

# Evolution of a climbing habit promotes diversification in flowering plants

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Key innovations are traits that are associated with the particular evolutionary ‘success’ of some taxonomic groups. Climbing plants depend on the availability of physical support to reach the canopy and thereby prevent shading by neighbouring plants. The present article shows that the evolution of a climbing habit in flowering plants constitutes a key innovation. A literature survey identified 48 pairs of sister groups from 45 families of flowering plants for which information on phylogenetic relationships, growth habit and species richness was available. In 38 cases, the climbing taxa were more diverse than their non-climbing sister groups. This pattern was highly significant. The same result was found when separate analyses were carried out for herbaceous and woody climbing plants, which differ in their constraints for successfully reaching a support.

**Keywords:** adaptive zone; climbing habit; diversity; key innovation; niche; vines

## 1. INTRODUCTION

A central question in evolutionary biology is why some taxonomic groups are remarkably more diverse than related groups (Futuyma 1998; Magallón & Sanderson 2001). Explanations for outstanding evolutionary ‘success’ in a particular lineage, measured by the proliferation of species (Hunter 1998), often involve key innovations, defined as traits that allow a clade to exploit a previously unused or under-utilized resource (Simpson 1953). Key innovation hypotheses are usually tested by comparing species richness in two related groups of equivalent age (sister groups) possessing and lacking the candidate trait (see Barraclough *et al.* (1998) for a discussion on the utility of sister-group analysis). This comparison is performed for each independent appearance of the trait, and statistical tests indicate whether the overall outcome is greater species richness in the lineages possessing the trait (Mitter *et al.* 1988; Hunter & Jernvall 1995; Bond & Opell 1998; Farrell 1998).

Climbing plants (vines) depend on the availability of a physical support to reach the canopy and thereby prevent shading by neighbouring plants. Vines that find a suitable support usually have a greater biomass and reproductive output than those that grow unsupported (Putz 1984; Puntieri & Pyšek 1993; Gianoli 2002). The evolution of a climbing habit has taken place many times during the course of plant evolution: more than 130 plant families include climbers (Gentry 1991). Vine species may represent more than 40% of species diversity in tropical forests (Schnitzer & Bongers 2002) and their dominance shows an increasing trend (Phillips *et al.* 2002). Surprisingly, to my knowledge, no study has addressed whether the climbing habit constitutes a key innovation in plants, i.e. whether there is greater species richness in climbing clades compared with non-climbing sister groups.

Vines in natural populations can increase their likelihood of encountering a suitable support by being able to climb on plants encompassing a wide range of stem/trunk diameters (Putz & Holbrook 1991). Constraints for successfully reaching a support differ for herbaceous and woody vines (Gentry 1991). Woody vines might be constrained

because there is a minimum diameter of tree required to be able to support the vine mass. Typically pioneer species rarely bear woody vines, partly owing to their flexible trunks, and thick woody vines are much less abundant than thin ones (Putz 1984). By contrast, there is no relationship between stem diameter and relative abundance of herbaceous vine species (Collins & Wein 1993). Consequently, it might be considered that such a constraint for support availability in woody vines would lessen the effect of the putative key innovation (development of a climbing habit) on taxonomic diversification, as compared to herbaceous vines.

I evaluated 48 cases of climbing taxa where phylogenetic information was available to determine non-climbing sister groups. I tested both the general hypothesis that the climbing habit in plants constitutes a key innovation, i.e. that climbing taxa are more diverse than their sister groups, and the specific prediction that woody vines would show a less pronounced pattern of greater species richness than herbaceous vines.

## 2. MATERIAL AND METHODS

### (a) Criteria for selection of taxa

First, plant families with a representative occurrence of climbing taxa were identified following the family description in Cronquist (1981). The literature was searched to retrieve both phylogenetic trees and information on the growth habit at the taxonomic level relevant for the hypothesis testing. To avoid overestimation of species in climbing genera, the study included only those genera with climbers as the main growth habit, and not merely a few species among a large total. Climbing plants were defined *sensu lato*, including scandent shrubs, herbaceous vines and woody vines (lianas). Epiphytes, hemiepiphytes, stranglers and parasitic plants were not considered.

When a phylogeny was available, sister-group comparisons of species richness between climbing and non-climbing clades were carried out. Identification of sister groups was obtained either from the particular phylogenetic studies or from sources of general scope (Angiosperm Phylogeny Group 1998, 2003; Barraclough & Savolainen 2001). The number of species for each group was

obtained from Mabberley (1997) or from more recent estimations appearing in specialized scientific articles on the corresponding family (86 references on the biology, phylogeny and species richness of each family are included in electronic Appendix A). If only rough estimations of species number in a given taxon were available, the upper limit of the estimated range was always considered. In some cases where the phylogeny was available, no comparison could be performed because of isolation of families lack of defined sister groups (paraphyletic groups), monogeneric families or habit variation within a genus. When there were interrelated, non-independent comparisons (i.e. polyphyly), the younger pair was always chosen. In some families a pair of sister groups with contrasting habits was chosen but they did not include all of the taxa within the family showing the specific trait. A total of 48 comparisons from 45 plant families were considered in the analysis, including 14 taxa of herbaceous vines and 34 taxa of woody vines. Systematic categories follow the Angiosperm Phylogeny Group (1998, 2003).

Despite its relevance for the topic, the geographical distribution of the clades is rarely addressed in comparisons of species richness aimed at testing key innovations. If the clades possessing the candidate trait are over-represented in the tropics in comparison with their sister groups, then it cannot be ruled out that the outcome of the test is associated with the renowned higher diversity of tropical taxa rather than with the putative key innovation. In the present study, I checked for the geographical distribution of taxa. Based on information available in Cronquist (1981) and Mabberley (1997), the geographical range of the compared clades was classified as tropical (including subtropical) and/or temperate. Only in three out of 48 comparisons was there a difference in geographical range between the climbing taxa and their sister groups. Moreover, in only one of these cases was the climbing taxon both more diverse and more strongly associated with tropical climates than its sister group. Therefore, there was no biogeographical bias underlying a hypothetical pattern of higher diversity of climbing taxa.

#### (b) Statistical analyses

The method of Slowinski & Guyer (1993) was used to test the general hypothesis that climbing clades are more diverse than their non-climbing sister groups. For each sister-group pair, the probability that the climbing clade is of size  $r$  or greater was calculated by the formula:  $P_c = p(r/n) + p(r+1/n) + \dots + p(n-1/n) = (n-r)/(n-1)$ , where  $n$  is the actual number of total species in both clades and  $r$  is the observed number of species in the climbing clade. The natural log of these independently calculated probabilities ( $P_c$ ) is summed for all pairs, multiplied by  $-2$ , and tested with Fisher's combined probability test (Sokal & Rohlf 1995), which compares the resulting value with a  $\chi^2$  distribution (d.f. =  $2k$ , where  $k$  is the number of pairs evaluated).

To compare the strength of the hypothetical pattern of greater species richness of climbing clades in herbaceous and woody vines, analyses were twofold. First, the method of Slowinski and Guyer was separately applied to each of these two groups as described above. Second, a  $2 \times 2$  table of contingency was built to evaluate, using a  $\chi^2$ -test, whether the disparity in species richness of the climbing and non-climbing taxa differed between herbaceous and woody vines.

### 3. RESULTS AND DISCUSSION

In 38 out of the 48 comparisons, the climbing taxa showed greater species richness than their non-climbing sister groups (table 1). This pattern was highly significant ( $\chi^2 = 180.74$ , d.f. = 96,  $p < 0.00001$ ; Fisher's combined

probability test) and supports the hypothesis that the climbing habit constitutes a key innovation for plants. The statistical strength of the pattern suggests that it would hold even if some of the phylogenetic hypotheses on which the determination of sister groups is based prove to be inaccurate. The separate analysis for herbaceous and woody vines showed that, in both groups, climbing taxa were significantly more diverse (herbaceous vines:  $\chi^2 = 62.75$ , d.f. = 28,  $p = 0.00018$ ; woody vines:  $\chi^2 = 117.99$ , d.f. = 68,  $p = 0.00017$ ; Fisher's combined probability test). The strong similarity between the latter results was confirmed by a test that indicated that the frequency of comparisons where species richness of the climbing taxa were greater than their sister groups was not different between herbaceous and woody vines (Yates' corrected  $\chi^2 = 0.21$ , d.f. = 1,  $p = 0.6483$ ; contingency table analysis). Consequently, the prediction of differences in the relative strength of the climbing habit as a key innovation in woody and herbaceous vines owing to biomechanical constraints was not supported. This suggests that the constraints imposed by the availability of suitable large-diameter hosts do not result in slower niche expansion and subsequent diversification compared with non-climbing species. It has been found earlier that woody and herbaceous families of flowering plants differ both in species richness (herbaceous families tend to have more species than woody families by a factor of 2.5: Ricklefs & Renner (1994)) and in the relative importance of abiotic and biotic dispersal for their taxonomic diversification (Tiffney & Mazer 1995).

Key innovations may boost diversification through different processes (Heard & Hauser 1995): (i) invasion of new 'adaptive zones' free from competitors or natural enemies; (ii) increase of fitness that leads one clade to replace another locally; or (iii) enhancement of conditions for reproductive or ecological specialization. Known cases of key innovations in plants include floral nectar spurs in *Aquilegia* (Ranunculaceae) that differ in length, orientation and colour and allow specialization to different pollinators (Hodges 1997), latex and resin canals that protect plants from herbivores and hence allow plant radiation in an adaptive zone of reduced herbivory (Farrell *et al.* 1991), and fleshy fruits in tropical understorey plants that promote isolation and speciation owing to limited seed dispersal by birds with occasional long-distance dispersal (Smith 2001). In the present case, explanations for the effect of climbing habit on clade diversification may include the following issues. First, in contrast with either erect or prostrate species, which occupy a narrow range of the light gradient, climbing species may use a very broad range of light conditions through both supported and unsupported individuals. Interestingly, it has been suggested that the proliferation of species within families might be related to the capacity of taxa to adopt different growth forms (Ricklefs & Renner 1994). Second, together with the occupation of such an expanded ecological niche, ranging from forest floor to understorey to forest canopy, access to pollinators and fruit/seed dispersers would be commensurably increased. Third, niche expansion may also entail exposure to a greater array of herbivores, whose pressure may promote the evolution of defensive secondary compounds in vines (Hegarty *et al.* 1991). Fourth, the

Table 1. Comparison of species richness of lineages composed of climbing plants and sister non-climbing groups. (For a given pair, the greater number of species is in bold.)

climbing plant taxa	number of spp.	sister group	number of spp.	habit of climbing taxa
Monimiaceae				
Palmerieae	<b>14</b>	Monimieae	3	woody
Hernandiaceae				
Hernandoideae				
<i>Illigera</i>	20	<i>Hernandia + Hazomalania</i>	<b>23</b>	woody
Hernandiaceae				
Gyrocarpoideae				
<i>Sparattanthelium</i>	<b>13</b>	<i>Gyrocarpus</i>	3	woody
Austrobaileyales				
Schisandraceae	<b>49</b>	Illiciaceae	42	woody
Piperaceae				
<i>Piper</i> sect. <i>Piper</i>	<b>300</b>	<i>Macropiper</i>	9	woody
Aristolochiaceae				
Aristolochieae	<b>358</b>	Bragantieae	26	woody
Ranunculaceae				
Clematidinae	<b>302</b>	Anemoninae	197	woody
Lardizabalaceae				
<i>Akebia + Boquila + Holboellia</i>				
+ <i>Lardizabala</i>				
+ <i>Sinofranchetia</i>				
+ <i>Stauntonia</i>	<b>43</b>	<i>Decaisnea</i>	1	woody
Sabiaceae				
Sabioideae	19	Meliosmoideae	<b>62</b>	woody
Cannabaceae				
<i>Humulus</i>	<b>3</b>	<i>Cannabis</i>	1	herbaceous
Moraceae				
<i>Ficus</i> subgenus <i>Ficus</i>				
sect. <i>Kalosyce + Rhizocladus</i>	<b>75</b>	sect. <i>Ficus</i>	60	woody
Phytolaccaceae				
<i>Ercilla</i>	2	<i>Anisomeria</i>	<b>3</b>	woody
Centrospermae				
Basellaceae	<b>22</b>	Didiereaceae	11	herbaceous
Polygonaceae				
Coccoloboeae	<b>157</b>	Triplaraceae	39	woody
Dilleniaceae				
<i>Hibbertia</i>	<b>115</b>	<i>Pachynema</i>	7	woody
Actinidiaceae				
<i>Actinidia</i>	<b>35</b>	<i>Clematoclethra</i>	12	woody
Ericales				
Marcgraviaceae	<b>130</b>	Pellicieraceae + Tetrameristaceae	5	woody
Caryophyllales				
Dioncophyllaceae +				
Ancistrocladaceae	<b>15</b>	Drosophyllaceae	1	woody
Passifloraceae				
Passifloreae	<b>650</b>	Paropsieae	25	herbaceous
Cucurbitales				
Cucurbitaceae	<b>845</b>	Anisophylleaceae	34	herbaceous
Cunoniaceae				
<i>Bauera + Aphanopetalum</i>	<b>6</b>	<i>Acrophyllum</i>	1	woody
Pittosporaceae				
<i>Billardiera</i>	<b>30</b>	<i>Bursaria</i>	7	woody
Fabaceae				
Papilionoideae				
Vicieae	307	Trifolieae	<b>427</b>	herbaceous
Fabaceae				
Papilionoideae				
milletioid/phaseoloid clade	<b>2888</b>	Indigoferae	710	herbaceous
Combretaceae				
Combretoideae				
<i>Calycopteris + Combretum + Quisqualis</i>	<b>267</b>	<i>Anogeissus + Conocarpus + Terminalia</i>	160	woody

(Continued.)

Table 1. (Continued.)

Dichapetalaceae					
<i>Dichapetalum</i>	124	<i>Tapura + Stephanopodium</i>	36	woody	
Euphorbiaceae					
Plukenetiae					
<i>Plukenetia + Romanoa</i>	17	<i>Haematostemon + Astrococcus + Angostyles</i>	4	herbaceous	
Rhamnaceae					
Ventilagineae	42	<i>Rhamneae + Maesopsideae</i>	260	woody	
Vitaceae					
<i>Vitaceae sensu stricto</i>	850	<i>Leea</i>	34	woody	
Linaceae					
Hugonioideae	61	<i>Linoideae</i>	240	herbaceous	
Malpighiaceae					
Stigmaphylloids	293	<i>Malpighioids</i>	87	woody	
Sapindaceae					
Paullinieae	441	<i>Thouinia + Allophylus</i>	29	woody	
Brassicales					
Tropaeolaceae	92	<i>Akaniaceae</i>	2	herbaceous	
Loganiaceae					
<i>Strychnos</i>	190	<i>Spigelia</i>	50	woody	
Apocynaceae s.l.					
Asclepiadoideae					
Asthephaninae	1041	<i>Asclepiadinae + Glossonematinae</i>	262	woody	
+ Metastelmatinae					
+ Oxypetalinae					
+ Gonolobinae					
Apocynaceae s.l.					
Periplocoideae					
<i>Baseonema + Batesanthus + Phyllanthera</i>	13	<i>Epistemma + Ischnolepis + Sacleuria + Sarcorrhiza</i>	8	woody	
Convolvulaceae					
Convolvuloideae	1600	<i>Humbertioideae</i>	1	herbaceous	
Polemoniaceae					
Cobaeoideae					
Cobaeae	18	<i>Bonplandieae</i>	2	woody	
Oleaceae					
Myxopyreae					
<i>Myxopirum</i>	4	<i>Nyctanthes + Dimetra</i>	3	woody	
Acanthaceae					
Thunbergioideae	150	<i>Acanthoideae + Nelsonioideae</i>	3228	herbaceous	
Bignoniaceae					
Bignonieae	350	<i>Crescentiae + Coleeae + Oroxyleae + Tecomeae</i>	318	woody	
Rubiaceae					
Ixoroideae					
<i>Sabicea + Pseudosabicea</i>	142	<i>Hekistocarpa + Tamridaea + Virectaria</i>	9	woody	
Arecaceae					
Calamoideae					
Plectocomiinae + Calaminae	525	<i>Pigafettinae</i>	2	woody	
Arecaceae					
Calamoideae					
Ancistrophyllinae	24	<i>Raphiinae + Lepidocaryinae</i>	54	woody	
Pandanaceae					
<i>Freycinetia</i>	180	<i>Pandanus + Sararanga</i>	702	woody	
Liliales					
Smilacaceae	320	<i>Liliaceae</i>	635	herbaceous	
Dioscoreales					
Dioscoreaceae	625	<i>Taccaceae</i>	31	herbaceous	
Araceae					
Monstereae	306	<i>Zamioculcadaeae</i>	6	herbaceous	

distinctive characteristics of climbing plants in resource allocation, for example, favoured transport tissues at the expense of supportive tissues and increased biomass allocation to leaves (Stevens 1987; Gartner 1991), might translate into a more efficient exploitation of light. The

occurrence of one or several of these events would grant climbing species the ecological opportunity that is considered a requisite for a trait to be considered a key innovation (Schluter 2000). Thus, according to theory (Simpson 1953), diversification should follow the spread of

a plant taxon into the ecologically open territory that the climbing habit may represent.

Species diversity in families of flowering plants has been recently related to the rate of neutral molecular change but not to morphological change rate (Barracough & Savolainen 2001). In addition, the role of ecological processes in speciation has been largely debated (Schluter 2000). Ecological change would be the main factor in the diversification of plant taxa when recently evolved species differ from their progenitors in the utilization of resources, while being only partially isolated by genetic barriers (Levin 2000). This is the case of the Hawaiian silversword alliance, a paradigmatic case of adaptive radiation (Schluter 2000) that occupies a very broad range of habitat types, yet many interspecific crosses remain fertile (Baldwin & Robichaux 1995). The same occurs in the previously mentioned *Aquilegia* species (Hodges 1997). Set at a broader scale, the present study uncovers a pattern of greater species richness associated with the evolution of a climbing habit in plants. Testing some of the hypothetical ecological mechanisms underlying such a pattern of macroevolution would help to appraise the importance of ecological processes in plant speciation.

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