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Population ecology of epiphytic angiosperms: A review

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Abstract: Epiphytic angiosperms represent *ca.* 10 % of the world's flowering plants and are key elements in tropical forests. Here we synthesize the available literature on their population ecology in an attempt to find patterns that may characterize them. Epiphytes tend to have specialized pollination systems frequently involving animal vectors, resulting in a mixture of selfing and outcrossing that ensures abundant seed production. Seed dispersal is anemochorous in 84 % of the species and is pivotal for the establishment of new local populations within metapopulation. Seed germination is highly dependent on specific environmental conditions, resulting in seedling establishment in particular microhabitats on phorophytes. Individual growth rates are slow and limited by the low water and nutrient availability characteristic of the epiphytic habitat. Population growth rates (λ) are close to unity and depend mostly on the survival of adults. This plant group is highly vulnerable to habitat loss and climate change.

Resumen: Las angiospermas epífitas representan *ca.* 10 % de las plantas con flores del mundo y son elementos clave en los bosques tropicales. Aquí sintetizamos la literatura disponible sobre su ecología de poblaciones en un intento por encontrar patrones que las puedan caracterizar. Las epífitas suelen tener sistemas especializados de polinización que con frecuencia involucran a vectores animales, lo cual determina que se presente una mezcla de autofecundación y polinización cruzada, lo que garantiza una producción abundante de semillas. La dispersión de semillas es anemócora en 84 % de las especies y es fundamental para el establecimiento de nuevas poblaciones locales en las metapoblaciones. La germinación de semillas dependen en gran medida de condiciones ambientales específicas, lo que resulta en el establecimiento de plántulas en microhábitats particulares sobre los forofitos. Las tasas de crecimiento individuales suelen ser lentas y están limitadas por la baja disponibilidad de agua y nutrientes que caracterizan el hábitat de las epífitas. Las tasas de crecimiento poblacional (λ) están cerca de la unidad y dependen principalmente de la supervivencia de los adultos. Este grupo de plantas es muy vulnerable a la pérdida de hábitat y al cambio climático.

Resumo: As angiospermas epífitas representam aproximadamente 10% das plantas com flores do mundo e são elementos-chave nas florestas tropicais. Nesta revisão sintetizamos a literatura disponível sobre a sua ecologia populacional, na tentativa de encontrar padrões que possam caracterizá-la. As epífitas tendem a ter sistemas especializados de polinização que envolvem frequentemente vetores animais, de que resulta uma mistura de autofecundação e fecundação cruzada, que garante a produção de sementes abundantes. A dispersão de sementes

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é anemocórica em 84 % das espécies e é fundamental para o estabelecimento de novas populações locais dentro da metapopulação. A germinação das sementes é altamente dependente de condições ambientais específicas, resultando no estabelecimento de plântulas em micro-habitats particular em forófitos. As taxas de crescimento individuais são lentas e limitadas pela água e baixa disponibilidade de nutrientes característicos do habitat das epífita. As taxas de crescimento populacional (λ) estão próximas da unidade e dependem principalmente da sobrevivência dos adultos. Este grupo de plantas é altamente vulnerável à perda de habitat e às mudanças climáticas.

Key words: Bromeliads, demography, forest canopy, metapopulations, seed dispersal, orchids.

Introduction

Epiphytes are a taxonomically heterogeneous group, composed of over 28,000 species belonging to 84 plant families, and representing an important proportion of the world's flora (Benzing 1990; Kress 1989). They are plants that establish on other plants, which they use as a substrate for growth, but without extracting any water or nutrient resources from them (Benzing 1990). Both vascular and non-vascular plants (*e.g.,* mosses and liverworts; Sequiera & Kumar 2008) are represented within this diverse group. Most epiphytes are angiosperm (24,748 species), within which the Orchidaceae (18,814 species) and the Bromeliaceae (1,170 species) are the plant families with the largest number of epiphytes (Zotz 2013). The highest diversity of epiphytes is generally found in humid tropical habitats, such as cloud forests and tropical rain forests, especially those in the neotropics (Benzing 1990; Gentry & Dodson 1987; Nieder *et al.* 2001). However, temperate humid and tropical dry forests may also hold large numbers of epiphytes (Gentry & Dodson 1987; Hietz & Hietz-Seifert 1995).

A large amount of information is available on the biology and ecology of epiphytes. They have been studied mainly from the morphological, ecophysiological and taxonomic points of view (Benzing 1978, 1990; Wanek & Zotz 2011; Zotz 2004b; Zotz & Hietz 2001). Information on their ecological features is generally related to the description of the epiphytic habitat, the adaptations that allow them to successfully exploit it, and the abiotic factors that limit their distribution and phorophyte preferences (Benzing 1990). Other epiphyte ecologists have concentrated on the analysis of epiphytic assemblages from the perspective of community ecology (Flores-Palacios & García-Franco 2003; Hietz & Hietz-Seifert 1995; Nadkarni 2000; Toledo-Aceves *et al.* 2012a; Zotz 2003). Promoted by the development of different techniques to access and study forest canopies (Perry 1978; Russell *et al.* 1990) there has been a substantial increase, in recent years, in the number of studies on epiphyte population ecology from which our knowledge of this interesting group has expanded. However, given the large number of epiphytic angiosperms, only little is known on the population ecology of this group of plants (Matallana *et al.* 2010; Mondragón 2011; Zotz *et al.* 2010). As epiphytes are subject to similar selective pressures given the particular habitat they occupy, it is reasonable to expect that they will also share similar demographic features, population numerical responses, and patterns of mortality, survival and reproduction. In this paper we focus on the population ecology of epiphytic angiosperms and review the literature that has been published on their reproduction, seed dispersal, early life cycle stages, growth and demography to address these questions. We also explore other related subjects, such as metapopulations and conservation ecology.

In the last decades plant population ecologists have been developing a host of analytical tools to explore the numerical behavior of populations in nature. Since the adequacy and convenience of population projection matrices was established in the early 1970's and applied to plants with complex life cycles (Caswell 2001), a large amount of literature has been produced on this subject. From the demographic data available, patterns have started to emerge that deserve attention and await explanation (*e.g.,* plants from early successional *vs.* late successional habitats, Franco & Silvertown 2004; Silvertown *et al.* 1993). Common demographic features have been found in species with similar life histories or life forms

(Franco & Silvertown 2004; Silvertown *et al.* 1993), or belonging to the same taxonomic family (Godínez-Álvarez *et al.* 2003). Also, over the last decade, the use of meta-analyses has grown among ecologists precisely with the hope of unraveling this type of obscure patterns that may enable a deeper understanding of biological systems (Arnqvist & Wooster 1995). In this context, the question arises as to whether epiphytes share a common set of demographic features, or rather they represent a diverse group in relation to their population ecology.

New ways of conceiving the character of epiphytic populations have also emerged since the metapopulation concept has been fruitfully applied to epiphytes, given the patchy nature of their local distributions and the evident colonization/extinction processes driving their larger-scale dynamics (Tremblay *et al.* 2006; Valverde & Bernal 2010; Winkler *et al.* 2009). Finally, conservation interests have also recently focused on the population ecology of epiphytes, associated to their presumed sensitivity to global climate change and their potential use as assessment tools to establish the conservation status of tropical forests (Hsu *et al.* 2012).

Given the wealth of population ecology topics that have recently been developed for epiphytes, the aim of this paper is to present a literature review on the population ecology of epiphytic angiosperms in order to analyze the information available on the subject in the search for patterns and processes that may be distinctive to this biological group. Where possible, the data obtained from the literature review were subjected to multivariate statistical analyses and meta-analyses to increase the level of objectivity of our conclusions (Arnqvist & Wooster 1995).

Reproduction and seed dispersal

Pollination

Epiphyte populations are often composed of scattered individuals or small, hyperdispersed clusters (Ackerman 1986; Benzing 1990). It is, therefore, expected that the interaction with pollinators would be more specialized among epiphytes than in terrestrial plants (Ackerman 1986; Benzing 1990; Carranza-Quiceno & Estévez-Varón 2008; Gentry & Dodson 1987; Hietz *et al.* 2006; van Dulmen 2001), which is indeed the case for many epiphytic orchids and aroids in the tropics (Gentry & Dodson 1987). However, contrary to this

pattern, Gentry & Dodson (1987), as well as Lehnebach & Robertson (2004), reported that many orchid-pollinator relationships are unspecialized and that flowers are visited by a wide range of insects. In addition, Gravendeel *et al.* (2004), in their study on epiphytism and pollinator specialization, found that the predominantly epiphytic subfamily Epidendroideae (Orchidaceae) shows a similar level of pollinator specialization compared to other families, from which the authors suggest that there is a trend for decreased rather than increased pollinator specialization in epiphytes. Supporting the latter idea, Navarro *et al.* (2007) reported that the epiphyte *Disterigma stereophyllum* (Ericaceae) shows a set of floral features that attract a wide variety of pollinators (bees and hummingbirds among them).

Either in specialized or unspecialized relationships, pollination systems among epiphytes clearly tend towards animal-mediated pollen transfer (Benzing 1990; Gentry & Dodson 1987; Madison 1977). For example, van Dulmen (2001) found that bees were the most common pollinator for the epiphytes of two contrasting rainforest habitats in Colombia, while Carranza-Quiceno & Estévez-Varón (2008) stated that birds are among the most common pollinators in epiphytic bromeliads. In the neotropics, trapline pollination (*i.e.,* by hummingbirds, bats, large bees and hawkmoths) is common among the epiphytes in the Bromeliaceae, Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae, and Rubiaceae, whereas pollination by deception is common in the Orchidaceae. Also, pollination by male euglossine bees, as they collect floral fragrances, is common in many Orchidaceae, Araceae, and Gesneriaceae epiphytes (Ackerman 1986; Damon & Salas-Roblero 2007; Gentry & Dodson 1987; Varassin & Sazima 2012).

Different strategies have evolved among epiphytes to attract pollinators and at the same time avoid pollinator competition. One of them involves the timing of flowering: the flowering of epiphytes is usually moderate during the peak flowering season of trees and lianas in tropical rainforests (Ackerman 1985; van Dulmen 2001). On the same line, Ackerman (1986) noted that epiphytes that use trapline pollination bloom for longer time periods and maintain a consistent daily production of a few flowers with high quality rewards, compared to epiphytes that use pollination by deception, among which mimicry (to insect brood sites, to mates, or to food resources) is the rule. In contrast, for the epiphytes that are pollinated by male euglossine bees the production

of floral fragrances is the key factor. Other ways of diversifying pollinator assemblages is through the presence of contrasting nectar and flower features. Perret *et al.* (2001) worked with *ca.* 70 species in the tribe Sinningieae (Gesneriaceae, many of which are epiphytes) and found that nectar composition was similar for hummingbird and bee-pollinated species, while the nectar of bat-pollinated species had a different chemical composition. At the same time, specific morphological traits were associated with each of these syndromes.

Breeding systems

No particular association between breeding systems and habitat or life history features has been demonstrated for epiphytes (Benzing 1990). However, most epiphytes are hermaphroditic (Bullock 1985; Bush & Beach 1995; van Dulmen 2001), in principle allowing for either selfing or outcrossing. Indeed, self-compatibility and autogamy seem to be widespread in this plant group (Table 1). For instance, self-compatibility and autogamy are prevalent among tropical lowland epiphytes (Gentry & Dodson 1987), and apparently most epiphytic orchids are self compatible, even though a few are regularly outcrossing (Dressler 1981). Many ant nest-garden and ant-fed epiphytic species have been reported to produce fruit without pollinator visitation (Madison 1979). Also among the Tillandsiodeae subfamily (Bromeliaceae), plants are predominantly self-compatible (Matallana *et al.* 2010). Selfing is also common in epiphytes that establish on short-lived branches (*i.e.,* atmospheric bromeliads or twig epiphytes; Gilmartin & Brown 1985; Hietz *et al.* 2006; Solis-Montero *et al.* 2005). In these ephemeral habitats the 'time limitation hypothesis' has been alluded to as a potential explanation for the evolution of selfing. In these cases, selfing is presumed to have evolved either as an indirect trade-off for shorter time to reproductive maturity - as it is frequently associated with a low investment towards floral displays, or as a direct consequence of selection for shorter pollination time, *i.e.,* the time between flower maturation and ovule fertilization (Snell & Aarsen 2005).

The available literature on the subject suggests that there is a continuum of breeding systems among epiphytes, from species with complete selfing due to cleistogamy (*Tillandsia capillaris*, *T. recurvata*; Gilmartin & Brown 1985; Soltis *et al.* 1987), to selfing with chasmogamous flowers (such as *Guarianthe aurantiaca, Cattleya patinii* and *Epidendrum latifolium*; Dressler 1981), to complete outbreeding (such as the dioecious *Catopsis berteroniana* and *C. sessiliflora*; Hietz *et al.* 2006; Mondragón & Ramírez-Morillo 2008) (Table 1), with selfing being more frequent in monocarpic than in polycarpic species (Benzing 2000).

It is generally thought that the balance between cross- and self-pollination in plant populations is typically a function of pollinator activity (Cruden & Lyon 1989). Even if cross-pollination is advantageous in principle, plants may retain the possibility for selfing when pollinators are scarce or inefficient (Eckert & Schaefer 1998). This may be the case for many epiphytes. However, cross pollination is clearly favored in some species, such as many bromeliads that show protogyny (Benzing 2000), in many orchids with highly attractive floral displays (Dressler 1981), and of course in dioecious species. In relation to the latter, the low frequency of dioecy among epiphytic angiosperms is noticeable (Table 1) (Benzing 1990; van Dulmen 2001).

We carried out a meta-analysis to investigate whether there is a significant effect of the plant family to which epiphyte species belong, on the expression of the autogamy and the self-incompatibility indices (AI and ISI in Table 1). Only the families Bromeliaceae, Gesneriaceae and Orchidaceae had enough data as to allow their inclusion in the analyses. The results showed that there is no evidence to suggest that AI and ISI differ between families (for AI, *LRT* = 0.6907, *P* = 0.780; and for ISI, *LRT* = 0.0877, *P* = 0.957; see *Appendix A* for details).

Seed dispersal

In epiphyte populations, seed dispersal may be conceived of as a bimodal process: seeds either remain close to their source (*i.e.* in the same phorophyte) or they leave their original phorophyte, in which case they are confronted with the highly risky process of crossing the habitat matrix where phorophytes are immersed and eventually finding a safe site for germination and growth. Despite the high risk involved in this process, the fact that so many epiphytes show long-distance seed dispersal adaptations makes it evident that its evolutionary advantages must outweigh its costs (Horvitz & Schemske 1986).

The importance of long-distance seed dispersal on population average fitness depends on habitat

Table 1. Breeding systems reported for different epiphyte species. The first five columns show the percentage of fruits produced under each pollination treatment (Nat = natural, Aga= agamospermy, Au= autonomous, S= selfing, C= cross pollination). Blank cells indicate that no information is available. After Matallana *et al.* (2010), the following columns show the autogamy index (*AI* = autonomous/cross), and the self-incompatibility index (*ISI*= selfing/cross). Finally, the breeding systems (Br. Sys.) are designated as self-incompatible (SI) when *ISI* values were below 0.30, and self-compatible or partially self-compatible (SC) when *ISI* values were above 0.30, or as indicated in the relevant reference. Ref= references, detailed in the footnote. Species marked with *(d)* are reported as dioecious.

Species	Nat	Aga	Au	S	C	AI	ISI	Br. Sys.	Ref
Bromeliaceae									
Aechmea araneosa			31.3	53.9	79	0.40	0.68	SC	1
Aechmea beeriana	97.9	0	0	0	70.7	0	0	SI	2
Aechmea capixabae			0	69.2	93.1	0	0.74	SC	1
Aechmea lamarchei			2.3	31.7	39.2	0.06	0.81	SC	1
Aechmea macrochlamys			53.3	70	100	0.53	0.70	SC	1
Aechmea mutica			13.6	42.4	61.4	0.22	0.69	SC	1
Aechmea nudicaulis			6.9	0	100	0.07	0	SI	1
Aechmea pectinata			0	0	96	0	0	SI	3
Aechmea pineliana			3.8	5.6	59	0.06	0.09	SI	1
Billbergia amoena			0	7.3	34.5	0	0.21	SI	1
Billbergia bradeana			0	56.5	55	0	1.03	SC	1
Billbergia euphemiae			0	0	61.1	0	0	SI	1
Billbergia horrid			0	0	50	0	0	SI	1
Billbergia vittata			0	0	37.5	0	0	SI	1
Catopsis compacta *(d)*	100	28.57			98	0	0	SI	4
Catopsis sessiliflora *(d)*	70.6								5
Edmundoa lindenii			75	92.9	88.5	0.85	1.05	SC	1
Guzmania nicaraguensis				62	100				6
Lymania smithii		90.3	89.2	77.9	81.3	0.99	0.86	SC	7
Neoregelia guttata			68.4	100	45	1.52	2.22	SC	1
Neoregelia macrosepala			0	10.8	28.6	0	0.38	SC	1
Neoregelia pauciflora			0	0	58.3	0	0	SI	1
Nidularium cariacicaense			87.5	90.5	76.5	1.14	1.18	SC	1
Nidularium procerum			10.2	16.7	22.2	0.46	0.75	SC	1
Pitcairnia brittoniana				100	100		1	SC	6
Portea fosteriana			1.7	10.5	88.7	0.02	0.12	SI	1
Quesnelia arvensis				20	70		0.29	SI	8
Quesnelia lateralis				7.6	80		0.10	SI	8
Quesnelia quesneliana			93.3	69.2	84.2	1.11	0.82	SC	1
Quesnelia strobilispica			26.3	24	52.9	0.50	0.45	SC	1
Racinaea spiculosa			54.5	79.2	100	0.55	0.79	SC	1
Tillandsia macdougallii		18.52	53.84	16.27	71.42	0.78	0.23	SI	4
Tillandsia magnusiana	83.33	15.38	62.07	63.33	68	0.88	1.25	SC	4
Tillandsia oaxacana	20	0	3.33	3.33	56.67	0.06	0.06	SI	4
Tillandsia brachycaulos	49.67	0	23.85	19.35	42.85	0.56	0.45	SC	9

Table 1. Continued.

Species	Nat	Aga	Au	S	C	AI	ISI	Br. Sys.	Ref
Tillandsia dasyliriifolia	87.4	0	93	92.7	90.5	1.03	1.02	SC	10
Tillandsia elongata	56.3	0	45.72	64.7	7.7	5.94	8.40	SC	9
Tillandsia geminiflora			87.5	69.4	42.9	2.04	1.62	SC	1
Tillandsia juncea	59.9		48	67	67	0.72	1.33	SC	5
Tillandsia multicaulis	41.2		0	3	56	0	0.04	SI	5
Tillandsia prodigiosa	73.91	64.7	95.8	93	95	1.01	0.98	SC	11
Tillandsia punctulata	25.4		0	0	42	0	0.14	SI	5
Tillandsia streptophylla	52.9	0	0	0	80.4	0	0	SI	12
Tillandsia stricta			0	6.3	14.3	0	0.44	SC	1
Tillandsia tenuifolia			0	80	100	0	0.80	SC	1
Vriesea aff. fenestralis			37.5	68.8	76.9	0.49	0.89	SC	1
Vriesea bituminosa			0	19.2	24	0	0.80	SC	1
Vriesea bracteosa				78	41		1.90	SC	6
Vriesea delicatula			40	87.5	70	0.57	1.25	SC	1
Vriesea ensiformis			36.4	87.5	37.5	0.97	2.33	SC	1
Vriesea friburguensis	58.16		6.77	58.97	55.17	0.124	1.069	SC	13
Vriesea gracilior			7.4	52.9	31.3	0.24	1.69	SC	1
Vriesea gigantea	47.92			85.42					14
Vriesea heterostachys				60	67		0.90	SC	8
Vriesea hydrophora				33.3	50		0.67	SC	8
Vriesea hygrometrica				89	46		1.935	SC	6
Vriesea incurvata				25	40		0.63	SC	8
Vriesea kautskyana			58.3	50	40	1.46	1.25	SC	1
Vriesea longicaulis			4.2	8.7	44.4	0.09	0.20	SI	1
Vriesea longiscapa				25	60		0.42	SC	8
Vriesea neoglutinosa				31	36.8		0.84	SC	8
Vriesea procera			54.5	79.2	100	0.55	0.79	SC	1
Vriesea ruschii			20	95	100	0.20	0.95	SC	1
Vriesea scalaris			94.4	37.5	69.2	1.36	0.54	SC	1
Vriesea simplex			20	35.3	40	0.50	0.88	SC	1
Vriesea sparsiflora				38.9	57		0.68	SC	8
Vriesea vagans			32.1	64.9	71.4	0.46	0.91	SC	1
Werauhia gladioliflora	87.5		90.8	97.3	94.4	0.96	1.03	SC	15
Werauhia sintenisii	97	0	100	93	92	1.09	1.01	SC	16
Ericaceae									
Disterigma stereophyllum	28.0		31.4	23	59.7	0.53	0.39	SC	17
Gesneriaceae									
Campanea grandiflora				75					6
Columnea microcalyx				45	67		0.672	SC	6
Columnea magnifica				73	64		1.141	SC	6
Drymonia conchocalyx				77	67		1.149	SC	6

Contd...

Table 1. Continued.

Species	Nat	Aga	Au	S	C	AI	ISI	Br. Sys.	Ref
Drymonia rubra				68	100		0.68	SC	6
Lentibulariaceae									
Utricularia praetermissa				83	67		1.239	SC	6
Lobeliaceae									
Burmeistera tenuifolia				77					6
Orchidaceae									
Acampe ochracea	41.31							SC	18
Acampe praemorsa	36.67							SC	18
Aerides odoratum	20.67							SC	18
Angraecum arachnites	41								19
Aspasia principissa	9.5			60	61		0.98	SC	20
Brassavola nodosa	12			100	67				21
Bulbophyllum lilacinum	25.54								18
Catasetum macrocarpum	7.1								19
Catasetum viridiflavum (d)				95.8					22
Cleisomeria lanatum	24.5								18
Cochleanthes lipscombiae	15								19
Comparettia falcate	15.7		0	53.85	86.36	0	0.62	SC	23
Coryanthes elegantium	25								24
Coryanthes leucocorys	0								24
Coryanthes macrantha	21								24
Coryanthes rodriguezii	43								24
Coryanthes trifoliata	40								24
Cymbidium aloifolium	12.82							SC	18
Dendrobium aphyllum	3.14							SI	18
Dendrobium monophyllum	6.6,7.8,6.3								25
Dendrobium toressae	19			88					19
Dendrochilum longibracteatum	0.02								19
Dilomilis montana	6.1 & 14.3								19
Elleanthus cf. brenesii	29								19
Encyclia cordigera	7			85	97				26
Earina autumnalis	30	0	0	55.3	60.6	0	0.913	SC	27
Earina mucronata	4.1	0	0	67.4	69.7	0	0.967	SC	27
Earina aestivalis	6.9	0	0	36.9	77.5	0	0.476	SC	27
Encyclia krugii	10			0	83.33		0	SI	28
Epidendrum ciliare	90			93	88	0	1.06	SC	29
Epidendrum exasperatum	2								30
Epidendrum obesum				33	41		0.805	SC	6
Gongora quinquenervis	1.1	0	0	35	73	0	0.479	SC	31
Ionopsis utricularioides	6			51 .32	89.71		0.99	SC	32
Jacquiniella leucomelana	16		2						5
Jacquiniella teretifolia	72		75						5
Laelia speciosa	14.9		0	83.3	66.7	0	1.25	SC	33
Leochilus scriptus	60			86.5					19

Contd...

Table 1. Continued.

Species	Nat	Aga	Au	S	C	AI	ISI	Br. Sys.	Ref
Lepanthes caritensis	0								34
Lepanthes eltoroensis	1.8								19
Lepanthes rubripetala	5								19
Lephantes rupestris	4.9 & 5.9								19
Lepanthes wendlandii	11.6								30
Lepanthes woodburyana	9.1								19
Luisia trichorhiza	41.67								18
Lycaste aromatica			0	8.00	39.00	0	0.21	SI	5
Micropera pallida	36.76								18
Micropera rostrata	10.48								18
Mormodes tuxtlensis (d)	3.3								19
Myrmecophila tibicinis	2.4			92					19
Mystacidium venosum			0	40	65	0	0.62	SC	35
Notylia nemorosa	0	0		5.8	64.8		0.089	SI	36
Oberonia falconeri	31.94								18
Oberonia rufilabris	14.41								18
Oncidium altissimum	2								19
Oncidium ascendens	6.8								37
Oncidium stipitatum	1.8								19
Pelatantheria insectifera	0							SI	18
Pholidota pallida	26.26								18
Pleurothallis cardiothallis				75	67		1.119	SC	6
Pleurothallis racemiflora	17.3								19
Polystachya concreta	10								19
Pomatocalpa undulatum	30.3								15
Prosthechea cochleata	4.6			54.5					19
Rhynchostylis retusa	34.78							SC	18
Rhyncholaelia glauca	13.6 & 6.7								38
Smitinandia micrantha	26.32								18
Sobralia amabilis				43	41		1.049	SC	6
Stanhopea insignis	25.3	0	0	92	90.5	0	1.02	SC	39
Stanhopea lietzei	16.8	0	0	63.6	65	0	0.98	SC	39
Stelis argentata	2.2			29.2					40
Stelis sp. 1	15								40
Stelis sp. 2	8								40
Stelis sp. 3	12								40
Stelis sp. 4	2								40
Tetramicra canaliculata	6			80					19
Tolumnia variegata	1.8				77.8				41
Winika cunninghamii	22.5	0	0	37.5	75	0	0.5	SC	27
Xylobium squalens	27			90					19

References are: 1 = Matallana *et al.* 2010; 2 = Nara & Webber 2002; 3 = Canela & Sazima 2003; 4 = Mondragón & Ramírez-Morillo 2008; 5 = Hietz *et al.* 2006; 6 = Bush & Beach 1995; 7 = Siqueira-Filho 2003; 8 = Martinelli 1994; 9 = González 2004; 10 = Ramírez-Morillo *et al.* 2004; 11 = Escobedo-Sarti 2007; 12 = Ramírez Morillo *et al.* 2009; 13 = Paggi *et al.* in 2013; 14 = Paggi *et al.* 2007; 15 = Cascante-Marín *et al.* 2005; 16 = Lasso & Ackerman 2004; 17 = Navarro *et al.* 2007; 18 = Huda & Wilcock 2008; 19 = cited in Tremblay *et al.* 2005; 20 = Zimmerman & Aide 1989; 21 = Schemske 1980; 22 = Zimmerman 1991; 23 = Rodríguez-Robles *et al.* 1992; 24 = Dodson 1965; 25 = Bartareau 1995; 26 = Janzen *et al.* 1980; 27 = Lehnebach & Robertson 2004; 28 = Ackerman 1989; 29 = Ackerman & Montalvo 1990; 30 = Calvo 1990; 31 = Martini *et al.* 2003; 32 = Montalvo & Ackerman 1987; 33 = Hernández-Apolinar 1992; 34 = Tremblay 1997; 35 = Luyt & Johnson 2001; 36 = Singer & Koehler 2003; 37 = Parra-Tabla *et al.* 2000; 38 = Flores-Palacios & García-Franco 2003; 39 = Pansarin & Amaral 2009; 40 = Christensen 1992; 41 = Ackerman & Montero 1985.

temporal and spatial heterogeneity (Howe & Smallwood 1982). Howe & Smallwood (1982) identified three potential advantages of long-distance seed dispersal: (1) it may allow seedlings to escape high density patches and, therefore, decrease density-dependent mortality near the mother plant; (2) it opens the possibility for the colonization of new habitat patches which may be ephemeral and/or competition free; and (3) seeds may be directly dispersed to highly specific microsites where establishment probabilities are higher. These hypotheses are complementary, rather than mutually exclusive. For epiphytes, the most likely advantages of seed dispersal are (2) and (3), given their characteristically discontinuous, heterogeneous and fragile habitat (Benzing 1990), along with their likely metapopulation structure (Laube & Zotz 2007; Valverde & Bernal 2010; Winkler *et al.* 2009) and their highly specific establishment microsites (Toledo-Aceves & Wolf 2008; Winkler *et al.* 2005). It is generally thought that competition is not an important process among epiphytes (Benzing 1990), while density-independent forces (*i.e.,* drought, strong winds) seem to play a major role as mortality factors (Benzing 1990; Hietz 1997; Larson 1992; Zotz 1998), as will be discussed below.

Hughes *et al.* (1994) have suggested that, as epiphytes often have very specific microsite requirements for establishment, dispersal by ballistic explosion or adhesion may be unsuitable because they are untargeted. These authors suggest that the most advantageous dispersal alternatives among epiphytes may be: (a) the production of large quantities of small, light seeds, thus increasing the probability that at least a few of them may arrive at safe sites; or (b) the use of biotic vectors that result in some degree of directed dispersal towards specific microsites. Indeed, Madison's (1977) paper about epiphyte seed dispersal shows that the most widespread seed dispersal strategies are anemochory (84 % of species) and zoochory.

Wenny (2001) re-evaluates the conditions under which directed seed dispersal may occur. He suggests that this phenomenon plays an important role in increasing seedling recruitment, as dispersal agents deposit seeds disproportionately in suitable locations. The question is how common and efficient this type of dispersal is in epiphyte populations. There are indeed some examples of directed seed dispersal in epiphytes. For instance, Guaraldo *et al.* (2013) describe a specialized relationship between small Neotropical passerines

(*Euphonia* spp.) that disperse the seeds of *Rhipsalis* spp., and Vander & Longland (2004) offer the example of epiphytic ant gardens to document this phenomenon, where seeds are dispersed by the combined activity of frugivorous birds (long-distance dispersal) and ants (directed short-distance dispersal). Epiphytes that form ant gardens occur in seven plant families (among them, the Bromeliaceae, the Araceae, and the Piperaceae). It is thought that the relationship between the epiphyte and the ant is highly specific and consistent through time and space, and is regulated by chemical signals (Benzing 1990; Orivel & Dejean 1999; Youngsteadt *et al.* 2009).

In the case of epiphytes whose seeds are dispersed by wind, several factors affect their fate. The height of release and the air turbulence strongly influence the dispersal distance (García-Franco & Rico-Gray 1988; Mondragón-Chaparro *et al.* 2006; Murren & Ellison 1998). Other factors such as the spatial distribution of reproductive adults, seed quantity and shape of the dispersal kernel also determine the seed dispersal pattern of epiphytes (Cascante-Marín *et al.* 2009; Harvey 1996; Yeaton & Gladstone 1982). Field observations suggest that the majority of seeds tend to fall near the mother plant, whereas long-distance seed dispersal is relatively rarer (Bernal 2006; García-Franco & Rico-Gray 1988; Mondragón-Chaparro *et al.* 2006; Paggi *et al.* 2010). However, data on genetic variability have sometimes contradicted this assumption, indicating that medium- and long-distance seed dispersal may be very common in some epiphyte populations (Ávila-Díaz & Oyama 2007; Trapnell *et al.* 2004; Ramírez-Padilla 2008).

Kelly (1985), Martínez-Meléndez *et al.* (2008), and Vieira & Izar (1999) suggested that in epiphyte communities there is a vertical stratification associated with seed dispersal syndromes. However, no general trend has been found, as epiphytes from different habitats behave differently. For example, in a tropical rain forest, wind-dispersed species occupy mainly the upper part of tree crowns (Kelly 1985), while in a cloud forest they are distributed in the lower canopy (Martínez-Meléndez *et al.* 2008). Regarding zoochorous epiphytes, in a tropical rain forests they seem to accumulate either in the upper trunk or the lower canopy, whereas in a cloud forest they may occur in any microhabitat (Kelly 1985; Vieira & Izar 1999).

Different morphological adaptations for seed dispersal may be found among epiphytes. Anemo-

chorous species often produce winged or plumose seeds. In twig orchids of the Oncidiinae and Sarcanthinae subtribes, seeds possess, a hooked testa that facilitates seed attachment to twig surfaces (Chase & Pippen 1988). Many tropical epiphytes fall on either of two extremes in relation to seed weight: they produce very tiny, easily dispersed seeds (*e.g.,* Orchidaceae and Tilladsioideae), or much larger seeds similar to, or larger than those of many shrubs (*e.g.*, Melastomataceae, Gesneriaceae, and some Bromeliaceae; Rockwood 1985). Tsutsumi *et al.* (2007) compared the seed morphology of epiphytic and terrestrial species in the genus *Liparis* (Orchidaceae), and showed that epiphytes tend to have larger embryos and smaller air spaces, and thus heavier seeds than their closely related terrestrial counterparts. Although such features may limit dispersal ability, larger embryos seem to be a result of a more advanced developmental stage and consequently may germinate earlier than smaller embryos. Thus, their relatively lower dispersal ability may be compensated by other advantages. Also, even if seeds are relatively heavy, they may have better dispersability if they are released from high microsites compared to those that are released almost at ground level.

Population genetics

Although strictly speaking population genetics is not part of population ecology (but rather of population biology), clearly the intricate breeding systems and seed dispersal patters, as well as the patchy distribution that characterize epiphytes, make them an interesting group to address genetic variation patterns within and between populations. Genetic diversity and breeding systems are intimately linked. As previously noted, the majority of epiphytes show mixed breeding systems, which in many cases include mechanisms that favor outcrossing (Table 1). This variation in breeding systems reflects on genetic diversity. For instance, *Tillandsia ionanta*, a predominantly outcrossing epiphyte, has F_{IS} values close to zero (0.056), while *T. recurvata*, a cleistogamous species shows an $F_{IS} = 1$, which reflects a total absence of heterocigotes (Soltis *et al.* 1987; working with allozymes).

Another factor that may influence genetic diversity is clonal propagation. In principle, this phenomenon may result in decreased genetic diversity because of the production of new ecological individuals with the same genotype, which

in turn increases the probability of geitonogamy and reduces the level of outcrossing. However, it has been shown in the orchid *Laelia rubescens* that what appears to be a large clone is in fact a mixture of several genotypes (Trapnell *et al.* 2004). On the other hand, species that propagate clonally may show stronger mechanisms favoring outcrossing; for instance, the clonal epiphyte *Tillansdia brachycaulos* showed an $H_0 = 0.503$, while the non-clonal *T. elongata* exhibited an $H_0 = 0.377$ (González 2004).

Seed dispersal also plays an important role in determining the genetic diversity within and between epiphyte populations. As discussed above, the seeds of many epiphytes are dispersed by wind. The resulting gene flow may determine a lack of genetic differentiation between populations (Ackerman & Ward 1999; Alcántara *et al.* 2006; Ávila-Díaz & Oyama 2007; Tremblay & Ackerman 2001). Occasional long distance seed dispersal events are important as gene flow agents, but also as means for the expansion of species distribution ranges through the foundation of new populations (Bernal 2006; García-Franco & Rico-Gray 1988; Mondragón-Chaparro *et al.* 2006; Paggi *et al.* 2010).

Many epiphytes, especially epiphytic orchids, have very small effective population sizes. Thus, despite being mainly outcrossing, they may suffer from high levels of endogamy and genetic diversity loss within local populations. The effect of low effective population sizes could be further accentuated by vegetative propagation, which increases the longevity of successful genotypes producing an apparently larger population with no increase in effective population size (Tremblay & Ackerman 2001). On the other hand, the distribution of epiphyte populations within the forest canopy may result in increased levels of genetic diversity, as panmictic reproduction becomes more likely when plants are distributed in a three-dimensional space, where the linear distance between individuals is reduced, than when they are distributed in a two-dimensional plane (Trapnell *et al.* 2004).

Beyond the population level, the use of genetic markers has proven a useful tool to address metapopulations questions in epiphyte populations. In *Tillandsia recurvata* paternity analyses based on microsatellites were used to determine the potential origin of the seedlings established in different local populations (*i.e.* trees) within a metapopulations (García-Morales 2007; Ramírez-Padilla 2008). The results showed that

seed dispersal is more widespread than originally suspected, and effectively completed the picture offered by the results of the field experiments on seed dispersal. In addition, the level of genetic variation within and between populations, which was thought to be very low in this apparently autogamous species (Soltis *et al.* 1987, with allozymes) turned out to be much higher than previously suspected (García-Morales 2007, using microsatellites). These results stress the need to develop appropriate genetic markers for the study of different ecological questions. In general, this is an underdeveloped field that clearly needs more attention among epiphyte researchers.

Early life cycle stages

Post-reproductive biology, particularly seed germination and seedling establishment, are among the most thoroughly investigated topics in epiphyte biology. Yet the knowledge on this subject is still limited, considering the large number of epiphytic species in nature, and most of this research has been interpreted from an ecophysiological viewpoint. The consequences of the fate of early-life cycle stages on the population dynamics of epiphytes have seldom been approached.

Seed germination

The seed germination of many epiphyte species has been studied under controlled conditions, and has shown that the germinability of most species is quite high (Table 2). However, seed germination experiments in the field have been carried out only for 27 epiphyte species, most of them in the Bromeliaceae family (~90 %). Seed germinability in the field varies from 0.0001 % to 96.8 %, with an average of 27.4 % (Table 2). In many species there is a large contrast between their potential (controlled conditions) and natural (in the field) germinability (*Aechmea bracteata*, *Laelia speciosa*, *Rhipsalis bacciferea*, *Tillandsia brachycaulos* and *T. eizii*; Table 2).

Germination rates in the field vary greatly between microsites. Tree crowns consist of a heterogeneous mosaic of microhabitats resulting from a complex combination of biotic and abiotic variables (Benzing 1978, 2000; Callaway *et al.* 2002; Hietz & Briones 1998; Madison 1977; Scheffknecht *et al.* 2012; Winkler *et al.* 2005). Within the canopy, radiation, temperature, wind velocity, and water and nutrient availability vary

spatiotemporally, creating microclimatic gradients that may differentially affect the germination of different epiphytic species (Benzing 1978; Hietz & Briones 1998; Zotz & Andrade 2002). These variables change from one phorophyte to another, depending on their height, crown size and shape, leaf habit, bark characteristics (texture, stability and water retention capacity), branch thickness, position in the canopy, the presence of allelopathic compounds or other minerals washed from the phorophyte, *i.e.,* lixiviates (Bennett 1986; Benzing 1978, 1990; Callaway *et al.* 2002; Castro *et al.* 1999; Frei *et al.* 1972; Mehltreter *et al.* 2005).

Water is considered the main limiting factor in the epiphytic habitat, and particularly so during the germination process. The seeds of many epiphytes are capable of a fast imbibition in small water amounts due to their small size (< 2 mm in 84 % of angiosperm epiphytes), their high surface-to-volume ratio (Madison 1977), and their frequently high permeability, as is the case for many epiphytic orchids and bromeliads (Benzing 2000; Rasmussen 2008; Toledo-Aceves & Wolf 2008; Yoder *et al.* 2000). In certain species, water absorption ability is increased by the presence of hydrophilic seed appendages that efficiently transfer water from the substrate to the seed (Wester & Zotz 2011). In most orchids water absorption is facilitated by their association with mycorrhizal fungi, generally of the genus *Rhizoctonia*, which starts at the time of seed germination (Arditti & Ghani 2000; Benzing 2000; Gowland *et al.* 2011).

In general, epiphyte seeds germinate soon after dispersal. Studies carried out in different ecosystems suggest that it is common for them (1) to lack dormancy, (2) to have a short longevity and do not form long-term seed banks, and (3) to be dispersed ripe at the end of an unfavorable or the beginning of a favorable season (Baskin & Baskin 2001; Benzing 2000; Garcia-Suarez *et al.* 2006; Goode & Allen 2009; Madison 1977; Toledo-Aceves & Wolf 2008; Winkler *et al.* 2005). The lack of seed dormancy has been documented for *Aechmea bracteata*, *Catopsis berteroniana*, *Tillandsia magnisuana* and *T. prodigiosa*, which may germinate readily after they enter in contact with water (Goode & Allen 2009). Other species, such as *Tillandsia eizii* and *T. califani*, may take two to three weeks to germinate (Garcia-Suarez *et al.* 2006; Toledo-Aceves & Wolf 2008). However, these processes tend to be much longer (*ca.* three months) under natural conditions, the triggering

Table 2. Seed germination percentages reported for some epiphytes in controlled conditions and in the field. Figures in parenthesis are germination percentages in the absence of light. Ref= references, detailed in the footnote.

Species	Controlled conditions (darkness)	Field conditions	Ref
Bromeliaceae			
Aechmea bracteata	100	1	1
Catopsis berteroniana	90 (80)	50.5[a]	2
Catopsis nutans		61.9	3
Catopsis sessiliflora		18.8	4
Guzmania monotachya		54.6	3
Tillandsia brachycaulos	100	3.19[b]	5
Tillandsia brachycaulos	73		6
Tillandsia bourgaei	100 (75)	28[a]	2
Tillandsia butzii		10	7
Tillandsia calothyrsus	100 (72.5)	29.4[a]	2
Tillandsia circinata		3	8
Tillandsia deppeana		7.2	4
Tillandsia eizii	92	4.7	9
Tillandsia elongata	82		6
Tillandsia flexulosa	100		10
Tillandsia fasciculata	100	57.9	3 & 10
Tillandsia guatemalensis	93-100	96.8[a]	11
Tillandsia imperialis	88.3	26.6	12
Tillandsia juncea		33.7	4
Tillandsia magnusiana	97.5 (90)	58.8[a]	2
Tillandsia multicaulis		0.2	4
Tillandsia multicaulis		14	7
Tillandsia prodigiosa	57.5 (35)	38.7[a]	2
Tillandsia punctulata		27.3	4
Tillandsia punctulata		32	7
Tillandsia recurvata	90-100	6.53	13 & 14
Viridantha plumosa	52.5 (57.5)	12.6	2
Werahuia gladioliflora		60.4	3
Cactaceae			
Epiphyllum phyllanthus	> 80 (~40)		15
Rhipsalis baccifera	80 (<1)	1.57	16
Orchidaceae			
Laelia speciosa	100	0.0001 [c]	17

(a) Mean seed germination from data obtained in different phorophytes; (b) Mean seed germination from data obtained at different heights on the phorophyte; (c) Ratio between emerging seedlings and number of fruits. References are: 1 = Goode & Allen 2009; 2 = Sosa-Luría 2008; 3 = Cascante-Marín *et al.* 2009; 4 = Winkler *et al.* 2005; 5 = Mondragón & Calvo-Irabiēn 2006; 6 = Chi 1996; 7 = Toledo-Aceves *et al.* 2012b; 8 = Benzing 1978; 9 = Toledo-Aceves & Wolf 2008; 10 = Bader *et al.* 2009; 11 = Castro-Hernández *et al.* 1999; 12 = Haeckel 2009; 13 = Fernández *et al.* 1989; 14 = Hernández-Rosas 2003; 15 = Simão *et al.* 2010; 16 = De la Rosa & Briones 2010; 17 = Hernández-Apolinar 1992.

factors being frequent rainfall and high relative humidity (Castro-Hernández *et al.* 1999).

As mentioned above, seed longevity in epiphytes is generally short. It is common to observe seed decomposition in the field shortly after seed dispersal (*e.g.,* in (*Tillandsia eizii, T. deppeana, T. guatemalensis, T. juncea, T. punctulata* and *Catopsis sessiliflora*; Garcia-Franco 1990; Toledo-Aceves & Wolf 2008; Winkler *et al.* 2005). However, certain seeds may retain. However, certain seeds may retain their germinability for one year (50 % germination in *A. bracteata*, and

80-95 % in *Viridantha plumose*, after 12 months of storage at room temperature; Goode & Allen 2009; D. Mondragón unpublished).

In habitats with a marked rainy season, epiphytes shed their seeds towards the end of the dry or the beginning of the humid season. Thus, the timing of seed germination and seedling emergence in natural population is coupled with both seed dispersal and the onset of the rainy season. These processes are enhanced on phorophytes whose bark absorbs and retains water (Benzing 2000; Callaway *et al.* 2002; Johansson 1974; Madison 1977; Mehltreter *et al.* 2005). This is an example of how certain phorophyte features may boost the germination of particular epiphyte seeds, resulting in a phenomenon similar to habitat selection, where high germination on specific phorophyte species (or in particular microsites within the phorophyte) reflects in an apparent preference in patch occupancy (Bernal *et al.* 2005).

In addition to water, radiation is also an important environmental factor affecting seed fate (Benzing 1978; Bernal *et al.* 2005; Castro *et al.* 1999; Chase 1987; Simão *et al.* 2010; Toledo-Aceves & Wolf 2008). Although many epiphyte seeds may germinate in both light and dark environments (Table 2), others have been reported to be inhibited by darkness or far-red radiation (*e.g., Tillandsia brachycaulos*; Graham & Andrade 2004); this suggests that light quality, rather than light intensity, may be most influential, which may have important consequences in terms of the type of microhabitats they occupy.

Seedling ecology

The seed-to-seedling transition is one of the most vulnerable stages in the life cycle of plants (Baskin & Baskin 2001) and epiphytes are no exception. From the hundreds, thousands and even millions of seeds that a plant produces (Madison 1977), only a small fraction germinate to become seedlings (Ackerman *et al.* 1996; Arditti & Ghani 2000; Benzing 1981), and those that germinate face a high mortality risk during the seedling phase. The most important mortality cause is drought, to which seedlings are highly vulnerable due to their high surface: volume ratio (Benzing 2000). However, as seeds germinate during the rainy season, some authors suggest that humidity is not as limiting as generally assumed (Cascante-Marín *et al.* 2008); in fact, early emerging seedlings may grow and store water for four to six months before the onset of the following dry

season. Also, association with mycorrhizal fungi in orchids plays a key role during this stage, as both water and nutrients are initially provided by the symbiotic fungus (Arditti & Ghani 2000; Rasmussen 2008).

Epiphytes display different photosynthetic metabolisms, most frequently CAM and C_3, which may play an important role in determining their early survival probabilities and the crown microenvironments each species may occupy. C_3 plants seem to occupy shaded microsites (Andrade *et al.* 2007; Griffiths & Smith 1983), whereas CAM plants are characteristic of external, relatively more exposed microsites, and also of relatively more arid environments (Andrade *et al.* 2007; Benzing 2000; Griffiths & Smith 1983; Hietz & Briones 1998; Reyes-García *et al.* 2012; ter Steege & Cornelissen 1989; van Leerdam *et al.* 1990; Winter *et al.* 1983). CAM metabolism is prevalent among some bromeliads, particularly in the adult stages (*e.g.*, atmospheric tillandsioid species), and in some epiphytic cacti such as *Hylocereus undatus*, *Selenicereus megalanthus*, and *Rhipsalis* spp. (Crayn *et al.* 2004; Griffiths & Smith 1983; Medina 1974; Stuntz & Zotz 2001; Weiss *et al.* 2010). Within the Orchidaceae, 35 % of the species present CAM metabolism and most of this percentage is composed of epiphytes; the rest are terrestrial orchids which are predominantly C_3 (Winter & Smith 1996; Zotz 2004b). Little is known about the activation process and timing of the CAM metabolism among the epiphyte species that present it, which is an important issue to address in the future. Interestingly, some epiphytes that occupy extremely shaded microsites have been characterized as CAM (Benzing 2000; Medina *et al.* 1989).

Several authors have studied the survival of epiphyte seedlings (Table 3), both as part of relatively controlled field experiments (60 % of studies) and through direct observations in natural conditions (40 %). Of the many mortality causes that have been reported for epiphyte seedlings, perhaps the most important is wilting due to drought (Benzing 2000; Hernández-Apolinar 1992; Larson 1992; Winkler *et al.* 2007). Other causes have also been mentioned, such as the presence of allelopathic compounds in the phorophyte bark that inhibit seedling growth (Bermudes & Benzing 1989; Madison 1977; Valencia-Díaz *et al.* 2010), and the instability of the substrate in the case of exfoliating trunks and fragile branches of many tree species (López-Villalobos *et al.* 2008; Zotz 1995). In relation to the latter, it has been

Table 3. Seedling survival percentages reported for different epiphyte species in field experiments and in natural (unmanipulated) conditions. Ref = references, detailed in the footnote.

Species	Observation time (months)	Field experiments	Natural conditions	Ref
Bromeliaceae				
Catopsis spp.	12		74	1
Catopsis nutans	24	6.8		2
Catopsis sessiliflora	12	7		3
Guzmania monostachia	24	7.9		2
Tillandsia brachycaulos	12		39	4
Tillandsia butzii	13		8.3	5
Tillandsia deppeana	12	11.6		3
Tillandsia eizii	12		9.3	6
Tillandsia fasciculata	24	10.1		2
Tillandsia guatemalensis	12		34.5	6
Tillandsia guatemalensis	7	19.5		6
Tillandsia juncea	12	17.8		3
Tillandsia multicaulis	12	0	11.5	3 & 5
Tillandsia paucifolia	12	1.5[a]		7
Tillandsia punctulata	12	10.4	36.5	3 & 5
Tillandsia spp.	12		81	1
Werahuia gladioliflora	24	7.1		2
Orchidaceae				
Dimerandra emarginata	12		< 50	8
Laelia speciosa	17		75	9
Tolumnia variegata	12		32.8	10

(a) Mean seedling survival from four cohorts. References are: 1 = Hietz 1997; 2 = Cascante-Marín *et al.* 2008; 3 = Winkler *et al.* 2005; 4 = Mondragón 2001; 5 = Toledo-Aceves *et al.* 2012b; 6 = Toledo-Aceves & Wolf 2008; 7 = Benzing 2000; 8 = Zotz 1998; 9 = Hernández-Apolinar 1992; 10 = Ackerman *et al.* 1996.

observed that thin branches subjected to high radiation and low humidity levels break rather easily (Hietz 1997; Winkler & Hietz 2001), and their fragility affects the survival not only of epiphyte seedlings, but also of larger individuals (Zotz *et al.* 2005). It is generally assumed that epiphyte mortality decreases with size (Haeckel 2009; Hietz 1997; Mondragón *et al.* 2004a; Zotz 1998; Zotz & Schmidt 2006; Winkler *et al.* 2007), as is the case with many other plant species. However, this relationship is unclear in some species, such as *Aspasia principissa* (Zotz & Schmidt 2006).

Many epiphytes have been reported to show vivipary (Madison 1977), described as the lack of seed dormancy, and thus germination takes place within the fruit. In these cases the dispersal unit is the seedling, which may establish readily as soon as it lands on an adequate substrate (Farnsworth 2000). However, among vascular epiphytes the term vivipary has been given two different connotations: (a) the process previous to dispersal consisting of seeds germinating within the fruit - commonly known as true vivipary; or (b)

the production of vegetative structures (*e.g.,* ramets, plantlets, or bulbils) that may detach from the parent plant and lead a physiologically independent life - commonly termed pseudovivipary or vegetative propagation (Benzing 2000; Farnsworth 2000). An example of the latter are the inflorescences of *Tillandsia flexuosa, T. paucifolia* and *T. utriculata*, that are known to produce plantlets whose establishment success is higher than sexually derived seedlings (Benzing 2000; Cota-Sánchez & Abreu 2007). As true vivipary has evolved independently several times in taxa with xerophytic traits (Farnsworth 2000), it is likely that in epiphytes it is more common than expected. Indeed, studies in Cactaceae of the tribes Hylocereeae and Rhypsalidae confirm the occurrence of true vivipary (Cota-Sánchez 2004; Cota-Sánchez & Abreu 2007).

Growth

Growth refers to the change in size, weight, form, and/or number of parts in a living organism (Chiariello *et al.* 1991; Hunt 2003). From the point

of view of population ecology, plant growth plays a major role as a demographic process, and consequently many demographic models are based on the rate at which individuals move along different size categories (as well as including other demographic processes such as survival, reproduction and vegetative propagation). Demographic studies carried out with epiphytes use some measure of plant size as a categorization variable to subdivide the population in classes; most of them (87 %) are based on measures of plant height or length, while a smaller proportion (13 %) use shoot or pseudobulb counts (Mondragón 2011).

Demographic models incorporate the probability of an individual in a particular size class moving to larger (or smaller) size classes within a specific time-step - generally a year -, which clearly depends on the rate at which individuals grow. However, such demographic studies rarely report mean individual growth rates. When these have been studied, they have shown that, compared to plants native to more mesic habitats, and even to terrestrial stress-tolerators, epiphytes tend to have slow relative growth rates (Chiariello *et al.* 1991; Hernández-Apolinar 1992; Hietz *et al.* 2002; Hunt 2003; Mondragón *et al.* 2007; Winkler *et al.* 2007; Zotz 2005; Zotz & Asshoff 2010; Zotz *et al.* 2005; Zotz & Schmidt 2006), as they are restricted by the low and unpredictable resource levels (particularly water and nutrients) characteristic of the epiphytic habitat (Benzing 2000; Laube & Zotz 2003; Schmidt & Zotz 2002; Zotz & Asshoff 2010; Zotz & Hietz 2001). In many cases seedlings and juveniles tend to have significantly higher relative growth rates compared to adult plants (Laube & Zotz 2003; Schmidt & Zotz 2002; Zotz & Asshoff 2010).

The slow growth rate of many epiphytes determines that the first reproduction is generally delayed, taking between 10 to 20 years. Such is the case of *Tillandsia circinnata* (Benzing 1981), *Laelia speciosa* (Hernández-Apolinar 1992), *Encyclia tampensis* (Larson 1992), *Tillandsia juncea*, *T. deppeana*, *T. punctulata* and *Catopsis sessliflora* (Winkler *et al.* 2007). However, the twig orchid *Erycina crista-galli* reaches maturity within its first year, when the pseudobulb reaches a height of 0.4 cm (Mondragón *et al.* 2007). In larger orchids the threshold size for a pseudobulb to become reproductive is *ca.* 3.5 cm in *Lycaste aromatica* and *Laelia speciosa* (Hernández-Apolinar 1992), 4 cm in *Artorima erubescens* (García-Soriano 2003), 4.5 cm in *Encyclia tampensis* (Larson 1992), and 5 cm in *Dimerandra emarginata* (Zotz 1998).

Some authors have documented the existence of spatial variation in growth rates between individuals of the same species, probably as a result of dissimilarities in the environmental conditions that prevail in different microhabitats within tree crowns (Cardelús & Mack 2010; Hietz *et al.* 2002) or between different phorophyte species (Bernal *et al.* 2005: Callaway *et al.* 2002; Cardelús & Mack 2010; Zotz 2005); while temporal variation in growth rates may be due to yearly differences in water availability (Zotz & Schmidt 2006). Within one year, there may be periods of active growth and episodes in which plants decrease in size due to drought (see, for instance, *Dimerandra emarginata*; Zotz 1998).

As mentioned above, the nutrient and water restrictions characteristic of the epiphytic habitat account to some extent for the slow relative growth rates of many epiphytes. In particular, nitrogen and phosphorous limitations restrict plant growth in some epiphytes, and the addition of both macronutrients results in an increased individual growth rate (Castro *et al.* 1999; Hietz & Wanek 2003; Laube & Zotz 2003; Zotz & Asshoff 2010; Zotz & Hietz 2001; Zotz *et al.* 2011). Fertilized plants may also develop longer inflorescences, with a relatively larger flower number, which results in a higher seed input per plant (Lasso & Ackerman 2013). However, Zotz & Asshoff (2010) found in *Guzmania monostachia*, *Tillandsia elongata*, and *Werauhia sanguinolenta* that a 100-fold increase in the N or P supply resulted in an increase in individual growth rate of only 15 to 33 %, which suggests that the positive effect of added nutrients is limited. This inherently slow growth rate and limited phenotypic plasticity is common among species that have evolved in nutrient poor environments (Grime 1979). Recent studies have suggested that P is even more limiting than N in the epiphytic habitat (Cardelús & Mack 2010; Zotz 2004a; Zotz & Asshoff 2010), and have shown that the use of both macronutrients vary among taxonomic groups (Cardelús & Mack 2010; Schmidt *et al.* 2001).

With regards to water limitations, Cardelús & Mack (2010) found that different taxonomic groups also differ in their water use efficiency. In general, bromeliads use water more efficiently than orchids and ferns. However, there is variation in water use efficiency also within the bromeliads depending on their photosynthetic metabolism (Hietz & Wanek 2003). Typically C_3 plants suffer more from water stress than CAM plants, and water stress is more intense in juveniles than in adults.

In addition to nutrients and water, the light environment also plays an important role in epiphyte growth. In many forests, this environmental feature is associated to the successional status of the forest, with early successional phases being characterized by higher radiation levels than late successional stands. Cascante-Marín *et al.* (2008) showed that the growth of *Catopsis nutans* and *Werauhia gladioliflora* was favored by the higher radiation levels of the early successional stages, while the growth of *Guzmania monostachia* and *Tillandsia fasciculata* was unaffected by forest successional stage.

The positive influence on plant growth of high radiation levels associated with the relative openness of the forest canopy has also been observed in the transition between montane cloud forest and temperate forests (Toledo-Aceves & Wolf 2008; Winkler *et al.* 2005). Variation in radiation levels within tree crowns also affects the growth of different species in distinct ways. *T. elongata* and *T. brachycaulos* plants showed higher relative growth rates and leaf production when growing under intermediate radiation levels (30 - 59 %) than when growing in lighter (> 60 %) or shadier microsites (11 - 29 %; Cervantes *et al.* 2005). This contrasts with *T. recurvata*, whose seedlings grew faster when exposed to high radiation levels in the most external parts of tree crowns (Bernal *et al.* 2005). On the other hand, *Vriesea sangui-nolenta* grew at a slower rate in relatively exposed conditions (60 % radiation) than in shadier microsites (30 %; Laube & Zotz 2003).

Many epiphytes grow through the emergence of new offshoots or ramets, which translates into vegetative propagation (García-Soriano 2003; Haeckel 2009; Martínez-García 2006; Mondragón 2001; Mondragón *et al.* 2004a; Mondragón & Ticktin 2011). Ramet production usually involves the growth of modules in the form of new rosettes that may eventually become physiologically independent from the mother plant while being genetically identical to it. This feature has been a source of confusion regarding the discrimination of semelparity and iteroparity in many epiphytes: when a species is classified as semelparous, it may be unclear whether this characterization refers to the genet or to the individual rosette. Indeed, many Tillandsias have semelparous rosettes while genets may be iteroparous given their ramet production ability (*e.g. Tillandsia brachycaulos*; Mondragón *et al.* 2004a). It is likely that the growth of individual ramets is quite different from that of sexually derived organisms; however, the distinction is seldom made when growth rates are reported. Mondragón (2001) and Mondragón *et al.* (2004a) explicitly mention that the growth rate of individual ramets is higher than that of seed-originated plants in *Tillandsia brachycaulos*, owing to the resource translocation that takes place from the mother plant to the emerging ramet. The same occurs in *Tillandsia macdougalli*, whose ramets may become reproductive within their first year of life (Mondragón & Ticktin 2011). It appears that some atmospheric bromeliads may show higher ramet growth rates than tank bromeliads (Mondragón & Ticktin 2011). In addition, vegetative spread may take place through plantlets that emerge from inflorescences (*e.g.* in *Tillandsia flexuosa*, *T. paucifolia* and *T. utriculata*), rather than from lateral rosettes. Apparently, such plantlets also grow faster than sexually derived seedlings (Benzing 2000).

An interesting issue regarding the growth traits of epiphytes is their potential response to increasing atmospheric CO_2 levels. Recent studies have demonstrated that higher atmospheric CO_2 concentrations result in increased individual growth rates (Fernandez Monteiro *et al.* 2009; Li *et al.* 2002; Weiss *et al.* 2010). Therefore, it has been suggested that epiphyte performance may improve in a CO_2-rich atmosphere, particularly during their initial life-cycle stages (Zotz *et al.* 2010). However, these results are still inconclusive and more information is still needed regarding how increased CO_2 levels may interact with other physical factors (Poorter & Navas 2003; Zotz *et al.* 2010).

Demography and population dynamics

The use of population projection matrices has grown in recent years, and their application to vascular epiphytes has not been an exception. We found results for 30 epiphytic angiosperms (15 bromeliads and 15 orchids), which add up to 38 populations (19 bromeliads and 19 orchids) and span a publication period of almost 20 years (Table 4), although half of these studies were published in the last seven years. Many other epiphytes have been studied from a demographic viewpoint, but only those reported in Table 4 were based on population projection matrices. In this section we focus on this set, explore the patterns observed amongst them and compare to other biological groups. We take advantage of the fact that most demographic results are generally given in standar-

Table 4. Main demographic results obtained from matrix analyses for different epiphyte species/populations. Columns are: Ab = abbreviation used for each species (different subindices for a single species correspond to populations at different sites; or, when marked with *, to different time periods for the same population); λ = finite population growth rate; *OPSI* = observed population structure index (ratio between the stage category with the highest relative number of individuals divided by the total number of stage categories defined for each population); *EF* = summed elasticity for fecundity, *EG* = growth, and *ES* = stasis/retrogression (after Silvertown *et al.* 1993); Q_s = annual seedling mortality rate; *F* = mean fecundity (in 'seedling' units). © = clonal spread was included in the matrix. References are detailed on the next page in the footnote.

Species	Ab	λ	*OPSI*	*EF*	*EG*	*ES*	Q_s	*F*	Ref
Bromeliaceae									
*Catopsis compacta$_1$**	Cb$_1$	1.069	0.60	0.058	0.255	0.687	0.083	2.350	14
*Catopsis compacta$_2$**	Cb$_2$	0.928	0.60	0.034	0.177	0.789	0.250	0.330	14
*Catopsis compacta$_3$**	Cb$_3$	1.042	0.60	0.086	0.362	0.552	0.166	8	14
Catopsis sessiliflora	Cs	0.82	0.40	0.020	0.090	0.890	0.610	4.429	1
*Tillandsia brachycaulos$_1$**	Tb$_1$	0.79	0.91	0.005	0.023©	0.976	0.714	0.019	2
*Tillandsia brachycaulos$_2$**	Tb$_2$	0.8	0.81	0.051	0.158©	0.841	0.210	0.022	2
*Tillandsia brachycaulos$_3$**	Tb$_3$	1.08	0.91	0.070	0.135©	0.764	0.330	0.705	2
Tillandsia carlos-hanskii$_1$	Tc-h$_1$	1.087	0.60	0.062	0.262	0.676	0.100	3	4
Tillandsia carlos-hankii$_2$	Tc-h$_2$	1.093	0.40	0.074	0.243	0.683	0.400	15.500	4
Tillandsia deppeana	Td	0.85	0.40	0.070	0.120	0.810	0.570	49.440	1
Tillandsia flexulosa	Tf	0.966	0.50	0.044	0.162	0.794	0.190	0.350	4
*Tillandsia imperialis$_1$**	Ti$_1$	1.01	0.375	0.026	0.22©	0.754	0.340	1.343	5
*Tillandsia imperialis$_2$**	Ti$_2$	0.965	0.375	0.023	0.198©	0.780	0.340	1.343	5
Tillandsia juncea	Tj	1.01	0.80	0.060	0.090	0.850	0.640	6.710	1
Tillandsia macdougallii	Tmc	0.927	0.50	0.008	0.129©	0.863	0.393	0.048	6
Tillandsia makoyana	Tma	1.059	0.17	0.177	0.418©	0.398	0.247	14.202	7
Tillandsia multicaulis	Tmu	0.96	0.40	0.050	0.070	0.880	0.660	8.240	1
Tillandsia punctulata	Tp	0.73	0.80	0	0.060	0.940	0.810	0.519	1
Tillandsia recurvata	Tr	1.127	0.50	0.106	0.300	0.593	0.200	0.748	8
Tillandsia violaceae	Tv	0.952	0.50	0.009	0.195©	0.797	0.286	0.288	6
Werauhia sanguinolenta$_1$	Ws$_1$	1.067	1	0.065	0.370	0.565	0.280	3.260	9
Werauhia sanguinolenta$_2$	Ws$_2$	1.04	1	0.047	0.274	0.674	0.300	14.600	9
Werauhia sanguinolenta$_3$	Ws$_3$	0.9	1	0.037	0.220	0.743	0.360	4.290	9
Werauhia sanguinolenta$_4$	Ws$_4$	1.109	0.214	0.070	0.368	0.554	0.190	19.400	10
Orchidaceae									
Artorima erubecens	Ae	1.024	1	0.0001	0.354©	0.646	0	0.017	11
Aspasia principissa	Ap	0.92	0.64	0.022	0.272	0.706	0.250	0.150	12
Encyclia chacaoensis	Ech	1.022	0.40	0.059	0.215	0.725	0.110	0.833	13
Erycina crista-galli$_1$	Ec-g$_1$	0.398	1	0.034	0.247	0.718	0.750	0.024	14
Erycina crista-galli$_2$	Ec-g$_2$	0.521	0.75	0.059	0.170	0.771	0.561	0.033	14
Guarianthe aurantiaca	Ga	0.987	0.60	0.021	0.154	0.825	0.107	0.064	3
Jacquiniella leucomelana	Jl	0.894	0.25	0.083	0.305	0.611	0.406	0.644	15
Jacquiniella teretifolia	Jt	0.976	0.50	0.058	0.206	0.736	0.255	1.755	15
Laelia speciosa	Ls	1.323	0.50	0.117	0.327	0.557	0.290	6.205	16
Lepanthes caritensis$_1$	Lc$_1$	0.995	0.50	0.002	0.114	0.884	0.059	0.017	17
Lepanthes caritensis$_2$	Lc$_2$	0.999	0.50	0.003	0.094	0.903	0.092	0.047	17
Lepanthes eltoroensis	Le	0.997	1	0.005	0.110	0.880	0.032	0.041	18
Lepanthes rubripetala	Lrb	1.012	1	0.032	0.148	0.820	0.220	0.150	19
Lycaste aromatica	La	0.949	0.50	0.007	0.126	0.867	0.482	0.055	15
Pleurothallis quadrifida	Pq	1.026	0.50	0.030	0.170	0.800	0.110	0.136	13
Tolumnia variegata	Tov	0.840	0.75	0.029	0.167	0.804	0.340	0.040	20

dized terms, so we apply meta-analyses to these results in the search for objective general patterns.

Only two plant families are represented in Table 4, from the *ca.* 50 angiosperm families that contain epiphytic species (Benzing 1990). All listed species are native to the New World and most inhabit tropical humid ecosystems (although a few thrive in temperate forests or relatively more arid ecosystems).

A variety of population growth rate values (λ) can be noticed in the data set, ranging from 0.398 in *Erycina crista-galli* to 1.323 in *Laelia speciosa*. Among the bromeliads (n = 24 cases), 50 % show a λ value above unity, while among the orchids (n = 19 cases) this happened only in 37 % of the cases (here we are not considering confidence intervals for λ values, but just describing the range of variation observed in this variable). The meta-analysis to test whether the λ values were affected by family showed that the effect of the plant family (Orchidaceae vs. Bromeliaceae) on λ was not significant (LRT = 0.4914, P = 0.4833; see Appendix B for details).

Apart from the λ value, several other demographic variables are reported in Table 4 such as the observed population structure index (*OPSI*), a proportional variable with values between zero and unity; as *OPSI* approached unity, populations were composed by a higher proportion of individuals in the larger stage category (see Table 4 for details). The meta-analysis showed that *OPSI* was not affected by family (LRT = 0.9092; P = 0.3403). Yet orchid populations tended towards larger *OPSI* values compared to bromeliads (Table 4). This pattern could indicate that small individuals are relatively more vulnerable among orchids than among bromeliads. However, the demographic data compiled for the present section showed that this was not the case: seedling mortality was higher in bromeliads (q_s weighted average = 0.387) than in orchids (q_s weighted average = 0.243) and the meta-analyses showed that the effect of family on seedling mortality was marginally significant (LRT = 3.0615; P = 0.0802). Some of the bromeliads cited in Table 4 that had high seedling mortality were *Catopsis sessiliflora* (0.61), *Tillandsia brachycaulos*[1] (0.71), *T. juncea* (0.64), *T.*

multicaulis (0.66) and *T. punctulata* (0.81). In contrast, only one orchid had seedling mortality > 60 % (*Erycina crista-galli*[1], 0.75) (the subindices associated to species Latin names follow the notation in Table 4). Orchids depend on early associations with mycorrhizal fungi, which may enhance their survival probability, yet its role in determining the seedling's vulnerability remains to be investigated in detail. Evidently, it is difficult to conclude in relation to this matter, as category definition differs between studies and species and it is likely that the fate of newly emerged orchid seedlings, which are extremely small, was not even recorded. In addition, the relatively large proportion of small individuals in some bromeliads (*e.g.*, *Tillandsia imperialis*, *T. makoyana*) could have been related to the occurrence of clonal spread in these populations, rather than to high seedling establishment/survival (Haeckel 2009; Martínez-García 2006).

Demographic elasticity patterns have become a useful numerical tool that can aid in the search for demographic patterns among plant species with different life histories (Silvertown *et al.* 1993, 1996), or with a common ancestry (Godínez-Álvarez *et al.* 2003). Here we explore to what extent this tool may allow us to identify shared and distinctive demographic features among epiphytes. The summed values of the three main demographic processes for each species/population are given in Table 4, and plotted in the demographic triangle in Fig. 1. As can be observed, most species/populations are located towards the lower right-hand portion of the triangle, implying that stasis (*ES*) is the demographic process with the highest elasticity values in most cases, followed by growth (*EG*). Only in one species, *Tillandsia makoyana*, was growth elasticity larger than stasis elasticity, although in a few of them the two values were quite close to each other (*i.e.*, *Werauhia sanguinolenta*[1] and [4], *Catopsis compacta*, *Artorima erubescens*, *Laelia speciosa*[2] and *Lepanthes rupestris*[2]). Compared to previous reports regarding elasticity patterns, epiphytes seem to behave similarly to long-lived forest understorey herbs, as well as shrubs and trees (Silvertown *et al.* 1993), and also to globose and articulated cacti (Godínez-Álvarez *et al.* 2003), in the sense that

References are: 1 = Winkler *et al.* 2007; 2= Mondragón 2001; 3= Mondragón 2009; 4 = Wester & Zotz 2010; 5 = Haeckel 2009; 6 = Mondragón & Ticktin 2011; 7 = Martínez-García 2006; 8= Valverde & Bernal 2010; 9 = Zotz 2005; 10 = Zotz *et al.* 2005; 11 = García-Soriano 2003; 12 = Zotz & Schmidt 2006; 13 = Mondragón & Ramírez-Morillo 2008; 14 = Mondragón *et al.* 2007; 15 = Winkler *et al.* 2009; 16 = Hernández-Apolinar 1992; 17 = Tremblay 1997; 18 = Tremblay & Hutchings 2002; 19 = Schödelbauerová *et al.* 2010; 20= Calvo 1993.
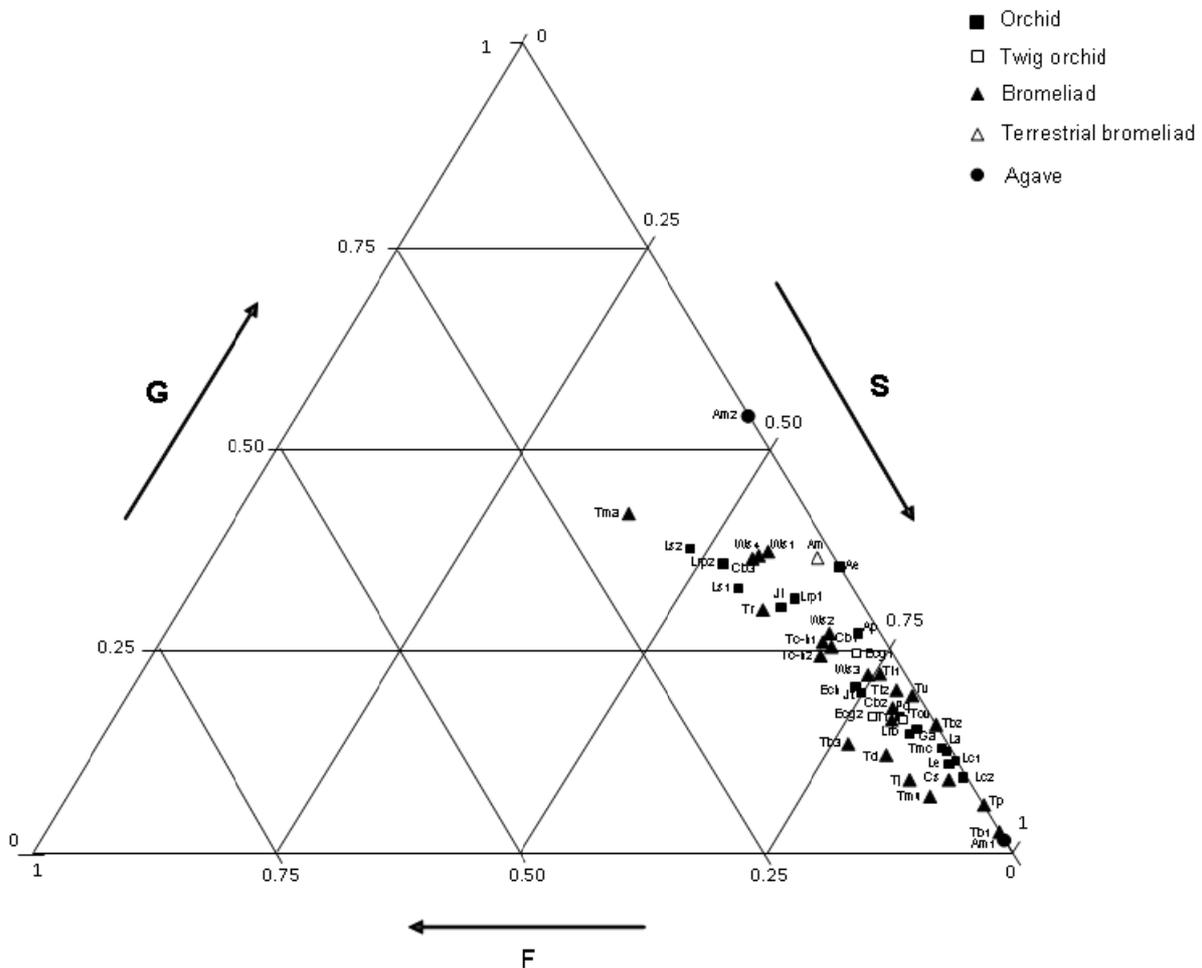
Fig. 1. Demographic triangle (following Silvertown *et al.* 1993) in which the summed elasticity values for the three main demographic processes (*S* = stasis, *G* = growth, and *F* = fecundity) are shown for each of the species/populations listed in Table 4. Nomenclature follows the abbreviations in Table 4. The different symbols represent distinct subgroups within the data set: black squares = orchids; grey squares = twig orchids; black triangles = bromeliads; grey triangle = terrestrial bromeliad (as an external group, for the sake of comparison); black circles = agave populations (as external groups, for the sake of comparison).

they tend to show high elasticities for the stasis components, *i.e.* the persistence of individuals in the same category (Fig. 1). Fecundity elasticity was below 15 % in all but one case (again, *T. makoyana*). Despite its apparent lack of relevance, an interesting pattern was found in this variable: the meta-analysis showed that there was a marginally significant negative association (*LRT* = 3.2349; *P* = 0.0719) between the summed elasticity for fecundity (*EF*) and the habitat index (*HI*, a quantitative score, ranging from 0 to 1, describing relative harshness of the habitat - see Appendix C). As *HI* increased (*i.e.*, the environment was relatively more benign, mainly in relation to water availability), the relative importance of fecundity to population dynamics decreased. Also, as has

been found in other studies (Godínez-Álvarez *et al.* 2003; de Kroon *et al.* 2000), fecundity elasticities were significantly and positively correlated with λ (*LRT* = 0.006; *P* = 7.38). And finally, λ values tended to be negatively associated with *HI*, although not significantly so (*LRT* = 2.5619; *P* = 0.1095), *i.e.* there was a tendency towards higher λ values occurring in habitats with lower *HI* values, which correspond to relatively harsher environments (see Appendix B for details on these meta-analyses).

The latter tendency contrasts with what has been found in other plant groups, where populations inhabiting relatively milder environments tend to show higher fecundity elasticities and higher λ values compared to those in harsher

habitats (Godínez-Álvarez *et al.* 2003), a pattern that results in their positioning closer to the centre of the demographic triangle (de Kroon *et al.* 2000). Yet we observe the opposite tendency among the epiphytes included in this review. The fine adaptations of epiphytes to the intrinsic harshness of the epiphytic habitat may account for this trend. Most epiphytes possess sophisticated mechanisms that allow them to successfully deal with the physiological aridity of the epiphytic habitat. In fact, they may be negatively affected by significant increases in humidity (*e.g.*, when they fall to the ground, it has been suggested that they die as a result of the sudden exposure to high humidity levels; Benzing 1990; Mondragón *et al.* 2004b). Thus, the demographic behavior outlined above (*i.e.*, relatively higher fecundity elasticities and λ values in harsher habitats) may be interpreted as a reflection of their ability across taxa to efficiently deal with such environmental conditions. Bromeliads in particular have been able to occupy the most extreme epiphytic habitats.

Interestingly, the two major taxonomic groups analyzed in this study (*i.e.,* bromeliads and orchids) were found intermingled in the demographic triangle, *i.e.* no clear differences between them could be noted. To explore the existence of other distinctive demographic features that could potentially discriminate between these two groups, we carried out a Principal Component Analysis (PCA) in which we incorporated a host of demographic variables in addition to the summed elasticities per demographic process. A total of 13 demographic variables were used (see Appendix C for details). The first component of the PCA (*x* axis in Fig. 2) accounted for 25.9 % of the overall variance, and the second component (*y* axis in Fig. 2) for 19.4 % (cumulative variance = 45.3 %). The first component showed a high correlation with λ, *EF* (fecundity elasticity) and *EG* (growth elasticity), and a negative correlation with *ES* (stasis elasticity) (Fig. 2a), whereas the second component showed a high positive correlation with the mortality of medium and large individuals (Q_m and Q_l), and to a lesser extent with seedling mortality (Q_s) (Fig. 2a) (see Appendix C for details of this analysis). In the resulting bi-plot (Fig. 2b), dots that are closer to each other are demographically more similar than dots located further apart. It may be observed that orchids and bromeliads are again intermingled in the bi-plot. Yet orchids form a group that predominantly span the lower left to upper right section of the bi-plot, whereas bromeliads are slightly more spread out

and preferentially spanning the upper left to lower right section of the bi-plot. This may indicate that the variables that vary the most among orchid populations (*e.g.,* the summed elasticities per demographic process, *ES*, *EF* and *EG*; Fig. 2a) tend to be different from the ones that vary most markedly between bromeliad populations (*e.g.*, seedling mortality - Q_s - and λ). Another interesting result of this analysis is that the twig orchids are surrounded by bromeliads in the bi-plot, and not by other orchids, which suggests that they share more demographic features with the former than with their taxonomically closer relatives (Fig. 2b).

Metapopulation dynamics

Although the metapopulation theory was originally developed in the field of animal ecology (Levins 1970), there has been an increasing influence of the metapopulation concept in plant population biology (Hanski & Gaggiotti 2004). The slower pace at which plant metapopulations have been addressed may be related to some of their biological peculiarities, such as seed banks and clonal spread, which may hinder the application of the traditional metapopulation concept (Husband & Barrett 1996). However, in the case of epiphytes, their naturally patchy distribution with local populations occupying patches (*i.e.*, phorophytes) embedded in a matrix of less suitable habitat makes them readily analyzable as metapopulations (Bernal *et al.* 2005; Snäll *et al.* 2005). Although some epiphytes may show low population densities as only one or two individuals occupy each phorophyte, many form more or less dense local populations in which tens or even hundreds of individuals may share the same phorophyte. Within a metapopulation, local populations are founded when dispersing seeds reach uncolonized trees, and they eventually become extinct if all individuals on a phorophyte die, or else when colonized trees fall down and pass away. The epiphyte-tree system has been described as a patch-tracking metapopulation in which colonizations are distance dependent and local extinctions are caused by deterministic patch loss (Snäll *et al.* 2003; Thomas 1994). Epiphyte metapopulations persist regionally due to a balance between colonizations and extinctions, and not necessarily through the long-term persistence of individual local populations. Hence, even when local populations on particular phorophytes are declining, the presence of an epiphytic species
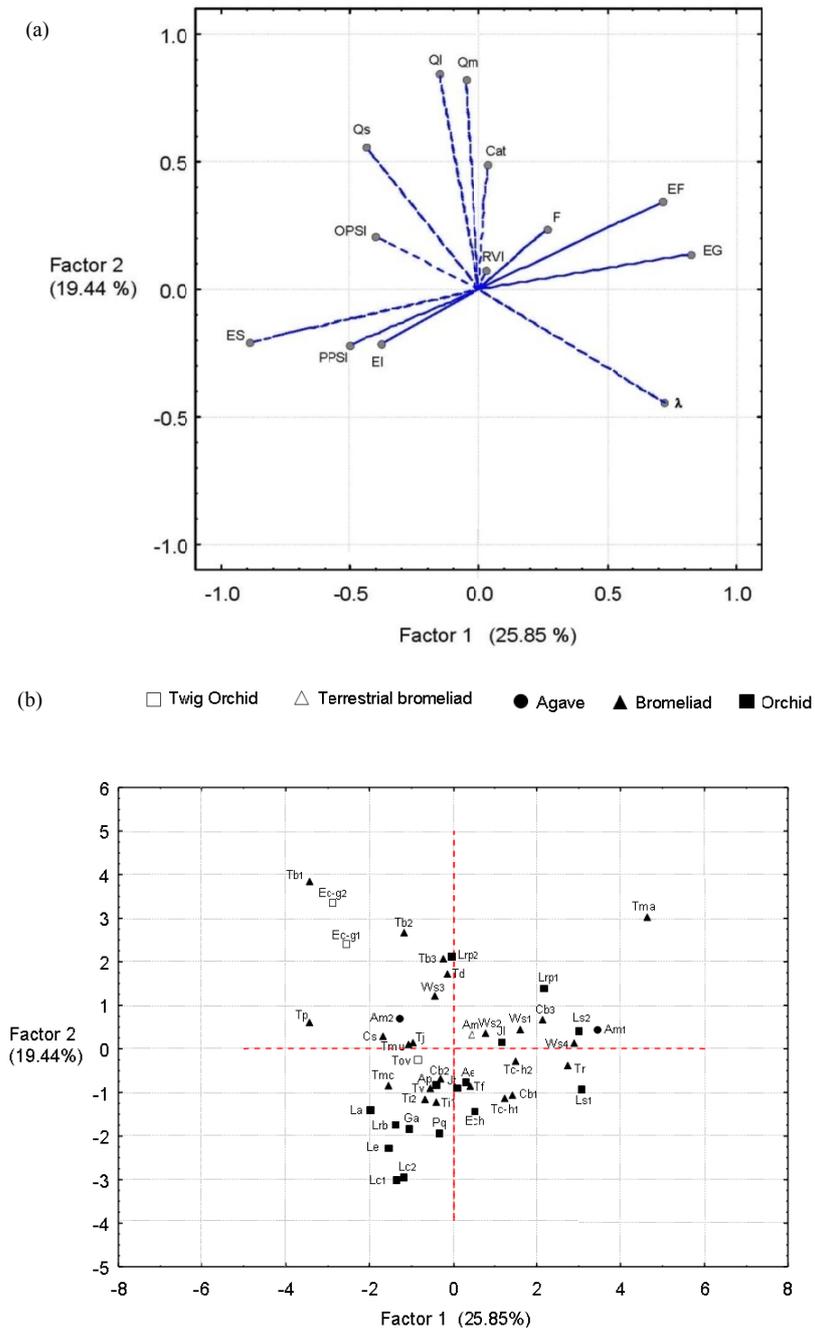
(a)

(b)

Fig. 2. Bi-plots derived from the PCA carried out with two descriptive variables (plant family, and species) and 13 demographic –response– variables for the different species/populations listed in Table 4 (see Appendix for details). In (a) each response variable is depicted as a vector in the two dimensional space (see text and Appendix C for variable abbreviations); the direction of each vector represents the way the relevant variable correlates with the two principal components represented by the two axis of the bi-plot, while vector size represents the strength of the correlation. In (b) the different species/populations are depicted as dots located in the two-dimensional space created by the first two principal components. Species/population names follow the abbreviations in Table 4. Symbols represent different subgroups within the data set: black squares = orchids; grey squares = twig orchids; black triangles = bromeliads; grey triangle = terrestrial bromeliad (as an external group, for the sake of comparison); black circles = agave populations (as external groups, for the sake of comparison).

within a forest community may be perceived as prevalent (Mondragón *et al.* 2004b; Tremblay *et al.* 2006; Zotz & Schmidt 2006).

Dealing with epiphytes through a meta-population perspective has been exemplified mostly for mosses and lichens (Löbel *et al.* 2006; Snäll *et al.* 2003, 2005). However, a few epiphytic angiosperms have also been studied as metapopulations: the orchids *Lepanthes rupestris* in Puerto Rico (Tremblay *et al.* 2006), and *Jacquiniella leucomelana*, *J. teretifolia* and *Lycaste aromatica* in a Mexican humid montane forest (Winkler *et al.* 2009); and the bromeliad *Tillandsia recurvata* in a Mexican semi-desert (Bernal *et al.* 2005; Valverde & Bernal 2010). Additionally, Laube & Zotz (2007) conducted another meta-population study with vascular epiphytes in Panama, but in this case they centered their analysis not on individual epiphyte populations/species, but on the phorophyte *Annona glabra*, which hosts *ca.* 60 epiphytic species.

Several interesting findings have emerged from these metapopulation studies with epiphytes. For instance, apparently epiphytes do not perceive the habitat in strictly binary terms (*i.e.*, colonizable patches vs. non colonizable habitat); rather, the different potential phorophytes form a gradient, with some more adequate than others for the establishment of local populations (Bernal *et al.* 2005; Boelter *et al.* 2011; Callaway *et al.* 2002; Mehltreter *et al.* 2005). This observation implies that the traditional usage of the metapopulation concept should be re-evaluated to make room for these relatively more complex metapopulations.

Another metapopulation subject that has been exemplified with epiphytes, at least in principle, has been the issue of asynchronous local population dynamics, which has been considered a prerequisite for metapopulation functioning (Hanski 1999). The large spatial extent and intensity of seed dispersal, along with the relative uniformity of the prevailing environmental conditions among local populations, may function as forces that homogenize local population dynamics, thus making them prone to correlated extinctions and preventing the development of real metapopulations (Liebhold *et al.* 2004; Tremblay *et al.* 2006). However, as mentioned above, the available literature on this subject supports the idea that seed dispersal among epiphyte local populations is a relatively weak homogenizing force, as most dispersed seeds remain within their original population and only a very low proportion reach other habitat patches (Bernal 2006; García-

Franco & Rico-Gray 1988; Mondragon & Calvo-Irabien 2006; Paggi *et al.* 2010). This fact may account for the observation that local populations do tend to function asynchronically (Tremblay *et al.* 2006; Laube & Zotz 2007; Valverde & Bernal 2010).

Some authors have suggested that in epiphyte metapopulations there must be a trade-off between the growth of local populations and the foundation of new populations. If too many seeds disperse out of the phorophyte, they have the potential to reach new phorophytes but at the expense of decreasing local population growth rate due to the lack of local recruitment (Winkler *et al.* 2009). Thus, enough seeds must disperse to reach new patches, but not so much as to deplete local populations from new recruits. This implies that, in order to understand epiphyte metapopulations, ecologists must be aware of both regional (between patches) and local (within patches) processes, which operate at different scales but are equally important to determine the dynamics of the system (Winkler *et al.* 2009; Zotz & Schmidt 2006).

Epiphytes and conservation

Epiphytes are currently considered one of the most threatened plant groups. This is in part due to their dependence on the presence/availability of host trees and the fact that most epiphytes satisfy their nutrient and water requirements directly from the atmosphere (Benzing 1998; Obregon *et al.* 2011; Zotz *et al.* 2010), which makes them vulnerable to potential atmospheric changes. In general, we were able to identify three major threats to the persistence of epiphytic populations: (a) climate change, (b) changes in land-use and vegetation cover, and (c) collection/harvesting of individuals from their natural populations.

Among the alterations that are already apparent as part of global climate change, it is clear that temperature is increasing, precipitation is decreasing (especially in subtropical areas), and atmospheric CO_2 concentration is rising (Murphy *et al.* 2004; Stainforth *et al.* 2005). It is estimated that these changes, especially the reduction in atmospheric humidity, will dramatically affect the performance of individual epiphytes, and, therefore, their population dynamics (Benzing 1990; Zotz *et al.* 2010). However, there are few studies that have directly documented the potential effect of climate change on epiphyte populations. Benzing (1998) reviews the importance of epiphytes for ecosystem functioning in tropical rain forests and discusses

their vulnerability in the face of climate change. He suggests that looking at the responses of epiphytes in terms of water content and carbon balance may account for their susceptibility to climate change. Although many epiphytes show CAM metabolism, temperatures a few degrees above the nocturnal optimum result in tissue desiccation or increase the saturation deficits in surrounding air masses, which reduces stomatal conductance and, therefore, CO_2 availability for photosynthesis (Benzing 1998). Additionally, high temperatures, high evaporative demands and nutritional stress, as well as excessive exposition to solar radiation, tend to promote CAM-idling, a variation in CAM metabolism in which the CO_2 produced by mitochondrial respiration becomes the only carbon source for photosynthesis, which implies that plants may survive, but not grow.

It is estimated that global climate change will result in a decrease in the incidence of fog in mountainous areas. Nadkarni & Solano (2002) investigated the potential effect of this decrease on the survival and growth of epiphytes, and observed that under drier atmospheric conditions there is higher leaf mortality, and lower leaf longevity and production. These environmental conditions may eventually result in the death of many epiphytes, thus driving a radical change in the composition and dynamics of the canopy community. Zotz *et al.* (2010) arrived at a similar conclusion, observing that among the environmental factors that may shift due to climate change, *i.e.* increased CO_2 and nutrient availability, and decreased atmospheric humidity, the latter may have the most dramatic effect on epiphyte communities, especially those from mountainous areas. A change in atmospheric temperature may produce a shift in the altitude at which clouds and fog are formed. Since atmospheric humidity is the main water source for many epiphytes, these alterations will have a dramatic effect on the distribution and abundance patterns of epiphytes. Hsu *et al.* (2012), in their paper about the simulation of the effects of climate change on a subtropical island in East Asia by year 2100 suggested that, as the distribution of epiphytes is strongly associated with particular forests types, epiphytes will shift to higher altitudes, *ca.* 400 m higher than their current distribution; as a result, epiphytic species are projected to lose 45-58 % of their current range due to global warming, with the consequent changes in spatial patterns of epiphyte richness. The belt of maximum richness is projected to shift to altitudes *ca.* 500 m higher than its current location. The

epiphytic species that are predicted to be most sensitive to climate change are those with a narrow distribution, or with a high sensitivity to temperature.

Regarding land-use change and habitat loss, several studies have demonstrated that epiphyte abundance and diversity have decreased due to the impact of human activities on the forests they inhabit; the severity of this impact depends on the type and magnitude of the disturbance, as well as on the type and structure of the vegetation cover replacing the original habitat (Adhikari *et al.* 2012; Hietz 1999; Köster *et al.* 2009, 2011; Wolf 2005). However, other evidence contradicts these reports. For instance, Hietz (2005) states that epiphyte diversity in coffee plantations under the shade of secondary vegetation is similar to that of primary forests; and Larrea & Werner (2010) found that epiphyte richness was equivalent in a mature forest, a forest cleared for cattle grazing, and in isolated remnant trees surrounded by pastures. However, the latter evidence is not conclusive, as it is based on observations carried out during relatively short time periods after disturbance, and many epiphytes may withstand long periods under stressful conditions before dying. On the other hand, there are some reports stating that richness, density and biomass of epiphytes increase with time in altered ecosystem (Benavides *et al.* 2006; Köster *et al.* 2009; Woods & DeWalt 2013), although there seems to be a dynamic species turnover after a disturbance, the mesic species (*e.g.,* Pteridophyta, Orchidaceae, Araceae) being substituted by more xerophytic ones (*e.g.,* Bromeliaceae, Cactaceae, Piperaceae) (Cascante-Marín *et al.* 2006; Padmawathe *et al.* 2004; Werner 2011; Werner & Gradstein 2008). A particular kind of disturbance is selective logging, which has been shown to decrease the abundance and species richness of vascular epiphytes (Wolf 2005). Obermüller *et al.* (2012) found that trees species that are more actively logged tend to bear a larger epiphytic load; according to their results, the preferred logged species hosted on average three times more epiphyte species per tree than other randomly selected trees, showing that a substantial portion of the local floristic richness may be lost due to logging.

The change in epiphyte species diversity and composition after a disturbance has been associated with two processes: dispersal constraints and alteration of microclimatic conditions. Regarding dispersal, it is believed that the epiphytic community is a reflection of the

abundance and composition of the propagule rain, which is in turn a function of seed production by each species (Yeaton & Gladstone 1982) in combination with the effectiveness of their dispersal means. In species whose seeds are dispersed by animal vectors, the seed dispersal curve may be dramatically affected by the spatial configuration and characteristics of the habitat patches remaining after the disturbance (del Castillo & Pérez-Rios 2008; Flores-Palacios & García-Franco 2003; Hietz 1999). In many orchids, the effect of fragmentation may also be noted on the dynamics of pollination, since the abundance and behavior of many insect pollinators may be altered (Parra-H. & Nates-Parra 2007; Powell & Powell 1987). Regarding the changes in micro-climatic conditions, disturbances frequently result in higher solar radiation, temperature and wind velocity, as well as lower humidity compared to the original conditions. The latter may result, again, in a gradual replacement of the mesic species by more xerophytic ones (Cascante-Marín et al. 2006; Padmawathe et al. 2004; Werner & Gradstein 2008; Wolf 2005). The rate at which these changes may take place also depends on the rate at which new potential phorophytes are colonized. Apparently, the recolonization rate in disturbed montane habitats is rather slow, and, therefore, the resulting epiphyte communities differ substantially from the original ones (Nadkarni 2000). However, recolonization rate in a shaded coffee plantation is relatively higher, thus the diversity of vascular epiphytes in such habitats may be recovered (Toledo-Aceves et al. 2012a).

The impact of habitat disturbance and loss on the extinction of epiphyte populations may be exacerbated in the case of rare, endangered or narrowly endemic species, as is the case of some orchids that have been reported from only one or two localities (Koopowitz et al. 1993; Roberts & Wilcock 2005).

Several measures may be taken to prevent the loss of epiphyte diversity in human-modified habitats. Wolf (2005) recommends allowing the persistence of the largest trees in sites where selective logging is practiced. These large trees tend to accumulate canopy soil (i.e., the mantle of death organic matter that collects on tree branches, derived from decaying epiphytes, decomposing tree bark, insect frass and intercepted litter) that some epiphyte species require, and serve as propagule sources for the colonization of new phorophytes. However, Padmawathe et al. (2004) sustain that the persistence of large trees is not enough to

ensure epiphyte conservation, as selective extraction alters the microclimatic conditions of the forest resulting in changes in species composition within the epiphytic community. As an alternative, they suggest preserving non-exploited patches within a matrix of exploited forest.

In sites with high disturbance levels due to land use change, the maintenance of agroforestry systems such as coffee or cacao plantations, where cultivated species are interspersed with native trees, favors the presence of a complex habitat with a variety of microenvironmental conditions. This type of productive systems allows the coexistence of different animal species, as well as a diverse array of potential phorophytes, which favors the persistence of epiphytic species with different ecophysiological requirements (Haro-Carrión et al. 2009; Hietz 2005; Scheffknecht et al. 2012; Solis-Montero et al. 2005; Sosa & Platas 1998); yet a species turnover process appears to take place after disturbance, with mesic species being replaced by more xeric ones due to changes in microclimatic conditions and an increase in herbivore pressure (Scheffknecht et al. 2012). In contrast, when forests are turned into grasslands, the potential habitat for epiphytes virtually disappears. In these cases, the presence of large remnant trees may become of paramount importance, as they can function as local refuges for epiphytes and future propagule sources during secondary succession (Hietz 1999; Köster et al. 2011). However, in remnant trees epiphyte mortality is high, relative growth rates are low, and the establishment rate of mesic species decreases substantially, which results in a loss of epiphyte diversity and the dominance of a few species that are tolerant to dryer conditions. Also, some tree species are much more efficient as epiphyte refuges than others, indicating that care should be taken when choosing the trees to be left standing during the activities leading to land use change (Köster et al. 2009; Lõhmus & Lõhmus 2010; Werner 2011; Werner & Gradstein 2008).

Another threat faced by epiphytes is plant extraction by collectors, the species in the Orchidaceae, Bromeliaceae and Araceae being the most affected (Flores-Palacios & Valencia-Díaz 2007; Hernández-Apolinar 1992; Mondragón & Villa-Guzmán 2008). The extraction of epiphytes for trade in European markets has been occurring since the first exploratory trips to the New World. Since then, the collection of epiphytic plants to adorn the gardens of the Old World has been a constant pressure to natural epiphyte populations

(Benzing 1990; Rauh & Rauh 1992). In addition, many local peoples have traditionally used some epiphytes as ornaments, medicine, food or fodder, as well as for fiber extraction and as religious offerings (Acebey *et al.* 2010; Flores-Palacios & Valencia-Díaz 2007; García-Soriano 2003; Haeckel 2008; Hernández-Apolinar 1992; Mondragón & Villa-Guzmán 2008; Salazar-Rojas *et al.* 2007; Thomas *et al.* 2011). In general, adult reproductive individuals are the targets of these collections (Guess & Guess 2002; Haeckel 2008; Hernández-Apolinar 1992; Mondragón & Villa-Guzmán 2008), which is demographically threatening as most epiphytic populations that have been studied demographically show that the survival of large reproductive individuals is highly relevant for population persistence (Mondragón 2009; Mondragón & Ticktin 2011; Winkler *et al.* 2007; Zotz *et al.* 2005).

It is thought that some natural populations of epiphytes have been driven to local extinction by excessive plant collection, while others have been substantially depleted. However, only a few studies have directly documented the impact of plant collection on epiphytic populations. One such study was carried out by Hernández-Apolinar (1992), who evaluated the population growth rate (λ) in two populations of the orchid *Laelia especiosa*, one subjected to plant collection (λ = 1.17) and another one with no extraction (λ = 1.32). Also, Mondragón (2009) evaluated the extinction probabilities of a population of the orchid *Guariante aurantica* under different collection intensities, and estimated that it would be drawn to extinction over the next 80 years if more than 5 % of adult individuals were collected each year.

Several measures have been taken to regulate the international and local trade of threatened species (*e.g.*, CITES) but the illegal trade of epiphytes is still high (Flores-Palacios & Valencia-Díaz 2007; Haeckel 2008; Solano *et al.* 2010). In the case of threatened bromeliads, two strategies have been proposed to reduce the effect of such collection pressure and to simultaneously allow for a sustainable exploitation of these species: limiting the collection of individuals to those that have naturally fallen from their host trees (Mondragón & Ticktin 2011), and extracting only from dense populations (< 9000 large plants ha^{-1}) with an even-sized structure, and only individuals established in the lower canopy (Wolf & Konings 2001).

Conclusions and perspectives

Epiphytes are a diverse plant group, not only taxonomically, but also in relation to their population ecology. The published literature on the subject reveals the existence of a host of reproductive, demographic and survival strategies among epiphytes. In relation to breeding systems, epiphytes may show from complete selfing (more frequent in monocarpic than in polycarpic species) to complete outbreeding. Cross-pollination is clearly favored in some species, although most epiphytes appear to retain the possibility for selfing.

Seed dispersal in epiphytes, along with their characteristic habitat occupancy patterns and relationships with their phorophytes, are responsible for the neat applicability of the meta-population concept to epiphytes. Despite the fact that this subject is of relatively recent development among plants, it has already been the focus of a number of interesting studies. It will no doubt keep on providing helpful insights, especially in the context of epiphyte conservation, which is a rapidly expanding field given the particularly high vulnerability of epiphytes to habitat loss.

The use of matrix modeling for epiphyte demographic analyses has proven successful given their versatility and adaptability to the complex life cycles of many epiphytes. An increasing number of epiphytic species are being studied under this approach, showing again that epiphytes are highly diverse and draw on a great variety of demographic strategies. Although epiphytes have patent physiological and morphological adaptations that allow them to successfully exploit the epiphytic habitat, our review has revealed that their demographic behavior does not allow an unambiguous identification of particular demographic traits that are exclusive to epiphytes. Furthermore, the two plant families from which most demographic studies on epiphytes have come from (*i.e.,* bromeliads and orchids) are not easily distinguished in relation to their population ecology.

Several subjects need to be addressed for us to deepen our understanding of epiphyte population ecology. First of all, a much larger number of species and from a larger array of plant families should be studied, as the available information is still quite limited considering the high number of

epiphytic species that have been described. The population genetics aspects of epiphyte populations have barely been explored. Also, although there is information about the incidence of CAM metabolism among epiphytes (Zotz 2004b), little is known about its activation process and timing, which is important to understand the dynamics of the early stages of plant development. Related to the latter, the role of mycorrhizal fungi in increasing seedling survival probability in orchids, and in general the ecological requirements for the establishment of epiphyte seedling is still to be investigated. Similarly, the fate of dispersing seeds and the relevance of long-distance seed dispersal for metapopulation dynamics is an exciting subject still awaiting analysis. Hopefully future studies on these subjects will complement the available information on epiphyte population ecology to offer an ever clearer outlook of the conservation issues associated with this interesting plant group.

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Appendices

Appendix A

Meta-analyses for the section on Breeding Systems

Two of the indices reported in Table 1 (AI and ISI) were subjected to a meta-analysis to test whether there is an effect of plant family on their value. The meta-analyses were ran with the Metafor package (in R), using the *rma* function. We used a mixed-effects model in which the independent variable was "Family" and the response variable was the index in question. The indices tested were the autogamy index (*AI*, the ratio between the percentage of fruits produced in the autonomous pollination treatment and the cross pollination treatment) and the self-incompatibility index (*ISI*, the ratio between the percentage of fruits produced in the selfing pollination treatment and the cross pollination treatment), which were the only variables in Table 1 for which enough data was available to run a meta-analysis. These response variables were given specific weights depending on the number of individuals used for their calculation (obtained from the relevant references); the weighting factor was the variance, obtained as $v = 1/(N - 3)$.

The independent variable, "Family", had only three levels: Bromeliaceae (with three species), Gesneriaceae (with five species) and Orchidaceae (with 69 species). The rest of the families did not have enough data as to be included in the analyses; also some of the species in these three families listed in Table 1 were left out of the analyses given the lack of data.

The response variables were tested for normality prior to the meta-analysis. The normality test used was the Lilliefors (an adaptation of the Kolmogorov-Smirnov test). For these analyses, the data were normalized using the transformation arcsin ($\sqrt{AI}$) and arcsin ($\sqrt{ISI}$).

The analyses were carried out by fitting two models to the data: a complete model which included the factor "Family", and another one that excluded it. The two models were evaluated using the Akaike information criterion (AIC) and given a relative likelihood value. The difference between the two models (which in this case evaluates the relevance of the factor "Family" in accounting for the variation observed in the response variable) was evaluated using the likelihood ratio test (LRT), from which the *P*-values were computed.

Appendix B

Meta-analyses for the section on Demography and Population Dynamics

Several meta-analyses were performed using some of the demographic data reported in Table 4 and A1 (the latter in Appendix C). As before, the meta-analyses were ran with the Metafor package (in R), using the *rma* function.

The first set of analyses tested the effect of the independent variable "Family" (Bromeliaceae and Orchidaceae) on the response variables λ, Q_s (seeling mortality) and *OPSI* (Observed Population Structure Index). We used a mixed-effects model. The response variables were given specific weights depending on the number of individuals used for their calculation (obtained from the relevant references); the weighting factor was the variance, obtained as $v = 1/(N - 3)$. Response variables were transformed for normality. The transformations used were exp (λ), arcsin($\sqrt{Q_s}$), and arcsin($\sqrt{OPSI}$), which fulfilled the normality criterion (Lilliefors test). Two models were fited to the data: a complete model including the factor "Family", and a second model that excluded it. The Akaike information criterion (AIC) and a relative like-lihood value were calculated for each model. The difference between the two models (which in this case evaluates the relevance of the factor "Family" in accounting for the variation observed in the response variables) was evaluated using the likelihood ratio test (LRT), from which *P*-values were computed.

The second set of analyses tested the association between different continuous variables (λ *vs. HI*, λ *vs. EF*, *HI vs. EF* - abbreviations as in Appendix C). The same type of procedure was followed as described in the previous paragraphs.

Appendix C

The Principal Component Analysis for the section on Demography and Population Dynamics

A Principal Component Analysis (PCA) was carried out to explore the relationships between the different demographic variables measured and reported in the literature from epiphyte populations. The variables included in the analysis were the following:
Descriptive/grouping variables:

Plant family – Four different plant family tags were used to distinguish between bromeliads (B),

orchids (O) and two additional groups which were incorporated for the sake of comparison: Agavaceae (two populations of *Agave marmorata*; Jiménez-Valdés *et al.* 2010), and terrestrial bromeliads (a population of *Aechmea magdalenae*; Ticktin *et al.* 2002).

Species - An abbreviation of the species name (and population number, when relevant) was included in the data base to identify the different populations in the output graphs (following the nomenclature given in Table 4).

Variables for analysis (detailed in Table 4 and Table A1):

Categories (*Cat*) - Number of size categories used to build population projection matrices. This number was multiplied by 0.1, to scale its value to a range comparable to the other variables. Thus, it ranged from 0.4 to 1.2.

Habitat Index (*HI*) - It aims to describe the relative harshness (in terms of atmospheric humidity) of the habitat where a species was studied. Of course, within the same habitat water availability may vary from one microsite to another, and even within the crown of the same tree; however, we intended this index as a general guideline to assess the relative benignity or hashnes of the habitat. Its value was assigned subjectively on a scale from 0 to 1 based on the vegetation type at the study site; the most humid environments (*i.e.*, tropical cloud forest) were assigned a value of 1, and the driest environments were given the lowest values (xerophytic shrubland, *HI* = 0.3). The remaining vegetation types were tropical rain forest in very humid areas (*HI* = 0.95), other tropical rain forest (*HI* = 0.9), temperate forest (*HI* = 0.8), temperate dry forest (*HI* = 0.6), tropical sub-perennial forest (*HI* = 0.5), electric cables near a subperennial dry forest (*HI* = 0.45), and tropical seasonally dry forest (*HI* = 0.4).

Projected population growth rate (λ) – It refers to the asymptotic population growth rate, λ, obtained from matrix analyses. For some species there were several λ values, either obtained from populations at different locations, or the same population during different time periods (marked in Table 4 with different subindex numbers associated with species names).

Observed Population Structure Index (*OPSI*) - With values ranging between 0 and 1, obtained as the size category with the largest number of individuals divided by the total number of size categories in which the population was subdivided. For instance, if the population was subdivided in 7 size categories (the smallest individuals being in category 1 and the largest in category 7), and size

category 5 was the one with the largest number of individuals in the observed population structure, then *OPSI* = 5/7 = 0.71. The value of *OPSI* approached unity in the populations dominated by larger individuals, and it approached cero in populations with a high proportion of small individuals.

Projected Population Structure Index (*PPSI*) - Similar to OPSI, but obtained from the stable size distribution (right eigen-vector) of the population projection matrix.

Reproductive Value Index (*RVI*) - Similar to *OPSI* and *PPSI*, but obtained from the vector of the size-specific reproductive values (left eigen-vector) of the population projection matrix. The value of *RVI* was 1 when the size category with the highest relative reproductive value was the largest one.

Elasticity of Fecundity (*EF*) - Summed elasticity for all the fecundity entries from a given population projection matrix.

Elasticity of Growth (*EG*) - Summed elasticity for all the growth entries from a given population projection matrix. It includes clonal spread, when this process was explicitly incorporated in a matrix.

Elasticity of Stasis (*ES*) - Summed elasticity for all the stasis and retrogression entries from a given population projection matrix.

Mortality of seedlings (Q_s), *medium-sized individuals* (Q_m) *and large individuals* (Q_l) - Proportion of seedlings (first size category in a matrix), medium-sized individuals (non reproductive categories, with the exception of seedlings), and large individuals (with reproductive potential) dying from one year to the next.

Mean Fecundity (*F*) - Mean fecundity value (in seedling units) obtained by averaging the fecundity entries of all the reproductive categories in a matrix.

The PCA incorporated these 13 variables for each species/population (see Tables 4 and A1). The main result of the PCA is an ordination bi-plot in which species/populations are represented as dots located in a two-dimensional space (Fig. 2). Dots located close to each other are demographically more similar than dots located further apart (Fig. 2b). In addition to the latter, different vectors, representing each variable included in the analysis, may be depicted in the two-dimensional space. The direction of each vector represents the way the relevant variable correlates with the two principal components (proxy variables, created by the analysis), which are in turn represented by the two axis of the bi-plot. Vector size represents the strength of the correlation (Fig. 2a).

Table A1. List of the epiphyte species/populations included in the Principal Component Analysis. Species names with different subindices correspond to populations at different sites; or, when marked with *, to different time periods for the same population. Only the variables omitted from Table 4 are shown. Nomenclature as follows: *HI* = habitat index; *Cat* = number of categories in which the populations were subdivided (times 0.1); *PPSI* = projected population structure index, *RVI* = reproductive value index; Q_m = mortality rate for medium-sized, and Q_l = for large individuals. See Appenndix C for a fuller description of variables. References are detailes in Table 4.

Species	Habitat	IE	Cat	PPSI	RVI	q_m	q_l
External groups							
Agave marmorata$_1$ (Agavaceae)	Xerophytic shrubland	0.3	1.2	0.08	1	0.064	0.108
Agave marmorata$_2$ (Agavaceae)	Xerophytic shrubland	0.3	1.2	0.08	1	0.088	0.118
Achmea magdalenae							
(terrestrial bromeliad)	Tropical rain forest	0.9	0.7	0.71	1	0.281	0.276
Bromeliaceae							
Catopsis compacta$_1$*	Temperate (oak) dry forest	0.5	0.5	0.4	1	0.0855	0.055
Catopsis compacta$_2$*	Temperate (oak) dry forest	0.5	0.5	0.6	1	0.143	0.100
Catopsis compacta$_3$*	Temperate (oak) dry forest	0.5	0.5	0.6	1	0.173	0.429
Catopsis sessiliflora	Montane moist forest	1	0.5	0.2	1	0.35	0.10
Tillandsia brachycaulos$_1$ *	Tropical dry forest	0.5	1.1	0.64	1	0.495	0.937
Tillandsia brachycaulos$_2$ *	Tropical dry forest	0.5	1.1	0.64	0.91	0.491	0.688
Tillandsia brachycaulos$_3$ *	Tropical dry forest	0.5	1.1	0.64	0.91	0.394	0.582
Tillandsia carlos-hankii$_1$	Temperate (pine-oak) forest	0.6	0.5	0.6	1	0.070	0.090
Tillandsia carlos-hankii$_2$	Temperate (pine-oak) forest	0.6	0.5	0.4	1	0.125	0.074
Tillandsia deppeana	Montane moist forest	1	0.5	0.4	1	0.28	0.35
Tillandsia flexulosa	Electric cables (in Panama)	0.4	0.4	0.25	1	0.08	0.13
Tillandsia imperialis$_1$ *	Low montane cloud forest	1	0.8	0.87	1	0.0464	0.0415
Tillandsia imperialis$_2$ *	Low montane cloud forest	1	0.8	0.75	0.62	0.0734	0.0585
Tillandsia juncea	Montane moist forest	1	0.5	0.2	1	0.26	0.04
Tillandsia macdougallii	Temperate (pine-oak) forest	0.6	0.6	1	1	0.180	0.077
Tillandsia makoyana	Tropical dry forest	0.4	0.6	0.17	1	0.6	0.52
Tillandsia multicaulis	Montane moist forest	1	0.5	0.2	1	0.27	0.09
Tillandsia punctulata	Montane moist forest	1	0.5	0.6	1	0.29	0.16
Tillandsia recurvata	Xerophytic shrubland	0.3	0.4	0.25	1	0.126	0.104
Tillandsia violaceae	Temperate (pine-oak) forest	0.6	0.6	0.66	1	0.093	0.113
Werauhia sanguinolenta$_1$	Tropical rain forest	0.9	0.7	0.14	1	0.25	0.125
Werauhia sanguinolenta$_2$	Tropical rain forest	0.9	0.7	0.14	1	0.225	0.11
Werauhia sanguinolenta$_3$	Tropical rain forest	0.9	0.7	0.14	1	0.42	0.236
Werauhia sanguinolenta$_4$	Tropical rain forest	0.9	0.7	0.14	1	0.23	0.145
Orchidaceae							
Artorima erubecens	Temperate forest	0.8	0.6	0.66	0.33	0.343	0.14
Aspasia principisa	Tropical rain forest	0.9	0.7	0.86	0.92	0.11	0.09
Enciclia chacaoensis	Tropical rain forest	0.95	0.4	0.5	1	0.125	0.06
Erycina crista-galli$_1$	Tropical rain forest	0.9	0.4	1	1	0.644	0.45
Erycina crista-galli$_2$	Tropical rain forest	0.9	0.4	0.75	1	0.617	0.54
Guarianthe aurantiaca	Tropical rain forest	0.9	0.5	1	1	0.102	0.049
Jacquiniella leucomelana	Montane moist forest	1	0.4	0.25	1	0.237	0.174
Jacquiniella teretifolia	Montane moist forest	1	0.4	0.5	1	0.125	0.152
Laelia speciosa	Temperate dry forest	0.6	0.4	0.5	1	0.15	0.084
Lepanthes caritensis$_1$	Tropical rain forest	0.9	0	0.75	1	0.037	0.005
Lepanthes caritensis$_2$	Tropical rain forest	0.9	0	0.75	1	0	0.0035
Lepanthes eltoroensis	Tropical rain forest	0.9	0.4	0.75	1	0.008	0.0085
Lepanthes rubripetala	Tropical rain forest	0.9	0.4	1	1	0.04	0.03
Lycaste aromatica	Montane moist forest	1	0.4	1	1	0.136	0.046
Pleurothallis quadrifida	Tropical rain forest	0.95	0.5	0.6	1	0.02	0.026
Tolumnia variegata	Tropical dry forest	0.5	0.4	0.5	1	0.18	0.13