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Habitat preferences of two New Zealand perching orchids with contrasting abundance and conservation status

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INTRODUCTION

The diversity of epiphytes is commonly higher in tropical parts of the world than anywhere else (Benzing 2012). In temperate Aotearoa/New Zealand (NZ), however, the biomass of epiphytes in some forests is significant and comparable to that in the tropics (Hofstede et al, 2001). Over 60 species of vascular epiphytes occur in NZ; most of them are ferns (ca. 39 species) and a few are woody or herbaceous plants (Oliver 1930). As in the tropics, orchids are also part of the NZ epiphytic flora but their diversity is low and only nine species occur there (de Lange et al. 2007, Beadel et al. 2010). *Drymoanthus* is a small genus of epiphytic orchids that includes only four species. *Drymoanthus adversus* and *D. flavus* are endemic to NZ, *D. minutus* is endemic to Australia and found in dry tropical rainforests of north-eastern Queensland, and *D. minimum* is endemic to wet tropical rainforests of New Caledonia. The latter two species are morphologically very similar to the NZ species of *Drymoanthus* (Molloy & St George 1994).

New Zealand *Drymoanthus* have a tropical look about them, with fleshy succulent leaves and long cordlike roots. They often perch high up on the trunk of their host going unnoticed by trampers due to their small size. Both orchids are similar in appearance though closer inspection reveals two subtly different plants. The most striking difference is that *D. flavus* (Figure 1A) is usually covered in dark purple spots on its leaves and fruits but not on the flowers. According to Molloy & St. George (1994) this is not always the case, and *D. flavus* may actually occur free of spots, making field identifications tricky. *Drymoanthus adversus* (Figure 1B) is normally a slightly larger plant with longer, more slender, glossy, succulent leaves that are thicker than *D. flavus* and are elliptic to oblong in shape; *D. flavus* has dull pale green leaves that are thinner, leathery and elliptic to lanceolate

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Figure 1. Plants of *Drymoanthus flavus* (A) and *D. adversus* (B) perching on *Olearia paniculata* and *Leptecophylla juniperina*, respectively. Photos by B. Cox.

(de Lange et al. 2007). Flowers in *D. adversus* are green to greenish-white with red to purplish flecks, and yellow with no spots in *D. flavus* (de Lange et al. 2007). Chromosome counts have shown *Drymoanthus adversus* is tetraploid (2n = 4x = 76) whereas *D. flavus* is diploid (2n = 38) (Molloy & St George 1994).

These two orchids also differ in abundance and conservation status. *Drymoanthus adversus* is not threatened; it is fairly widespread throughout both the North and South Islands, but considered to be more common in the North Island. On the other hand, *D. flavus* is naturally uncommon throughout most of the country even though it is mostly sympatric with *D. adversus* except for the southern part of the South Island where *D. flavus* tends to be dominant and sometimes the only species present (Molloy & St George 1994). According to Molloy & St George (1994) orchid collectors pose a threat to rare endemic orchids such as *D. flavus* and de Lange et al. (2007) states indiscriminate collection have stripped bare some well-known populations in the lower North Island. *Drymoanthus flavus* is currently classified as At Risk—Naturally Uncommon (de Lange et al. 2013). This means that populations of *D. flavus* are naturally small and widely scattered.

The distribution and abundance of epiphytic orchids can be affected by numerous factors. Host availability, bark texture, host age and structure, and the presence of allelopathic chemicals in the bark, which may affect seed germination, are only some of them (Benzing 1979; Migenis & Ackerman

1993; Tremblay et al 1998; Gowland et al. 2011; Wyse & Burns 2011; Crain 2012). Habitat preferences of orchid mycorrhizal fungi add another level of complexity to the orchid-host interaction as these fungi are essential for the orchid seeds to germinate (Tremblay et al 1998; Gowland et al. 2011). Interestingly, despite the habitat demands this three-species interaction may impose on orchids, host specificity seems to be uncommon among epiphytic orchids (see Gowland et al. 2011) but not inexistent. For instance, host specificity has been confirmed in some species of the tropical orchid genus *Lepanthes*, some Malaysian and Philippine orchids (Migenis & Ackerman 1993) and in two species of *Sarcochilus* from the Australian temperate dry rainforests (Gowland et al. 2011). Some of these orchids are restricted to a single host and their long term conservation depends on the suitable management and protection of their host.

Habitat preferences of NZ epiphytic orchids are largely unknown. Lists of host species have been compiled for some orchids (de Lange et al. 2007) and bark features of trees hosting four species of epiphytic orchid in the Auckland region compared (Wyse & Burns 2011). However, studies exploring the influence that habitat preferences may have on abundance and distribution of our native epiphytic orchids are missing. In this study we aim to characterise the habitat that *D. adversus* and *D. flavus* occupy in a protected area of the Wellington region, and we investigate whether their contrasting local abundance is linked to habitat preferences. More specifically we focused on the following questions:

1. Do *D. adversus* and *D. flavus* have a preference for a host species?
2. Do *D. adversus* and *D. flavus* have a preference for host size?
3. Are *D. adversus* and *D. flavus* commonly associated with other vascular epiphytes?
4. Are *D. adversus* and *D. flavus* commonly associated with non-vascular epiphytes such as lichens, liverwort and moss?

METHODS

Field sites

This study was conducted within a protected area of the Wellington region in the southern North Island. Due to differences in the vegetation and forest structure within the area, two sites were included in the study. In the first one (Site 1), observations aimed to investigate the interaction of *Drymoanthus* with other vascular epiphytes. The vegetation here consisted of mixed lowland podocarp/broadleaved forest with species such as rimu, miro, mataī, kahikatea and pukatea (Sawyer 2005). On Site 2, we studied the interaction between orchid presence and abundance with host size and the orchids' association with non-vascular epiphytes. At this site the vegetation consisted of a mixture of variously-aged beech forest and scrub with black beech on dry exposed ridges and spur tops and hard beech on less steep slopes (Sawyer 2005).

Survey design

The first site (Site 1) was in a valley. Here we conducted a visual search for all vascular epiphytes occurring along a 0.45 km section of an established track and all trees within 15 m of either side of the track. Based on the methodology used by Burns & Dawson (2005), each potential host was searched until it was deemed that all vascular epiphyte species had been found. The time this initial search took was noted and a further search was conducted for one-third of that time. To obtain an accurate representation of the identity and occurrence of each epiphyte, two observers scanned each host tree simultaneously and then notes were compared. Visual searches were conducted by the naked eye and assisted by two sets of binoculars, each with a different level of magnification. Those trees supporting vascular epiphytes were identified to species and their resident vascular epiphytes recorded.

The second site (Site 2) was a steep west-facing slope. A 60 × 60 m plot was established in a representative section of the forest and the presence of *Drymoanthus* species and other epiphytes was conducted for every tree or shrub in the plot. Site 2 was dominated by trees no taller than 15 m, making it very easy for one observer to search and accurately count and identify all epiphytes. Epiphytes were surveyed here in the same fashion as Site 1, with the only differences being that the number of individuals of *D. adversus* or *D. flavus* on each host was counted and the diameter at breast height (d.b.h.) measured for host and non-host trees of > 5 cm d.b.h. The d.b.h. measurement is considered a good indicator of the size of the host trees as the measurement often correlates with height and tree age (Zotz & Vollrath 2003). In Site 2, *Drymoanthus* individuals were also found perching on a few medium size shrubs (c. < 2.5 m high) with sympodial growth (no single main trunk). The d.b.h. of these shrubs was not measured because they had multiple trunks and measurements are not comparable with those of monopodial species (one main trunk only); furthermore, their trunks were mostly below 5 cm d.b.h. Lastly, the presence of non-vascular epiphytes such as bryophytes (mosses and liverworts) occurring in direct contact with the orchids was recorded and bryophyte samples collected from selected hosts and later identified. Tree ferns may also provide sites for epiphytes but were here excluded as their growth habit and trunk structure are sufficiently different to warrant a separate study (see Burns & Dawson 2005).

Statistical analyses

Analysis of variance (ANOVA) to test size difference (i.e., d.b.h.) between hosts and non-host trees and correlation between orchid abundance and host size were performed with the program SPSS (SPSS: IBM Corporation 2013). The interaction between *Drymoanthus* species and other vascular epiphytes was investigated by calculating incidence functions for each species of vascular epiphyte found on hosts at Site 1. Incidence functions describe the probability of occurrence of a species with respect to the number of species occurring on each host and are considered an accurate representation of the distributional ecology of a species (Diamond 1975; Gotelli & Graves 1996).

RESULTS

Host diversity

Drymoanthus individuals were found on 19 native species in both study sites combined (Table 1); most of them were tree species and only four were medium size shrub species. *Drymoanthus adversus* had the greatest diversity of hosts and it was found on all 19 species and at both study sites. Furthermore, *D. adversus* was observed on three previously unrecorded hosts; *Dicksonia squarrosa* (tree fern), *Lophomyrtus obcordata* (shrub) and *Metrosideros fulgens* (vine). Up to 30 potential host species were recorded in Site 2 but *D. adversus* was restricted to three species only (Table 1). On the other hand, *D. flavus* was only found at Site 2 and on two shrub species (*Leptecophylla juniperina* and *Olearia paniculata*) (Table 1). Both orchids co-occurred on *O. paniculata* but were never found growing together on *L. juniperina*. Overall, *D. adversus* and *D. flavus* occurred most commonly on *O. paniculata* (14.5% and 11.6% respectively, Fig. 2), which was the least abundant host species in Site 2 (Fig. 2). Conversely, only 12.8% of *Fuscospora solandri* trees, the most abundant host species in Site 2 (Fig. 2), had *D. adversus* perching on them and none had *D. flavus*.

Host size preference and orchid abundance

The d.b.h. of 554 *Fuscospora solandri* trees was measured at Site 2; most of the trees were less than 10 cm d.b.h. (Fig. 3) and only nine were larger than 50 cm (Fig. 3). Host trees had a significantly larger d.b.h. than non-host trees (ANOVA $F_{1,\,553}$ = 113.47, p = 0.000; Fig. 3) and their size ranged between 7.8 and 63.7 cm (Fig. 3). As for the shrubs hosting *Drymoanthus adversus* or *D. flavus*, their branches were rarely >5 cm diameter. The number of orchids on *F. solandri* trees ranged from 1 to 306 individuals. There was a significant but moderate positive correlation between the size of the host and the number of *D. adversus* plants found on the host (r = 0.349, d.f. = 48,

Table 1: List of hosts of *Drymoanthus adversus* and *D. flavus* at Site 1 (1) and Site 2 (2). T: tree, Shr: Shrub.

Host	***D. adversus***	***D. flavus***
Beilschmiedia tawa (T)	1	
Carpodetus serratus (T)	1	
Dacrycarpus dacrydioides (T)	1	
Elaeocarpus dentatus (T)	1	
Elaeocarpus hookerianus (T)	1	
Fuscospora solandri (T)	1,2	
Knightia excelsa (T)	1	
Leptecophylla juniperina (Shr)	1,2	2
Leucopogon fasciculatus (Shr)	2	
Lophomyrtus bullata (T)	1	
Lophomyrtus obcordata (T)	1	
Melicytus ramiflorus (T)	1	
Metrosideros robusta (T)	1	
Myrsine australis (T)	1,2	
Olearia paniculata (Shr)	2	2
Olearia rani (Shr)	1	
Prumnopitys ferruginea (T)	1	
Pseudopanax crassifolius (T)	2	
Weinmannia racemosa (T)	1	

$P < 0.05$) and larger *F. solandri* trees had slightly more individuals on their trunks than those of smaller d.b.h. The four largest trees in the plot had the larger numbers of orchids, each with > 100 individuals.

Association with other epiphytes

Incidence functions showed that the occurrence of *Drymoanthus adversus* decreased and remained low as the number of species of vascular epiphytes on the host increased (Fig. 4). Conversely, the occurrence of other vascular epiphytes such as *Asplenium flaccidum, Griselinia lucida* and *Pyrrosia eleagnifolia* rapidly increased as more species of epiphytes were present on the host.

Association with moss and liverworts

Nine species of moss, two of liverwort and one of lichen were recorded on the most common hosts at Site 2 (Table 2). Almost 90% of the orchids recorded in Site 2 were growing in direct contact with these non-vascular

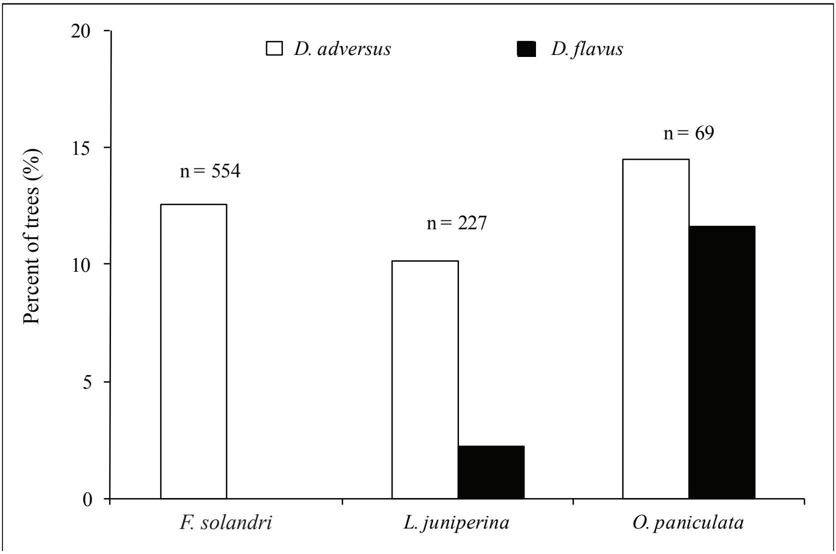

Figure 2. Percentage of individuals of *Fuscospora solandri*, *Leptechophylla juniperina* and *Olearia paniculata* with *Drymoanthus adversus* and *D. flavus* at Site 2. Number above bars of each host species indicates the total number of individuals in the plot.

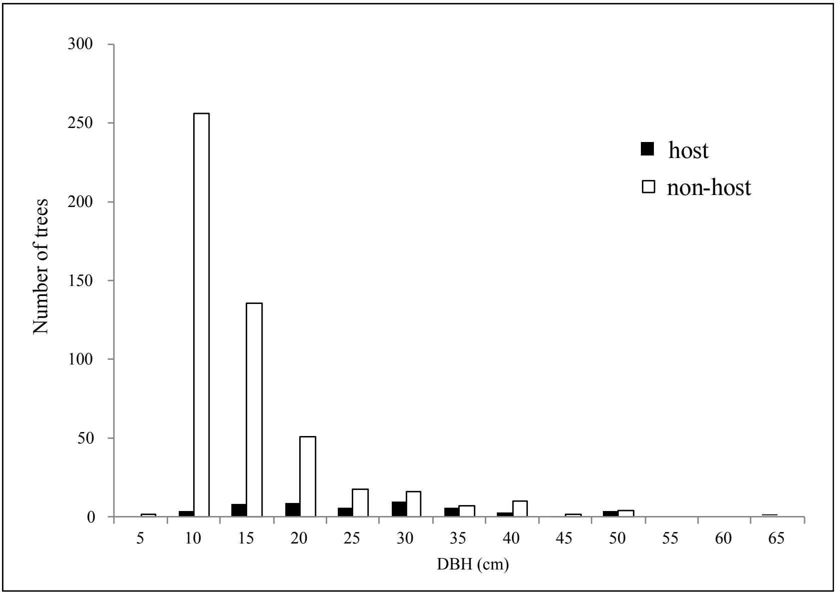

Figure 3. Size distribution of host (n= 52) and non-host (n= 502) trees of *Fuscospora solandri* with *Drymoanthus adversus* at Site 2. Mean d.b.h. and standard deviation of host and non-host was 249.67 ± 121.9 and 123.30 ± 123.3, respectively.

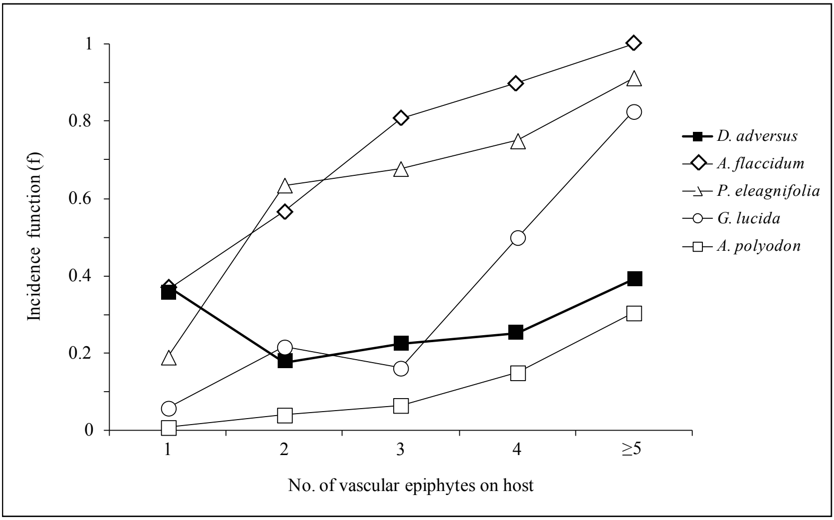

Figure 4. Incidence function of *Drymoanthus adversus* at Site 1 and associated vascular epiphytes (*Asplenium polyodon*, *Asplenium flaccidum*, *Griselinia lucida* and *Pyrrosia eleagnifolia*).

Table 2. List of non-vascular epiphytes in direct contact with plants of *Drymoanthus adversus* and *D. flavus* occurring on three host species at Site 2. M: moss, Ln: lichen, L: liverwort.

Host species	**Non-vascular epiphytes**
Leptecophylla juniperina	*Thuidium furfurosum* (M)
	Camptochaete arbuscula (M)
	Zygodon intermedius (M)
	Macromitrium sp. (M)
	Dicranoloma menziesii (M)
Olearia paniculata	*Pseudocyphellaria* spp. (Ln)
Fuscospora solandri	*Dicnemon calycinum* (M)
	Hypnum cupressiforme (M)
	Dichelodontium nitidum (M)
	Macromitrium longipes (M)
	Drepanolejeunea aucklandia (L)
	Metalejeunea cucullata (L)
	Pseudocyphellaria spp. (Ln)

epiphytes and only one plant of *Drymoanthus adversus*, perching on *Fuscospora solandri*, with none (Fig. 5). The lowest percentage of orchids growing in contact with mosses/liverworts was recorded on the shrub *O. paniculata*, with c. 30% (Fig. 5). On this host, however, orchid roots were commonly growing amongst *Pseudocyphellaria* lichens.

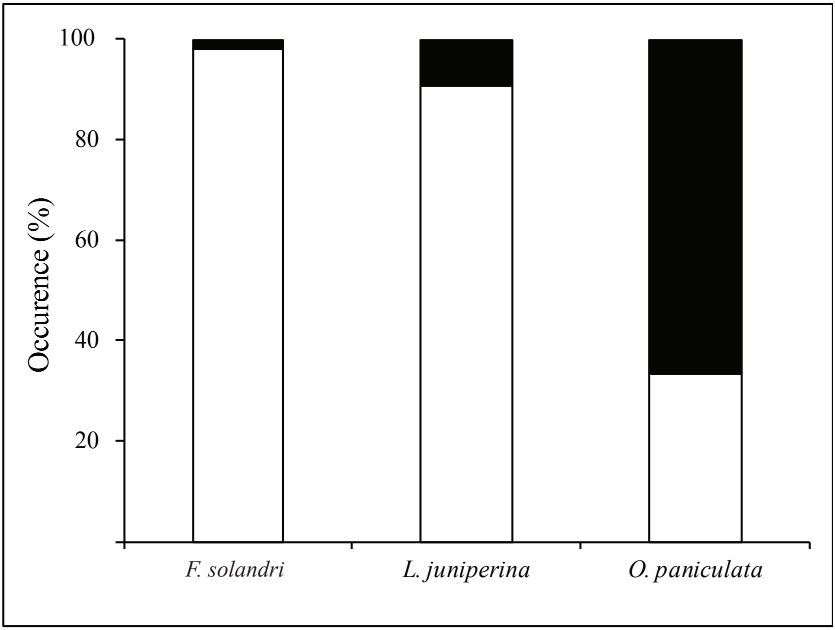

Figure 5. Occurrence of bryophytes (moss or liverworts) in direct contact with *Drymoanthus* species for each host species (*Fuscospora solandri*, *Leptecophylla juniperina*, *Olearia paniculata*) at Site 2. Open bars indicate presence of bryophyte, and filled bars indicate absence of bryophyte.

DISCUSSION

We investigated the habitat preferences of *Drymoanthus adversus* and *D. flavus*, two native epiphytic orchids with contrasting abundance and conservation status. Our results indicate that *D. adversus* is not biased towards a particular host species and it may grow on a range of native species and of different growth habit (e.g. trees, shrubs and vines). This confirms previous claims that *D. adversus* has an ample habitat range (Molloy & St. George 1994) establishing even on introduced species such as willow (Johns & Molloy 1983) and sometimes on rocks (de Lange et al. 2007). On the contrary, *D. flavus* appears to be more selective, or at least so in our study area, where *D. flavus* was only found at one study site and on only two host species, *Olearia paniculata* and *Leptecophylla juniperina*. Interestingly, *O. paniculata* was the least abundant species in the site but the host where most of the *D. flavus* plants were found. Furthermore, at least 10 other species previously reported as hosts of *D. flavus* by Molloy & St. George (1994) were found in our study site but none had *D. flavus* on them. What is preventing *D. flavus* from colonising these potential hosts? Our observations suggest that the occurrence of *D. flavus* at a specific site may not only depend on host availability but also on other factors such as the presence of a specific mycorrhizal fungus on the host and suitable micro-habitat conditions for the symbiosis to form (e.g. bark texture and presence of moss). Orchid mycorrhiza are believed to be responsible for host specificity in some Australian epiphytic orchids related to *Drymoanthus* (Gowland et al. 2011) and the Costa Rican *Lepanthes* which is range restricted despite its strong preference for a widespread host species (Tremblay et al. 1998).

Our study has also shown that hosts for *Drymoanthus adversus* are generally larger trees (d.b.h. > 25 cm) and that, to some extent, its abundance is correlated to host size. However, we believe these patterns do not reflect the orchid habitat preferences, but colonisation likelihood. Host size, measured as d.b.h., is a reflection of age and, therefore, represents the time the tree has been available for the orchid seeds to reach and establish (Gowland et al 2011). Also, the larger the surface area the greater the chance for orchid seeds to land on the host (Migenis & Ackerman 1993). Time and surface area may explain the large number of *Drymoanthus* plants found in the largest trees at Site 2 (> 200). However, in the case of *Fuscospora solandri*, age also means a change in the bark surface and older trees are generally rougher in texture (Fig. 6) which may facilitate the establishment of orchids and other non-vascular epiphytes. On the contrary, *D. flavus* seems to be a twig epiphyte and shows a preference for small diameter branches (< 5 cm); however, due to its low abundance in the site (55 individuals in 13 shrubs), this should be further investigated.

The order in which *Drymoanthus* and other vascular and non-vascular epiphytes colonise their hosts is so far unknown. Burns & Dawson (2005) have studied the interaction between epiphytes in NZ and suggested epiphytes rely on the formation of networks, or communities, to create or make habitat available for newcomers. Our observations suggest the opposite for *D. adversus*. This orchid has a preference for unoccupied hosts, free from other vascular epiphytes and its occurrence decreases when other epiphytes appear (Fig. 4). Based on these observations it is likely that *D. adversus* is the first species to colonise a host and it is subsequently outcompeted as the host becomes more crowded and new habitat is accessible to other vascular epiphytes. This early coloniser strategy is in line with the weedy nature of some orchids and their opportunistic use of resources (Rasmussen 1995), generally appearing in sites that have been recently disturbed and in early successional stages (Hutchings 1989; Rasmussen 1995).

In our study, over 90% of the orchid individuals or clumps observed were growing in direct contact with moss or liverworts. This orchid-moss/liverwort association is not unique to *Drymoanthus* and it has been reported before in overseas orchids (Tremblay et al. 1998; Scheffknecht et al. 2010; Gowland et al. 2011; Crain 2012) and in several NZ epiphytes including orchids (Wyse & Burns 2011). Crain (2012) proposed four hypotheses to explain this strong association. Firstly, bryophytes may provide a moist heterogeneous substrate for the extremely fine orchid seeds to land on and establish as opposed to smooth, dry bark. Secondly, bryophytes may support the growth of the mycorrhizal fungi that orchids rely on. Thirdly, bryophytes may leach nutrients into water which could become available to orchids. Lastly, bryophytes may help to buffer orchid roots from drought conditions by slowing desiccation. Similar to bryophytes, lichens may also facilitate orchid seeds' establishment and field experiments elsewhere have demonstrated their presence favours the establishment of bromeliad seeds on smooth bark hosts (Callaway et al. 2001). In our study we found species of the lichen *Pseudocyphellaria* associated with *D. flavus* growing on *Olearia paniculata*, a host with a flaky bark (Fig. 6), and once with *D. adversus* on *Fuscospora solandri*, a host with smooth bark when young but rough bark when older (Fig. 6).

In conclusion, this study has shown that *Drymoanthus adversus* is not biased towards a specific host species but to host size and it is most commonly found on larger trees. On the contrary, *D. flavus* is restricted to smaller hosts and biased towards the least abundant host found in our study site (i.e., *O. paniculata*), which may suggest some degree of preference. Both orchids grow commonly in direct contact with non-vascular epiphytes such as bryophytes or lichens, which may facilitate seed attachment to the bark and germination. However, the establishment of other vascular epiphytes seems to have a negative effect on *D. adversus* limiting its occurrence to empty hosts. Finally, our findings suggest that the distribution and abundance of these orchids may also depend on factors other than host availability and size. For instance, the habitat preference of each of these orchids' mycorrhiza and the specificity of this interaction may influence the local distribution and abundance of *Drymoanthus* species. These aspects of the mycorrhiza-host-orchid interaction have never been researched in *Drymoanthus* or in any of our native epiphytic orchids. Besides providing an insight into our epiphytic orchids' distribution and colonisation patterns, these studies will give us the knowledge necessary to implement management tools and propagation techniques to assist with the re-establishment of fallen plants and eliminate the collection of plants from wild populations.

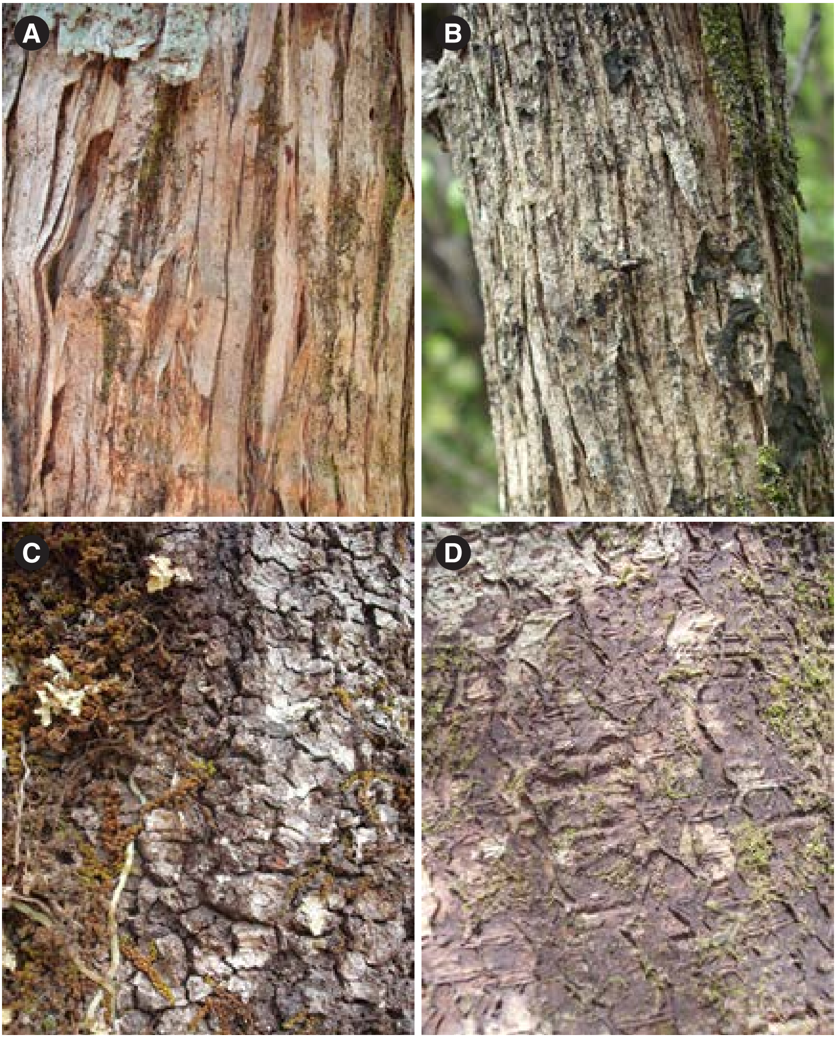

Figure 6. Bark surface of most common host species for *Drymoanthus adversus* and *D. flavus* found on Site 2. (A) *Olearia paniculata*; (B) *Leptecophylla juniperina*; (C) *Fuscospora solandri* (old tree); (D) *F. solandri* (young tree).

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