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When facilitation meets clonal integration in forest canopies

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Summary

- Few studies have explored how – within the same system – clonality and positive plant–plant interactions might interact to regulate plant community composition. Canopy-dwelling epiphytes in species-rich forests provide an ideal system for studying this because many epiphytic vascular plants undertake clonal growth and because vascular epiphytes colonize canopy habitats after the formation of nonvascular epiphyte (i.e. bryophyte and lichen) mats.
- We investigated how clonal integration of seven dominant vascular epiphytes influenced inter-specific interactions between vascular epiphytes and nonvascular epiphytes in a subtropical montane moist forest in southwest China.
- Both clonal integration and environmental buffering from nonvascular epiphytes increased survival and growth of vascular epiphytes. The benefits of clonal integration for vascular epiphytes were higher when nonvascular epiphytes were removed. Similarly, facilitation from nonvascular epiphytes played a more important role when clonal integration of vascular epiphytes was eliminated. Overall, clonal integration had greater benefits than inter-specific facilitation.
- This study provides novel evidence for interactive effects of clonality and facilitation between vascular and nonvascular species, and has implications for our understanding of a wide range of ecosystems where both high levels of clonality and facilitation are expected to occur.

Introduction

The study of biotic interactions is essential for developing a predictive understanding of community assembly (Kraft & Ackerly, 2010; Michalet *et al.*, 2015; Chalmandrier *et al.*, 2017; Lekberg *et al.*, 2018; Tylianakis *et al.*, 2018) and ecosystem responses to environmental change (Harley, 2011; Cavieres *et al.*, 2014; Polle & Luo, 2014; Graff & Aguiar, 2017). Although studies of natural communities for a long time assumed that the dominant form of the inter-specific interaction was competition (i.e. negative interactions; Connell, 1983; Kunstler *et al.*, 2012; Bödeker *et al.*, 2016; Lekberg *et al.*, 2018), the role of facilitation (positive interactions) has recently been realized in many ecosystems (Callaway *et al.*, 2002a; Brooker *et al.*, 2008; He *et al.*, 2013; Ettinger & Hillerislambers, 2017; Filazzola *et al.*, 2018). Whilst competition may drive species extinctions and diversity loss (Hautier *et al.*, 2009; He *et al.*, 2013) and negatively affect ecosystem stability (Ives *et al.*, 1999; Loreau & de Mazancourt, 2013; Douda *et al.*, 2018), facilitation can maintain diversity (Butterfield *et al.*, 2013; Cornacchia *et al.*, 2018), particularly in harsh environments where species often rely on each other to persist (Cardinale *et al.*, 2002; Cavieres *et al.*, 2014; Le Bagousse-Pinguet *et al.*, 2014; Barron-Gafford *et al.*, 2017).

Whilst generating a recent surge of interest in plant community ecology (Choler *et al.*, 2001; Brooker *et al.*, 2008; Cavieres *et al.*, 2014; Douda *et al.*, 2018; Filazzola *et al.*, 2018), positive plant–plant interactions are nothing new for researchers working on clonal plants. Within clonal plants, patchily available resources can be shared between ramets through physiological integration, thus enhancing the survival and growth of ramets in otherwise resource-poor patches (Hartnett & Bazzaz 1983; Alpert 1991; Song *et al.*, 2013). Although there are many studies of intra-specific facilitation through clonal integration (Song *et al.*, 2013; Roiloa *et al.*, 2014; Wang *et al.*, 2017; Duchoslavova & Jansa, 2018), few studies have examined how clonal integration and inter-specific facilitation might interact (Brooker, 2017). This is notable given that both phenomena are considered more common in some kinds of environments, for example in severe environments such as arctic and alpine ecosystems (Brooker, 2017), and forest canopies with regards to epiphytes (i.e. plants which grow on, but do not parasitize, other plants; Barkman, 1958). The epiphyte–host interaction is a well-known form of commensalistic facilitation, and the traits of host trees may play key roles in germination and performance of epiphytes (Callaway *et al.*, 2001, 2002b; Burns & Zotz, 2010). However, we know very little about the interaction of epiphytes within the canopy, and how such an interaction is affected by clonal integration.

Forest canopies offer an excellent opportunity for exploring interactions between clonality and inter-specific facilitation. Forest canopies represent the functional interface between 90% of the Earth's terrestrial biomass and the atmosphere, and include some of the most threatened terrestrial ecosystems (Ozanne *et al.*, 2003; Ellwood & Foster, 2004; Zotz, 2016). They house 40–50% of terrestrial biodiversity, and epiphytes are a key component of forest canopies and play important roles in maintaining biodiversity (Ozanne *et al.*, 2003; Ellwood & Foster, 2004; May, 2010) and ecosystem functioning (Umana & Wanek, 2010; Lowman & Schowalter, 2012; Zotz, 2016). Also epiphytic ferns provide a highly suitable group for studying intra-epiphyte interactions as they represent a high percentage of the vascular epiphytic diversity in subtropical and temperate zones with seasonal climates (Watkins *et al.*, 2007; Chen *et al.*, 2019). Perhaps surprisingly, given their high diversity, epiphytic habitats can still be considered 'harsh': tree crowns are characterized by a limited storage capacity for available nutrients and water, sporadic and dilute nutrient inputs, low physical stability, and extreme fluctuations in moisture and temperature (Lowman & Schowalter, 2012; Zotz, 2016). To adapt to such harsh habitats, many vascular epiphytes, and almost all bryophytes and lichens, are capable of clonal growth, potentially allowing physiological integration (Lu *et al.*, 2015, 2016; Chen *et al.*, 2019).

At the same time as promoting clonality and physiological integration, the severe environments of the forest canopy could also be locations where facilitation between neighbouring but physiologically-independent individuals is important. For example, during the development of the epiphyte community, vascular epiphytes establish after the development of epiphytic mats consisting of bryophytes, lichens, and canopy humus (Barkman, 1958; Nadkarni & Haber, 2009; Zotz, 2016). The net inter-specific interaction of epiphytes and their physiologically-independent neighbours may not be competition but facilitation. However, the simultaneous occurrence of physiological integration between the ramets of clonal epiphytes might reduce their dependence on – and alter the balance of their net interactions with – physiologically independent neighbours.

We conducted a field experiment combining neighbour removal and rhizome severing treatments with seven dominant vascular epiphytes (all rhizomatous clonal species) in forest canopies in a primary montane moist forest in southwest China. We explored (1) whether net interactions between vascular and nonvascular epiphytes are negative or positive, and (2) whether altering the level of physiological integration between ramets of vascular epiphytes also alters their interactions with their physiologically-independent nonvascular neighbours. In particular, we expect that dependence on clonal integration will increase once nonvascular neighbours are removed, and likewise that beneficial effects of having physiologically-independent neighbours are greatest for physiologically-isolated ramets.

Materials and Methods

Study site

The experiment was conducted in a primary subtropical montane moist forest in the Ailao Mountain National Nature Reserve in Yunnan Province, southwest China. The mean air temperature is 11.6°C, the mean annual precipitation is 1859 mm, with 86% of rainfall occurring in the rainy season (May–October) and 14% in the pronounced dry period from December to April (Song *et al.*, 2016). The dominant tree species in this forest include *Lithocarpus xylocarpus*, *Castanopsis wattii*, *L. hancei*, *Schima noronhae*, *Machilus viridis*, and *Hartia sinensis*. The forest is inhabited by a diverse community of epiphytes, including 125 species of seed plants, 93 species of ferns and lycophytes, and *c.* 300 nonvascular epiphytes. In the epiphytic community, eight of the nine dominant vascular epiphytes are ferns, and seven of these ferns produce long, creeping rhizomes (Lu *et al.*, 2016).

Study species

We chose the seven dominant rhizomatous epiphytic ferns as our study species: *Araiostegia perdurans* (Christ) Cop., *Arthromeris lehmannii* (Mett.) Ching, *Lepisorus scolopendrium* (Buchanan-Hamilton ex Ching) Mehra & Bir, *Oleandra wallichii* (Hook.) C. Presl, *Polypodiastrum argutum* (Wall. ex Hook.) Ching, *Polypodiodes subamoena* (C. B. Clarke) Ching and *Selliguea connexa* (Ching) S. G. Lu, Hovenkamp & M. G. Gilbert (Supporting Information Methods S1). These species mainly inhabit tree barks, branch junctions and rocks (Flora of China: http://foc.iplant.cn/).

Experimental design

We chose 60 host trees with a diameter at breast height of at least 30 cm from three dominant canopy species (*L. xylocarpus*, *C. wattii* and *L. hancei*), that is 20 tree individuals from each host tree species. For each epiphyte species, we selected 120 ramets of a similar size (indicated by initial frond length; Notes S1; Table S1) on these host trees, and randomly subjected them to two rhizome severing treatments (rhizome severed or intact) crossed with two neighbour removal treatments (removed or not removed) (Fig. S1). There were 30 replicates for each treatment. The 120 ramets of each epiphytic fern were distributed in three species of host trees, with 10 individual trees from each host tree species. Thus, for each epiphytic fern, there were 30 individual trees hosting these 120 ramets, with each individual host tree having four ramets treated with each of the four treatments. Also, each individual tree hosted three to four epiphytic fern species (Fig. S1).

For the severed treatment we cut off the two rhizomes that were connected to each ramet halfway from the ramet, and for the intact treatment we left the two rhizomes unsevered. Severance of connections between ramets is widely accepted in the study of clonal integration (Hartnett & Bazzaz 1983; Alpert, 1991; Pennings & Callaway, 2000; Roiloa *et al.*, 2014; Wang *et al.*, 2017; Duchoslavova & Jansa, 2018). It is generally assumed that such a method does not cause physical damage to the disconnected ramet(s), not least in our system because there is always some distance from the severing point(s) to the disconnected ramet. Although we cannot exclude the potential for increasing disease infection from the severing point(s), we did not observe any indications of infection following severing. Also, many studies (e.g. Alpert, 1991; Wijesinghe & Handel, 1994; Saitoh *et al.*, 2002; Yu *et al.*, 2002) have shown that severance of the connection(s) between adjacent ramets of the same age and size in homogeneous environments does not harm the two ramets that are disconnected. For the neighbour removal treatment we carefully removed only the shoots of mosses and lichens leaving intact the bulk of the epiphytic mat around the ramet, and for the neighbour present (not removed) treatment we left the mosses intact. In previous studies, we found strong effects of clonal integration in distance of 10 or 20 cm (Lu *et al.*, 2015, 2016) so chose to use 15 cm as a removal area for this study (also see Choler *et al.*, 2001 for neighbour removal *c.* 15–20 cm). And there was no clear sign of moss or lichen regrowth during the experiment. The experiment started on 14–25 June 2014 and ended on 14–19 October 2014.

Measurements and analyses

At the end of the experiment, the survival status of each ramet was recorded and the surviving ramets ($n = 582$) were harvested. A ramet was considered dead if all its fronds were shed, dried or withered. For each surviving ramet, we measured frond length. Then we measured its biomass (roots and shoots) after drying at 70°C for 48 h.

We analysed the data using the open-source software R (v.3.6.0; R Development Core Team, 2019). Data on ramet survival were analysed with a generalized linear mixed model with a binomial error distribution using the package ‘LME4’ (Bates *et al.*, 2019). Biomass of surviving ramets was analysed with a linear mixed model using the package ‘NLME’ (Wang *et al.*, 2017; Pinheiro *et al.*, 2019). In both the survival and biomass models, we included epiphyte species, severance, removal and their two- and three-way interactions as fixed terms. We accounted for differences in initial size of the epiphyte ramets by including initial size (frond length) as a covariate in the model (Ning *et al.*, 2016). Furthermore, we accounted for variation among host species and host trees (treeID) by including them as random terms, with individual host trees nested within host species. To improve normality of the residuals, the biomass data were log-transformed before analysis.

In the (generalized) linear mixed models described earlier, we assessed the significance of the fixed terms with log-likelihood-ratio tests (Zuur *et al.*, 2009). In these tests, a model with the term of interest is compared to a model without the term of interest, and the calculated log-likelihood ratios are approximately χ^2 distributed (Ning *et al.*, 2016). Specifically, we sequentially removed three-way interactions, two-way interactions, the three main effects, and the covariate, and compared the fit of the simplified to the more complex model. If the fit of the models differed significantly then there was a significant effect of that factor. We treated epiphyte species as a fixed term because, in addition to searching for a general trend across species, we were also interested in species-specific impacts of clonal integration and neighbour removal. As we indeed detected a significant interaction effect of species × severance × removal, we also analysed the data separately for each epiphytic species using similar methods.

Results

Overall, epiphyte species and initial size affected substantially both ramet survival and biomass (Fig. 1; Table 1 – significant species (Sp) and initial size effects). Rhizome severance (Se) negatively affected survival and biomass, but such effects differed greatly among species (Fig. 1; Table 1 – Sp × Se effects). Neighbour removal (R) also reduced survival and biomass, and this effect on survival was irrespective of species (Table 1 – ns Sp × R interactions). There was also a significant two-way interaction between severance and removal, indicating that the negative impacts of severance were greater when neighbours were removed (Fig. 1; Table 1 – Se × R interaction effect); this interaction effect on survival and biomass also differed between species (Table 1 – Sp × Se × R effect).

At the individual species level (Table 2), rhizome severance significantly decreased ramet survival of all seven species, and also significantly reduced biomass of surviving ramets of six species with *O. wallichii* showing a trend in the same direction ($P = 0.065$). Neighbour removal significantly decreased ramet survival of all species except *A. perdurans*, *O. wallichii* and *P. subamoena* (Table 2; Fig. 1a,d,f). Neighbour removal also decreased biomass of surviving ramets of five species (*A. perdurans*, *O. wallichii*, *P. argutum*, *P. subamoena*, *S. connexa*), with *L. scolopendrium* showing a trend in the same direction ($P = 0.066$; Table 2; Fig. 1h,j–m,n). Initial size had no effects on ramet survival of any epiphyte species, while it significantly affected biomass of surviving ramets of all epiphyte species (Table 2).

For all seven epiphyte species except *P. argutum* there were significant severance × removal interaction effects on survival (Table 2; Fig. 1a–d,f,g). In five cases (*A. perdurans*, *A. lehmannii*, *O. wallichii*, *P. subamoena* and *S. connexa*) the negative effect of rhizome severance on ramet survival was significantly stronger when the neighbours were absent (removed) than present (Fig. 1a, b,d,f,g). For four species (*A. lehmannii*, *P. argutum*, *P. subamoena* and *S. connexa*) there were significant severance × removal interaction effects on biomass (Table 2; Fig. 1i,l,m,n). As for the

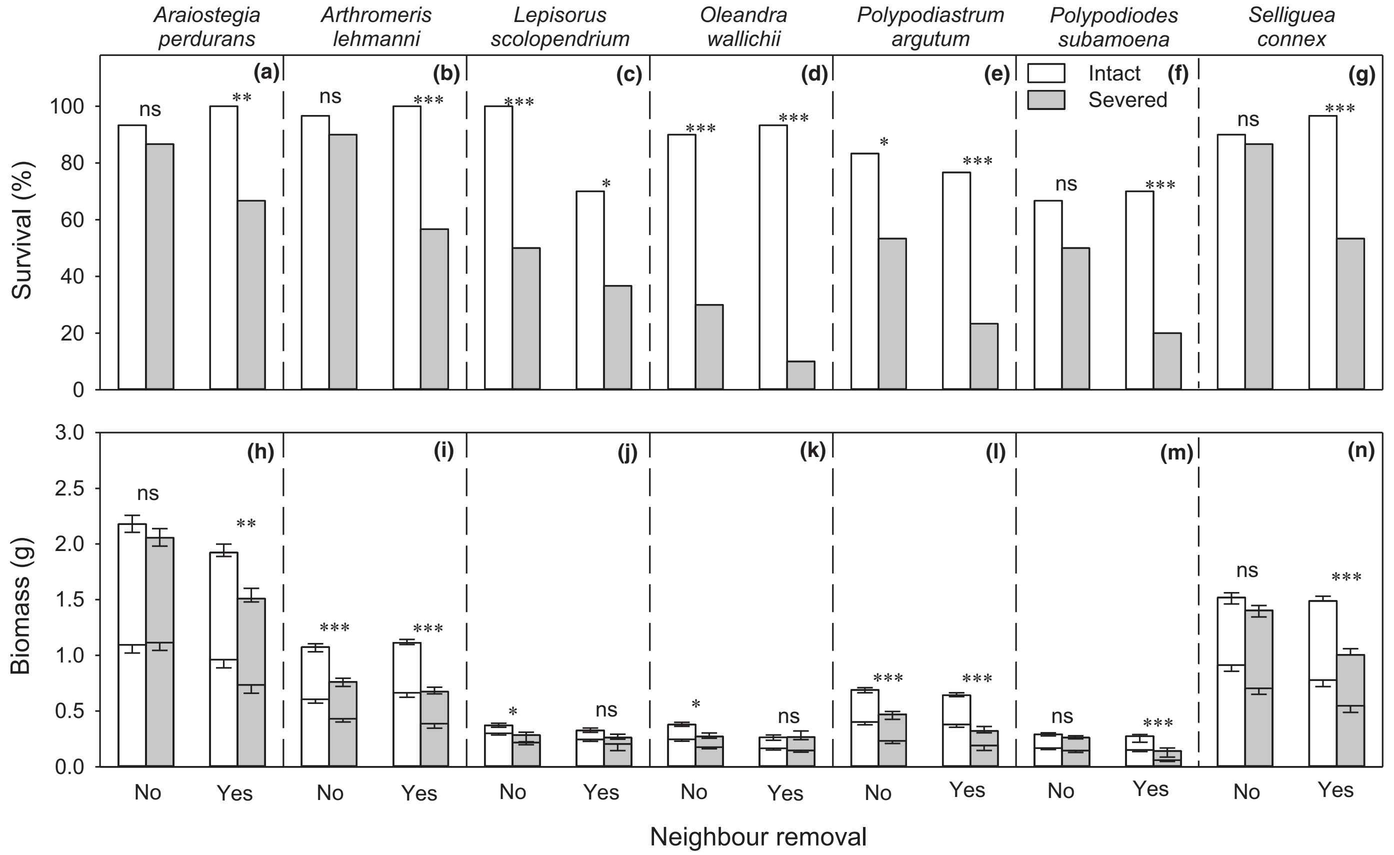

Fig. 1 Ramet survival (a–g) and biomass (mean ± SE, h–n) of the seven epiphytes with rhizomes severed or not (intact) and with neighbours removed (absent) or not (present). For biomass, the upper and lower parts of each bar stand for shoot and root biomass, respectively. Significance of difference (***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P > 0.05$) between the two severance treatments within each removal treatment.

Table 1 Effects of epiphyte species, rhizome severance, neighbour removal and their interactions on ramet survival and biomass of the clonal epiphytes.

	Survival			Biomass[1]		
Effect	DF	χ^2	*P*	DF	χ^2	*P*
Initial size	1	36.2	< 0.001	1	778.5	< 0.001
Epiphyte species (Sp)	6	54.9	< 0.001	6	541.1	< 0.001
Severance (Se)	1	163.4	< 0.001	1	151.3	< 0.001
Removal (R)	1	26.8	< 0.001	1	61.2	< 0.001
Sp × Se	6	16.3	0.012	6	31.5	< 0.001
Sp × R	6	1.8	0.936	6	18.3	0.006
Se × R	1	7.8	0.005	1	19.9	< 0.001
Sp × Se × R	6	21.8	0.001	6	20.7	0.002
Random	*n*	SD		*n*	SD	
Host species	3	0.005		3	< 0.001	
TreeID (Host)	60	0.483		60	0.237	

[1] Data are log-transformed. The number of surviving ramets is 582. Epiphyte species, severance and removal were used as fixed factors, initial size as a covariate, and host tree species (Host) and individual host trees (TreeID) as random factors; TreeID was nested within Host.

interactive effect of severance × removal on survival, the negative effect of rhizome severance on biomass was significantly stronger when neighbours were absent.

Discussion

Clonal integration can give support to individuals in unfavourable conditions and buffer the negative effects of patchy resources (Hartnett & Bazzaz 1983; Alpert 1991; Song *et al.*, 2013; Duchoslavova & Jansa, 2018). In general epiphytes can take up the majority of water and nutrients from the atmosphere through their leaves, especially those species with particularly absorptive foliage (Benzing, 1998; Reyes-García *et al.*, 2012). However, for almost all of the vascular epiphytes that we examined, ramet survival and growth were enhanced by clonal integration, a result consistent with previous studies in the same region (Lu *et al.*, 2015, 2016). The forest canopy is heterogeneous and unpredictable; canopy soils are patchy, forming mainly in the junction of trunks and branches. Through physiological connections, ramets can share resources to ameliorate microhabitat patchiness, and clonal integration has been shown to enhance nitrogen assimilation and allow pre-acclimation to highlight conditions for shaded, connected ramets, thus promoting the opportunistic expansion of these colonizers (Lei *et al.*, 2014).

As with rhizome severance, the effects of neighbour removal were species-specific. Such effects were broadly negative for *A. lehmannii*, *L. scolopendrium*, *P. argutum* and *S. connexa*, meaning that nonvascular neighbours buffered the stresses experienced by target vascular epiphytes in forest canopies. Positive interactions

Table 2 Effects of rhizome severance, neighbour removal and their interaction on survival and biomass of each of the seven clonal epiphytes.

		Survival		Biomass[1]	
Epiphyte species	Effect	χ^2	P	χ^2	P
Araiostegia perdurans	Initial size	1.5	0.215	121.6	< 0.001
	Severance (Se)	11.9	< 0.001	13.1	< 0.001
	Removal (R)	1.3	0.247	24.5	< 0.001
	Se × R	5.2	0.023	2.5	0.117
Arthromeris lehmannii	Initial size	0.02	0.900	73.5	< 0.001
	Severance (Se)	19.0	< 0.001	65.4	< 0.001
	Removal (R)	6.6	0.010	0.8	0.364
	Se × R	3.8	0.051	8.0	0.005
Lepisorus scolopendrium	Initial size	< 0.01	0.978	12.5	< 0.001
	Severance (Se)	25.3	< 0.001	16.1	< 0.001
	Removal (R)	7.7	0.006	3.4	0.066
	Se × R	7.5	0.006	0.03	0.864
Oleandra wallichii	Initial size	0.8	0.369	13.1	< 0.001
	Severance (Se)	77.6	< 0.001	3.4	0.065
	Removal (R)	2.6	0.109	12.8	< 0.001
	Se × R	7.4	0.006	2.6	0.110
Polypodiastrum argutum	Initial size	< 0.01	0.990	47.1	< 0.001
	Severance (Se)	23.3	< 0.001	64.5	< 0.001
	Removal (R)	5.2	0.023	12.1	0.007
	Se × R	1.1	0.298	8.7	0.003
Polypodiodes subamoena	Initial size	0.03	0.867	15.6	< 0.001
	Severance (Se)	14.4	< 0.001	15.6	< 0.001
	Removal (R)	2.5	0.114	7.6	0.006
	Se × R	4.0	0.046	11.2	< 0.001
Selliguea connexa	Initial size	0.04	0.850	112.5	< 0.001
	Severance (Se)	12.0	< 0.001	24.9	< 0.001
	Removal (R)	4.0	0.046	20.0	< 0.001
	Se × R	5.4	0.020	15.4	< 0.001

[1] Data are log-transformed. Degree of freedom is one for all the effects. Severance and removal were used as fixed factors, initial size as a covariate. Host tree species and individual host trees (nested within host tree species) were included as random factors, but were not shown here for simplicity.

can strongly influence local diversity in many harsh environments (Cardinale *et al.*, 2002; Kikvidze *et al.*, 2005; Butterfield *et al.*, 2013; Cavieres *et al.*, 2014; Barron-Gafford *et al.*, 2017; Lekberg *et al.*, 2018), and such effects may be operating in this ecosystem. However, this study showed weaker inter-specific facilitation effects for *A. perdurans*, *O. wallichii* and *P. subamoena*, all of which are outer-branch species (Fig. S1). Compared to branch junctions, outer branches lack resources because there is less canopy soil and a scarcer epiphytic mat. According to the stress-gradient hypothesis, we might expect positive interactions to be greater under higher stresses (Callaway *et al.*, 2002a; Maestre *et al.*, 2009; Dohn *et al.*, 2013; Ettinger & Hillerislambers, 2017; Filazzola *et al.*, 2018), but there is also evidence that the degree of facilitation from inter-specific neighbours can depend on the stress-tolerance of the target plant (Michalet *et al.*, 2006). These species may be more tolerant to stress, and thus benefit less from inter-specific facilitation. However, they still appear to benefit from clonal integration, indicating that the mechanisms driving inter- and intra-specific facilitation may differ.

The interactive effects of clonal integration and neighbour removal indicate that for some species dependence on clonal integration was greater when neighbours were removed. To the best of our knowledge this is the only experimental study that has shown such interactive effects, a topic area which clearly needs greater research effort (Brooker, 2017). Notably, there were no interaction effects of integration and neighbour removal on the survival of *P. argutum* or biomass of *A. perdurans*, *L. scolopendrium* and *O. wallichii*. Again this may be related to the common locations of epiphytes and their ability of stress tolerance. Therefore, our results demonstrate, along with general trends, variation in species-level responses which may relate to the different morphological traits and biological habits of these species. Unpicking these species-level differences will need more research and detailed studies of their physiological processes and responses.

Importantly, clonal vascular epiphytes may have effects as ecosystem engineers: whilst anchoring the plant and helping it search for patchily distributed resources, rhizome networks are also available for anchoring other epiphytes in these harsh unstable habitats (Mehltreter *et al.*, 2010; Lu *et al.*, 2016), forming a framework that maintains the community (Nadkarni & Haber, 2009; Angelini & Silliman, 2014; Woods *et al.*, 2015). Poor performance of epiphytic ferns could, therefore, have cascading effects on a wide range of biodiversity both within the forest canopy and other closely-connected ecosystems (Ellwood & Foster, 2004; Angelini & Silliman, 2014; Zotz, 2016).

Overall we conclude that for vascular epiphytes in forest canopies clonal integration has in general greater benefits than inter-specific facilitation from nonvascular epiphytes. Also, many vascular epiphytes in forest canopies depend less on inter-specific facilitation due to their clonal integration. According to the stress-gradient hypothesis, a testable prediction would be that the negative impact of both severing rhizomes and removing the neighbours on at least some vascular epiphytes would be greater under higher environmental stress (Dohn *et al.*, 2013; He *et al.*, 2013; Ettinger & Hillerislambers, 2017; Filazzola *et al.*, 2018), as the connected vascular epiphytes are relatively less impacted by this stress – and hence less dependent on facilitation – thanks to their clonal integration. In addition, we might expect the role of facilitation from nonvascular epiphytes to be particularly important at stages of the vascular epiphyte where clonal integration is not possible, e.g. when these plants are developing from spores or seeds. Both of these predictions would be readily testable in canopy systems, helping to plug a gap in our current understanding of both facilitation and plant clonality (Brooker, 2017), and providing important information for underpinning the conservation of these species-rich and poorly-understood ecosystems.

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Author contributions

F-HY and H-ZL conceived the ideas and designed methodology; H-ZL and L Song collected the data; H-ZL, F-HY and W-YL analysed the data; H-ZL, RB, F-HY, L Song, L Sack and J-LZ led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Experiment design: host trees and epiphytic location (A) and four treatments (B).

Methods S1 Details of seven epiphyte species, three host tree species and experiment design.

Notes S1 Details of leaf length of seven epiphyte species.

Table S1 Statistical comparison (ANOVA) of the initial sizes (leaf length) of epiphyte ramets among treatments ($p1$) or among host species ($p2$).

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