



Vascular epiphytes in the temperate zones – a review

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Abstract

Vascular epiphytes are typically associated with tropical rainforests, whereas their occurrence in temperate forests is little appreciated. This review summarises the available information on epiphytism in the temperate zones ($> 23.5^\circ$ latitude), which has not been reviewed comprehensively for more than a century, and critically analyses the proposed mechanisms behind the observed biogeographical patterns. Although in the temperate zone epiphytic vascular plants are rarely as impressive as in tropical forests, there are noteworthy exceptions. Temperate rain forests of Chile and New Zealand, or montane forests in the Himalayas are comparable to many tropical forests in terms of epiphyte biomass and diversity, but differ in their taxonomic spectrum: temperate epiphyte communities are generally dominated by ferns and fern-allies. Other temperate areas are not, however, necessarily barren of epiphytes, as repeatedly implied. Quite in contrast, local populations of epiphytes in a large number of other non-tropical areas in both the southern and the northern hemisphere can be quite conspicuous. The proposed reasons for the latitudinal gradients in epiphyte abundance and diversity (water scarcity or low temperatures) are not fully convincing and, moreover, still await experimental verification. Other factors, both historical (e.g., Pleistocene extinctions) and ecological (e.g., prevalence of conifers in the northern hemisphere), should also be taken into consideration to obtain a comprehensive explanation of the extant global distribution of vascular epiphytes.

Introduction

A latitudinal gradient in diversity with a maximum in the tropics characterises most groups of organisms (Ricklefs and Schluter 1993). The trend can be very steep in some cases. Vascular epiphytes, in particular, seem so tightly associated with the wet tropics, that definitions of tropical rain forests frequently include the presence of this growth form (e.g., Richards 1996; Schimper 1903; Webb 1959). Local diversity can be impressive: in tropical montane forests species numbers of the canopy-based flora sometimes outnumber the sum of all other plant life-forms (Kelly et al. 1994). North and south of the tropics, however, there

is a steep decline in epiphyte abundance and diversity. Not surprisingly then, reviews of vascular epiphytism (e.g., Benzing 1995; Gentry and Dodson 1987; Lüttge 1989b; Nieder and Barthlott 2001; Zotz and Hietz 2001) mention vascular epiphytes outside the tropics only very briefly. Moreover, many of these reviews suffer from a north-temperate bias. For example, holarctic *Polypodium* species were called the *only* vascular epiphytes in the temperate climate by Lüttge (1989a) and Nieder and Barthlott (2001), thus ignoring the rich epiphyte floras of, e.g., New Zealand or Chile (for a critique of this bias from a southern hemisphere perspective compare, e.g., Dawson 1980). The most in-depth treatment of vascular epiphytes in

the temperate zones is still Schimper's seminal monograph (1888), in which he described the global occurrence of vascular epiphytes and also tried to identify the mechanisms behind latitudinal trends.

The observation that the epiphytic habit among temperate vascular plants is most prevalent in oceanic climates characterised by relatively high humidity and few incidences of frost has prompted two principal explanations for the global pattern described above, both of which are based on *current* ecological conditions. While Schimper (1888) stressed low water availability in the temperate zones, Benzing (1990) and others (e.g., Ellenberg 1988; Nieder and Barthlott 2001) emphasised the importance of frost. Other explanations, e.g., the possibility that Pleistocene extinctions have led to a currently unsaturated 'epiphytic niche', biotic interactions with potential host trees, and/or biogeographical considerations, e.g., the effect of distance to potential (tropical) source areas, are rarely discussed in the literature (but see Dawson 1986; Gentry and Dodson 1987; or Khullar 1981).

In summary, our understanding of the global occurrence and ecology of temperate-zone vascular epiphytes may be even more biased and fragmentary than our knowledge of tropical species. Hence one of the principal goals of this review is to provide a stimulating basis for future research with temperate epiphytes. To achieve this end, this review will – for the first time in more than a century – provide a comprehensive compilation of the information on vascular epiphytes outside the tropics, that is beyond 23.5° north and south. Secondly, based on the available information and on previous hypotheses given in the literature, it will discuss the possible mechanisms leading to the observed global distribution (for a complete bibliography on vascular epiphytes in the temperate zones see Zotz 2003).

A definition of 'epiphyte'

Epiphytism grades into the soil-rooted habit. Many epiphytes grow occasionally on rocks or soil as long as competition by terrestrial plants is low (e.g., Dawson 1988). Similarly, many terrestrial plants may grow occasionally on living substrate as 'accidental epiphytes' (Zotz and List 2003). A formal distinction between obligate epiphytes (> 95% of all individuals of a species in a particular region are growing epiphytically), accidental epiphytes (> 95% of all

individuals in a region are growing terrestrially), and facultative epiphytes (proportions between these two extremes) was introduced by Ibisch (1996). Obligate epiphytes are also called 'true', 'typical' or 'holo-epiphytes'. This review will focus on holoepiphytes, and in the following 'epiphyte' will be used in this sense.

Vascular epiphytism in the temperate zones

The pronounced asymmetry in the latitudinal trend from the tropics to the two temperate zones was first noted more than a century ago by Schimper (1888) and has also been discussed by Gentry and Dodson (1987) and Benzing (1990). For example, while there are just two species of epiphytes in Caverns State Park in USA (30° N), there are 15 such species in Puyehue National Park in Chile (41° S) (Gentry and Dodson 1987). The diverse epiphyte floras of southern Chile and New Zealand include many taxa with tropical affinities, but also a number of temperate elements. Autochthonous development is indicated, for example, by the frequent occurrence of monotypic taxa, e.g., the epiphytic grass genus *Microlaena* of New Zealand, the fern genus *Synammia* of Chile, as well as genera like *Griselinia* (Griselinaceae) or *Luzuriaga* (Smilacaceae), which are restricted to Chile and New Zealand (Dawson 1966). The most diverse region in respect to vascular epiphytes in the north-temperate zone is the Himalayas (Schimper 1888), but locally abundant epiphyte populations can also be found in temperate East Asia (Kolbeck 1995; Miyawaki and Nakamura 1988; Ohwi 1965), the Caucasus (Derzhavina and Shorina 1992), Central Europe (Zotz 2002), the British Isles (Rübel 1912; Tansley 1939), several Atlantic islands (Bennert et al. 1992; Page 1977), and Northwest North America (Sillett 1999; Sillett and Bailey 2003).

Temperate Australasian region

Vascular epiphytes are a regular, albeit not very conspicuous, component of rainforests in Tasmania (Jarman and Kantvilas 1995; Jarman et al. 1986) and temperate Australia (Herbert 1960; Webb 1959). New Zealand, however, is much more noteworthy for its rich epiphyte flora. In-depth treatments of New Zealand epiphytes can be found in Oliver (1930), Dawson (1988), and Dawson and Sneddon (1969). Epiphyte richness is greatest in damp podocarp forests (for climate data compare Table 1), but a few

Table 1. Synopsis of climate data from representative climate diagrams (Walter and Lieth 1967) from temperate regions with vascular epiphytes. Given are mean annual temperature (MT, in °C), number of month with minimum temperatures < 0 °C (F), annual precipitation (AP, in mm), and number of dry months (DS).

Region	MT	F	AP	DS
Atlas	14	2-8	400-800	4
Ireland	10-12	1-6	> 1000	0
Eastern Himalayas	13-18	3-5	> 1000	2-5
Japan	15-18	several	1000-2900	0
South Africa, western region with summer rain	12-17	3-5	800-1300	0-5
Valdivia region, Chile	12	0	2700	0
NSW Tasmania	13-14	0-3	> 1000	0
New Zealand	10-15	0-10	> 1000	0
Northwest USA	10	0-9	> 1000	0

species (e.g., the orchid *Earina mucronata*) may also extend into drier, more open forests. Oliver (1930) lists 50 species of 'typical' epiphytes, corresponding to c. 2% of the total flora of New Zealand. Locally, however, epiphytes may account for a much higher proportion of the vascular flora. For example, the epiphytic habit is represented by 22 species (= 13% of all vascular plants) at Mt Karioi, North Island (37° S) (Clayton-Greene and Wilson 1985), by 32 species (= 12%) in the Kaitake range of Egmont National Park (39° S) (Clarkson 1985) or even 20% of all species in the Maungataniwha Ranges (35° S) (35 of 174 species, Dawson and Sneddon 1969). In contrast to the tropics, but similar to all other temperate epiphyte floras, ferns and fern-allies represent a much higher percentage of the total diversity, typically about 70% (Table 2). Another difference compared to typical epiphyte communities in the tropics (compare, e.g., Nieder et al. 2000, Zotz et al. 1999) is the large percentage of accidental epiphytes. For example, in a New Zealand *Nothofagus* forest only 14 of the total 55 species growing epiphytically were obligate epiphytes (Hofstede et al. 2001).

The geographic origin of the New Zealand flora is discussed in detail by Dawson (1986). He proposed that most taxa with epiphytic habit evolved during the Tertiary, when rain forests were widespread in mid-latitudes of both hemispheres. In contrast to their northern counterparts, they survived Pleistocene glaciations in refugia available due to New Zealand's narrow landmass, which provided a strongly oceanic climate. New Zealand's rainforests not only harbour a large number of vascular epiphytes, but also share many other features with tropical rainforests, for example, special growth habits such as lianas, tree ferns, palms, and strangling hemi-epiphytes (Dawson

1988). Another striking feature are epiphytic *Collospermum* and *Astelia* species (Liliaceae) with water-impounding foliage, analogous to many Neotropical bromeliads.

Temperate South America

The epiphyte flora of Argentina has already been covered in some detail by Schimper's (1888) classic monograph (see also, e.g., Drehwald 1995). There are a number of epiphytic taxa restricted to temperate South America, for example the fern genus *Synammia* and the monotypic genus *Pfeifferia* (Cactaceae), although most species have unambiguous tropical affinities. Classic studies on the vegetation of Chile include Schmithüsen (1956) and Oberdorfer (1960). Although neither monograph is focussed on epiphytes, Oberdorfer (1960), in particular, provides detailed species lists of the moist, epiphyte-rich *Nothofagus* forests of southern Chile (39 – 43° S). These 'Valdivian rain forests' (compare Table 1) are especially noteworthy for their epiphytes, but a few ferns (*Grammitis magellanica* and *Hymenophyllum* spp.) can be found as far south as Tierra del Fuego (growing on trunks of *Nothofagus* and *Drymis*, compare Moore 1983). Near Valdivia, epiphytes account for c. 10% of all vascular plants (Arroyo et al. 1995; Oberdorfer 1960). As with the flora as a whole (Arroyo et al. 1995), there are a large number of endemic epiphytes. This high degree of endemism is probably the result of long-lasting isolation, but also due to the fact that refugia near the ocean or farther north were available during times of glaciation in the south (reaching only 42 °S, Arroyo et al. 1995). Like New Zealand's rain forests, the tropical aspect of the vegetation is further intensified by the occurrence of

Table 2. Proportion of major taxonomic groups among the total number of vascular epiphyte species in the temperate zones and the tropics (only moist and wet tropical forests are included). (O = Orchidaceae, F = ferns (including fern-allies), B = Bromeliaceae, A = Araceae, P = Piperaceae, E = Ericaceae). Presented are total species numbers (T) and percentages for each taxon per region/country, and the averages (SD) for all temperate and tropical entries, respectively.

Country or region	Vegetation type	total	O%	F%	B%	A%	P%	E%	source	comments
Rio Palenque, Ecuador	lowland	238	34	12	8	15	8	1	(Dodson and Gentry 1978, Gentry and Dodson 1987)	
Barro Colorado Island, Panama	lowland	186	44	22	10	16	5	0	(Croat 1978, Zotz and Ziegler 1997)	
La Selva, Costa Rica	lowland	368	30	18	8	22	3	0	(Ingram et al. 1996)	only holocpiphytes
Surumoni, Venezuela	lowland	36	50	25	6	6	3	0	(Nieder et al. 2000)	
Bafou, Cameroon	lowland - 800 m a.s.l.	44	68	30	0	2	0	0	(Sonke et al. 2001)	
Nimba, Liberia	submontane, 800 - 1300 m a.s.l.	153	66	25	0	1	2	0	(Johansson 1974)	
montane rainforest, Zaire	montane, c. 900 m a.s.l.	106	55	39	0	0	3	0	(Biedinger and Fischer 1996)	
Tjibodas, Java	montane, c. 1400 m a.s.l.	100	40	20	0	0	4	8	(Went 1940)	
Monteverde, Costa Rica	montane, c. 1500 m a.s.l.	256	36	22	9	5	5	4	(Ingram et al. 1996)	
Omitemi, Mexico	montane, c. 2000 m a.s.l.	54	54	15	7	2	7	0	(Meave et al. 1992)	
Cajunuma, Ecuador	montane, c. 2900 m a.s.l.	104	46	32	6	3	2	3	(Bøgh 1992)	only holocpiphytes
La Carbonara, Venezuela	montane, c. 2300 m a.s.l.	181	52	31	6	4	6	1	(Engwald 1999)	only holocpiphytes
Reserva Otonga, Ecuador	montane, 1700 - 2200 m a.s.l.	127	41	28	6	12	2	8	(Nowicki 2001)	only holocpiphytes
Rio Gujalito, Ecuador	montane, 1800 - 2200 m a.s.l.	122	57	22	10	3	2	4	(Rauer and Rudolph 2001)	only holocpiphytes
Reserva Biologica S. Francisco, Ecuador	montane, 1800 - 2100 m a.s.l.	340	45	25	14	6	4	1	(Bussmann 2001)	
Reserva Biologica S. Francisco, Ecuador	montane, 2100 - 2450 m a.s.l.	283	54	23	11	4	4	2	(Bussmann 2001)	
San Andrés Tlalnelhuayocan, Mexico	cloud forest, c. 1600 m a.s.l.	82	38	28	20	4	6	0	(Flores-Palacios and García-Franco 2001)	
Average percentage tropical forests		48 (10)	24 (6)	7 (5)	6 (6)	4 (2)	2 (3)			
New Zealand	Temperate rain forest	50	12	70	0	0	4	0	(Oliver 1930)	only 'typical epiphytes'
Egmont National Park, New Zealand	Temperate forest	32	16	69	0	0	0	0	(Clarkson 1985)	
Mt. Karioi, New Zealand	Temperate forest	22	14	68	0	0	0	0	(Clayton-Greene and Wilson 1985)	
Maungataniwha Range, New Zealand	Temperate rain forest	35	14	57	0	0	0	0	(Dawson and Sneddon 1969)	
Japan	Temperate forest	52	35	63	0	0	0	2	(Ohwi 1965)	
Parque Nacional Tolhuaca, Chile	Temperate forest	6	0	83	0	0	0	0	(Ramírez 1978)	
Fundo San Martín, Valdivia, Chile	Aeotoxicicon wood farm	16	6	63	6	0	0	0	(Riveros and Ramírez 1978)	
Isla de Quinchao, Chile	Temperate rain forest	8	0	63	0	0	0	0	(Troncoso and Torres 1974)	
Canary Islands	Laurel forest	5	0	100	0	0	0	0	(Page 1977)	mostly facultative epiphytes
Azores	Temperate forest	7	0	100	0	0	0	0	(Bennett et al. 1992, Ward 1970)	mostly facultative epiphytes
North Korea	Temperate forest	9	0	100	0	0	0	0	(Kolbeck 1995)	
Temperate North America (excl. Florida)	Temperate forest	7	0	86	14	0	0	0	(Lellinger 1985)	mostly facultative epiphytes
Nainital, Western Himalaya, India	Montane forest, 1850 m a.s.l.	17	24	76	0	0	0	0	(Gupta 1968, Verma and Khullar 1980)	
Average percentage temperate forests		9 (11)	77 (16)	2 (4)	0	0.3 (1.1)	0.1 (0.5)			

other life forms typically restricted to wet tropical forests: for example, the hemi-epiphytic strangler *Pseudopanax laetevirens* (Araliaceae) reaches 50° S.

Himalayan region and temperate Asia

Schimper (1888) was first to point out the unique epiphyte flora of the Himalayas, which has epiphytic *Ribes*, *Euonymus*, *Thalictrum*, or *Rhododendron* species in addition to taxa of unequivocally tropical affinities. Epiphytic orchids, for example, are mostly represented by large tropical genera such as *Bulbophyllum*, *Coelogyne*, *Dendrobium*, *Eria* and *Oberonia* (Hajra 1996; Mehra and Vij 1974). Similarly, the fern flora has strong floristic affinities with tropical Burma and Malaysia, and with the Yunnan and Szechwan provinces of China (Bir 1989). The degree of endemism in some groups can be quite high. There are, e.g., 58 endemic fern species, constituting nearly 12% of all Himalayan pteridophytes (Bir 1989). These have probably evolved *in situ* during the uplift of the Himalaya in the late tertiary (Punetha and Kholia 1998). While annual precipitation in the east reaches up to 3000 mm (Table 1), the monsoon climate is associated with a 2-months to 5-months dry season. Many of the ferns are drought-deciduous and survive seasonal drought as dormant rhizomes (Gurung 1985). As in the tropics, epiphyte abundance is highest at intermediate elevations (1500 – 2400 m), i.e., there exists a so-called ‘mid-altitude bulge’ (Gentry and Dodson 1987). The abundance of epiphytic orchids decreases much more rapidly above the upper limit of this bulge; epiphytic ferns may be found even above 3500m, where frost is frequent (Mehra and Vij 1974). The important role of epiphytic vegetation to the primary production in these forests is indicated by their large contribution to total chlorophyll. Singh and Chaturvedi (1982), studying a number of *Quercus* forests, report that epiphytic ferns accounted for almost as much chlorophyll as terrestrial herbs.

There is a striking difference in the abundance of epiphytes in the Eastern and Western Himalayas, which has been attributed to changes in water availability by most authors (e.g., Bir 1989; Mehra and Vij 1974). Khullar (1981), however, argued that low moisture can only partly explain the paucity of epiphytes in the western region. One important additional factor may be the identity of potential host trees. It is frequently observed that conifers are only used as phorophytes when trunk and branches are

covered with a layer of humus or bryophytes (e.g., Bir 1989; Mehra and Bir 1964). Thus, if angiosperms are much better epiphyte hosts than gymnosperms, the greater dominance of conifers in Western Himalayan forests may also play a role in this biogeographical pattern (Khullar 1981).

Information on vascular epiphytes in temperate East Asia is scarce. However, one study reports a high proportion of epiphytic ferns in Yunnan (China) (Lu 1992), another describes epiphytes as a significant component of North Korean forests (Kolbeck 1995). The flora of Japan (Ohwi 1965) lists 52 species of vascular epiphytes (c. 1 % of the total flora), again most of them ferns (Table 2). The remaining taxa are almost all orchids and mostly found in the southern islands of Japan.

Europe and North America

Many reviews state that there are no vascular epiphytes in central Europe (e.g., Ellenberg 1988; Nieder and Barthlott 2001). For example, Nieder and Barthlott (2001) claim that *Polypodium vulgare* can only thrive where frost spells are rare, e.g., in southwestern England. This ignores observations on the epiphytic occurrence of this species in wet montane forests of the Alps (e.g., Stäger 1908; Wilmanns 1968). Recent studies on *P. vulgare* in a montane forest in the Swiss Alps (47 °N) quantified its local abundance with densities of more than 300 plants ha⁻¹ and attachment heights of up to 14m (Zotz 2002; Zotz and List 2003). While the climate is very humid at this site (annual precipitation c. 1500 mm) with no dry season, there is long-lasting frost in winter. Dense moss cushions (mostly *Antitrichia curtipendula*) provided some buffer against short-term extremes of air temperature, but thermal conditions of lithophytically and epiphytically growing individuals were virtually identical (Zotz, unpubl. data). Besides its frequent occurrence throughout montane forests in the northern Alps, species of the *P. vulgare* complex are also regularly found as epiphyte in more oceanic climates of southern Europe, e.g., in Italy (Béguinot and Traverso 1905), Corsica (Fliche 1902) or the damp forests of northern Portugal (Schimper 1888). In Great Britain, the Azores and the Canary Islands other epiphytic taxa appear, e.g., Hymenophyllaceae or Grammitidaceae (Bennert et al. 1992; Page 1977; Rübél 1912; Tansley 1939). Overall, however, epiphytes are rare in all these floras. For example, on the

Canary Islands, epiphytes account for just 0.2% of the total number of species (Kunkel 1993).

While Europe is separated from possible wet-tropical sources by the Sahara, North America has been reached in the Holocene by a number of epiphyte species belonging to large tropical genera (Gentry and Dodson 1987). *Tillandsia usneoides*, the northernmost species of this group, reaches 36° N latitude (Garth 1964). Farther north, members of the *Polypodium vulgare* complex are occasionally found growing as epiphytes in the North-eastern United States and Canada (Johnson 1921; Maycock 1975), but occur much more frequently as epiphytes in the Pacific Northwest (Scoggan 1978; Sillett 1999; Sillett and Bailey 2003). Yet, compared to its southern counterpart in Chile, the temperate rainforest of the west coast of North America is rather species-poor, not only in respect to epiphytes (Alaback 1991; Arroyo et al. 1995).

Non-tropical Africa

Although the African continent south and north of the tropics is rather arid (Knapp 1973), there is a rich epiphyte flora in the western, more mountainous parts of South Africa. For example, there are a large number of epiphytic orchids from Transvaal to the south, which reach the southern tip of Africa, for example *Aerangis*, *Polystachya*, or *Tridactyle* species (Ball 1978). In regions with winter rainfall, which host about a third of the orchid flora of South Africa, epiphytic forms are absent (Schelpe 1978). Remarkably, there are also reports of vascular epiphytes from Mediterranean Northern Africa, where they are quite frequently found on summer-green *Quercus faginea*: Knapp (1973) mentions *Polypodium australe*, a close relative of *P. vulgare*, and *Davallia canariensis*. Forests dominated by this oak are found from Tunisia westwards to the Rif-area in Morocco and characterise the most humid areas in altitudes of 1000 – 2000 m a.s.l., e.g., north facing slopes and shaded valleys. Fliche (1902) observed epiphytic *Polypodium* in Algeria, in Haute Kabylie and in the forêt de l'Edough.

Epiphyte communities – a comparison between the temperate zones and the tropics

Although bryophytes clearly prevail in temperate epiphytic plant communities (Barkman 1958), the previous paragraphs showed that epiphytic vascular plants are not as exceptional in temperate forests as implied by many reviews (even when ignoring the large num-

ber of 'accidental epiphytes'). Although the gradient between the tropics and the temperate zones is generally steep, epiphyte communities in parts of Chile, New Zealand and the Himalayas certainly rival those of many tropical forests in biomass and *relative* species diversity: take, for example, the large proportion of vascular epiphytes in local inventories (Dawson and Sneddon 1969) or the high epiphytic biomass (Hofstede et al. 2001) in the New Zealand rainforest (for epiphyte biomass see also Sillett and Bailey 2003). *Absolute* species numbers, however, are much higher in moist and wet tropical systems (Table 2). Irrespective of the absolute or relative contribution to the local or regional flora, there is a dramatic shift in the taxonomic composition of epiphytic communities. While those of tropical moist and wet forests are dominated by orchids (which account for almost half of all epiphyte species there), ferns and fern-allies are by far the most speciose group in temperate-zone epiphyte communities. Orchids may still be conspicuous in some temperate forests (e.g., in Southern Japan or the Himalayas), but most other important epiphyte taxa (Bromeliaceae, Araceae, Piperaceae, Ericaceae; all families with at least 700 epiphyte species globally) are completely or almost completely absent in canopy-dwelling flora outside the tropics (Table 2). The reasons for the prevalence of ferns in the temperate zones are unclear. Although most ferns prefer mesic environments, some species exhibit a desiccation tolerance superior to most vascular plants, others are poikilohydrous or drought-deciduous. Many ferns may tolerate even severe frost and tiny, easily dispersed propagules are an important attribute of epiphytism in this group irrespective of latitude. Remarkably, epiphytic ferns also reach higher altitudes in tropical mountains than other epiphyte taxa (M. Kessler, pers. comm.).

Epiphytism in the tropics and the temperate zones also differs in the speed of speciation. The evidence for autochthonous evolution in the temperate zones (e.g., Dawson 1970) suggests at the same time very little subsequent speciation: many temperate genera are monotypic or consist of very few species. This contrasts sharply with the stunning species numbers of genera like *Pleurothallis* or *Stelis* in the tropics. Gentry (1982) called the extreme epiphyte diversity in the northern Andean cloud forest an 'evolutionary explosion' and provided an example of possible speciation in an orchid in just a few decades (Gentry and Dodson 1987).

A final distinction between the tropics and the temperate zones concerns the proportion of obligate vs. accidental epiphytes. At least in lowland tropical forests accidentals are rare, whereas their number frequently exceeds the number of obligate epiphyte species in the temperate zones (Punetha 1989; Sharp 1957; Tewari et al. 1985; Zotz and List 2003), even in regions with a rich epiphyte flora such as New Zealand (e.g., Hofstede et al. 2001).

What limits epiphytism in the temperate zones?

The temperate regions with a rich epiphyte flora (i.e., New Zealand, Southern Chile, Himalayas, Japan) are characterised by humid climates with few incidences of frost (Table 1). This observation has prompted two principal explanations for the global pattern described above. Schimper (1888) stressed low water availability in the temperate zones, Benzing (1990) and others (e.g., Ellenberg 1988; Nieder and Barthlott 2001) emphasised the importance of frost. One possible test of the proposed mechanism behind latitudinal trends is the consistent influence of the same factors at a smaller scale (Huston 1999). Indeed, low moisture availability has been identified as the major constraint for epiphytism in the tropics (Gentry and Dodson 1987) and low temperatures have been used as to explain changes in species abundance with altitude (although evidence is mostly circumstantial). It should be emphasised that epiphytes comprise a very diverse group, both taxonomically and ecologically (Benzing 1990) and it seems unlikely that there is a single, universal mechanism underlying their global distribution. For example, it is reasonable to assume 'tropical' families such as Araceae to be limited mostly by low temperature in extra-tropical regions, but less so for cosmopolitan ferns and fern-allies, which are known to tolerate substantial freezing as terrestrials (Kappen 1964). In addition, there are other explanations, which are rarely discussed in the literature, e.g., the possibility that Pleistocene extinctions have led to a currently unsaturated 'epiphytic niche', biotic interactions with potential host trees, and/or biogeographical considerations, e.g., the effect of distance to potential (tropical) source areas (but see Dawson 1986; Gentry and Dodson 1987; or Khullar 1981). Unfortunately, not a single experimental study has been published on the subject to date.

Arguably, low moisture availability limits the development of epiphytism more than any other environmental factor in the temperate zones, similar to the tropics (Gentry and Dodson 1987). However, even in

the driest tropical forests there are generally at least some epiphytes (Mooney et al. 1989; Murphy and Lugo 1986), a few species may even be found in deserts as long as there is regular moisture input from mist (MacMahon and Wagner 1985). Many moist temperate forest, on the other hand, harbour no or only very few epiphytes, while the Himalayas with several months of drought (Table 1) have a rich epiphyte flora. Thus, moisture availability alone can only explain part of the latitudinal trend. This emphasises the role of dispersal barriers or, conversely, the importance of geographic proximity to tropical sources for the diversity and abundance of vascular epiphytes in temperate areas (compare, e.g., western Europe with the Himalayas).

Cold temperatures, let alone long-lasting frost is likely to constitute a major limiting factor for most tropical taxa (Benzing 2000; Larson 1992), but not for all (Halbinger 1941). Garth (1964) suggested that temperature itself is not determining the northern limit of *Tillandsia usneoides* in North America. The only temperate species studied in this respect is *Polypodium vulgare* (Kappen 1964). In the Swiss Alps, epiphytic *P. vulgare* experience severe frost for weeks without suffering any visible damage (Zotz, unpubl. data). Similar to seasonally low temperatures in the temperate zones, recurring nocturnal frost in upper montane areas in the tropics may be the reason for the upper *altitudinal* limits of vascular epiphytes (Kessler 2002). In conclusion, low temperatures are likely to act as a major filter for many of the tropical (lowland) epiphyte taxa (Hall 1958, Wurthman 1984), but we still lack quantitative studies on the frost tolerance of epiphytes from the temperate zones and tropical montane areas.

Differences in Pleistocene history between hemispheres are a potentially important, yet mostly neglected aspect towards a comprehensive explanation of current global distributions. Temperate areas, featuring a high number of epiphytes today (i.e., Chile, New Zealand, Himalayas, Japan), have all been affected very little by Pleistocene glaciations and/or provided refugia allowing survival of tertiary vegetation (e.g., Arroyo et al. 1995; Dawson 1986). Similar to terrestrial flora, temperate epiphyte communities are possibly far from saturated, especially in Europe with its much poorer flora compared to North America or eastern Asia (Röhrig 1991). Unfortunately, direct evidence for possible changes in the epiphyte floras is very limited due to the poor fossil record of vascular epiphytes (Collinson 2000). While

regions with Pleistocene refugia (e.g., in Chile, New Zealand) feature many autochthonous taxa, the 'epiphytic niche' in other areas (e.g., Southeast United States) was probably refilled in the holocene by plants from lower latitudes or by newly evolved members with the epiphytic habit (e.g., species of the *Polypodium vulgare* complex, e.g., Europe or North America). This scenario emphasises the influence of a historical component in creating the global patterns of species distributions (Ricklefs et al. 1999).

Although probably of minor importance, the possible role of host plant identity should not be ignored either. It has been observed repeatedly that conifers are poor hosts for epiphytes (Bir 1989; Garth 1964; Kolbeck 1995; Kramer 1993). Similar observations have been made in the Swiss Alps (Zotz and List 2003): although spruce trees were much more abundant than *Acer* trees, epiphytic *P. vulgare* plants were exclusively found on the angiosperm. There are a number of possible reasons, which are, e.g., related to bark chemistry (Bir 1989) or tree architecture (Garth 1964). Moreover, conifers with dense foliage intercept a much higher proportion of rainfall and feature significantly reduced stem flow compared to deciduous angiosperms (Garth 1964), leading to considerably reduced water supply to epiphytes. Needle-leaved conifers being poor hosts could also be part of the reason for the asymmetry in epiphytism between northern and southern hemisphere. Purely coniferous moist montane forests as well as mixed montane forests are unique to the northern hemisphere (Box 2002). If temperate forests in the southern hemisphere under otherwise similar environmental conditions feature a 'better' suite of potential host trees (compare, e.g., temperate rain forests in North and South America, Alaback 1991), development of epiphytism may be enhanced.

In summary, after reviewing the occurrence of vascular epiphytes outside the tropics I discussed the possible mechanisms behind the observed latitudinal trend. While acknowledging low water availability and low temperatures as the principal mechanism(s) behind the observed latitudinal trend (although experimental evidence is still lacking) I suggest to explore other variables as well in seeking explanations for the global variation in epiphyte diversity and abundance.

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