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INSULAR WOODINESS ON THE CANARY ISLANDS: A REMARKABLE CASE OF CONVERGENT EVOLUTION

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Premise of research. One of the most conspicuous aspects of island floras is the relatively high proportion of woody species. Often, but not always, these woody species have developed wood on the islands and have evolved from herbaceous continental ancestors, a phenomenon known as insular woodiness. Shifts from herbaceousness toward increased woodiness also occur on continents (the broader term "secondary woodiness" is more appropriate here and includes insular woodiness), but comprehensive worldwide knowledge about secondary woodiness within angiosperms remains lacking. We update hypotheses regarding the herbaceous ancestry of woody Canarian lineages in a molecular phylogenetic context and investigate the possible link of secondary woodiness and paedomorphic wood features in the Carlquistian sense.

Methodology. We have assembled available literature data from molecular phylogenetic studies, wood anatomical descriptions, floras, and taxonomic revisions to identify the native secondarily woody taxa.

Pivotal results. In total, at least 220 native Canary Island species of flowering plants, from 34 genera representing 15 families, are truly insular woody. This represents a significant portion of the native nonmonocot angiosperm species on the Canaries, and all of the insular woody species have paedomorphic wood features in the Carlquistian sense, although this wood anatomical syndrome might be more related to particular life forms. The majority of these insular woody groups typically grow in the markedly dry lowland regions, suggesting a possible link between secondary woodiness and increased drought resistance.

Conclusions. The Canary Island flora is characterized by at least 38 independent shifts toward insular woodiness, representing an important portion of the endemic angiosperms on the archipelago. These convergent evolutionary events emphasize the remarkable lability in growth forms between herbaceous and woody lineages, but it remains puzzling which environmental variables trigger these shifts and how these independent shifts are regulated genetically.

Keywords: Canary Islands, convergent evolution, insular woodiness, molecular phylogeny, protracted juvenilism, secondary woodiness, wood anatomy.

Online enhancements: appendix tables.

Introduction

Darwin's five-year odyssey aboard the HMS *Beagle* was the beginning of numerous discoveries of unknown life forms that formed the basis for his pioneering evolutionary theory (Darwin 1859). Not surprisingly, his ideas originated when he visited islands, which are still considered to be laboratories of evolution because of their isolated position and relatively small size, in combination with a high diversity in habitats and an often dynamic geological history in terms of volcanic and erosional activity (Carlquist 1974; Givnish 1998; Emerson 2002; Whittaker et al. 2008; Losos and Ricklefs 2009; Whittaker and Fernández-Palacios 2010; Bramwell and Caujapé-Castells 2011). Gigantism in relatives of small continental animals or flightlessness in birds are examples of insular animal evolution, but insular floras also typically include species with remarkable adaptations, such as a pronounced development of woodiness. This so-called insular woodiness was described and interpreted correctly by Darwin:

> Again, islands often possess trees or bushes belonging to orders which elsewhere include only herbaceous species; now trees ... generally have, whatever the cause may be, confined ranges. Hence trees would be little likely to reach distant oceanic islands; and an herbaceous plant, ... when established on an island and having to compete with herbaceous plants alone, might readily gain an advantage by growing taller and taller and overtopping the other plants. If so, natural selection would often tend to add to the stature of herbaceous plants when growing on an island, to whatever order they belonged, and thus convert them first into [insular woody] bushes and ultimately into trees. (Darwin 1859, p. 392)

Darwin's hypothesis that at least some woody island species evolved wood on the islands and are thus derived from continental herbaceous colonizers is supported by recent molec-

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ular phylogenetic results for many woody island genera: to name just a few, *Aeonium* and *Echium* on the Canary Islands (Böhle et al. 1996; Mes and 't Hart 1996); *Viola* and the silverswords *Argyroxiphium*, *Dubautia*, and *Wilkesia* on the Hawaiian islands (Baldwin et al. 1991; Ballard and Sytsma 2000); *Eryngium* and *Senecio* (formerly *Robinsonia*) on the Juan Fernandez Islands (Calviño et al. 2010; Pelser et al. 2010*b*); *Dendrosicyos* on Socotra (Schaefer et al. 2009); *Nesohedyotis* on St. Helena (Lens et al. 2009); and *Fitchia* and *Plakothira* on Polynesian islands (Hufford et al. 2003; Crawford et al. 2009). Darwin's insular-woodiness hypothesis is further supported by (1) the excellent dispersal mechanisms of many herbaceous plant groups that have reached isolated islands, (2) the relatively young age (~5 Myr or less) of several insular woody groups, based on molecular divergence estimates (Baldwin and Sanderson 1998; Carine 2005; Fiz et al. 2008; Kim et al. 2008; Feodorova et al. 2010), and (3) the presence of specific wood features in these secondarily woody species ("paedomorphosis" sensu Carlquist 1962; "protracted juvenilism" sensu Carlquist 2009, 2012); molecular phylogenies have confirmed the evidence for an herbaceous ancestry adduced well before the molecular era (Carlquist 1962, 1969*a*, 1969*b*, 1970*a*, 1970*b*, 1970*c*, 1974, 1985; Carlquist and Eckhart 1982; Cumbie 1983; however, see "Discussion" about interpreting this wood anatomical syndrome).

Insular woody species do not comprise the entire island flora, as is evident from the following three points. First, several authors have advocated that many of the woody island species can best be interpreted as evolutionary remnants of ancient lineages instead of as recent lineages, because it was—and still is—generally accepted that the shift from (primary) woodiness toward herbaceousness is much more common than the opposite shift (i.e., from herbaceousness toward secondary woodiness) in flowering plants (Lems 1960; Bramwell 1972; Cronk 1987, 1992). The evergreen laurel forests in the Canary Islands, dating back ~65 Myr (paleotropical flora with Thetian-Tertiary origin; Fernández-Palacios et al. 2009; fig. 1*A*) and composed mainly of primarily woody trees having only woody relatives, provide one of the best-known examples demonstrating the validity of this relict hypothesis. Second, our ongoing broad-scale attempt to review habit shifts from herbaceousness toward increased woodiness within angiosperms shows that a majority of them (more than 200 genera, including at least one secondarily woody species) do not occur on islands (F. Lens, unpublished data). For these woody continental taxa, the term "insular woodiness" should be replaced by the more general term "secondary woodiness" to define all woody taxa characterized by an herbaceous ancestry; "insular woodiness" should be applied only to woody island taxa that have developed woodiness on the islands, and it should be considered part of the broader term "secondary woodiness." Therefore, not all woody island species with an herbaceous ancestry are by definition insular woody. For instance, the woody genus *Scalesia*, endemic to the Galapagos Islands, is secondarily (not insular) woody, because its closest relatives are the woody Andean *Pappolobus* species (Schilling et al. 1994); the woody *Scalesia-Pappolobus* clade is embedded in a largely herbaceous group consisting of *Helianthus*, *Simsia*, and *Viguiera* pro parte. The same is true for the woody Hawaiian lobeliads, which are secondarily woody (Givnish et al. 2009). Third, insular floras still include a significant proportion of herbaceous species that apparently did not evolve into shrubs or trees, for whatever reason. In conclusion, it is also important to critically examine the origin of woodiness of native woody island plants when they belong to families with many insular woody species (e.g., Asteraceae).

Since the number of secondarily woody genera within angiosperms is much higher than anticipated (F. Lens, unpublished data), we decided to focus first on the Canary Islands, an active volcanic archipelago off the coast of West Africa that includes seven main islands ranging in age from 1 to 21 Myr (Coello et al. 1992). This archipelago is unique, compared to other oceanic islands, for two main reasons: (1) the dynamic link between island age (increasing from west to east) and height, which results in marked habitat differences and strong influences of humid trade winds on the northeastern mountain slopes of the higher islands; and (2) the proximity of the African mainland and the presence of several volcanic sea mounts around the Canary Islands, which may have facilitated dispersal between the continent and the archipelago by serving as "stepping stones" during glacial periods, when sea levels were lower (García-Talavera 1997; Geldmacher et al. 2001; Fernández-Palacios et al. 2009).

This review on the Canary Islands has several main objectives: (1) to give a sound estimate of the minimum number of insular and secondarily woody species and to identify the number of habit shifts, based on a molecular phylogenetic context and wood anatomical observations, (2) to discuss the association of secondary woodiness with paedomorphic wood characters in the Carlquistian sense, (3) to comment on the recent versus relict origin of insular woody groups, and (4) to bring forward some arguments for a new hypothesis linking secondary woodiness with drought resistance for several groups in the Canary Islands and beyond.

Material and Methods

As explained above, not all woody island groups are insular woody. Therefore, it is crucial to distinguish between insular woody species that have developed into shrubs on the islands, secondarily woody species that have developed wood from a continental (secondarily) woody ancestor, and primarily woody species derived from continental (primarily) woody relatives. The first difficulty is how to distinguish woody from herbaceous species. In nonmonocot flowering plants, this is not so straightforward as it may seem, because the anatomical boundary between herbaceous and woody species is known to be fuzzy (Lens et al. 2012*a*). Most angiosperm herbs of the traditional dicot lineages produce various amounts of wood tissue at the basal part of the stem, even in small, herbaceous species such as *Arabidopsis thaliana* (Carlquist 2009; Dulin and Kirchoff 2010; Schweingruber et al. 2011; Lens et al. 2012*b*). The amount of wood development in herbaceous stems is always limited, ranging from just a few wood cells in the vascular bundles to a narrow, complete wood cylinder, while in woody species there is a gradual increase in the wood cylinder that usually extends into the upper parts of the branches. However, it remains challenging to draw the line between herbaceous and truly woody species, even in groups where detailed diameter measures of entire stems and wood

Fig. 1 Illustrations of the woody habit of Tenerife species. *A*, Overview of laurel forest with primarily woody species in Anaga, close to Casa Forestal, Tenerife. *B–G*, Truly insular woody species. *B*, *Argyranthemum frutescens*. *C*, *Aeonium urbicum*. *D*, *Echium leucophaeum*. *E*, *Crambe arborea*. *F*, *Lobularia canariensis*. *G*, *Descurainia bourgeauana*.

cylinders were made in combination with detailed wood anatomical observations (Lens et al. 2012*a*). Therefore, in order not to overestimate the number of insular or secondarily woody taxa, we prefer to exclude any life form intermediate between herbaceousness and woodiness, and we discard the—often confusing—transitional life forms that are mentioned in species descriptions: among others, “suffrutescent herbs,” “lignified herbs,” “woody herbs,” “herbs or subshrubs,” and “weakly lignified shrublets.” The insular woody shrubs that we identified on the Canary Islands are mostly small shrubs, rarely exceeding 2 m tall (fig. 1*B*–1*G*), and occasionally small trees or climbing species up to 5 m.

From the continuous anatomical variation between herbaceous and woody species, it is not surprising that botanists interpret the term “woodiness” in different ways and often make their decisions without any anatomical observations, which further complicates things. For instance, in the molecular phylogeny of *Pericallis* (Asteraceae), Panero et al. (1999) sequenced 15 species, of which six were considered woody. In our interpretation, only *Pericallis appendiculata* can be considered a truly woody shrub; the five other so-called woody species would be better interpreted as herbaceous species with a woody basal part, meaning that Panero et al.’s hypothesis of two independent shifts toward insular woodiness is not valid. Another example is the molecular phylogenetic study of *Tolpis* by Moore et al. (2002), who concluded that woodiness arose in the common ancestor of all extant *Tolpis*, followed by two independent reversals to an herbaceous habit. Although there is indeed an anatomical difference in wood formation among different *Tolpis* species, this difference is only trivial, so we have excluded this genus from our analysis of woody species. The same is true for the Crassulaceae genera *Aichryson* and *Monanthes*. When two literature sources contradict each other—for instance, Mes and ’t Hart (1996) considered fewer *Aeonium* species to be woody than did Bramwell and Bramwell (1974)—the stricter circumscription of woodiness (in this case, that of Mes and ’t Hart 1996) was followed.

After the life forms were defined, the next step was to assemble independent molecular and anatomical data, because investigating merely wood anatomical characters or molecular phylogenetic data may easily lead to misinterpretation of the origin of woodiness in a particular group (Lens et al. 2009, 2012*a*; Dulin and Kirchoff 2010). Therefore, we consulted 61 molecular phylogenetic publications about Canary groups that included herbaceous as well as woody species, and we retrieved habit and habitat information for the species used in these phylogenies based on 47 revisions and flora volumes. Furthermore, we searched for wood anatomical features with protracted juvenilism in 23 wood anatomical papers and in original sections of wood samples that we collected during our Tenerife expedition in spring 2011. The sections were made according to a previously described standard protocol (Lens et al. 2007). Our sections were screened for the presence of an abundance of upright and square cell shapes of ray cells and for flat or decreasing length-on-age curves for vessel elements, two wood characters that are frequently used to point to secondarily woody taxa (fig. 2; however, see “Discussion” on how to interpret this). We have used a comprehensive phylogenetic framework to assess whether Carlquistian paedomorphic features are present only in secondarily woody species or whether these features represent a particular function that could explain their presence in secondarily as well as primarily woody species with similar growth forms. For a list of other examples of protracted juvenilism in wood, we refer to Carlquist (2009, 2012).

Results

The results of this literature search are summarized in table 1 (woody taxa with clearly herbaceous origin) and the appendix, available in the online edition of the *International Journal of Plant Sciences* (table A1: list of insular and secondarily woody species; table A2: list of ambiguous genera), with reference to the number of secondarily or insular woody species and the total number of species per genus (phylogenetic placement follows the APG III [2009] classification system), the diversity in habit, the habitat of secondarily woody species in and outside the Canary Islands, the presence of protracted juvenilism in wood characters, remarks on the number of habit shifts, and information about insular or secondary woodiness. Table 1 shows that secondarily woody species are present in 46 genera belonging to 18 families; among these, wood development in 34 genera, representing 15 families (fig. 3), did evolve on the Canary Islands, and such species should thus be called insular woody. In the genus *Convolvulus*, only one of two independent shifts has led to insular woodiness, while the other probably represents secondary woodiness. Table A2 shows that the origin of woodiness in 17 genera cannot be assessed with certainty at this moment. The five families that are represented in table A2 but not in table 1 are Rosaceae, Urticaceae, Plumbaginaceae, Acanthaceae, and Scrophulariaceae; these could potentially be added to the list of families with secondarily (insular) woody species on the Canary Islands. Nevertheless, current evidence rather points to primary woodiness in the genera *Gesnouinia* and *Forsskaolea* (both Urticaceae) and in *Gymnocarpos*, *Paronychia*, and *Polycarpaea* (all Caryophyllaceae), so these should probably be discarded, but more data are needed to confirm this.

Figure 2 and table 1 show that most of the insular and secondarily woody genera from which the wood anatomy is known are characterized by multiseriate rays with mainly square to upright ray cells and by flat to continuously decreasing length-on-age curves for vessel elements. Sometimes, scalariform intervessel pitting with wide apertures or multiseriate rays with exclusively upright cells are also observed. Occasionally, rays are absent. However, the studied wood sample of *Pterocephalus* does not show protracted juvenilism in its wood. In table A2, the same picture arises: mainly square to upright ray cells in most species but no wood features with protracted juvenilism in *Marcetella moquiniana*.

Figure 3 shows a phylogenetic overview of the 34 insular woody angiosperm genera, based on table 1. Insular (and secondary) woodiness on the Canary Islands is mostly confined to the euasterid clades, especially in the Lamiales and Asterales. In the rosids, only three families contain insular woody species: Brassicaceae (five genera, although the closest relatives of *Parolina* remain incompletely known), Fabaceae (*Lotus* and *Ononis*), and Malvaceae (*Navaea*). Outside rosids and asterids, the genus *Aeonium* is the only group that has evolved into insular woody species.

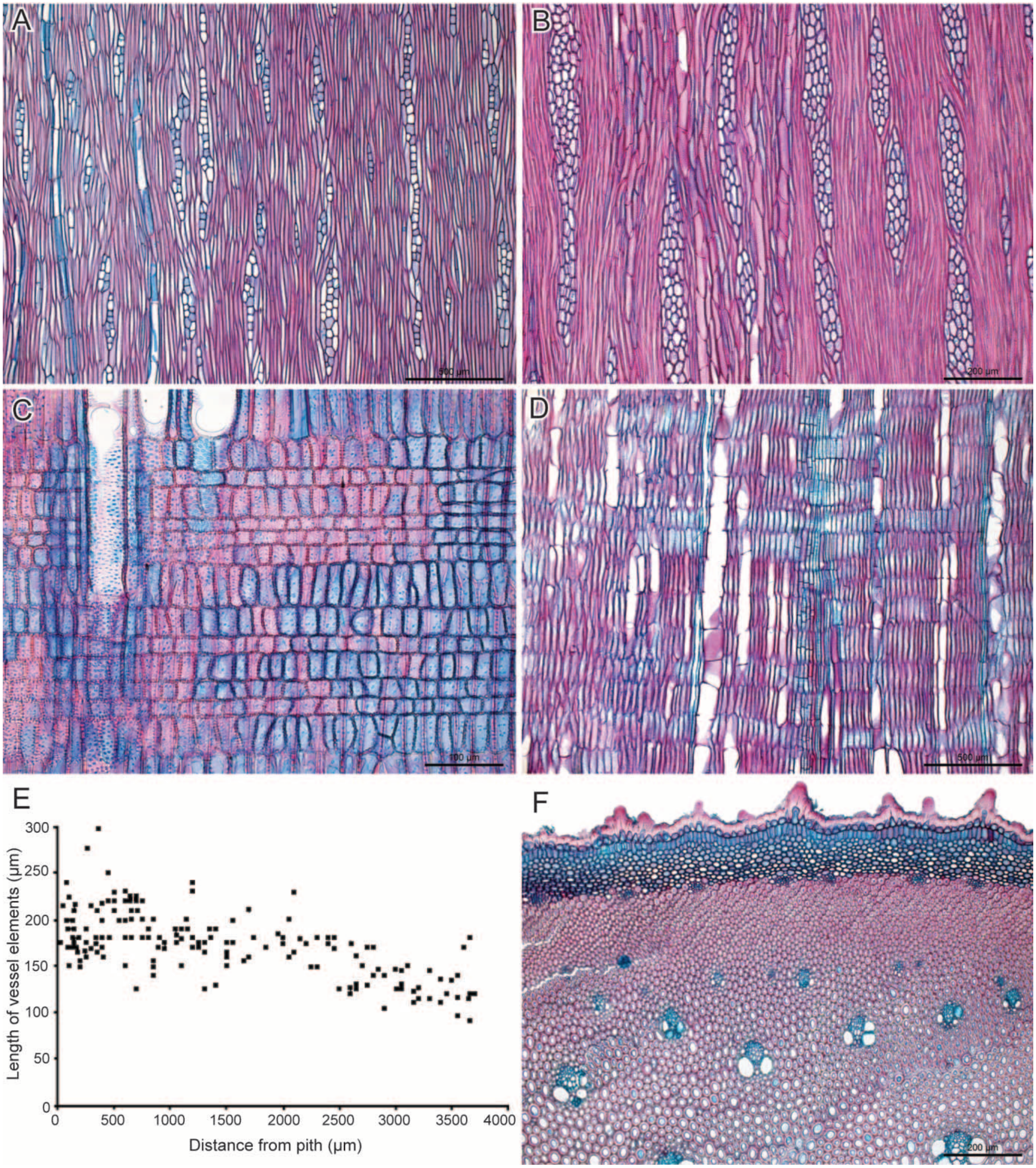


Fig. 2 Wood anatomy of native Canary Island species, showing LM pictures of protracted juvenilism in wood features of truly insular woody species (*A–D*), a length-on-age curve for vessel elements (*E*), and an LM section of a "woody" monocot, *Asparagus scoparius*, without cambium formation (*F*). *A*, *Rumex lunaria*, tangential section, illustrating mainly upright ray cells. *B*, *Argyranthemum adauctum*, tangential section, showing mainly upright ray cells. *C*, *Echium leucophaeum*, radial section, showing mixed square and upright ray cells. *D*, *Lobularia canariensis*, radial section, with vague rays consisting of upright cells only. *E*, *Campylanthus salsoloides*, decreasing length-on-age curve for vessel elements. *F*, *Asparagus umbellatus*, cross section through outer stem part of "woody" monocot stem without cambium activity.

Table 1

Canary Island (CI) Genera That Include Woody Species That Have Evolved from Herbaceous Ancestors, with Reference to Their Systematic Position within Angiosperms, Species Composition, Habit, Habitat, Paedomorphic Wood Anatomical Features, Number of Shifts toward (Insular or Secondary) Woodiness, and References Used

APG III classification; APG order; family, genus[a]	Habit of entire genus	Habitat of secondarily woody species		Protracted juvenilism in wood	References	Remarks
		On the CI	Outside the CI			
Unplaced in core eudicots:						
Saxifragales:						
Crassulaceae:						
Aeonium (18/28/36)	Herbs or shrubs ≤1 m, sometimes more	Dry and rocky areas from sea level (dry costal zones) to the forest zones (≤1500 m asl, occasionally on subalpine rocks ≤2000 m asl)	Dry and rocky areas of Cape Verde Islands, Azores, Madeira, SW Morocco, NE and East Africa, Yemen	Flat LOA curve for vessel elements, scalariform intervessel pitting with wide apertures, no rays	Bramwell and Bramwell 1974; Carlquist 1974; 't Hart and Koek-Noorman 1989; Mes and 't Hart 1996; Thiede and Eggli 2007; Mort et al. 2010	Growth form boundaries not well defined; Mes and 't Hart (1996) include fewer truly woody species (shrubs) than Bramwell and Bramwell (1974), so we follow the former, which means that 2 independent shifts toward insular woodiness have occurred; *Aichryson* and *Monanthes* occasionally shrublets, but treated as not woody enough
Eurosids I:						
Fabales:						
Fabaceae:						
Lotus (incl. *Dorycnium*; 7/20/150)	Herbs or shrubs ≤2 m	Dry coastal regions, pine forests and montane scrub in mountain zone >1000 m asl	Cape Verde Islands, California offshore islands (e.g., Guadeloupe and San Clemente), Mediterranean	Flat or decreasing LOA curve for vessel elements, multiseriate rays with mainly upright cells or procumbent to square cells (F. Lens, pers. obs.)	Carlquist 1974; Allan and Porter 2000; Allan et al. 2004	≥2 independent shifts toward insular woodiness throughout the genus on the CI; putative back-colonization from the CI to NW Africa
Ononis (3/16/86)	Mainly herbs, sometimes small shrubs	*Ononis christii*: xerophytic shrub endemic to Mount Pico de la Zarza at 800 m asl (Fuerteventura), *O. angustissima*: dry coastal regions	Moroccan cedar forests at high altitudes, mountains of SW Europe, dry lowland areas of SW Mediterranean to central Asia	Multiseriate rays with mainly square to procumbent cells	Bramwell and Bramwell 1974; Schweingruber 1990; Turini et al. 2010	Multiple shifts toward insular woodiness within the genus (probably ≥6, of which 2 were on the CI); most CI species are herbaceous
Malpighiales:						
Euphorbiaceae:						
Euphorbia (25/25/~2000)	Herbs, shrubs or trees ≤30 m	Drier coastal regions (subgenus *Esula*), occasionally in laurel forests	Drier coastal regions or laurel forests of Cape Verde Islands, Azores, Madeira (subgenus *Esula*), predominantly in wet montane forest understories or bogs in Hawaii (subgenus *Chamaesyce*)	Long vessel elements, wide scalariform intervessel pitting in the succulent species, multiseriate rays with only upright cells or mixed upright, square, and procumbent	Carlquist 1970*b*, 1974; Bramwell and Bramwell 1974; Wagner et al. 1990; Press and Short 1994; Yang and Berry 2011; Horn et al. 2012	Primarily as well as secondarily woody species; secondary woodiness evolved ≥7 times throughout the genus, of which 2 were on the CI; woodiness on the CI did not develop on the islands

Table 1

(*Continued*)

APG III classification; APG order; family, genus[a]	Habit of entire genus	Habitat of secondarily woody species		Protracted juvenilism in wood	References	Remarks
		On the CI	Outside the CI			
Eurosids II:						
Brassicales:						
Brassicaceae:						
Brassica (1/3/~40)	Mostly herbs, occasionally shrubs (*B. oleracea*)	*B. oleracea* (walking-stick cabbage): irrigated gardens of the dry lowland areas and more humid zones	Comparable situation in Channel Islands, Mediterranean region	Flat LOA curve for vessel elements, multiseriate rays with procumbent to square ray cells (F. Lens, pers. obs.)	Kowal and Cutler 1974; Appel and Al-Shehbaz 2003; Warwick and Sauder 2005; Franzke et al. 2009; Warwick et al. 2010	Local inhabitants of the CI imported seeds of *B. oleracea* ~2000–3000 yr ago, resulting in the walking-stick phenotype
Crambe (13/13/41)	Herbs or shrubs ≤2 m	Humid laurel forest, pine forest or dry lowland scrub	Madeira: in ravines, rocks, and cliffs, mainly in the western part usually near the coast ≤100 m asl	Multiseriate rays with mainly upright and square cells	Carlquist 1971, 1974; Bramwell and Bramwell 1974; Press and Short 1994; Francisco-Ortega et al. 1999, 2002	Woodier species (e.g., *C. arborea*) grow in dryer lowland habitat, less-woody species in the laurel forests (e.g., *C. strigosa*)
Descurainia (7/7/45)	Herbs or shrubs ≤1 m	Lowland scrub, pine forest, high-altitude desert ecological zones >2000 m asl	Not applicable	Multiseriate rays with mainly upright and square cells	Carlquist 1971, 1974; Bramwell and Bramwell 1974; Goodson et al. 2006; Franzke et al. 2009	Closest relative of insular woody *Descurainia* clade is *D. tanacetifolia*, including *D. tanacetifolia* ssp. *suffruticosa*, which is a "woody herb" with only a woody basal stem part; since we do not consider this species a truly woody species, *Descurainia* can be considered an example of insular woodiness
Erysimum (3/3/~180)	Herbs or shrubs ≤2 m	Lower and forest zones ≤1000 m asl, high-altitude zone 1500–2200 m asl	Madeira (rocks, laurel forests), NW Africa, California offshore islands (e.g., Guadeloupe and San Clemente)	Multiseriate rays with mainly upright and square cells (F. Lens, pers. obs.)	Carlquist 1971, 1974; Bramwell and Bramwell 1974; Press and Short 1994; Warwick et al. 2010	Woodiness not evolved on the CI
Lobularia (1/3/4)	Herbs or shrubs ≤0.7 m (*L. canariensis* ssp. *fruticosa*)	*L. canariensis* ssp. *palmensis*: in and below forest zones, on cliffs at 500–1600 m asl; most subspecies of *L. canariensis* grow in the xerophytic zone 0–600 m asl	Woodiest taxon *L. canariensis* ssp. *fruticosa*: steep cliffs and gravelly slopes of Cape Verde Islands, sometimes in dry coastal zone but more often in more mesic montane conditions, 200–1250 m asl	Rays very vaguely present, consisting of few upright ray cells (F. Lens, pers. obs.)	Borgen 1987; Appel and Al-Shehbaz 2003; Beilstein et al. 2008	Most drought-tolerant species in the genus are the annuals *L. arabica* and *L. libyca* growing in deserts or xerophytic seashore communities outside the CI
Parolinia (6/6/6)	Shrubs ≤4 m	Dry sunny slopes 100–500 m asl	Not applicable	Multiseriate rays with mainly square to procumbent cells	Bramwell 1970; Carlquist 1971, 1974; Bramwell and Bramwell 1974; Khosravi et al. 2009	Relatives are not yet discovered, but likely woody *Diceratella*, herbaceous *Anastacia*, or herbaceous *Morettia* are good candidates; still some doubt about insular or secondary woodiness

Resedaceae:						
Reseda (incl. *Oligomeris*, *Randonia*, *Ochradenus*; 1/5/~77)	Herbs or small shrubs	Dry coastal regions	Desert shrubs from the SE Mediterranean region to the Middle East and West Pakistan, Socotra, western and central Sahara Desert, South Arabian Peninsula, Socotra Islands	Multiseriate rays with mainly upright and square cells	Bramwell and Bramwell 1974; Carlquist 1998*b*; Kubitzki 2003; Martín-Bravo et al. 2007	4 independent colonizations to the CI in the genus, of which 2 resulted in secondary woodiness; the secondarily woody CI species (*R. scoparius* and *Oligomeris linifolia*) have woody relatives
Malvales:						
Malvaceae:						
Lavatera (1/3/18)	Herbs or shrubs	Dry lowland scrub, open areas at borders of laurel forest	Dry regions of California, Mexico, Ethiopia, western Australia	Multiseriate rays consisting of mixed upright, square, and procumbent body ray cells	Bramwell and Bramwell 1974; Schweingruber 1990; Fuertes Aguilar et al. 2002; Bayer and Kubitzki 2003; Escobar García et al. 2008	Highly polyphyletic; CI species *L. acerifolia* is sister to woody *L. maritima*, so no truly insular woody species; secondary woodiness developed ≥3 times
Navaea (1/1/1)	Shrubs	Northern slopes of the oldest parts of the island Tenerife, lowland regions	Not applicable	?	Bramwell and Bramwell 1974; Fuertes Aguilar et al. 2002; Bayer and Kubitzki 2003; Escobar García et al. 2008	*N. phoenicea* is placed basal to the *Lavatera-Malva* complex, so possibly insular woody relict taxon
Sister to asterids:						
Caryophyllales:						
Amaranthaceae:						
Bassia (incl. *Chenoleoides*; 1/1/21)	Herbs or small shrubs	Dry beach vegetation	Dry regions in western Mediterranean to East Asia	Multiseriate rays with mainly upright cells	Bramwell and Bramwell 1974; Kadereit and Freitag 2011; Heklau et al. 2012	Woodiness not evolved on the CI; sister species of *B. tomentosa* is also woody and grows from Morocco to Iraq
Salsola (5/5/116)	Herbs or small shrubs	Dry lowland regions	Dry regions in northern Africa and Asia	Multiseriate rays with mainly upright cells	Schweingruber 1990; Kühn 1993; Kadereit et al. 2006; Wen et al. 2010	≥2 independent colonizations toward the CI; woodiness not evolved on the CI; all the woody species also occur on the continent; successive cambia present
Sarcocornia (1/1/16)	Herbs or small shrubs	Coastal salty soils	Coastal salty soils or deserts throughout the world	?	Scott 1977; Wilson 1980; Kühn 1993; Kadereit et al. 2006	Woodiness not evolved on the CI; all the woody species also occur on the continent
Suaeda (4/5/~100)	Mainly herbs, sometimes small shrubs	Dry and salty coastal regions	Sea coasts and inland saline soils throughout the world	Multiseriate rays with mainly upright cells or rays absent	Hopkins and Blackwell 1977; Schweingruber 1990; Kühn 1993; Schütze et al. 2003; Heklau et al. 2012	≥3 independent colonizations toward the CI; woodiness not evolved on the CI; all the woody species also occur on the continent; successive cambia present
Traganum (1/1/2)	Small shrubs ≤1 m	Sand dunes, coastal regions	Drier parts in northern Africa, eastern Mediterranean	Raylessness	Bramwell and Bramwell 1974; Kühn 1993; Akhani et al. 2007; Heklau et al. 2012	Close relatives are secondarily woody continental species, so *Traganum* is not truly insular woody
Caryophyllaceae:						
Silene (1/26/~700)	Herbs or small shrubs ≤1 m	*S. berthelotiana*: open spots in pine forests	Open and dry alpine vegetation on Hawaiian Islands ≤3500 m asl	Multiseriate rays with upright ray cells or raylessness	Bramwell and Bramwell 1974; Carlquist 1974, 1995; Wagner et al. 1990; Bittrich 1993; Eggens et al. 2007; Harbaugh et al. 2010; Greenberg and Donoghue 2011	Probably ≥2 independent shifts to insular woodiness in the genus, of which 1 was on the CI, but phylogeny is too poorly resolved

Table 1

(Continued)

APG III classification; APG order; family, genus[a]	Habit of entire genus	Habitat of secondarily woody species		Protracted juvenilism in wood	References	Remarks
		On the CI	Outside the CI			
Polygonaceae:						
Rumex (1/5/~200)	Mostly herbs, rarely shrubs ≤2 m or vines ≤12 m	Dry coastal regions and midelevation scrub	Hawaiian Islands (variable: mesic to wet forest and subalpine woodland 660–3050 m asl), China (dry mountain slopes at 600–3200 m asl)	Multiseriate rays with a mix of procumbent, square, and upright cells	Bramwell and Bramwell 1974; Carlquist 1974, 2003*a*; Brandbyge 1993; Wagner et al. 1990; Anjen et al. 2003; Sanchez and Kron 2008; Sanchez et al. 2009; Burke et al. 2010	1 shift toward insular woodiness
Euasterids I:						
Gentianales:						
Gentianaceae:						
Ixanthus (1/1/1)	Suffrutescent herbs to small shrubs ≤2 m	Moist laurel forest habitat	Not applicable	Wood rayless in earlier portion, rays relatively infrequent with mainly upright cells	Bramwell and Bramwell 1974; Carlquist 1974, 1984; Thiv et al. 1999; Struwe et al. 2002; Thiv and Kadereit 2002; Mansion and Struwe 2004	Most individuals growing in the wild can be considered woody herbs, but others are woodier
Rubiaceae:						
Rubia (1/2/~80)	Mostly herbs, occasionally shrubs (*R. fruticosa*)	*R. fruticosa*: very common throughout the dry lower zones	High-elevation semideserts and steppes in central Asia, often 1000–3000 m asl	Flat LOA curve for vessel elements, raylessness	Bramwell and Bramwell 1974; Koek-Noorman 1976; Ehrendorfer and Schönbeck-Temesy 2005; Bremer and Eriksson 2009	Herbaceous *R. angustifolia* grows in much more humid conditions (e.g., laurel forests)
Lamiales:						
Lamiaceae:						
Lavandula (5/5/~36)	Herbs or shrubs	Commonly in dry coastal regions ≤600 m asl or in pine forests ≤1600 m asl	Cape Verde Islands	Mainly upright to square cells in multiseriate rays	Bramwell and Bramwell 1974; Carlquist 1992*a*; Upson and Andrews 2004	Probably primary woodiness (subgenera *Subaudia* and *Lavandula*) as well as insular woodiness (subgenus *Fabricia*)
Micromeria (15/15/~70)	Herbs or shrubs	Mainly in dry to medium-dry lowland habitats, occasionally in pine forests or in high-altitude desert ecological zone	Similar dry habitats in Madeira and Cape Verde Islands	Rays vaguely present, uniseriate with few upright cells	Bramwell and Bramwell 1974; Schweingruber 1990; Meimberg et al. 2006; Bräuchler et al. 2010	1 shift toward insular woodiness
Salvia (4/4/~900)	Herbs and shrubs ≤2 m, sometimes more	Commonly found in the dry lower zones, occasionally in montane region	Equatorial uplands of Africa (SW, NW, and NE of Africa, Madagascar, Somalia) and South America, SW US	Mainly upright to square cells in multiseriate rays	Epling 1938; Bramwell and Bramwell 1974; Carlquist 1974, 1992*a*; Hedge 1974; Walker et al. 2004	Several independent shifts toward insular woodiness within the genus, of which probably 1 was on the CI
Sideritis (24/24/~148)	Herbs or shrubs	All ecological zones from dry coastal region to more humid montane and pine forests ≤2100 m asl, humid laurel forests	Dry or exposed habitats in Madeira	Mainly upright to square cells in multiseriate rays	Bramwell and Bramwell 1974; Press and Short 1994; Barber et al. 2002; Bendiksby et al. 2011	1 shift toward insular woodiness

Plantaginaceae:						
Campylanthus (1/1/12)	Shrubs ≤2 m	Dry lower zone, often on rocks and cliffs	Dry regions in Cape Verde Islands, NE Africa, Socotra, Yemen, Pakistan	Decreasing LOA curve for vessel elements, mainly upright to square cells in multiseriate rays (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Fischer 2004; Albach et al. 2005	1 shift toward insular woodiness on the CI
Digitalis (incl. *Isoplexis*; 3/3/23)	Herbs and shrubs ≤2 m	Often in laurel forests or in pines forests at 600–1000 m asl	Madeira (laurel forests)	Decreasing LOA curve for vessel elements, mainly upright to square cells in multiseriate rays (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Carlquist 1974; Press and Short 1994; Bräuchler et al. 2004; Albach et al. 2005	1 shift toward insular woodiness
Globularia (incl. *Lytanthus*; 3/3/23)	Herbs and (sub)shrubs ≤2 m (*G. salicina*)	Dry coastal regions, mountain cliffs ≤1600 m asl, cliffs in pine zone	Cape Verde Islands	Mainly upright to square cells in multiseriate rays	Bramwell and Bramwell 1974; Carlquist 1974, 1992*b*; Albach et al. 2005	1 shift toward insular woodiness
Kickxia (1/5/9)	Herbs or small shrubs	Dry rocky slopes, basalt cliffs	Dry regions of northern Africa, eastern Mediterranean, southwestern Asia	?	Bramwell and Bramwell 1974; Ghebrehiwet 2001; Fischer 2004; Albach et al. 2005	1 shift toward insular woodiness on the CI
Plantago (3/14/~250)	Rosette herbs, (sub)shrubs ≤2 m, miniature trees ≤1 m	Dry coastal region, rocky places in forest zone and below, rocky places from lower zone to the mountains, high-altitude mountains ≤1800 m asl among rocks and boulders	Hawaiian Islands (*P. princeps*: rain forests, mesic forests, waterfalls), Juan Fernandez Islands, South America and Africa (equatorial uplands), St. Helena	Raylessness (except in larger stems)	Carlquist 1970*c*, 1974, 1992*b*; Bramwell and Bramwell 1974; Wagner et al. 1990; Rønsted et al. 2002; Albach et al. 2005; Dunbar-Co et al. 2008	Several independent shifts toward insular woodiness within the genus; on the CI, 3 colonizations, of which ≥1 resulted in insular woodiness; putative back-colonization from the CI to NW Africa
Solanales:						
Convolvulaceae:						
Convolvulus (11/14/~200)	Herbs, shrubs, trees, or lianas ≤4 m	Dry coastal zone, laurel forests, often on rocks or cliffs	Madeira (mainly in humid gullies and ravines among rocks), Selvagems, Mediterranean	Rays with mainly upright or mainly procumbent ray cells	Sa'ad 1967; Bramwell and Bramwell 1974; Carlquist 1974; Carlquist and Hanson 1991; Press and Short 1994; Stefanović et al. 2002; Carine et al. 2004	2 independent shifts toward the CI leading to secondary woodiness; insular woodiness in *C. caput-medusae*, *C. scoparius*, *C. floridus* is doubtful because of close relationship with woody continental *C. dorycnium*; also back-colonization toward continent
Unplaced:						
Boraginaceae:						
Echium (19/25/60)	Shrubs ≤3 m, rosette trees ≤4 m	Dry coastal rocky regions, cliffs, semidesert habitats, laurel forests, high-altitude desert ecological zone	Cape Verde Islands, Madeira (sea cliffs and dry rocky slopes along roads, laurel forests)	Multiseriate rays with a mix of procumbent, square, and upright cells or with mainly upright ray cells	Carlquist 1970*a*, 1974; Bramwell and Bramwell 1974; Press and Short 1994; Böhle et al. 1996; García-Maroto et al. 2009	1 major shift toward insular woodiness, 3 reversals back to secondary herbaceousness
Euasterids II:						
Apiales:						
Apiaceae:						
Bupleurum (2/3/~190)	Mostly herbs, occasionally shrubs (e.g., *B. salicifolium*)	Often on cliffs in the lower zone ≤1000 m asl, mountain region	*B. salicifolium*: scattered in dry, rocky places throughout the mountains of Madeira, generally >1000 m asl	?	Bramwell and Bramwell 1974; Cannon 1994; Neves and Watson 2004	*B. fruticosum* is primarily woody, from molecular data and wood anatomy; putative back-colonization from the CI to NW Africa

Table 1

(Continued)

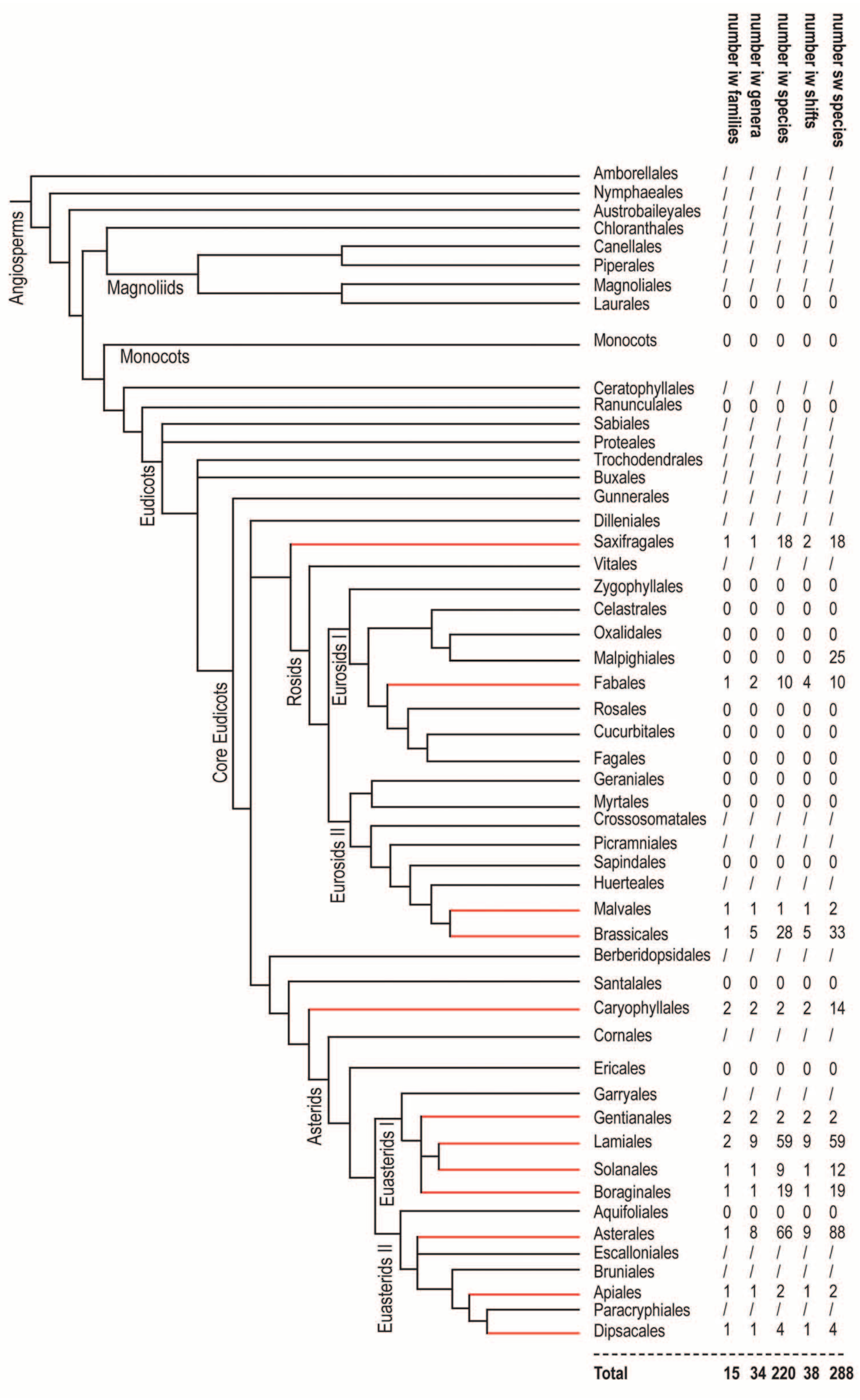
APG III classification; APG order; family, genus[a]	Habit of entire genus	Habitat of secondarily woody species		Protracted juvenilism in wood	References	Remarks
		On the CI	Outside the CI			
Asterales:						
Asteraceae:						
Argyranthemum (19/19/23)	Shrubs ≤1.5 m	Dry coastal regions, pine forests, laurel forests, high-altitude desert zone 1900–2200 m asl	Mainly on wet coastal cliffs, Madeira	Multiseriate rays with mainly upright and square cells (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Press and Short 1994; Francisco-Ortega et al. 1997; Anderberg et al. 2007; Oberprieler et al. 2009	1 shift toward insular woodiness
Asteriscus (4/5/8)	Herbs or shrubs ≤0.7 m	Dry coastal zones, semiarid mountain slopes, or laurel forests	Cape Verde (arid slopes), Moroccan desert	?	Bramwell and Bramwell 1974; Halvorsen and Borgen 1986; Francisco-Ortega et al. 2001*b*; Goertzen et al. 2002; Anderberg et al. 2007; Anderberg 2009	2 independent shifts toward insular woodiness; woody shrubs taller in laurel forests
Atractylis (3/3/30)	Herbs or small shrubs	Rocky coasts near the sea	Not applicable	?	Bramwell and Bramwell 1974; Anderberg et al. 2007; Susanna and Garcia-Jacas 2009	1 shift toward insular woodiness
Bethencourtia (segregated from *Senecio*; 3/3/3)	Shrubs ≤1 m	Dry midelevation rocks, borders of laurel forests, high-altitude desert zone ~2000 m asl	Not applicable	?	Bramwell and Bramwell 1974; Anderberg et al. 2007; Pelser et al. 2007, 2010*a*; Nordenstam et al. 2009	1 shift toward insular woodiness
Carlina (5/5/28)	Herbs, shrubs, or treelets ≤3 m	High-altitude desert zone 1900–2100 m asl, dry cliffs in dry lower zone 150–600 m asl, cliffs and rocks in lower zone	SE Aegean Islands	Multiseriate rays with upright to square cells (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Carlquist 1974; Anderberg et al. 2007; Susanna and Garcia-Jacas 2009; Wahrmund et al. 2010	1 shift toward insular woodiness on the CI
Cheirolophus (16/16/25)	Shrubs ≤3 m	Often in dry coastal region on cliffs, occasionally in high-altitude desert zone 2000–2200 m asl	Western Mediterranean, northern Africa, and Macaronesia	Multiseriate rays with upright to square cells (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Susanna et al. 1999; Anderberg et al. 2007; Susanna and Garcia-Jacas 2009	Macaronesian group monophyletic but with woody ancestors
Kleinia (segregated from *Senecio*; 1/1/~50)	(Succulent) herbs or (succulent) shrubs ≤2 m	Very common in the dry lower zone	Africa, Madagascar, Arabia, east to India and Sri Lanka, often in dry areas	Multiseriate rays with upright to square cells (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Carlquist 1974; Pelser et al. 2007, 2010*a*; Nordenstam et al. 2009	Also many woody species outside the CI, so woodiness probably did not evolve on the CI
Launaea (1/4/54)	Herbs or (rosette) shrubs ≤2 m	Extremely dry coastal regions, especially on the southern slopes, ≤700 m asl	Dry regions (often semidesert areas) of Mediterranean region (incl. Balearic Islands), Atlas Mountains (NW Africa), Saharo-Arabian region, Irano-Turanian region, India	Multiseriate rays with mainly upright to square cells (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Kilian 1997; Anderberg et al. 2007; Kilian et al. 2009	Woodier species occur in much more arid environments; woody species not confined to islands, so it might be that woodiness did not evolve on the CI

Pericallis (1/13/15)	Herbs or small shrubs	Mainly in laurel forests, sometimes in pine forests	Laurel forests of Madeira	?	Bramwell and Bramwell 1974; Panero et al. 1999; Anderberg et al. 2007; Pelser et al. 2007, 2010*a*; Nordenstam et al. 2009	≥2 independent shifts toward insular woodiness, according to Panero et al. 1999; however, according to Bramwell and Bramwell 1974, only *P. appendiculata* should be considered a truly woody species, while the others are (woody) herbs; we follow the more strict definition of Bramwell and Bramwell 1974
Sonchus (25/33/~92)[b]	Herbs, (rosette) shrubs, or trees ≤5 m	Mainly on coastal cliffs and lower dry zones, also in more humid forest (pine and laurel) zones	Cape Verde Islands, Madeira (coastal cliffs and rocks, wet ravines 800–1200 m asl), Juan Fernandez Islands, San Ambrosio Islands	Flat LOA, relatively long vessel elements, scalariform intervessel pitting with wide apertures, rays with mainly upright cells	Carlquist 1962, 1974; Bramwell and Bramwell 1974; Press and Short 1994; Kim et al. 2007	3 independent shifts toward insular woodiness throughout the genus, of which 1 was on the CI; primary as well as secondary herbaceousness
Gonospermum (incl. *Lugoa*; 6/7/7)	Shrubs ≤4 m	Lower zones and laurel forest zones on cliffs, 100–1000 m asl	Not applicable	Multiseriate rays with mainly upright to square cells (F. Lens, pers. obs.)	Bramwell and Bramwell 1974; Carlquist 1974; Francisco-Ortega et al. 2001*a*; Anderberg et al. 2007; Oberprieler et al. 2009	CI *Tanacetum* is sister to CI *Gonospermum*, but resolution is poor
Dipsacales:						
Caprifoliaceae:						
Pterocephalus (4/4/~30)	Herbs or shrubs	Coastal rocks, in mountain areas and upper forest zone ≤1900 m asl, high-altitude desert zone 2000–2200 m asl	Irano-Oriental region, extending to eastern Mediterranean, Macaronesia, eastern Africa, and central Asia	Absent	Bramwell and Bramwell 1974; Carlquist 1982; Press and Short 1994; Carlson et al. 2009	1 shift toward insular or secondary woodiness on the CI; still some doubt about insular or secondary woodiness

Note. APG = Angiosperm Phylogeny Group; LOA curve = length-on-age curve; pers. obs. = personal observation.

[a] The three numbers in parentheses are the number of native secondarily woody species on the CI, the number of CI species, and the total number of species. Insular woody genera are underlined.

[b] Includes *Atalanthus*, *Babcockia*, *Chrysoprenanthes*, *Dendroseris*, *Lactucosonchus*, *Sventenia*, and *Thamnoseris*, among others.



	number iw families	number iw genera	number iw species	number iw shifts	number sw species
Amborellales	/	/	/	/	/
Nymphaeales	/	/	/	/	/
Austrobaileyales	/	/	/	/	/
Chloranthales	/	/	/	/	/
Canellales	/	/	/	/	/
Piperales	/	/	/	/	/
Magnoliales	/	/	/	/	/
Laurales	0	0	0	0	0
Monocots	0	0	0	0	0
Ceratophyllales	/	/	/	/	/
Ranunculales	0	0	0	0	0
Sabiales	/	/	/	/	/
Proteales	/	/	/	/	/
Trochodendrales	/	/	/	/	/
Buxales	/	/	/	/	/
Gunnerales	/	/	/	/	/
Dilleniales	/	/	/	/	/
Saxifragales	1	1	18	2	18
Vitales	/	/	/	/	/
Zygophyllales	0	0	0	0	0
Celastrales	0	0	0	0	0
Oxalidales	0	0	0	0	0
Malpighiales	0	0	0	0	25
Fabales	1	2	10	4	10
Rosales	0	0	0	0	0
Cucurbitales	0	0	0	0	0
Fagales	0	0	0	0	0
Geraniales	0	0	0	0	0
Myrtales	0	0	0	0	0
Crossosomatales	/	/	/	/	/
Picramniales	/	/	/	/	/
Sapindales	0	0	0	0	0
Huerteales	/	/	/	/	/
Malvales	1	1	1	1	2
Brassicales	1	5	28	5	33
Berberidopsidales	/	/	/	/	/
Santalales	0	0	0	0	0
Caryophyllales	2	2	2	2	14
Cornales	/	/	/	/	/
Ericales	0	0	0	0	0
Garryales	/	/	/	/	/
Gentianales	2	2	2	2	2
Lamiales	2	9	59	9	59
Solanales	1	1	9	1	12
Boraginales	1	1	19	1	19
Aquifoliales	0	0	0	0	0
Asterales	1	8	66	9	88
Escalloniales	/	/	/	/	/
Bruniales	/	/	/	/	/
Apiales	1	1	2	1	2
Paracryphiales	/	/	/	/	/
Dipsacales	1	1	4	1	4
Total	**15**	**34**	**220**	**38**	**288**

Fig. 3 APG III (2009) phylogeny showing all ordinal lineages including truly insular woody species (red branches) of the Canary Islands with reference to the number of families, genera, species, and shifts. A solidus (/) indicates that there are no native species belonging to this group on the Canary Islands. iw = insular woody; sw = secondarily woody.

Table 1 also indicates that most of the insular woody species are confined to the dry lower zone of the Canary Islands, although the genera *Argyranthemum*, *Crambe*, *Echium*, *Gonospermum*, *Sideritis*, and *Sonchus* are much more widespread and also occur in pine forests and the much more humid laurel forests. However, when one looks carefully at the distribution of these six insular woody genera within the laurel forests, most of them typically occur in the lower, drier laurel forest parts intermixed with pine forests or in sunny places and rocks within the laurel forests (del Arco et al. 2010). *Ixanthus* and *Digitalis* are typical shrubs of the laurel forests, but these shrubs never produce thick, woody stems. A small percentage of the insular woody species—for instance, species of the genera *Aeonium*, *Descurainia*, *Echium*, *Micromeria*, and *Pterocephalus*—also occur in the high-altitude desert from 1900 to 2500 m asl, where frost occurs. Evidently, frost temperatures increase with increasing height, especially during the winter months January and February, but strong frost events below −6°C do not occur (Martín Osorio et al. 2007).

According to the latest land plant checklist of the Canary Islands (Arechavaleta et al. 2010), the current flora contains ~1337 native species of flowering plants, of which 1104 are traditional dicots and 234 are monocots (table 2). Within the traditional dicots—the angiosperm lineages that are capable of producing wood by a vascular cambium—it is surprising to see that 59% of the species are herbaceous (increasing to 66% within angiosperms as a whole), 26% are secondarily woody (including 20% insular woody species), and 11% are primarily woody; in 4% of the species, the origin of woodiness remains doubtful. When only the endemic species of traditional dicots are taken into account, the number of herbaceous endemics significantly drops, from 59% to 34%, while the proportions of secondarily and insular woody species increase drastically (from 26% to 46% and from 20% to 40%, respectively).

Discussion

Differences in Colonization and Radiation Events among Insular Woody Lineages

As summarized in table 2 and figure 3, 38 shifts to insular woodiness on the Canary Islands gave rise to 220 truly insular woody species belonging to 34 genera and 15 families, representing a significant proportion of the native traditional dicots (20%). Of the 15 largest Canary Island genera with 10 or more endemic species (Whittaker and Fernández-Palacios 2010, p. 229), nine are characterized by insular woody species (*Aeonium*, *Argyranthemum*, *Convolvulus*, *Crambe*, *Echium*, *Lotus*, *Micromeria*, *Sideritis*, and *Sonchus*), in total representing almost 70% of the insular woody species found. Most of these larger radiations are characterized by a single colonization followed by radiation into several insular woody species, while *Aeonium*, *Convolvulus*, and *Lotus* are characterized by two shifts (table 1). In *Asteriscus* and *Ononis*, two independent shifts have led to only a handful of species, while the genera *Campylanthus*, *Ixanthus*, *Kickxia*, *Lobularia*, *Pericallis*, *Rubia*, *Rumex*, and *Silene* each harbor only one insular woody species (table 1). This demonstrates that radiations within a limited number of insular woody genera (9 out of 34) greatly contributed to the Canary Island flora, but the reason for this remains a mystery. Most likely, many more herbaceous colonizers must have reached the Canary Islands from the African continent or the Mediterranean region, leading to potentially even more insular woody species, but not every colonization event resulted in a successful settlement on the island (Whittaker and Fernández-Palacios 2010).

Although colonizations from the mainland toward the Canary Islands were plentiful, Caujapé-Castells (2011) demonstrated, on the basis of molecular phylogenies, that "biodiversity boomerangs" from the islands toward the mainland have occurred in at least 30 genera, of which six include insular woody species (*Aeonium*, *Bupleurum*, *Convolvulus*, *Lotus*,

Table 2

Overview of the Life Forms of Native Angiosperms on the Canary Islands

	Traditional dicots	Monocots
Total number of native angiosperm species	1104	234
Secondarily woody species	288 (26%)	Not applicable
Insular woody species (included in secondarily woody species)	220 (20%)	Not applicable
Primarily woody species	122 (11%)	Not applicable
Herbaceous species	649 (59%)	232 (99%)[a]
Potential secondarily or insular woody species	45 (4%)	Not applicable
Endemic species	507 (46%)	25 (11%)
Secondarily woody endemic species	234 (46%)[b]	Not applicable
Insular woody endemics (included in secondarily woody endemics)	202 (40%)[b]	Not applicable
Primarily woody endemics	64 (13%)[b]	Not applicable
Herbaceous endemics	174 (34%)[b]	24 (96%)[c]
Potential secondarily or insular woody endemics	35 (7%)[b]	Not applicable

Note. The proportions of secondarily woody species, insular woody species, primarily woody species, and herbaceous species are compared to the total number of native flowering plants species. Percentages in rows after "Endemic species" are based on the endemic species. Data were compiled on the basis of the checklist of Arechavaleta et al. (2010).

[a] Two native *Dracaena* spp. were excluded.

[b] Percentage is based on the 507 endemic species.

[c] The exception is *Dracaena tamaranae*; see "Herbaceousness Prevails in Canary Island Angiosperms" for details.

Navaea, and *Plantago*). Consequently, mainland northwest Africa not only is one of the main sources of the present Canary Island flora (ranked second after the Mediterranean region) but is also a substantial historical sink for the archipelago's biodiversity (Caujapé-Castells 2011). This is especially true for the so-called Macaronesian enclave, the coastal region of northwestern mainland Africa between Agadir (Morocco) and Nouadhibou (Mauritania).

Age of Insular Woody Lineages

Dating estimates of Canary genera with insular woody species are known for only a few genera, such as *Aeonium*, *Convolvulus*, *Crambe*, *Echium*, *Sideritis*, and *Sonchus* (Kim et al. 2008; García-Maroto et al. 2009). These age estimates indicate that the insular woody subgroups evolved ~8.5–8 Ma (*Aeonium* and *Crambe*), 5.5 Ma (*Sonchus*), ~3 Ma (*Sideritis* and *Echium*; Kim et al. 2008), and ~1.5 Ma (*Convolvulus*; Carine 2005), while García-Maroto et al. (2009) found an older age for the insular woody subgroup of *Echium* (~6 Ma). Therefore, although information about the evolutionary age of insular woodiness is very incomplete and potentially prone to errors, the available dated phylogenies point to recent radiations as well as older relict insular woody groups. Generally, this agrees with the concept of Vargas (2007), who searched for molecular phylogenies to reveal crown-based lineages (recent clades) versus stem-based lineages (lineage relictualism). According to this concept, four insular woody genera should be considered relicts (*Argyranthemum*, *Crambe*, *Ixanthus*, and *Navaea*), while seven are regarded as recent clades (*Aeonium*, *Asteriscus*, *Echium*, *Gonospermum*, *Pericallis*, *Sideritis*, and *Sonchus*). However, at least one crown-based lineage (*Aeonium*) is much older than some of the stem-based lineages, assuming that not all crown-based groups have to be recent (and vice versa: not all lineage-based groups are by definition relicts).

The younger insular woody lineages are especially interesting to investigate in the light of major paleoclimatic drought events, such as the formation of the Sahara (starting 5–6 Ma; Potts and Behrensmeyer 1992; Schuster et al. 2006) and the onset of cooler and drier periods during the glaciation cycles, co-occurring with lower sea levels (during the past 2–3 Myr; García-Talavera 1997; Geldmacher et al. 2001; Meco et al. 2005, 2006; Fernández-Palacios et al. 2009). If many insular woody groups would have ages of 3 Myr or younger, as demonstrated in some of the large insular woody subclades of *Convolvulus* (Carine 2005) and *Sideritis* (Kim et al. 2008), or if some other insular woody groups have radiated in that period (as García-Maroto et al. 2009 demonstrated for *Echium*), this would provide extra arguments for our new hypothesis linking secondary woodiness with increased drought resistance (see below for more arguments).

Protracted Juvenilism in Wood: Interpret with Caution!

Table 1 shows that most of the insular and secondarily woody genera are characterized by protracted juvenilism in their wood, which is also confirmed in the genera with an ambiguous origin of woodiness. Decreasing or flat length-on-age curves for vessel elements and an abundance of square to upright cells in rays are commonly found (fig. 2), while other forms of paedomorphosis in the Carlquistian sense, such as scalariform intervessel pitting with wide apertures, rays with exclusively upright cells, or raylessness, are scarce (Carlquist 2009, 2012). Although the value of these wood features for identifying secondarily woody groups has been validated in our study on the basis of independent molecular phylogenies, one should always be careful when interpreting this wood anatomical syndrome. First, "protracted juvenilism" should replace the commonly used term "paedomorphosis" (Carlquist 1962), which actually is incorrect with respect to secondary woodiness because secondarily woody taxa add a woody growth stage on top of the ancestral herbaceous growth stage (i.e., peramorphosis; Olson 2007). Second and more important, there is growing evidence that protracted juvenilism in wood features is related to the specific growth forms, such as rosette trees, stem succulents, or slender-stemmed shrubs, that were investigated by Carlquist (1962) in his pioneering paedomorphosis paper, instead of representing information about the evolutionary origin of woodiness of a particular taxon. This is further emphasized by one of Carlquist's most recent reviews, where he links protracted juvenilism in wood with sympodial growth forms that are characteristic in early-diverging, (primarily) woody angiosperms (Carlquist 2009). Independent molecular phylogenies show that many more primarily woody taxa with growth forms comparable to the ones commonly found in secondarily woody taxa also exhibit, for example, rays with mainly upright cells, such as those in the ericaceous dwarf shrubs *Cassiope*, *Corema*, and *Empetrum* (Carlquist 1989), the pachycaul rosette trees in the epacrids clade of Ericaceae (Lens et al. 2003), and the *Moringa* bottle trees (Olson and Carlquist 2001). The same is true for the tall, primarily woody stem succulents in the family Didiereaceae (e.g., *Alluaudia*, *Decarya*, and *Didierea*) that are derived from the smaller *Calyptrotheca*-like shrubs (Carlquist 1998*a*; Applequist and Wallace 2000). Also, with regard to the length-on-age curves for vessel elements, the link between Carlquistian paedomorphosis and secondary woodiness is not straightforward: Mabberley (1974) emphasizes that the shape of the curves depends on the position in the stem and does not fit with Carlquist's ideas on paedomorphosis, while it has been known for a long time that flat length-on-age curves for vessel elements are characteristic of primarily woody species with storied cambia (Bailey 1923). In conclusion, protracted juvenilism in wood features is present in secondarily woody species, but these wood features seem to be more closely associated with primarily or secondarily woody taxa that have specific plant habits.

If protracted juvenilism is indeed strongly linked to life forms showing limited growth, then these characters should have a function. For instance, Carlquist (2012) hypothesized that upright ray cells in wood are more efficient than square or procumbent ones in vertical flow of sugar transport, which would make sense because radial transport in woody taxa with limited wood accumulation is of less significance. That may explain why upright ray cells are gradually replaced by procumbent ray cells in mature wood of tall secondarily woody trees, such as *Nesohedyotis*, that can grow up to 7 m in height (Lens et al. 2009). Likewise, wide-gaping intervessel pits are often present in the wood of stem succulents, which may or may not be secondarily woody. Apparently, the vessel walls in these succulents do not need to be reinforced mechanically by smaller pits, likely because the turgor pressure in the water-filled cells provide enough mechanical strength (Dulin and Kirchoff 2010). A possible function for the flat or continuously decreasing length-on-age curves of vessel elements in woody plants has not been forthcoming. Vessel elements are known to be shorter in species from dry environments (Carlquist 1966; Baas et al. 1983) or in small shrubs (Baas et al. 1984), and there might be a greater chance for air bubbles to be trapped more frequently near the vessel element tails when vessel elements are shorter (Carlquist 2012). However, there is general consensus that the length of entire vessels greatly overwhelms the importance of vessel element length in the water transport mechanism of plants (Sperry et al. 2007; Lens et al. 2011).

Why Does Insular Woodiness Occur on the Canary Islands and Beyond?

A sound explanation for why insular woodiness has evolved so many times in parallel during the evolution of flowering plants on islands is lacking. Various island hypotheses have been put forward, such as (1) the competition hypothesis (plants gain competitive advantage by growing taller into shrubs and trees; Darwin 1859; Tilman 1988; Givnish 1995), (2) the longevity hypothesis (woody plants live longer and are able to produce more seeds; Wallace 1878), (3) the moderate-insular-climate hypothesis (release from seasonality allows herbs to grow throughout the year and become woody; Carlquist 1974, 2012), and (4) the herbivore hypothesis (absence of large native herbivores on islands allows herbaceous plants to grow longer and become woody; Carlquist 1974). The first hypothesis was extended by Givnish (1998; taxon-cycling hypothesis) and the second by Böhle et al. (1996; promotion-of-outcrossing hypothesis), but convincing experimental data for all these hypotheses are scarce to absent. For instance, in an attempt to investigate the adaptive significance of herbaceous plant height in the understory of forests, a 7% increase in leaf cover of herbaceous plants led roughly to a doubled maximum leaf height (proxy for plant height). In other words, herbaceous species growing in dense herb communities develop taller stems than do herbaceous species occurring in low-density herb habitats, which is in line with the competition hypothesis (Givnish 1982). However, to our knowledge, it has not been proved that island species would grow in higher-density communities than continental species. The outcrossing hypothesis was supported by field observations on St. Helena investigating the tall *Nesohedyotis arborea* trees up to 7 m. The trees showed limited gene flow, which would be likely more severe in smaller-stature plants (Percy and Cronk 1997).

We agree with Carlquist that a moderate climate, in particular the absence of frost temperatures, in most of the oceanic islands is definitely an important condition for herbaceous plants to develop insular woodiness. Interestingly, Sinnott and Bailey (1915) argued that the onset of cold winters in the temperate zones, due to refrigeration of the climate since the beginning of the Tertiary, caused the evolution from primary woodiness toward herbaceousness. This old idea can be confirmed by our ongoing broad-scale secondary review project, which shows that secondarily woody species generally do not occur in cold temperate or boreal to arctic regions where frost regularly occurs. However, some secondarily woody species do survive frost, especially in tropical alpine environments, such as the pachycaul rosette trees of *Espeletia* (Rauscher 2002), *Dendrosenecio* (Nordenstam et al. 2009), and lobelioids (Givnish et al. 2009); the small, shrubby Hawaiian species of *Silene* (Eggens et al. 2007); and some shrubby Canarian groups (table 1). Our broad-scale review also indicates that a single environmental variable such as temperature cannot be the only explanation driving increased woodiness: secondarily woody species hardly occur in lowland tropical rain forests, but they do occur in diverse warm habitats ranging from very wet tropical forests of, among others, the Hawaiian Islands (*Asinidendron*; Weller et al. 1995) or Southeast Asia and the Pacific (*Cyrtandra*; Cronk et al. 2005) to markedly dry deserts, such as coastal regions of Peru and Chile (*Nolana*; Dillon et al. 2007) or the North African deserts (*Henophyton*; Warwick et al. 2010). Most likely, a complex mix of abiotic and biotic factors can induce secondary woodiness in many groups, and these variables may change, depending on the group under study.

We believe that—at least in some herbaceous groups—drought may trigger wood formation, which has never been hypothesized before in relation to secondary woodiness. This idea comes from our ongoing review, which demonstrates that a majority of the angiosperm genera that include secondarily woody species are restricted to dry continental regions with at least a few months of drought per year (coastal Mediterranean regions, steppes in Central Asia, and even [semi-]deserts across the world; F. Lens, unpublished data). A possible link between insular woodiness and dry habitats can also be confirmed for the Canary Island flora, where 58% of the insular woody species grow in the dry coastal regions up to 700 m asl (fig. 1*B*) and another 6% grow in the high-altitude desert above 2000 m asl (fig. 1*G*), while only 11% are found in the humid laurel forests (fig. 1*A*). Moreover, plotting habitat type data on molecular phylogenies supports the hypothesis that the dry habitats are ancestral within Canary Island clades exhibiting insular woodiness, as intensively studied in, for instance, *Descurainia* (Goodson et al. 2006), *Echium* (García-Maroto et al. 2009), and *Micromeria* (Meimberg et al. 2006). Although plants can rely on different mechanisms to cope with drought stress (deep root systems, C_4 or CAM metabolism, stem succulence, leaf adaptations), additional evidence for this new hypothesis could be found in the ability of stems to avoid air bubble formation (i.e., embolism resistance) in vessels. A direct causal link between survival of plants and embolism resistance during extreme drought has been highlighted, suggesting that embolism resistance is an important adaptive trait (Maherali et al. 2004; Brodribb and Cochard 2009; Brodribb et al. 2010; Choat et al. 2012). At this moment, no experiments have been carried out showing that embolism resistance in stems of insular woody species would be stronger than that in the stems of closely related herbaceous species. However, there are preliminary results in *Arabidopsis* that may point to this correlation: Tixier et al. (2013) found that short-day *Arabidopsis thaliana* plants with more wood development are significantly more embolism resistant than long-day plants with less wood development. Moreover, embolism resistance in stems of the woody mutant is ~1 MPa more negative than the values obtained for the wild-type stems (Lens et al. 2013). Future experiments will indicate whether this assumption can be generalized using additional species growing in the wild.

Herbaceousness Prevails in Canary Island Angiosperms

Despite massive convergent evolutionary trends toward insular woodiness on the Canary Islands, it is intriguing to see that the majority of native angiosperms have never evolved to insular woodiness (66% of the angiosperm species, 59% of the native traditional dicots, and 34% of the endemics are herbaceous; table 2). As most herbaceous traditional dicot species still produce a small amount of wood at the base of their stems (Carlquist 2009; Dulin and Kirchoff 2010; Schweingruber et al. 2011; Lens et al. 2012*a*, 2012*b*), it is unlikely that the ability to turn on the molecular wood pathway has been lost in these species. This is suggested in the herbaceous model plant *A. thaliana*, which develops into a woody shrub by knocking out only two flowering-time genes (Melzer et al. 2008). Moreover, there is growing evidence that at least some key genes associated with the shoot apical meristem are also expressed in the cambial zone during secondary growth (Schrader et al. 2004; Aichinger et al. 2012), explaining why there is a strong evolutionary pressure for these wood-inducing genes to be maintained in herbaceous plants (Spicer and Groover 2010). Anyway, many herbaceous lineages on the Canary Islands were not triggered to develop into shrubs, and this does not seem to be disadvantageous, considering the vast number of herbs. The lack of development into shrubs might be related to (1) much shorter generation times, leading to higher rates of molecular evolution (Smith and Donoghue 2008), (2) the possible occurrence in specific microhabitats that do not require much allocation of energy and resources in wood formation within stems, (3) the ability of herbaceous species to deal with unfavorable periods as seeds (avoidance strategy), or (4) gene mutations blocking (part of) the molecular wood pathway. In the literature, several potential advantages of shrubbiness over herbaceousness are mentioned (Stutz 1989), such as a reuse of old tissue (more energy efficient), taller habit (harvesting more sunlight), or photosynthesis during the entire year (through evergreen leaves or chlorophyll contained in the bark of overwintering stems). Among the endemic species within the traditional dicots (table 2), the 202 insular woody species slightly outnumber the 174 herbaceous species, assuming that both life forms represent equally advantageous strategies to cope with the environmental conditions on the Canaries.

Surprisingly, the Canary monocots include only 25 endemics, of which one (*Dracaena tamaranae*) forms a vascular cambium producing amphivasal vascular bundles embedded in parenchyma to the inside and parenchyma to the outside, a peculiar monocot anatomy characteristic of the entire genus (Cheadle 1937; Tomlinson and Zimmermann 1969). This form of secondary growth in *Dracaena* is not an island phenomenon, however, since the distribution of the genus extends to the warmer regions of the Old World (Bos 1998). Also, species of the genus *Asparagus* are described as shrubs, but on the basis of original anatomical sections, there is no sign of vascular cambium formation (fig. 2*F*; cf. the native palm species *Phoenix canariensis*).

Suggestions for Future Research

Besides screening for more secondarily woody species around the world, future research on secondary woodiness should be focusing on the questions (1) Why do herbaceous species develop into shrubs? and (2) What is the molecular pathway that triggers wood development in secondarily woody species? We propose an integration of ecology, evolution, and developmental studies (eco-evo-devo), which is a modern approach in systematics to bridge understanding between genotype and phenotype, to contribute to solving these major questions.

1. Integrating georeferenced environmental data and evolutionary biology is an efficient way to reveal new insights into the ecological causes of evolutionary patterns (Kozak et al. 2008; Evans et al. 2009; Yesson et al. 2009; Boucher et al. 2012). On the basis of this niche-modeling approach, we hope to find environmental variables that are tightly linked to either the insular woody or the herbaceous life form on the Canary Islands. If it turns out that drought resistance parameters play an important role in at least some of the secondarily woody groups, experimental hydraulic experiments will be performed in herbaceous and woody stems to validate whether secondarily woody stems are more embolism resistant than stems of herbaceous relatives (Lens et al. 2013).

2. The woody *Arabidopsis* lab mutant shows that a “simple” genetic mechanism can turn an herb into a secondarily woody shrub, demonstrating that at least some herbaceous plants retain the genetic capability to develop into woody shrubs (Oh et al. 2003; Groover 2005; Spicer and Groover 2010), but we need to identify how the “flowering-time” signal is transferred to the “woody-growth” regulator in this species. A next step would be to compare the results in *Arabidopsis* to those in insular woody species in different branches of the angiosperm tree of life, using comparative transcriptomics of nonmodel species (Strickler et al. 2012). This strategy will allow us to find whether homoplastic evolution toward secondary woodiness in flowering plants develops via a similar molecular mechanism (parallel evolution) or whether dissimilar molecular pathways are responsible for these independent shifts (convergent evolution; Scotland 2011). Before this is clarified, it is better to describe an independent evolution of a given phenotype as convergence (Scotland 2011).

One of the most remarkable habit shifts on the Canary Islands is the evolution of some insular woody groups toward secondary herbaceousness. This has happened at least three times in *Echium* (García-Maroto et al. 2009) and once in *Sonchus* (Kim et al. 2007). These two genera provide excellent case studies to investigate the habit shifts in more detail.

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