explain the observed data. The combined probability matrix ASB presented the lowest AIC value, for which the combination between abundance, size and bark texture of host trees was the best model to predict interaction frequencies in this network. Abundance was the variable that contributed the most to explain the observed patterns, and the combination between abundance and the other factors was better than the other combinations and the factors alone.

Network metrics such as nestedness and interaction evenness were predicted by models including abundance, while no model predicted connectance (Fig. 5). As expected, the null model did not predict any of the metrics. Models which did not include abundance were as bad as the null model.

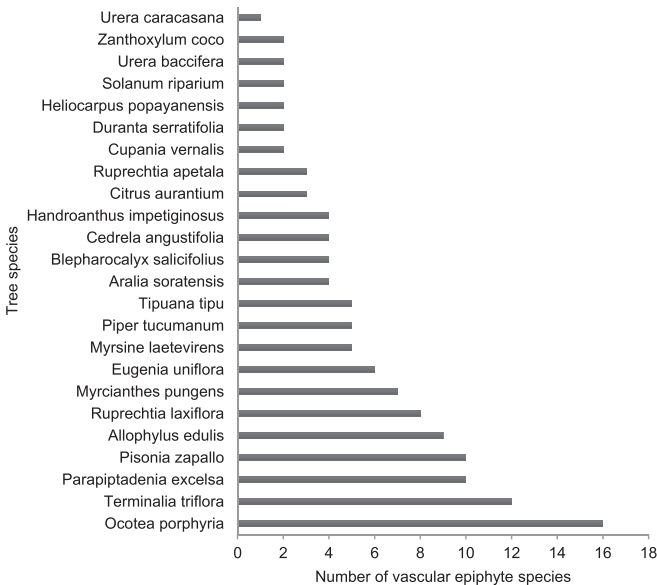


Fig. 2. Number of vascular epiphyte species interacting with each tree species in a subtropical forest of Argentina.

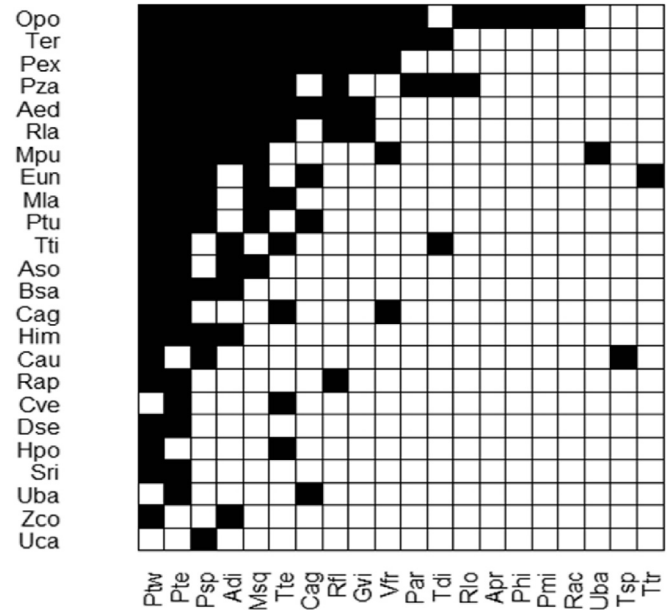


Fig. 3. Occurrence of vascular epiphyte species (columns) in tree host species (rows) in a subtropical forest of Argentina. See Tables 1 and 2 for tree and vascular epiphyte species abbreviations.

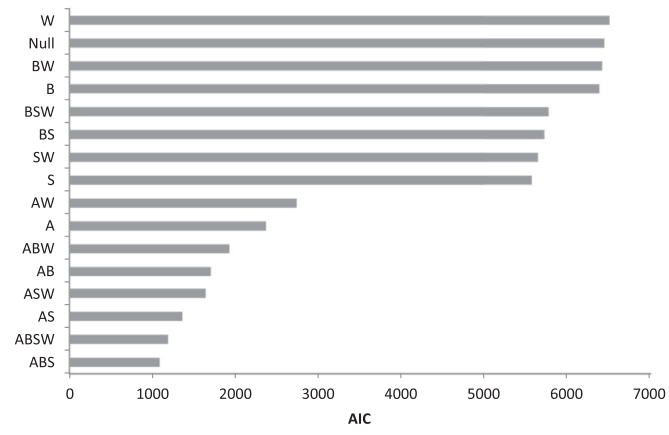


Fig. 4. AIC values of the models used to predict network structure. Abbreviations: A (abundance), B (bark texture), W (wood density), S (trees size).

4. Discussion

We recorded 20 vascular epiphyte species interacting with 24 tree species, similarly to other subtropical forests of northwestern Argentina (Ayarde, 1995; Malizia, 2006; Roldán, 1995). Due to the lower latitude, this forest presents a lower richness than that reported in other subtropical forests of the region (47 vascular epiphyte species in Brown, 1990). We recorded fewer species of vascular epiphytes compared to that found in other studies assessing the interactions among vascular epiphytes and host trees with a network approach (77 species in Burns and Zotz, 2010; 105 species in Silva et al., 2010; 103 species in Zhao et al., 2015). Several of these studies were conducted in temperate forests (Burns, 2008; Piazzon et al., 2011; Taylor et al., 2016) or tropical forests (Burns and Zotz, 2010; Sáyo et al., 2013; Zhao et al., 2015) and some of them considered only a part of the vascular epiphyte assemblage (Sáyo

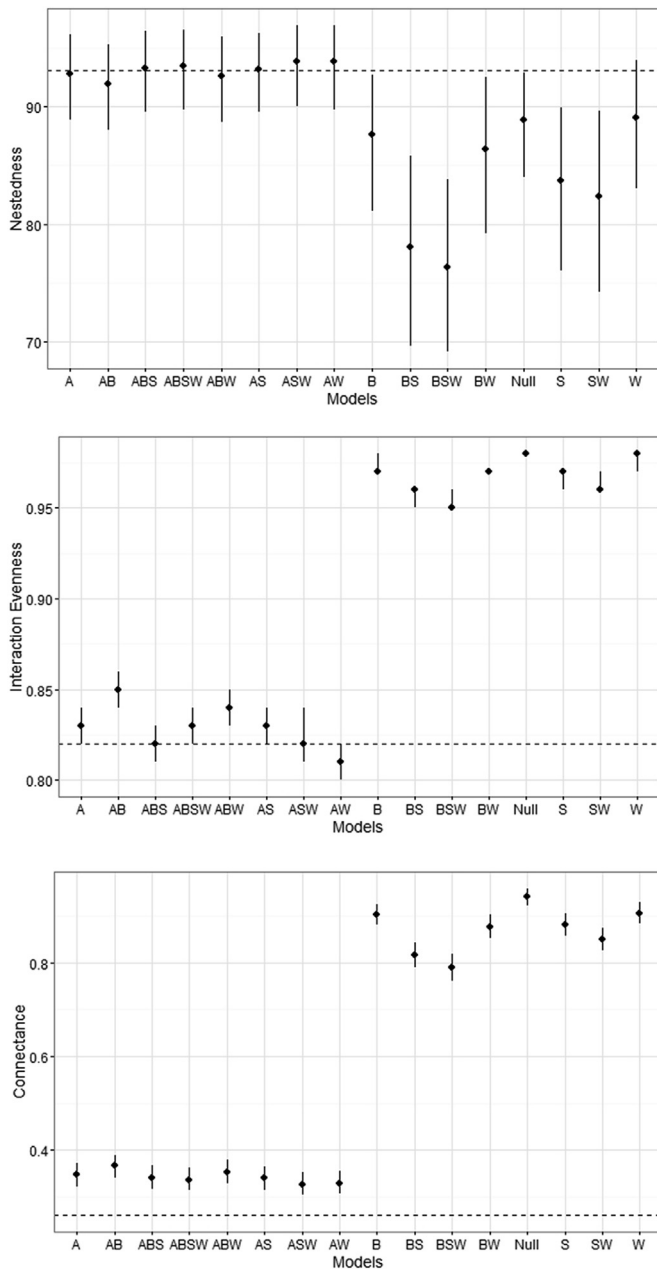


Fig. 5. Probability models used to predict nestedness, interaction evenness and connectance values of the observed network. The horizontal black dotted line represents the metric value based on the observed network. Circles with confidence intervals represent the value of the metric predicted by each model. A (abundance), W (wood density), B (bark texture), S (trees size) represent the models and combinations tested.

et al., 2013; Silva et al., 2010). Therefore, this study represents one of the first assessments in subtropical forests and considering the whole assemblage of vascular epiphytes.

The vascular epiphyte-host tree network showed a nested structure, low specialization and high interaction evenness. These results are consistent with previous research about networks between obligate vascular epiphytes and host trees (e.g. Blick and Burns, 2009; Burns, 2007; Piazzon et al., 2011; Sáyago et al., 2013; Silva et al., 2010; Zhao et al., 2015). Nestedness was higher than expected by chance, suggesting that interactions among vascular epiphytes and host trees are deterministically assembled and that certain processes may be involved in structuring these

networks (Silva et al., 2010). Some of the suggested processes involved are vascular epiphyte succession, species abundance, host tree traits, and network size (Blick and Burns, 2009; Burns, 2007; Silva et al., 2010; Taylor et al., 2016). In particular, succession is one of the most discussed processes in several vascular epiphyte-host tree networks (Blick and Burns, 2009; Burns, 2007; Silva et al., 2010; Taylor et al., 2016). This process was suggested by Burns (2007), who argued that succession occurs as a result of facilitation between vascular epiphyte species, leading to a sequential colonization of vascular epiphytes on trees as they grow. In temperate forests of New Zealand, it has been suggested that “nest epiphytes” are involved in this process, by accumulating water and organic debris and allowing the establishment of woody shrubs and hemi-epiphytes (Taylor et al., 2016). In the studied subtropical forest, *Aechmea distichanta* seems to act similarly, allowing the establishment of facultative epiphytes such as *Ureca baccifera*, and obligate vascular epiphyte species as *Phlebodium areolatum* and *Rhypsalis floccosa* (Brown, 1990). However, this concept is yet speculative and needs to be further investigated to evaluate its possible link with nestedness (Blick and Burns, 2009).

Nestedness also showed that specialization is low, and most of the interactions occurred among generalist vascular epiphytes species and generalist host tree species (e.g. Silva et al., 2010). In fact, the recorded value of specialization was lower than that previously reported for other vascular epiphyte-host tree networks (Sáyago et al., 2013; Taylor et al., 2016; Zhao et al., 2015). This is not surprising because specificity is expected to be weaker in structurally dependent plants, which cannot actively search for appropriate hosts and thus only have the option of establishing or perishing at the location where diaspores were carried by chance (Wagner et al., 2015). However, low specialization can be beneficial for vascular epiphytes, since several species can be adequate hosts, making them less vulnerable to disturbances (Sáyago et al., 2013).

The structure of the vascular epiphyte-host tree network was explained by species abundances, which suggests that species interact randomly, resulting in interaction frequencies which are proportional to relative species abundances (Canard et al., 2014; Vázquez, 2005; Vázquez et al., 2007). Abundance was cited as an important factor explaining the structure of other vascular epiphyte-host tree networks (Burns, 2007; Piazzon et al., 2011; Sáyago et al., 2013), and of other types of interaction networks (Marcilio-Silva et al., 2015; Olito and Fox, 2014; Vázquez et al., 2009). However, vascular epiphyte-host tree networks are not a simple random encounter of individuals, and other biological factors influence the establishment of interactions (Sáyago et al., 2013). Phylogeny, host traits and species spatial overlap were among the factors assessed for explaining the structure of other vascular epiphyte-host tree networks; although, to date, no evidence of phylogeny as an explanatory factor has been found (Sáyago et al., 2013; Silva et al., 2010).

In addition to abundance, the vascular epiphyte-host tree structure was also explained by tree traits such as tree size and tree bark texture. Host trees provide of different conditions or traits that influence the interactions with plants that rely on them (Sáyago et al., 2013; Sfair et al., 2010). The importance of tree size and bark texture as relevant features for vascular epiphytes establishment and growth has been reported in several studies. Tree size, measured here as tree diameter, involve several aspects which might represent plausible mechanisms for explaining interactions between vascular epiphytes and host trees. For example, larger trees provide of more surface and microhabitats, and longer exposure time for the colonization of vascular epiphytes (Burns, 2008; Hietz and Hietz-Seifert, 1995; Woods et al., 2015; Zhao et al., 2015). Large trees also have more surface for fog interception, which might be particularly important for many epiphytes (Pérez-

Harguindeguy et al., 2013). Bark texture is important for vascular epiphytes establishment and growth, since it involves capture and/or storage of water, nutrients and organic debris of trees and epiphytes (Callaway et al., 2002; Johansson, 1974). In particular, rough barks exhibit fissures that capture water and nutrients for vascular epiphytes more efficiently than smooth barks, which in this study had a lower score (Callaway et al., 2002; Johansson, 1974; Wyse and Burns, 2011). However, it is important to note that fissured barks are more important to certain groups of vascular epiphytes, but not to those living in twigs and wires. Therefore, future studies should assess the influence of this factor over particular groups of vascular epiphytes. Bark texture and trees size were also important in an interaction network between bromeliads and host trees in a tropical dry forest of Mexico; however, in that network, the best model also included species spatial overlap and tree wood density (Sáyago et al., 2013). Species spatial overlap was not considered in our study because plots presented the same composition of species, due to their proximity and to the similar successional stage of these old-growth forests.

Wood density was expected to be a relevant factor, due to its relation with tree traits that may be favourable for epiphytes, such as growth, longevity and structural strength. Higher wood density of trees involve longevity and slow growth (Easdale, 2006), which affect the exposure time to vascular epiphyte seed rains (Sáyago et al., 2013). Also, falling branches affecting epiphyte communities (Sarmiento Cabral et al., 2015) may be reduced in higher wood density trees due to their relation with structural strength and branch stability. However, in this study, wood density was not a significant factor. We believe this could be at least partially explained by the influence of particular species. For example, in the studied forest, wood density of *Ocotea porphyria* (the tree species hosting more vascular epiphytes; Brown, 1990; Cabrera, 1976) does not rank among the highest.

The factors assessed in this study were also useful to explain certain network metrics, particularly nestedness. The best model explaining nestedness included abundance and size of trees as factors. Abundance may generate nestedness because abundant species interact more frequently, and less abundant species interact less frequently (Vázquez, 2005). Nestedness might also result from trees size, when vascular epiphyte assemblages on small-diameter trees form perfect subsets of vascular epiphyte assemblages on large-diameter trees (Taylor et al., 2016; Zhao et al., 2015). For example, in New Zealand temperate forests, sites with a higher percentage of large diameter trees were on average significantly nested (Taylor et al., 2016). In Brazilian gallery forests, it was also suggested that nestedness might be due to the thickness distribution of the host trees, since host trees with more orchid epiphyte species were often those with higher basal area (Silva et al., 2010). In the studied subtropical forest, trees size explained nestedness due to the fact that large-diameter tree species (e.g. *Ocotea porphyria*, *Terminalia triflora*, *Parapiptadenia excelsa*, *Pisonia zapallo*) hosted more vascular epiphyte species than small-diameter tree species (e.g. *Urera caracasana*, *Urera baccifera*, *Solanum riparium*).

5. Conclusion

In this study, we observed that the vascular epiphyte-host tree interaction network in a subtropical forest of Argentina exhibits a nested structure, high interaction evenness, and low specialization, similarly to several other networks including obligate vascular epiphytes. Using the conceptual and methodological framework proposed by Vázquez et al. (2009) we observed that interactions between vascular epiphytes and host trees were mainly related to species abundances, and to tree size and tree bark texture. In other words, abundant species interact more frequently, but host tree

traits are also important to predict interactions. This is one of the first studies assessing different factors to explain the structure of a vascular epiphyte-host trees network in a subtropical forest, and that considers the whole assemblage of the sampled community.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2016.10.007>.

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