



Ecosystem engineering by *Fascicularia bicolor* in the canopy of the South-American temperate rainforest



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ABSTRACT

Ecosystem engineers are organisms that modify habitats and resource flows, they therefore could have a disproportionate impact on the diversity of ecological communities. Evidence suggests that trash basket epiphytes (TBE) can be considered ecosystem engineers of forest canopies, due to their relationship with arboreal soil availability and treetop communities. Here we evaluated whether the TBE *Fascicularia bicolor* (Bromeliaceae), modulates temperature and humidity in the forest canopy. We also investigated if this bromeliad is related with greater arboreal soil accumulation and is associated to higher diversity of other epiphytic plants and invertebrates in the canopy of the South-American temperate rainforest (SATR), in Chile. We measured temperature and humidity in ten trees within the forest before and after the experimental addition of *F. bicolor*. We also related the presence of *F. bicolor* with occurrence of soil macrofauna and other canopy dwelling plants in a comparative field survey.

Temperature variability in the canopy was reduced by *F. bicolor*. Soil availability was higher in sites with mats of *F. bicolor*. The richness of vascular epiphytes was unaltered by the presence of *F. bicolor*, but species composition differed between sites with and without mats on each tree. At the group level, the cover of lichens and bryophytes was greater in sites without *F. bicolor*, while vascular epiphytes show a larger cover in sites with *F. bicolor*. The species richness of invertebrates increased in treetop sites colonized by *F. bicolor* but species composition was not different from soil in branch bifurcations. Our results show that *F. bicolor* must be considered in forest management practices to determine which trees must be logged, in order to preserve the viability of populations of these key organisms in the treetops of South-American temperate rainforests.

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1. Introduction

Ecosystem engineers are species that transform their habitat by creating new structures (e.g., beaver dams; Jones et al., 1994; Wright et al., 2002), or by changing the environmental conditions with their mere presence (e.g., shading trees; Jones et al., 1994; Jones et al., 1997). In both cases engineers are able to directly or indirectly regulate the flow of resources in the environment, thus greatly impacting the landscape architecture and the community's structure and composition.

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Ecosystem engineers have such a great effect on their environment that they help to determine the inclusion or exclusion of species in the transformed area, depending on the attributes of the former habitat and organisms' ability to take advantage of the new environmental conditions created by the engineer species (Crain and Bertness, 2006; Jones et al., 1997). Therefore, species distribution and diversity patterns across different landscapes can be partially explained due to the presence and effects of ecosystem engineers. Identifying engineer species in different ecosystems could provide insightful information to understand the mechanisms that structure ecological communities, and contribute to the improvement of current resource management and biodiversity conservation protocols (Crain and Bertness, 2005).

The importance of ecosystem engineers in less explored habitats such as forest canopies is little known, despite the existence of clear examples of canopy dwelling organisms that are able to alter arboreal communities (Angelini and Silliman, 2014; Ellwood et al., 2002; Gonçalves-Souza et al., 2010; Karasawa and Hijii, 2006; Mccracken and Forstner, 2014; Richardson, 1999; Stuntz et al., 2002; Yanoviak et al., 2004). Forest canopies are considered one of the last biotic frontiers of terrestrial ecosystems (Nadkarni et al., 2011) and hold a large portion of forest biodiversity (Ozanne et al., 2003). One of the most conspicuous structural components of forest canopies are “epiphytes”, i.e. vascular and non-vascular plants that use trees as substrates for support without extracting nutrients from their host. Epiphytes represent a significant percentage of forest biodiversity in tropical and temperate forests (Gentry and Dodson, 1987; Kelly et al., 1994; Zotz, 2005). In South-American temperate rainforests seven trees of *Fitzroya cupressoides* (Cupressaceae) can hold up to 48 species of vascular epiphytes, non-vascular epiphytes and vines (Clement et al., 2001). Hofstede et al. (2001) reported at least 40 vascular canopy dwelling plants in a Lowland temperate forest in New Zealand. Epiphytes support a carpet-like layer of arboreal soil along the vertical profile of their host-trees (Nadkarni, 1984a,b; Nadkarni and Longino, 1990) and can harbor an enormous diversity of invertebrates (Ellwood and Foster, 2004; Stuntz et al., 2002). Thus, epiphytes enhance structural diversity throughout trees’ vertical profiles by creating new habitat conditions quite different from bare trunks and branches.

Several studies have documented the ecological importance of epiphytes as drivers of forest biodiversity. For instance, Cruz-Angón et al. (2009) found that abundance of bird individuals in coffee plantation plots with epiphytes increase by 90% and the number of species is 22% higher when compared with plots where epiphytes were removed. The epiphytic bromeliad *Tillandsia usneoides* increase invertebrate richness by 70% by offering a more suitable environment for invertebrates, reducing the risk of predation and modulating temperature and humidity stress (Angelini and Silliman, 2014). Tank bromeliads are particularly known for supporting several species within the forest canopy, including a specialized aquatic community (Armbruster et al., 2002; Richardson, 1999). Gonçalves-Souza et al. (2010) found that tank bromeliads act as “biodiversity amplifiers”, increasing in 40% spider diversity. Armbruster et al. (2002) reported 11,219 individuals of 354 morphospecies inhabiting 209 bromeliads in the Yasuni Reserve (Ecuador), while Richardson (1999) found 15,599 individuals of 282 morphospecies from 120 tank bromeliads sampled in the Luquillo Forest (Puerto Rico). In tropical South East Asian rainforests, the presence of *Asplenium* ferns practically doubles the invertebrate biomass in the canopy (Ellwood and Foster, 2004). Besides their impact on forest diversity, epiphytes also support essential functional groups in the treetops, such as soil decomposers (Díaz et al., 2012). Thus, epiphytes can directly or indirectly modify their surroundings, influencing the amount of resources available and therefore change the number of species and functional groups inhabiting the canopy.

Epiphytic species which affect the canopy’s habitat due to their accumulation of organic matter in focal points of trees are called trash-basket epiphytes (TBE; sensu Benzing, 1990). Most of these epiphytes are characterized by their funnel-like shape, where litter is collected, accumulated and decomposed (Benzing, 1990; Ingrouille, 1995). The importance of TBE in the structure of canopy communities has been overlooked in most forest ecosystems; however, their relationship with the occurrence of soil invertebrates in the canopy has been widely recognized in ecological literature (Beaulieu et al., 2010; Ellwood et al., 2002, 2004; Gibernau et al., 2007; Karasawa and Hijii, 2006; Wardle et al., 2003). Existing evidence suggests that TBE could be considered as ecosystem

engineers since TBE: (i) contribute to accumulate organic matter in the treetops (Benzing, 1990; Díaz et al., 2010; Ellwood and Foster, 2004), (ii) modulate micro-environmental conditions by reducing air temperature oscillations (Turner and Foster, 2006), (iii) create a more stable habitat for canopy dwelling invertebrates (Turner and Foster, 2006).

1.1. The TBE *Fascicularia bicolor* in South-American temperate rainforests

South-American temperate rainforests (SATRs) are distributed along the west side of the Andes, in southern Chile and westernmost Argentina. These forests are a vanishing ecosystem, threatened by the expansion of exotic tree monocultures, agriculture, grazing, and logging (Armesto et al., 1998; Echeverría et al., 2006). Most taxa of the SATRs share floristic and faunistic relationships with tropical forests due to their common origin during the Tertiary (Villagrán and Hinojosa, 1997). During the Quaternary drastic climatic and geological changes depauperated the existing flora and fauna, causing these forests to become a simplified ecosystem, rich in families and genera but poor in number of species (Hinojosa and Villagrán, 1997; Villagrán and Hinojosa, 1997). This ecosystem represents an opportunity to understand general ecological processes while avoiding the high complexity and diversity of most tropical forests.

In the SATRs the only TBE is the endemic *Fascicularia bicolor* (Bromeliaceae). This species has long leaves arranged in a rosette form with an extremely short stem or no stem at all while mats are generally formed by multiple rosettes growing together (Zizka et al., 1999). According to Zizka et al. (1999) there are two subspecies of *F. bicolor*: *F. bicolor* ssp. *bicolor*, a mostly saxicolous plant associated with coastal lands, and *F. bicolor* ssp. *canaliculata*, which is a frequent epiphyte in lowland old-growth forests. *Fascicularia bicolor* becomes more abundant in large old trees, where it is associated with around 50% of the arboreal soil along the vertical profile of their hosts (Díaz et al., 2010). Furthermore, the rosette shape of this plant acts like a natural littertrap, where debris from epiphytes and the host tree accumulates and decomposes, fostering a focal accumulation of canopy soils. By promoting the accumulation of arboreal soils, this TBE could influence a large part of the SATR canopy’s community, including functional groups such as decomposers and predators. However, traditional foresters and rural people tend to see this large epiphyte as a “parasitic plant” and a “sign of forest decay”. Therefore, trees colonized by *F. bicolor* are frequently targeted for selective logging in management plans of native forest in Chile (G. Ortega, personal observation). In addition, *F. bicolor* has been cultivated as an ornamental plant and introduced to Europe where it has been reported naturalized (Marchante et al., 2008; Nelson and Zizka, 1997).

By understanding the links between *F. bicolor*, the habitat provided by its host-trees and the other species inhabiting the vertical profile of trees, it is possible to visualize consequences of the loss of this TBE in a forest stand in the SATR. This information could be useful to improve forest management plans in the SATR and also to predict potential effects of *F. bicolor* in its non-native range. In this context, we evaluated the importance of *F. bicolor* within the canopy community, following four specific predictions: (i) *F. bicolor* modulates both the air temperature and humidity in the forest canopy, (ii) The presence and abundance of *F. bicolor* in focal points of trees is associated with higher diversity and abundance of other epiphytic plants, (iii) *F. bicolor* provides accumulation sites for organic matter and arboreal soil, and (iv) The arboreal soils associated with *F. bicolor* enhances the diversity and abundance of soil invertebrate macro-fauna. We therefore explored variations within the canopy habitat related to the occurrence of *F. bicolor* in order to

provide insights about the links between this TBE and forest biodiversity.

2. Materials and methods

2.1. Study site

The study was conducted in the Arboretum of the Universidad Austral de Chile (hereafter Arboretum, 39°48'S, 73°15'W) and the Parque Oncol (39°41'S, 73°20'W). The Arboretum is a 60 ha experimental forest; it is property of the Universidad Austral de Chile and is located adjacent to Valdivia's city limits. The forest is dominated by *Nothofagus dombeyi*, *N. obliqua* (both Nothofagaceae), *Aextoxicon punctatum* (Aextoxicaceae) and several species of the Myrtaceae family. This is a remnant patch of the native forest which formerly covered the entire area, with many large trees older than 100 years-old and up to 30 m in height. On the other hand, Parque Oncol is a private reserve in the coastal range near the city of Valdivia, including 754 ha of old-growth and second-growth temperate rainforest, surrounded by a matrix of pine tree plantations, pastures for cattle grazing and secondary forests subjected to firewood extraction (G. Ortega, *personal observation*). The Oncol forest is dominated by evergreen species, with a multilayered canopy and frequent emergent trees (30–35 m tall). The dominant species are the emergent *Eucryphia cordifolia* (Eucryphiaceae), *Laureliopsis philippiana* (Monimiaceae), *Amomyrtus luma* and *A. meli* (Myrtaceae).

2.2. Study design

We evaluated our four predictions by combining different approaches. First, we conducted a field experiment at the Arboretum site to describe the relationship between *F. bicolor* presence, air temperature and air humidity in the canopy. Second, we conducted comparative surveys to describe the arboreal soil accumulation under the natural conditions at the Parque Oncol site. Finally, at the Oncol site, we used the cover of canopy dwelling plant species, the richness of vascular plants inhabiting the canopy and diversity of soil macro-fauna found along the vertical profile of trees as indicators of the relation between *F. bicolor* and the canopy's community structure.

2.3. Effects of *F. bicolor* on air temperature and humidity

To evaluate the effects of *F. bicolor* on air temperature and humidity, we selected 10 *Nothofagus obliqua* trees of ca. 25 meters tall and 1 meter of diameter at breast height (DBH) in the Arboretum site. Air temperature and humidity of the inner canopy of each selected tree were measured before and after the experimental addition of living mats of *F. bicolor*. This field experiment was performed during March 2014 (last month of the southern summer). The mean temperature in the area during summer 2014 was 12.4 °Celsius (ranging from 2.2 °C to 27.2 °C) and precipitations reached up to 114.9 mm distributed in ten days with a maximal rain event of 44 mm fallen in a single day (Dirección meteorológica de Chile, 2014). First, we took four hemispherical photographs, each separated by at least one meter, on the southern side of every experimental tree to sought similar sampling points. The location of our sampling points to the south of each tree helped to prevent direct sunlight during midday (the solar declination was around -7.81° to the 0 azimuth during the study period; NOAA, 2016). Each photo was taken from between 10 and 15 meters above the ground. Photographs were analyzed to estimate direct solar radiation, indirect solar radiation and site openness (DSR, ISR and SO, respectively) with the software Gap Light Analyzer 2.0 (Frazer

et al., 1999). With this information, we selected one sampling point per tree by minimizing the standard deviation of DSR, ISR and SO reported by the software, across all trees. The selected sampling points averaged 3.8 mol/m²/d of DSR (SD = 0.68) and 2.92 mol/m²/d of ISR (SD = 0.68), and 10.4% of site openness (SD = 2.60). After selecting the sampling points, three HAXO 8 temperature and humidity sensors (Logtag Recorders Inc., Auckland, New Zealand) were vertically arranged every 30 cm along the trunk (hereafter, “upper”, “mid” and “lower” sensors) at each sampling point. All sensors were attached to the trunk, secured with a small rope and an aluminum nail and protected from direct rain and solar incidence with a small roof of waterproofed paperboard placed ca. five cm above each sensor. Sensors recorded the variations in air temperature and humidity along the tree trunks for 15 days. After that time, the trees were haphazardly assigned to a treatment and control group. For the treatment group (five trees), a mat of *F. bicolor* was attached over each mid-sensor while the control group remained unchanged. After the attachment of the mats, the distance between the upper and lower sensor and the mat root-ball was around 15 cm. Humidity and temperature were monitored for another 15 days after the addition of *F. bicolor*. These mats were previously collected from fallen trees in Parque Oncol, and were stored in a garden at the Arboretum site for a month so they could acclimate to the new conditions before their attachment to the experimental trees. *F. bicolor* is very resistant to damages from manipulation (Nelson and Zizka, 1997) and present a dense and compact root system, holding most of its associated arboreal soil, however, the mats were supported with a small net to ensure their integrity during the experiment.

From the recorded data we calculated “temperature variations” as the difference between the minimum and maximum air temperature recorded each day. Mean air humidity per day was also calculated. To evaluate whether the addition of *F. bicolor* to the experimental trees decreased the daily temperature range and increased mean humidity, we applied a General Linear Mixed Model (GLMM; Zuur et al., 2009) to each response variable, using the experimental tree and the sensor within the tree as random factors to test the interaction between the tree groups (control and treatment), sensor locations (upper, mid and lower) and the addition of *F. bicolor* mats to the experimental trees. The response variables were normalized with Box-Cox transformations before the analyses (Box and Cox, 1964).

2.4. Litter and soil accumulation

We selected 10 *Eucryphia cordifolia* trees in the Parque Oncol study site to evaluate whether *F. bicolor* was associated with larger accumulations of organic matter and arboreal soil in their host trees. Trees had between 70 and 150 cm of diameter at breast height (DBH) and were over 20 meters tall. The *F. bicolor* mats were found between 0.5 and 23.2 meters above the forest floor, with 44% above 10 meters. To access to the canopy, we used single and double rope techniques (Perry, 1978). We sampled 58 points with *F. bicolor* mats (all of them with leaves larger than 15 cm) and 57 points without mats along the vertical profile of all of the trees (with means of 5.8 ± 3.08 and 5.7 ± 3.06 points per tree, respectively). The points without mats were located on the same trees and at similar heights and exposures as the sampled points with mats. At each sampling point, we used a circular plot of 150 cm perimeter to delimit the sampling area where litter occurrence, arboreal soil depth, trunk or branch diameter and inclination were registered. The occurrence (presence-absence) of litter and the depth of the arboreal soil were used as a proxy of arboreal soil accumulation. Soil depth corresponded to the average of four haphazard measurements of depth at different locations within each circular plot. Finally, the inclination of the branch or the trunk

Table 1
Model selection for temperature variations (difference between the daily minimum and maximum temperature) and mean daily humidity for the treatment before and after the addition of *F. bicolor* mats.

Model	Intercept	Time	Location	Treatment	Time: location	Time: treatment	Location: treatment	Time: location: treatment	Df	AICc
<i>Temperature</i>										
1	3.68	+	+	+	+	+	+	+	15	3767.34 ^a
2	3.54	+	+	+	+	+	+	+	13	3768.16
3	3.64	+	+	+	+	+	+	+	11	3769.05
4	3.74	+	+	+	+	+	+	+	12	3772.36
5	3.93	+	+	+	+	+	+	+	8	3773.46
<i>Humidity</i>										
1	82.70	+	+	+	+	+	+	+	15	7245.65 ^a
2	82.98	+	+	+	+	+	+	+	13	7253.69
3	82.82	+	+	+	+	+	+	+	12	7254.70
4	82.61	+	+	+	+	+	+	+	11	7257.93
5	87.71	+	+	+	+	+	+	+	8	7270.82
6	81.78	+	+	+	+	+	+	+	6	7280.49
Parameters	Estimate	Standard error	t-value	Probability						
<i>Selected model for temperature</i>										
Intercept	3.68	0.25	14.61	<0.01**						
Time-after	1.31	0.32	4.15	<0.01**						
Treatment-treatment trees	-0.03	0.36	-0.09	0.93						
Location-up	-0.02	0.32	-0.06	0.95						
Location-mid	-0.02	0.32	-0.06	0.95						
Time-after:treatment trees	-0.21	0.45	-0.46	0.64						
Time-after:location-up	0.16	0.45	0.35	0.73						
Time-after:location-mid	0.08	0.45	0.18	0.85						
Treatment trees:location-up	-0.07	0.45	-0.17	0.87						
Treatment trees:location-mid	0.01	0.45	0.01	0.99						
Time-after:treatment trees:location-up	-0.07	0.63	-0.11	0.92						
Time-after:treatment-trees:location-mid	-1.24	0.63	-1.97	0.05 [†]						
<i>Selected model for humidity</i>										
Intercept	82.70	6.84	12.10	<0.01**						
Time-after	-3.87	2.12	-1.82	0.07						
Treatment-treatment trees	-6.25	9.67	-0.65	0.54						
Location-up	-0.71	9.67	-0.07	0.94						
Location-mid	-1.57	9.67	-0.16	0.87						
Time-after:treatment trees	-0.48	3.00	-0.16	0.87						
Time-after:location-up	-0.15	3.00	-0.05	0.96						
Time-after:location-mid	0.72	3.00	0.24	0.81						
Treatment trees:location-up	-14.50	13.67	-1.06	0.30						
Treatment trees:location-mid	-18.74	13.67	-1.37	0.19						
Time-after:treatment trees:location-up	5.21	4.24	1.23	0.22						
Time-after:treatment-trees:location-mid	-1.89	4.24	-0.45	0.66						

Time indicates the effect of the different days of the assay grouped before and after the mats of *F. bicolor* were added to the experimental trees, location included the effect of the sensor in the upper, lower or middle position, treatment refers to the addition of *F. bicolor* mats, and the combination of factors indicates the interactions. + indicate several estimated levels of model parameters for categorical variables. Interactions between pairs of predictor variables are expressed as "A:B".

^a Selected model for temperature and humidity data.

was measured and classified in four categories: one (-1° to -45°), two (-46° to -89°), three (90° – 46°) and four (45° – 0°), considering 0° as a completely horizontal position, 90° as a completely vertical position and negative values as negative inclinations. We also recorded the number of mats attached to surfaces with inclination between -80° and 80° , to assess the importance of colonization of *F. bicolor* on nearly vertical sections of the trees. Category one for the inclination variable was omitted from further analyses because it only occurred once.

We evaluated the influence of height, branch diameter, inclination category, azimuth category and *F. bicolor* presence on the occurrence of litter and the soil depth in the canopy using GLMM. Height and branch diameter were correlated, then both variables were alternatively tested in different models to avoid overfitting. The tree was included in all the tested models as a random factor. Our modeling approach to evaluate litter occurrence was to use a binomial distribution with logit link function. Several plausible models were fitted to our dataset and the final model was selected according to the lower Akaike Information Criterion (AIC). The soil

depth was transformed by logarithm and analyzed in a GLMM with Gaussian distribution. Different alternative models were evaluated and the one with lower AIC was selected to further interpretation.

2.5. Influences of *F. bicolor* on epiphytes and invertebrates

In order to assess whether *F. bicolor* could be associated with changes in relative abundance of other epiphytes, we recorded the percentage of cover of bryophytes, lichens (each of them as a group to avoid taxonomic uncertainty) and species of vascular plants within the circular plots previously described (58 plots with *F. bicolor* mats and 57 plots without mats). Then, we calculated the mean cover of vascular epiphytes for each plot. The fieldwork was performed by three researchers previously trained on another project to standardize estimations of epiphytic cover (Díaz, 2012). Each tree was sampled by one researcher, considering that we were looking for differences related to the presence of *F. bicolor* on the canopy and not differences between trees. To evaluate the association of *F. bicolor* with invertebrate richness and composition,

we focused on soil macro-fauna since this fauna is most likely absent from the canopy when arboreal soil is also absent (Díaz et al., 2012). We used a 15 cm diameter soil-corer and 20 cm long knives to collect 1,000 cm³ soil samples. Knives were required because in most cases was not possible to cut the woody roots of *F. bicolor* and other vascular epiphytes with the corer. Thus, soil samples were initially larger than needed but were later reduced to the desired size. We collected 23 soil samples from large *F. bicolor* mats and 12 from trunk bifurcations on the 6 largest *E. cordifolia* trees found in Parque Oncol. Additionally, we took 20 soil samples from the forest floor to compare this habitat's invertebrate richness, abundance and composition with that of the forest's canopy. All of the samples were stored individually in labeled plastic bags and taken to the laboratory to extract soil invertebrate macro-fauna with a Berlese-Tullgren funnel (Beaulieu et al., 2010). We identified individuals at the order and family level and used morphospecies to estimate richness, abundance and species composition with a dissecting microscope and specialized literature (Oliver and Beattie, 1996; Yanoviak et al., 2004). Morphospecies are currently being assigned to species by invertebrate specialists in an ongoing parallel project. After the invertebrate extraction, soil samples were oven-dried at 60 °C until a constant weight

was reached. It is important to note that the dry weight of the soil samples was highly variable, reaching 51.8 g (SD = 27.3 g) for *F. bicolor* samples, 55.5 g (SD = 26.7 g) for soil samples on branch bifurcations and 170.2 g (SD = 43.8 g) for forest floor samples. An examination of scatterplots by each invertebrate morphospecies showed that there are no relations between the samples' dry weights and the number of individuals. Then, we decided to compare richness, abundance and composition of invertebrate macro-fauna between habitat types without standardize the number of individuals by sample weight.

We examined the variations on the mean cover (VMC) of vascular plants, bryophytes and lichens with the following formula:

$$VMC = \frac{(\text{sites With } F. \text{ bicolor} - \text{Without } F. \text{ bicolor})}{\text{sites Without } F. \text{ bicolor}}$$

The VMC allowed us to estimate the magnitude of differences in the mean cover of each epiphytic group found in sampling points with or without *F. bicolor*. To evaluate the relation of *F. bicolor* with species richness in the forest we followed the approach of Karasawa and Hijii (2006). Data was divided into three groups: (1) samples without *F. bicolor*, (2) samples where *F. bicolor* was present, and (3) all the samples obtained on the vertical profile of trees

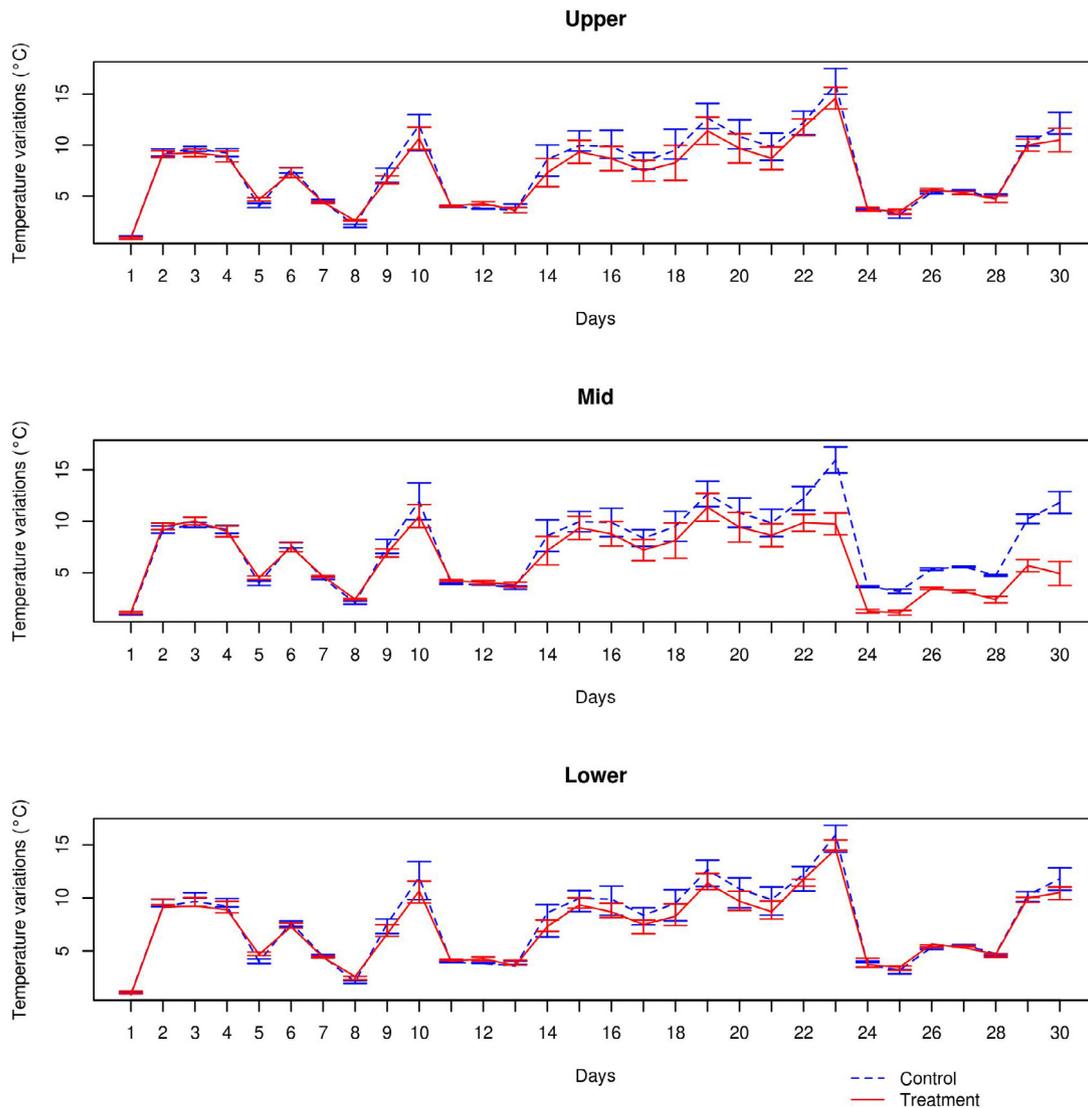


Fig. 1. Daily temperature variations (difference between minimal and maximal temperature per day) registered in the study trees before and after the addition of *F. bicolor* over mid sensors in the treatment group.

(with and without *F. bicolor*). This method provides a way to compare richness between sites within a tree with and without *F. bicolor* and the influence of this epiphyte in overall species richness on the trees. Additionally we considered forest floor samples as a separate group on the evaluation of invertebrate richness. To compare the richness of vascular plants and soil macro-fauna between the different groups of samples we used rarefaction analysis. The rarefaction technique allowed us to avoid biases caused by different sampling efforts (Gotelli and Colwell, 2001). We used sample-based rarefaction analysis for vascular plants and individual-based rarefaction for invertebrate macro-fauna. We also estimated Renyi evenness curves to graphically compare evenness from the different groups of samples evaluated (Kindt and Coe, 2005). Finally, we performed a permanova to determine if the occurrence of *F. bicolor* is related to changes in species composition for vascular plants and invertebrate macro-fauna along trees' vertical profile (Anderson and Walsh, 2013). The cover of vascular epiphytes was transformed by square root before the analysis to improve homocedasticity. All statistical analyses and graphs were performed in R 3.2.3 (R Core Team, 2015) with the packages vegan (Oksanen et al., 2017), iNEXT (Hsieh et al., 2016), nlme 3.1 (Pinheiro et al., 2016), lme4 (Bates et al., 2015) and BiodiversityR (Kindt and Coe, 2005).

3. Results

3.1. Air temperature and humidity

Temperature variability registered by the mid sensors was significantly influenced by the addition of *F. bicolor* mats to the experimental trees, while no changes were observed in the sensors located away from the mats (Table 1). After the addition of

F. bicolor, the daily temperature variations registered in the mid-sensors averaged 2.58 °C less in experimental trees than in control trees, although upper and lower sensors located above and below the mid-sensors did not register significant differences in daily temperature variations after the addition of *F. bicolor* (Fig. 1). We also found that *F. bicolor* had no effect on the daily mean air humidity. Changes in air humidity were not related to the addition of *F. bicolor* (Table 1).

3.2. Litter and soil accumulation

We found 31% of the mats of *F. bicolor* (n = 18) attached to vertical surfaces of the trees, ranging from –80° to 80° inclinations. Litter occurred in 55% of the points with *F. bicolor* (n = 32) and only 12% (n = 7) of the points without *F. bicolor*. The selected model showed that the occurrence of litter retained in the canopy is related to the presence of *F. bicolor*, but is also affected by the inclination and diameter of branches (Table 2). The inclusion of *F. bicolor* in the final model significantly increased the model's fit and produced the largest increment in the odds of litter occurrence. The soil depth tends to increase when *F. bicolor* is associated to positive branch inclination (larger than 90°). Height and azimuth category were also retained in the final model but no significant effects were found (Table 3).

3.3. Canopy dwelling plants and invertebrates

We found 21 vascular plant species from 12 genera in the sampled trees at the Parque Oncol study site (Table 4). Most of the vascular plants found were epiphytes (12 species), mainly from the fern genus *Hymenophyllum* (Hymenophyllaceae; nine species). We also found seven climber species, two mistletoes and one

Table 2
Estimated model parameters for logistic regression comparing the occurrence of litter among the inclination of branches, the diameter of the trunk or branches and the presence of *F. bicolor* mats in the canopy of *E. cordifolia* trees in Parque Oncol, southern Chile.

Model	Intercept	Azimuth category	Diameter	<i>F. bicolor</i>	Inclination category	Height	Azimuth category: <i>F. bicolor</i>	Diameter: <i>F. bicolor</i>	<i>F. bicolor</i> : Inclination category	<i>F. bicolor</i> : Height	Df	AICc
1	-4.00		0.04	+	+						6	112.80 ^a
2	-5.84		0.04	+							4	116.29
3	-4.01	+	0.04	+	+						9	118.29
4	36.31	+	0.02	+	+		+	+	+		15	118.61
5	0.87			+	+	-0.09					6	118.93
6	-0.32			+	+						5	119.07
7	-5.91	+	0.04	+							7	121.46
8	-2.33			+							3	122.12
9	-1.93			+		-0.05					4	123.58
10	-0.26	+		+	+						8	124.05
11	-0.26	+		+	+						8	124.05
12	0.83	+		+	+	-0.09					9	124.33
13	-2.16	+		+							6	127.43
14	37.76	+		+	+	-0.08	+		+	+	15	127.95
15	-1.81	+		+		-0.04					7	129.16
16	-3.99		0.03								3	140.85
17	-0.55					-0.02					3	149.35
18	-0.82	+									5	153.57

Selected model

Variables	Estimated parameters	Standard error	Z value	Probability
Intercept	-4.00	2.30	-1.74	0.08
With <i>F. bicolor</i>	2.59	0.64	4.06	***
Inclination two	-3.63	1.45	-2.50	*
Inclination three	-2.34	1.17	-2.00	*
Diameter	0.04	0.02	2.01	*

+ indicate several estimated parameters for categorical variables. Interactions between pairs of predictor variables are expressed as "A:B".

*** P < 0.001.

^a Selected model for litter occurrence.

* P < 0.05.

Table 3

Estimated model parameters for soil deep as a result of the inclination and azimuth of each sampling point, the diameter of the trunk or branches and the presence of *F. bicolor* mats in the canopy of *E. cordifolia* trees in Parque Oncol, southern Chile.

Model	Intercept	Azimuth category	Diameter	<i>F. bicolor</i>	Inclination category	Height	Azimuth category: <i>F. bicolor</i>	Diameter: <i>F. bicolor</i>	<i>F. bicolor</i> : Inclination category	<i>F. bicolor</i> : Height	Df	AICc
1	2.28	+		+	+	-0.01	+		+		16	595.85 ^a
2	-3.51	+		+	+						9	603.63
3	-3.51	+		+	+						9	603.63
4	-3.11			+	+						6	604.18
5	-5.45	+		+							7	605.73
6	1.29	+	0.01	+	+		+	+	+		16	606.10
7	-4.99			+							4	606.35
8	-5.19	+		+	+	0.14					10	606.46
9	-4.93			+	+	0.13					7	607.01
10	-6.57	+		+		0.16					8	607.35
11	-6.33			+		0.15					5	608.11
12	-2.41	+	-0.01	+	+						10	612.21
13	-2.29		-0.01	+	+						7	612.77
14	-4.24	+	-0.01	+							8	614.15
15	-3.90		-0.01	+							5	614.60
16	-3.23	+									6	639.64
17	-3.57					0.15					4	644.50
18	-1.72		-0.01								4	650.69

Selected model

Variables	Estimated parameters	Standard error	t value	Probability
Intercept	2.28	3.87	0.59	0.56
With <i>F. bicolor</i>	-6.23	4.55	-1.37	0.17
Inclination three	-7.66	3.49	-2.20	*
Inclination two	-6.31	3.68	-1.71	0.09
Azimuth north	-0.62	2.09	-0.29	0.77
Azimuth south	-1.27	1.93	-0.65	0.51
Azimuth west	0.60	1.69	0.36	0.72
Height	-0.01	0.13	-0.08	0.94
With <i>F. bicolor</i> : Inclination three	7.95	3.92	2.03	*
With <i>F. bicolor</i> : Inclination two	3.89	4.57	0.85	0.40
With <i>F. bicolor</i> : Azimuth north	2.17	2.89	0.75	0.45
With <i>F. bicolor</i> : Azimuth south	4.05	2.83	1.43	0.16
With <i>F. bicolor</i> : Azimuth west	2.68	2.48	1.08	0.28
With <i>F. bicolor</i> : Height	0.24	0.17	1.40	0.16

+ indicate several estimated parameters for categorical variables. Interactions between pairs of predictor variables are expressed as "A:B".

^a Selected model for soil deep.

* P < 0.05.

hemiepiphyte (Table 4). The mean cover of vascular plants was 44% higher in plots with *F. bicolor* compared to plots without this TBE, while bryophytes and lichens mean cover were lower by 24% and 14%, respectively (Table 4). We found no differences in richness of vascular epiphytes between plots with and without *F. bicolor* mats (Fig. 2A), but species evenness was higher in plots without *F. bicolor* (Fig. 2C). Regarding changes in species composition, the occurrence of *F. bicolor*, height and azimuth have significant influence (Table 5).

We collected 210 invertebrate individuals inhabiting *F. bicolor* mats; while only 57 were obtained from plots without *F. bicolor* and 67 from forest floor samples (Table 6). The most abundant invertebrate order was Arachnida, with 223 individuals from 20 morphospecies, most of them of the subclass Acari. Invertebrate species richness in soil samples from mats of *F. bicolor* was greater than that from branches, but similar to the species richness found when all of the samples from the vertical profile of trees were grouped together or when compared to that of forest floor samples (Fig. 2B). Evenness tended to be higher in mats of *F. bicolor* than in

plots without it, but the largest evenness was observed in forest floor samples (Fig. 2D). Permanova results showed that the composition of soil invertebrate species did not differ among samples taken in *F. bicolor* mats, branch bifurcations or the forest floor (Table 5). No effects of height on the tree or sample weight were observed.

4. Discussion

4.1. Environmental changes driven by the TBE *F. bicolor*

Our evidence indicates that the trash-basket epiphyte *Fascicularia bicolor* is able to create new patches of habitat within the vertical profile of its host tree. The decreased oscillations in the daily air temperature within the area occupied by *F. bicolor* mats could be related to its leaves and the organic matter accumulated within each mat, similar to Freiberg's (2001) proposal. When the temperature is high, the leaves, litter and debris could decrease temperature by

Table 4
Mean cover of canopy dwelling plants in plots with and without mats of *F. bicolor* in Parque Oncol, southern Chile. VMC indicate differences in cover percentage.

Species	With <i>F. bicolor</i>	Without <i>F. bicolor</i>	VMC
Vascular plants	27.16	18.89	0.44
Epiphytes	30.01	20.21	0.45
<i>Fascicularia bicolor</i> (Ruiz & Pav.) Mez	48.12	12.50	2.85
<i>Grammitis magellanica</i> Desv.	5.00		
<i>Hymenophyllum caudiculatum</i> (Mart.)	42.78	45.63	-0.06
<i>Hymenophyllum cruentum</i> Cav.	46.67	45.50	0.03
<i>Hymenophyllum cuneatum</i> (Kunze)	35.00	9.27	2.77
<i>Hymenophyllum dentatum</i> Cav.	17.75	15.35	0.16
<i>Hymenophyllum dicranotrichum</i> (C. Presl) Sadeb.	19.08	22.54	-0.15
<i>Hymenophyllum krauseanum</i> Phil.	4.00	7.00	-0.43
<i>Hymenophyllum pectinatum</i> Cav.	6.17	4.14	0.49
<i>Hymenophyllum peltatum</i> (Poir.) Desv.		5.00	
<i>Hymenophyllum plicatum</i> Kaulf.	8.67	6.50	0.33
Hemiepiphyte	7.50	5.00	0.50
<i>Raukua laetevirens</i> (Gay) Frodin	7.50	5.00	0.50
Mistletoes	12.50	10.50	0.19
<i>Antidaphne</i> sp.	15.00	1.00	14.00
<i>Notanthera heterophyllus</i> (Ruiz & Pav.) G. Don	10.00	20.00	-0.50
Climbers	22.30	17.16	0.30
<i>Gaultheria insana</i> (Molina) D.J. Middleton	24.58	17.14	0.43
<i>Griselinia racemosa</i> (Phil.) Taub.	38.29	29.17	0.31
<i>Griselinia ruscifolia</i> (Gay) Ball	17.00	14.43	0.18
<i>Hydrangea serratifolia</i> (Hook. & Arn.) Philf.		12.50	
<i>Luzuriaga polyphylla</i> (Hook.f.) J.F. Macbr.	13.14	17.73	-0.26
<i>Mitriaria coccinea</i> Cav.	12.50	1.00	11.50
<i>Sarmienta repens</i> (Ruiz & Pav.)	5.50	5.44	0.01
Non vascular epiphytes			
Bryophytes	58.51	77.18	-0.24
Lichens	16.32	18.90	-0.14

shading the root-ball (Jian et al., 2013), while at lower temperatures the organic matter could warm the mat with the energy released from the decomposition process (Freiberg, 2001). This two alternative process can explain the reduced temperature variation observed in sites where *F. bicolor* was attached on the experimental trees. In contrast, we found that *F. bicolor* did not directly affect the mean air humidity registered daily; however, this result should be viewed with caution because could be related to the environmental conditions during the experiment rather than a total absence of effects. Ten scattered rain events occurred during the experimental evaluation of temperature and humidity, but the low temperatures registered in the same days could have reduced water evaporation from the root-ball of *F. bicolor*. Also, the focal accumulation of arboreal soil can have other water related effects, at different seasons and time scale that could require attention. For instance, Jian et al. (2013) showed that the epiphytic fern *Haplopteris zoosterifolia* benefits from growing on the root-ball of *Asplenium nidus* when facing drought conditions because this substrate can store up to 300% of its dry weight in water. Also, the experimental study of Vergara (2013) in the SATR, showed that greater volumes of arboreal soils could store water for a long time while still supporting species that are very sensitive to drops in air humidity.

The morphological attributes and growth form of *F. bicolor* could help explain its influence on organic matter retention in the treetops. The mats of *F. bicolor* consist of several rosettes of thorny leaves, which create an intricate bush-like structure. These

mats are frequently attached to branch bifurcations, although our results show it is also common to see individuals attached to vertical portions of the trunk (31% of the mats in our study). Therefore, *F. bicolor* could enhance organic matter deposition and retention in the host tree's architecture by: (1) increasing the complexity of branches and trunk bifurcations that normally intercept litter falling from the crown (i.e. large horizontal branches) and by (2) providing new deposition sites when mats are attached to vertical trunks, which are otherwise hardly available for organic matter deposition.

Arboreal soils associated with trash basket epiphytes like *F. bicolor* could be important sources of nutrients for the TBE and other canopy organisms. For instance, in the tropical forests of Malaysia the nitrate concentration in the stemflow below mats of *A. nidus* was found to increase by around 35% compared to that found above these plants (Turner et al., 2007). Litter degradation is a predominant source of nitrate in forest ecosystems, thus the increased nitrate concentration below the ferns can be attributable to the decomposition of the litter trapped in the TBE mats (Turner et al., 2007). It must be taken into account that decomposition rates could greatly differ between tropical and temperate areas (Parton et al., 2007). In the SATR, (Tejo et al., 2008) showed that nitrogen availability is higher in winter season, probably related to a lower microbial activity and decreased plant growth. However, it is likely that if all the decomposition process is naturally fast in tropical forests or slow in temperate forests, the relative importance of TBE species within their corresponding ecosystem could still be significant. More research is needed to reveal if nutrients released from TBE in tropical and temperate forests influence the community's composition at the canopy level.

The attributes that allow TBE species to retain organic matter in the canopy contribute to nutrient redistribution within the vertical profile of trees. In a system with few epiphytes colonizing the trees, the abscised leaves and other organic debris reach the forest floor and the nutrients can be recovered by the trees. While in a system where epiphytes act as litter traps suspended above the forest floor, a portion of the organic matter falling from trees will not be able to reach the forest floor; this organic matter will decompose in the forest canopy and be incorporated to the epiphyte compartment without being available for the tree immediately. Benzing and Seemann (1978) proposed the term "nutritional piracy" to describe this situation and showed that under restrictive nutritional conditions, there could be detrimental effects on the host tree. According to Benzing and Seemann (1978) proposal, trash-basket epiphytes like *F. bicolor*, *A. nidus* and others could be seen as large nutritional pirates whose occurrence increases nutrient removal from a normal cycle. However, beyond the tree perspective, organic matter retention by TBE increases the opportunities for canopy organisms to access nutrients by relocating these resources within the vertical profile of the forest. In addition, epiphytes also have been proposed as nutrients capacitors for the forest, because they can incorporate nutrients from allochthonous sources such as precipitation, dust or the atmosphere into the forest (Nadkarni, 1984a,b). Such nutrients are later incorporated into the forest nutrient's cycles via decomposition throughfall, or litterfall.

4.2. Canopy dwelling plants and invertebrates

Ecological and physiological restrictions can explain the differences in abundance of bryophytes, lichens and vascular plants in sites with or without *F. bicolor* on the same trees. Vascular plants of the canopy require a deeper substrate to grown, thus vascular plants will be favored by greater arboreal soil accumulations associated with *F. bicolor*. On the other hand, bryophytes and lichens are considered primary colonizers of the forest canopy (Dudgeon,

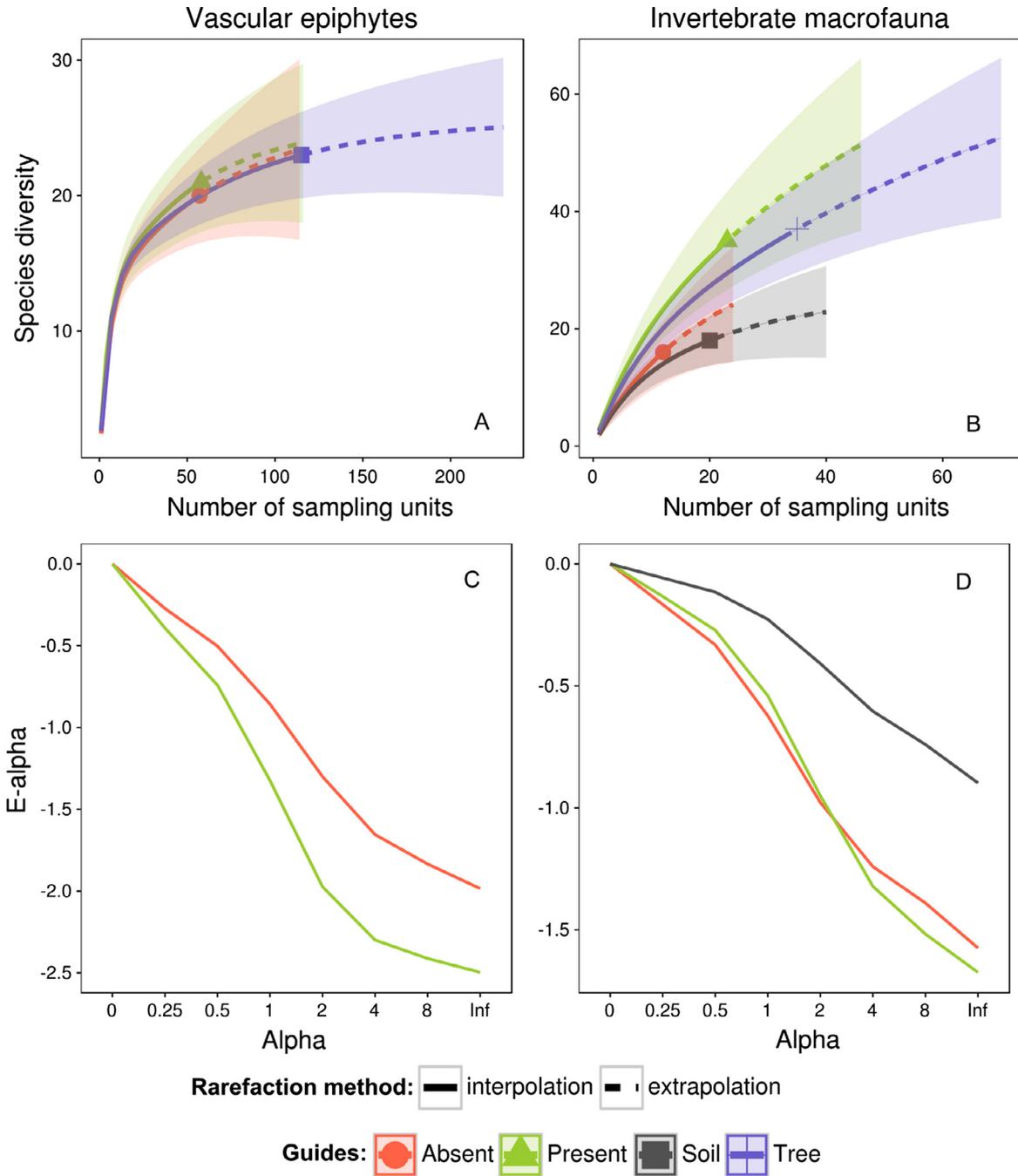


Fig. 2. Species richness (A and B) and evenness (C and D) of vascular plants and invertebrate macro-fauna found on *Eucriphia cordifolia* trees in Parque Oncol, southern Chile. The X axis in A and B show the number of samples required to reach each point of the rarefaction curves and the Y axis show the corresponding number of species estimated. Light colors indicate the confidence interval for each curve. The C and D plots show the Renyi evenness profile for vascular plants and invertebrate macro-fauna occurring in sites with *F. bicolor* (green), without *F. bicolor* (red) and forest floor (dark line in D panel). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

1923) and their propagules are not restricted to developed substrates to establish. Species sensitive to desiccation such as *Hymenophyllum* ferns (Saldaña et al., 2014) could grow better in the shade of the foliage of a TBE like *F. bicolor*, or could be supported by the water retention in the arboreal soil associated with the TBE (Vergara, 2013). However, *Hymenophyllum* ferns also respond to light availability (Saldaña et al., 2014) and have a complex reproductive cycle with two kind of individuals (sporophytes and gametophytes) which can have completely different habitat requirements (Rumsey et al., 1998). Thus, specific habitat requirements of each species can help to explain a differential pattern in composition within the studied microhabitat types.

Arboreal soils are an important component for the canopy's invertebrate fauna. Therefore, species that support the formation and storage of arboreal soils play an important role in forest canopies as habitat providers for invertebrates (Ellwood and Foster, 2004). Lack of difference in species composition between the compared habitats suggests that there are no exclusive species in the soil associated to *F. bicolor* mats, similar to that observed in the fern *Asplenium nidus* (Karasawa and Hijii, 2006). However, soil invertebrates are restricted by soil availability within the canopy, which increase with the presence of *F. bicolor* when it creates new deposition sites on their host trees. The litter trapped in *F. bicolor* mats can provide habitat and food to a wide variety of

Table 5
Permanova results for vascular plants and invertebrate macro-fauna diversity on *Eucryphia cordifolia* trees in Parque Oncol, southern Chile.

Source	SS	Df	F	Probability
<i>Vascular epiphytes</i>				
<i>F. bicolor</i> (presence-absence)	1.73	1	5.25	***
Height	4.61	1	13.98	***
Azimuth category	1.61	3	1.62	*
Inclination category	0.51	1	1.55	0.13
Residuals	34.26	104		
<i>Invertebrate macro-fauna</i>				
Sample groups	0.70	2	0.77	0.90
Height	0.49	1	1.09	0.34
Sample weight	0.25	1	0.56	0.97
Residuals	14.53	32		

Results are presented according to a marginal test of significance for each predictor variable. Sample groups for invertebrate macro-fauna consider sampling points with and without *F. bicolor* and forest floor samples.

SS = sums of squares.

* $P < 0.05$.

*** $P < 0.001$.

Table 6
Number of morphospecies and number of total individuals of invertebrate macro-fauna for each taxa in plots with mats of *F. bicolor*, without mats of *F. bicolor* and on the forest floor under large *E. cordifolia* trees in Parque Oncol, southern Chile.

Clase	Number of morphospecies				Number of individuals			
	With <i>F. bicolor</i>	Without <i>F. bicolor</i>	Forest floor	Total	With <i>F. bicolor</i>	Without <i>F. bicolor</i>	Forest floor	Total
Annelida								
Clitellata	1	0	0	1	1	0	0	1
Arthropoda								
Arachnida	16	7	11	20	143	36	44	223
Chilopoda	1	1	1	1	1	1	4	6
Entognatha	5	1	2	5	11	1	7	19
Insecta	11	4	4	12	42	10	12	64
Symphyla	1	0	0	1	1	0	0	1
Crustacea								
Malacostracea	2	2	0	2	11	9	0	20
Total	37	15	18	42	210	57	67	334
Number of samples	23	12	20		23	12	20	
Mean per sample	2	1	1		9	5	3	

invertebrates, increasing their biomass and thereby increasing the abundance of functional groups such as decomposer organisms (Beaulieu et al., 2010; Díaz et al., 2012; Ellwood and Foster, 2004). Finally, invertebrates are poikilotherms, therefore extremely high or low temperatures can be detrimental for their metabolism (Meehan, 2006). *Fascicularia bicolor* offers a more stable environment for soil macro-fauna inhabiting the canopy by reducing temperature variability. This effect is shared by other TBE species (Turner and Foster, 2006) but could also be an attribute of soil accumulation rather than the TBE itself (Freiberg, 2001).

4.3. Trash basket epiphytes as ecosystem engineers: consequences of *F. bicolor* for forest conservation and management

Our findings support the hypothesis that *F. bicolor* is an ecosystem engineer that creates habitat and resources, influencing ecosystem processes and biodiversity in the forest's canopy. In addition, the consequences of greater organic matter accumulation associated with the presence of TBE such as *F. bicolor* could be relevant in relation with its abundance. For instance, in coastal temperate forests of southern Chile *F. bicolor* is associated with ca. 50% of the arboreal soil (around 60 kg dry weight per tree) accumulated in the canopy (Díaz et al., 2010). The effects of *F. bicolor* on the habitat and species in the vertical profile of trees have been largely overlooked in the SATR because of the lack studies describing canopy communities and biodiversity patterns. *Fascicularia bicolor*

could contribute to enhancing canopy biodiversity and redistributing nutrients within the vertical profile of the forest, and should be explicitly included in management and restoration plans in the South-American temperate region. Like other ecosystem engineer species, there could be also negative effects associated to *F. bicolor* which need to be investigated because engineer species can be able to transform their surroundings independently of the context where they are. Future research needs to address the influence of *F. bicolor* regarding the consequences of enhancing the abundance and composition of invertebrates on the vertical profile of trees, the contribution of this TBE to nutrient cycles and even the potential effects of this specie on its introduced range in North-America and Europe (GBIF, 2001; Nelson and Zizka, 1997).

The ecological effects of *F. bicolor* could be shared by other TBE species in many forest ecosystems, based on their strong structural and functional similarities (Zona and Christenhusz, 2015). All of these species share a common factor, they accumulate litter in the canopy increasing the amount of arboreal soil, and thus increasing resources, habitat, species, and functional groups within the vertical axis of the forest. Since TBE accumulate arboreal soils, they not only increase the amount of habitat available for soil invertebrates, they also potentially change nutrient cycling at the canopy level in several tropical and temperate forests. In addition, the importance of the habitats created by TBE species in the tree-tops may become critical under a climate change scenario where expected mean air temperatures will increase and daily variations

could become more intense (Hsu and Wolf, 2013). This could be a general process in forest canopies, driven by different taxa in each region, and largely overlooked by managers and those in charge of conservation planning. TBE can be biological indicators of the associated canopy biodiversity, which could be helpful in restoration and conservation efforts in degraded forests where canopy biodiversity is declining.

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