

The importance of tree species and size for the epiphytic bromeliad *Fascicularia bicolor* in a South-American temperate rainforest (Chile)

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Bromeliads are a numerous family of vascular epiphytes, though only one epiphytic species inhabits South-American temperate rainforests: the endemic *Fascicularia bicolor*. This bromeliad is an important driver of canopy biodiversity, but attributes of its hosts are mostly unknown. Here we report (i) the tree species colonized by *F. bicolor*, (ii) the relationship between tree size and presence of *F. bicolor* and (iii) the relation between tree size and the number of mats of *F. bicolor* inhabiting each colonized tree. We sampled 231 trees in seven forest plots recording their species, diameter, heights, and the number of *F. bicolor* mats growing on them. The dataset was analyzed with a zero-inflated model to relate host tree attributes with *F. bicolor* occurrence and abundance in a single statistical approach. The occurrence and abundance of *F. bicolor* depend on host-species identity and diameter. *F. bicolor* colonization in slow-growing trees started at smaller DBH than that required for other tree species. Nonetheless, the overall occurrence of *F. bicolor* relies on large trees above 50 cm DBH for most host species. The number of mats occurring on each colonized tree depends on the interaction between tree height and species suggesting the importance of space available for colonization along the tree-trunk, and differential effects due to species' traits. Currently, large trees and old-growth forests are scarce within the distribution range of *F. bicolor*, which could seriously affect the long-term conservation of this endemic epiphyte, along with the canopy properties and species associated with it.

Keywords: Forest Canopy, Epiphytes, Bromeliads, South American Temperate Forests

Introduction

Bromeliaceae is the second largest family among Neotropical vascular epiphytes, with 1770 epiphytic species, representing 60% of the family (Zotz 2013). Epiphytic bromeliads can provide important habitat for other canopy-dwelling organisms, fostering biodiversity in the upper layer of the

forest. For example, tank bromeliads are known to retain water and debris in their rosettes, which support fully-fledged communities in the treetops. Another bromeliad, *Tillandsia usneoides*, creates intricate shelters which reduce predation risk to invertebrates (Angelini & Silliman 2014). Epiphytic bromeliads can modify canopy environ-

ments by creating habitat patches with distinct characteristics, increasing beta-diversity (Angelini & Silliman 2014, Ortega-Solís et al. 2017). Hence, threats to the conservation of bromeliad species could be detrimental for other canopy organisms.

The underlying ecological processes explaining the occurrence and the number of epiphytic bromeliads on individual trees – as well as other canopy dwelling plants – include the increase in surface available for colonization by epiphytic propagules during tree growth (Flores-Palacios & García-Franco 2006), the time that each tree has been available for epiphyte colonization (Merwin et al. 2003), chemical or physical attributes of the bark (Hietz et al. 2012), or the distance from propagule sources (i.e., neighbouring trees or stands – Paggi et al. 2010). However, most of these processes are tied to tree ontogeny (Taylor & Burns 2015). As time passes, trees increase their diameter and height until they reach their maximum height, when only diameter and branches continue growing. Over time, branches create a complex crown, the bark of several tree species increases its roughness, and epiphyte colonization occurs whenever diaspores are able to reach their host. Once established, the epiphyte assembly creates its own dynamics, similar to those described in the crowns of long-lived trees in the Northern Hemisphere (Sillett &

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Van Pelt 2007, Ishii et al. 2018). Beyond the value of the specific ecological processes that explain the colonization of epiphytes, most of these processes are intrinsically correlated to variables commonly recorded in forest inventories, such as tree species, diameter at breast height (DBH) and height. Thus, the knowledge about basic attributes of the host-trees is simple but critical information required to include epiphytes conservation in sustainable forest management.

Here we evaluate the relationship between the colonization of trees by *Fascicularia bicolor* (Ruiz & Pav.) Mez, and DBH, height and species of each host tree. *Fascicularia* is a single species genus with two subspecies, according to Zizka et al. (1999): *F. bicolor* subsp. *bicolor* (mostly associated with coastal rocky areas) and the epiphytic *F. bicolor* subsp. *canaliculata* (hereafter referred to as *F. bicolor*). The latter subspecies is a trash-basket epiphyte whose mats capture a large amount of organic debris in the forest canopy (Díaz et al. 2010, Ortega-Solis et al. 2017). Like other trash-basket epiphytes, *F. bicolor* influences the presence and abundance of other epiphytic plants and invertebrates in the vertical profile of the forest by creating habitat patches on host trees (Ortega-Solis et al. 2017). Despite its potential importance for canopy biodiversity, no specific studies relating *F. bicolor* with the attributes of its hosts have yet been conducted.

While not included in the IUCN or Chilean red lists, Zizka et al. (2009) recommend monitoring population trends of *F. bicolor canaliculata*. Besides, a recent industrial project involving forest intervention has proposed to relocate *F. bicolor* individuals as part of their environmental compensation measures (Comisión de Evaluación Ambiental 2011). However, the selection of host-trees and other environmental management practices concerning *F. bicolor* rely on anecdotal information and field observations, without a quantitative background. In this context, the goals of our research were to determine: (i) which tree species were colonized by *F. bicolor*; (ii) what tree size indicated the potential break-point at which tree individuals become suitable hosts for *F. bicolor*; and (iii) the relation between the number of mats of *F. bicolor* and host tree species and size. We provide basic knowledge about the host-trees of *F. bicolor* as a first step to include the species in conservation and management plans of the threatened South American temperate rainforest (SATR – Myers et al. 2000).

Material and methods

Study area

This study was conducted in Parque Oncol (39° 41' S, 73° 20' W), a private protected area in the Coastal Range of Valdivia, southern Chile. Parque Oncol is made up of 754 hectares of old-growth and sec-

ondary forests between 500-710 m a.s.l. The study site is surrounded by a matrix of exotic pine tree plantations, agricultural grasslands and native forests, the latter with varying degrees of human disturbance. The forest is dominated by broad-leaved evergreen species such as *Laureliopsis philippiana* (Looser) Schodde (Athrospermataceae), *Saxegothaea conspicua* Lindl. (Podocarpaceae), *Eucryphia cordifolia* Cav. (Cunoniaceae) and *Drimys winteri* J.R.Forst. & G.Forst. (Winteraceae – Ortega-Solis et al. 2017). The Oncol area was subject to selective logging by the locals up to 1985 (P. Alba, pers. comm.). Then, a Chilean timber company acquired Oncol, and transformed it in a natural reserve in 1989 as a measure of environmental compensation (Hora & Marchant 2016).

Study design

We established seven 20 × 20 m plots in the old-growth forest in Parque Oncol, with elevation ranging from 500 to 600 m a.s.l. Plots were located at least 100 m from each other. In each plot, we recorded species, DBH, and the height of all trees with DBH greater than 5 cm. Tree height was measured with a hypsometer when possible or estimated by measuring neighbouring trees when necessary. Standing dead trees were grouped as “snags”, since we could not identify their original species.

We performed a ground-based census to record the number of *F. bicolor* mats growing on each tree, using binoculars (Celestron® outland 10 × 40, CA, USA) when required. *Fascicularia bicolor* occurs in large mats between 0.5 and 23.2 metres above the forest floor (Ortega-Solis et al. 2017), and no similar epiphytic species inhabit SATR; therefore, the presence of mats was easily determined from a ground-based perspective. Mats include from one to multiple rosettes growing together, but individual rosettes cannot be counted or measured from the ground. Therefore, we counted each full mat as a proxy of the number of successful colonization events (at least one individual established and passed the seedling stage). We did not count *F. bicolor* seedlings (plants whose leaves were about 15 cm in length or smaller) both because of the low probability of detecting the ones growing at high height on trees and their uncertain long-term survival rate.

Data analysis

Since the response variable contained many zeros, we used a Zero-Inflated Poisson (ZIP) model to analyse the relationship between the presence of *F. bicolor* in the sampled trees with DBH, height, and tree species. Zero-Inflated Poisson models are two parts models that fit Poisson and binomial distributions to datasets with a large amount of zeros. Binomial distribution is applied under the assumption that the excess of zeros in the data is produced by the existence of true and false zeros. Then, counts and false zeros (or structural zeros)

are modelled with a Poisson distribution. In our case, false zeros could be trees where only seedlings were growing or those with mats that could not be seen from the ground. An additional variable named tree size index (TSI) was added to the dataset as a proxy for the joint effect of height and DBH. We calculated the TSI using the formula to estimate the lateral surface of cones (eqn. 1):

$$TSI = \frac{\pi \cdot DBH}{2} \cdot \sqrt{\left(\frac{DBH}{2}\right)^2 + Height^2} \quad (1)$$

We emphasise that TSI is not a measure of tree surface, since branches and trunk deviations are not considered. However, TSI allowed to evaluate the joint effect of DBH and height on the abundance of *F. bicolor* mats without testing the interaction between both, thereby decreasing model complexity.

We build a set of nine full models alternating DBH, height, and TSI as fixed effects in the two parts of the model (counts and zeros). In addition, species and the two-way interactions between species and DBH, height, and TSI were included as fixed effects in the count portion of the models. Plot was considered as random effect in both the parts of the models, whereas species was added as random factor in the zero-excess part. Then, we fitted all the possible reduced models by removing interactions and fixed effects from the original set (see Tab. S1 in Supplementary material). The most parsimonious model was selected for interpretation with the corrected version of Akaike's information criterion (Burnham & Anderson 2004). Snags, host species with less than five trees found, those with only one tree colonized by *F. bicolor*, and species where *F. bicolor* was completely absent were excluded from regression analyses, because their inclusion produced unreliable results or complete separation issues. We applied a complimentary Chi-squared test to examine if the number of host-trees per species was associated with tree species abundance in the forest plots. The latter analysis was performed in a data subset with individuals larger than 34 cm DBH of all species (the minimum DBH of a colonized tree in our dataset). Statistical tests were performed in R ver. 3.6.1 (R Core Team 2019) using the package “glmmTMB” (Brooks et al. 2017).

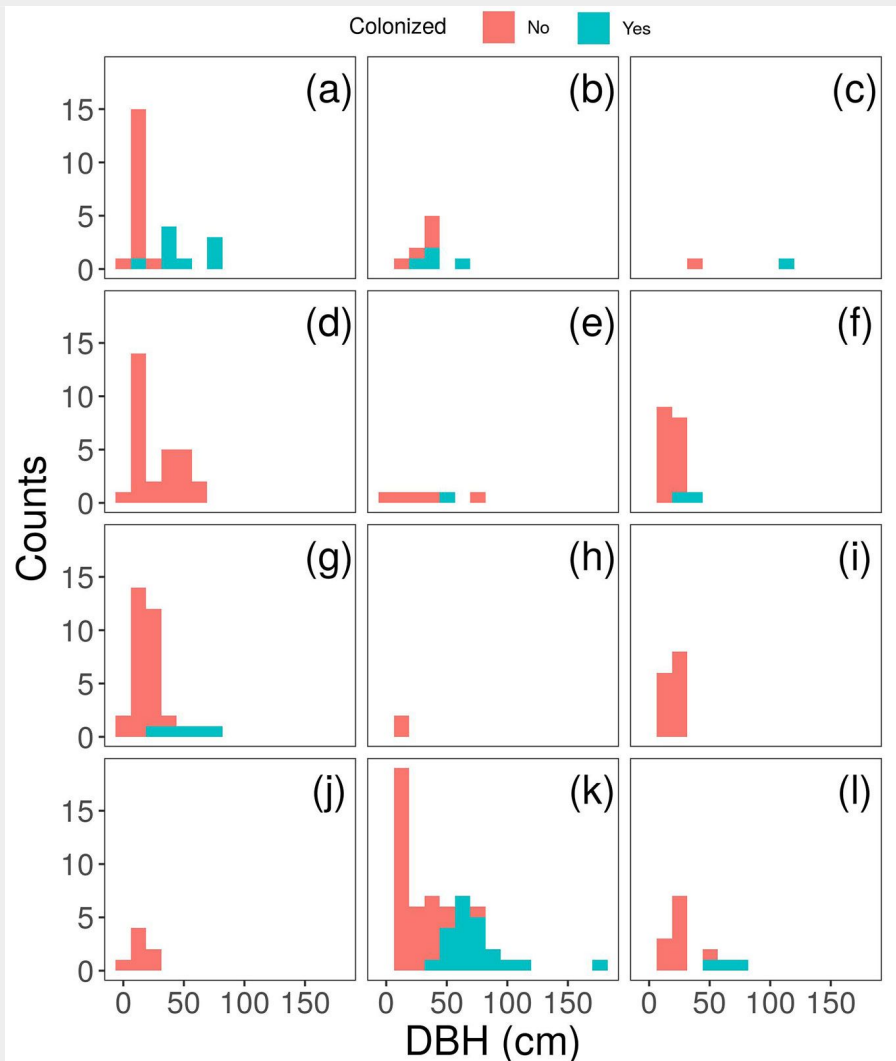
Results

We found 15 tree species totalling 231 individual trees and snags (Tab. 1) with DBH ranging from 5 to 181 cm (Fig. 1), and heights between 3 and 26 m. The most common tree species was *Saxegothaea conspicua*, followed by *Laureliopsis philippiana*, *Drimys winteri* and *Amomyrtus luma* (Molina) D.Legrand & Kausel (Myrtaceae) (Tab. 1). The DBH distribution was typically skewed with a high abundance of small trees and fewer large ones (Fig. 1). Mats of *F. bicolor* were found on 20% of the sampled trees, with most of them on *S. con-*

Tab. 1 - Total sampled trees per species, number of colonized trees and total mats of *F. bicolor* found on each colonized tree species in Parque Oncol. Physical features of the bark were classified on a scale from low (+) to high (+++) importance of each variable based on personal observations. Minus sign (-) show the absence of the corresponding feature. Shade tolerances are shown as intolerant (+), semi-tolerant (++), and tolerant (+++) according to Lusk (1999), Gutiérrez & Huth (2012), and Donoso Zegers (2015).

Species	Bark features			Shade tolerance	Total trees	Colonized trees	Total mats
	Roughness	Peeling	Fissured				
<i>Amomyrtus luma</i>	-	++	-	+++	26	9	50
<i>Amomyrtus meli</i>	-	+++	-	+++	10	4	7
<i>Dasyphyllum diacanthoides</i>	+	-	+	++	3	1	22
<i>Drimys winteri</i>	+	-	-	++	30	0	0
<i>Eucryphia cordifolia</i>	+++	-	+	++	7	1	1
<i>Gevuina avellana</i>	+	-	-	++	19	2	2
<i>Laureliopsis philippiana</i>	++	-	-	+++	34	5	30
<i>Lomatia ferruginea</i>	++	-	-	+	1	0	0
<i>Myrceugenia parvifolia</i>	++	+	-	++	1	0	0
<i>Myrceugenia planipes</i>	++	+	-	+++	3	0	0
<i>Ovidia pillopillo</i>	+	-	-	+	1	0	0
<i>Podocarpus nubigenus</i>	++	+	++	++	15	0	0
<i>Raukaua laetevirens</i>	+	-	-	+	8	0	0
<i>Saxegothaea conspicua</i>	+	+	+++	+++	57	22	161
<i>Weinmannia trichosperma</i>	+	-	+	+	1	0	0
Snags	-	-	-	-	15	3	22
Total Result	-	-	-	-	231	47	295

Fig. 1 - Diameter at breast height distribution per tree species in Parque Oncol, Chile. Colours show non-colonized (red) and colonized (green) trees. Panels: (a) *Amomyrtus luma*, (b) *Amomyrtus meli*, (c) *Dasyphyllum diacanthoides*, (d) *Drimys winteri*, (e) *Eucryphia cordifolia*, (f) *Gevuina avellana*, (g) *Laureliopsis philippiana*, (h) *Myrceugenia planipes*, (i) *Podocarpus nubigenus*, (j) *Raukaua laetevirens*, (k) *Saxegothaea conspicua*, and (l) snags. *Lomatia ferruginea*, *Myrceugenia parvifolia*, *Ovidia pillopillo*, and *Weinmannia trichosperma* were excluded because only one individual of each species was found (with 5, 8, 25, and 31 cm DBH, respectively).



Tab. 2 - Estimated parameters of the selected Zero-Inflated Poisson model for the number of *F. bicolor* mats. Counts of mats were fitted to a conditional model with Poisson distribution (cond), while the zero inflation was evaluated with a logistic model (zi). Intercept (cond) corresponds to *Amomyrtus luma*. (A:B): interaction terms. Random effects are not shown. A full model selection table is reported in Tab. S1 (Supplementary material).

Parameter	Estimate	Standard error	z-value	p-value
Intercept (cond)	2.91	0.92	3.16	<0.01
Height (cond)	-0.13	0.05	-2.42	0.02
<i>Amomyrtus meli</i> (cond)	-5.07	2.20	-2.31	0.02
<i>Laureliopsis philippiana</i> (cond)	-2.76	1.81	-1.52	0.13
<i>Saxegothaea conspicua</i> (cond)	-1.94	0.90	-2.17	0.03
Height: <i>Amomyrtus meli</i> (cond)	0.29	0.13	2.28	0.02
Height: <i>Laureliopsis philippiana</i> (cond)	0.16	0.09	1.68	0.09
Height: <i>Saxegothaea conspicua</i> (cond)	0.22	0.06	3.62	<0.01
Intercept (zi)	7.68	2.25	3.41	<0.01
DBH (zi)	-0.24	0.07	-3.61	<0.01

spicua (Tab. 1). Colonized trees tend to have higher DBH than non-colonized individuals in each species. No mats of *F. bicolor* were found on *D. winteri* or *Podocarpus nubigenus* Lindl. (Podocarpaceae), despite their high abundance compared to other tree species at the study site (Tab. 1). The number of colonized trees was not related to the total abundance of species ($\chi^2 = 28.8, p < 0.001$). Our final ZIP model included an interaction between height and species in the count portion and DBH in the zero inflated part (Tab. 2). The probability of having true zeros decay up to 50%

between 25 and 50 cm DBH for the species included in the model (Fig. 2). The minimum height of a colonized tree was 10 m (Fig. 3).

Discussion

The epiphyte *Fascicularia bicolor* colonizes many, but not all the tree species in our study site. This could be related to multiple variables, such as bark properties and the processes related to the ontogeny of each tree species (e.g., increase in bark roughness, longevity, size and structural changes in the trunk and branches). For instance,

the large and long-living conifer *S. conspicua* (>750 yrs – Lusk 1999) develops a hollow trunk and generates adventitious roots along its internal walls which provide continuous structural strength to assure tree survival (Donoso 2006). Such features make large individuals of *S. conspicua* to have sinuous shapes, cavities, and uneven wrinkled surfaces along the main trunk and branches, which could facilitate the accumulation of detritus, small vascular and non-vascular epiphytes, and arboreal soil, followed by the establishment of large epiphytes like *F. bicolor*.

The absence of *F. bicolor* on *D. winteri* is consistent with Muñoz et al. (2003), who related low epiphyte richness and abundance on *D. winteri* to its smooth bark. However, in our study *F. bicolor* was found on *A. luma* and *A. meli*, which have a smoother and decorticating bark (Donoso 2006). Other epiphytic bromeliads have also been reported inhabiting tree species with peeling bark (López-Villalobos et al. 2008). This evidence suggests that factors other than smooth bark could also explain the absence of *F. bicolor* on *D. winteri*. For instance, the bark of *D. winteri* contains tannins, alkaloids and other substances (Woda et al. 2006) which could negatively affect the establishment of epiphytes. In addition, *Drimys winteri* reaches large sizes in a short time, while *A. luma* and *A. meli* have long lifespans with slow growth rates (Donoso 2006), suggesting that the age of the trees could be an important factor. As an example, in an ongoing study, two 30 cm DBH cross sections of *A. luma* showed

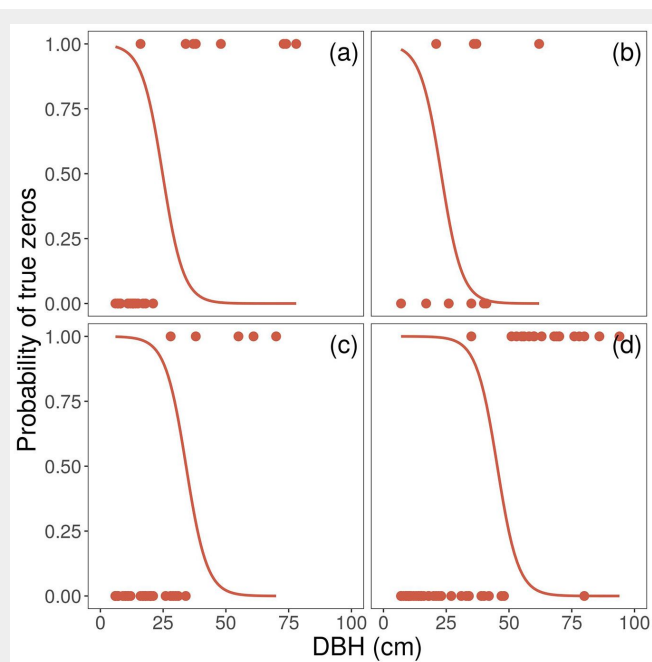


Fig. 2 - Probability of true zeros. Points show trees colonized and not colonized by *F. bicolor*. Lines represent the predicted probability of true zeros. Tree species are shown in the following order: (a) *Amomyrtus luma*, (b) *Amomyrtus meli*, (c) *Laureliopsis philippiana*, and (d) *Saxegothaea conspicua*.

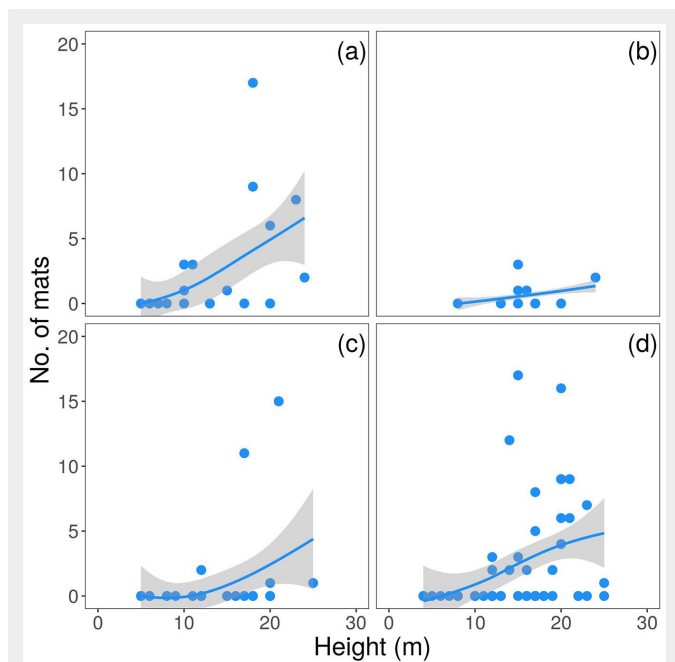


Fig. 3 - Observed (points) and predicted (lines) number of mats per host tree species. Lines show probably LOESS curves fitted to the data. (a) *Amomyrtus luma*, (b) *Amomyrtus meli*, (c) *Laureliopsis philippiana*, and (d) *Saxegothaea conspicua*.

an age of around 185 years, while the core of a living tree of *D. winteri* 1 m in DBH showed an age of 200 years (Díaz & Christie, unpublished data). The slow growth rates of *A. luma* could also explain why the probability of finding a colonized tree reaches 50% at a lesser DBH than required for other hosts (Fig. 2).

Muñoz et al. (2003) indicated that large trees of *P. nubigena* are a common host for many epiphytic species in the SATR; however, we found no *P. nubigena* individuals colonized by *F. bicolor*. According to local people, *P. nubigena* was intensively logged in the area for timber (P. Alba, pers. comm.), and nowadays it is difficult to find large individuals of this species (Fig. 1). We only found *P. nubigena* individuals with a DBH less than 50 cm, which could explain the absence of *F. bicolor* mats growing on them. Logging before 1985 could also be related to the scarcity of large *E. cordifolia* or *W. trichosperma* individuals. *Eucryphia cordifolia* is a highly valued source of firewood in southern Chile and *W. trichosperma* was commercialized to extract tannins for the leather industry (Ramírez et al. 1989). However, no stumps or other evidence was found to support that logging took place within our study plots. Other sampled species, such as the understory tree *L. ferruginea* and the hemiepiphytic *R. laetevirens* do not reach large sizes.

Regarding the number of mats per tree, the interacting effect of height and species suggests height to increase the availability of microsites along the tree-trunk (Fig. 3), but the intensity of such an effect depends on the tree species. Bromeliads suffer dispersal limitation, which could involve that once a tree has been colonized many propagules from the first colonizer individual would establish on the same host or neighbouring trees (Cascante-Marín et al. 2006). Therefore, it is likely that the higher the first *F. bicolor*'s individual become established in a host, the larger amount of microsites will be available for the next generation along the tree trunk. As indicated before, the influence of DBH on the probability of finding a colonized tree could result not only from an increased size but from the time that each tree has been available for colonization (Fig. 2).

Implications for sustainable forest management

The functional roles and biomass input of *F. bicolor* are noteworthy, considering that it can be found associated with forests between 33° and 42° S, one of the most threatened ecosystems on the planet (Myers et al. 2000). Much of these forests are secondary and highly degraded (CONAF 1999). The lack of large trees in second-growth or degraded forest stands can limit the long-term viability of local populations of *F. bicolor* and its ecological role in the forest. This epiphyte is associated with 50% of arboreal soils and epiphytic green tissues (Díaz et al. 2010), enhancing the cover

of vascular epiphytes (Ortega-Solís et al. 2017), and providing habitat to invertebrates living along the vertical profile of trees (Ortega-Solís et al. 2017, Vera & Schapheer 2018). Although the conservation status of *F. bicolor* has not been assessed in the current IUCN Red List, monitoring of population trends is recommended (Zizka et al. 2009).

Despite protection efforts, forests in southern Chile are still subject to illegal logging to produce firewood and charcoal (Moorman et al. 2013). Therefore, producing basic ecological knowledge to support the development of sustainable forestry in the SATR is necessary. Here we show that conserving tree species large-sized, and with a wrinkled surface (such as *Saxegothaea conspicua*) could be beneficial for epiphytes like *F. bicolor*. However, there are open questions regarding dispersal strategies of *F. bicolor*, or the effects of physical and chemical attributes of the tree-bark on propagule establishment. We also emphasize that further research is needed to elucidate host-tree requirements of other epiphytic species, and to integrate such information in forest management strategies.

Conclusions

Our findings provide an initial approach to evaluate the characteristics necessary to support a substantial population of *F. bicolor* within a forest stand. *F. bicolor* does not colonize all tree species, but large trees of its host species could be crucial for the establishment and population's viability of this bromeliad. Large trees are complex organisms that can support many other species due to their attributes: rough bark, trunk cavities, horizontal and well-developed branches among others (Lindenmayer & Laurance 2017). These features offer a wide microhabitat range, absent in young small trees. Here, we focused on the host' requirement for *F. bicolor*, but additional research is needed to elucidate the potential changes in canopy biodiversity related to local extinctions of this large epiphyte.

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Supplementary Material

Tab. S1 - Model selection table for the number of mats of *F. bicolor* per tree.

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