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HISTORICAL EFFECTS AND SORTING PROCESSES AS EXPLANATIONS FOR CONTEMPORARY ECOLOGICAL PATTERNS: CHARACTER SYNDROMES IN MEDITERRANEAN WOODY PLANTS

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Abstract.—Ecological patterns are not only a consequence of adaptive processes, but also influenced by phylogenetic constraints, historical effects, and sorting processes. In contrast to the attention paid to the influence of phylogeny on interspecific ecological patterns, historical effects and sorting processes have been considered less frequently. This article shows that, for the woody flora of western Andalusia, southwestern Spain, these factors may be of substantial importance for explaining covariation among life-history traits (and associated "character syndromes") in plant communities. Multivariate analysis of the covariation across genera of 10 qualitative characters (related to general habit and reproductive biology) revealed a dominant life history–reproductive gradient (called "dimension 1") defining two distinct groups of genera and associated syndromes. Syndromes may largely be explained by reference to historical effects and species sorting processes, without recourse to adaptive explanations. Lineage age (as estimated from paleontological and biogeographical data) explained a significant proportion of intergeneric variation in position along dimension 1. Many character associations contributing to the syndromes vanished after the sample was split into groups based on lineage age, and those remaining occurred exclusively within the group of "old" (pre-Mediterranean) genera. No supporting evidence was found for the contribution of differential extinction of pre-Mediterranean genera to observed syndromes. Differential diversification of lineages as a function of life-history and reproductive characteristics did contribute significantly.

Ecologists study thin temporal slices of historically dynamic systems. Evolutionary ecologists, in particular, attempt to interpret the array of ecological patterns found in these contemporary slices in terms of adaptive processes undergone by species and populations (Orians 1962; Lack 1965; Harper 1967). By using taxonomic entities (ordinarily species) as sampling units, patterns are often inferred from the distribution of ecologically relevant attributes, or their covariation, among taxa co-occurring on a particular spatial scale (e.g., local or regional). These patterns depend simultaneously on the identity of the taxa involved and on their attributes. As neither the traits of the taxa nor their involvement in a given local or regional assemblage are entirely the result of adaptive changes, ecological patterns should not be expected to be solely the consequence of adaptations. Further factors must thus be taken into consideration to explain them. For convenience, these may be grouped under the labels "phylogenetic constraints," "historical effects," and "species sorting processes," as outlined be-

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low. I admit, however, that the precise conceptual limits and operational relationships between these three broad categories of phenomena may often prove difficult to trace, as illustrated by the diverse usages of these and comparable terms found in the literature (see, e.g., Fowler and MacMahon 1982; Wanntorp 1983; Lechowicz 1984; Huey 1987; Gould 1989; Gould and Woodruff 1990).

Phylogenetic constraints, also sometimes referred to as "phylogenetic inertia" (Wilson 1975), "historical constraints" (Wanntorp 1983), or "historical factors" (Pearson et al. 1988), set limits on the evolution of individual species (Gould and Lewontin 1979; Felsenstein 1985; Gould 1989). They are taxon specific, and a particular taxon, regardless of where it occurs, may be forced into certain combinations of character states by virtue of these constraints. In animal species assemblages, for instance, phylogenetic constraints are responsible for a substantial proportion of observed interspecific variation in life-history attributes (see, e.g., Wiklund and Karlsson 1984; Cheverud et al. 1985; Pagel and Harvey 1988; Pearson et al. 1988; Bell 1989; Lessios 1990). In plant communities, phylogeny has been shown to be an important factor in explaining patterns of interspecific variation in seed size (Hodgson and MacKey 1986; Mazer 1989), flowering phenology (Kochmer and Handel 1986), flower duration (Stratton 1989), and features of fruit and fruiting synchrony of animal-dispersed plants (C. M. Herrera 1986, 1992; Gorchov 1990).

Historical effects become relevant explanations for ecological patterns whenever an understanding of the latter requires a knowledge of past historical states or contingencies. In contrast to phylogenetic constraints, historical effects are mainly site specific. As stated by Gould and Woodruff (1990, p. 75), "History represents a class or category of explanations, not a particular scenario," and the details of processes and mechanisms involved in historical explanations will differ from one particular study system to another. In the context of this article, historical effects are considered in relation to the dynamics of regional taxonomic assemblages and the long-term persistence of ecologically relevant characteristics of the taxa involved. As revealed by biogeography and paleontology, contemporary regional species assemblages represent transitory amalgamations of taxa that originated at different geological times and thus, presumably, in different ecological scenarios. This juxtaposition of taxa having temporally and ecologically disparate origins, and whose characteristics may have remained essentially unchanged over long time periods, may lead to contemporary patterns that are best explained as a consequence of historical effects (see Lechowicz 1984 for an example of this approach). In these instances, some present-day patterns would constitute "ecological phantoms" conceptually analogous to the "genetic phantoms" of Gould and Woodruff (1990).

Species sorting processes are also related, although for different reasons, to the long-term dynamic nature of species assemblages. They simultaneously involve taxon-specific and site-specific components. The lineages represented in a regional species pool may intrinsically differ in their rates of extinction and speciation (Stebbins 1951; Stanley 1979). In the long run, differential diversification rates (originations minus extinctions) of lineages possessing different attributes may give rise to distinct patterns in the distribution of such attributes across taxa, brought about by some process akin to what has been variously termed "selective extinction and speciation" (Fowler and MacMahon 1982), "species selection" (Stanley 1975, 1979), and lineage "sorting" (Vrba and Gould 1986). There has been a vigorous controversy in recent years with regard to the meaning of, and actual mechanisms involved in, species selection and related processes (see, e.g., Hull 1980, 1988; Hoffman 1984, 1989; Vrba 1984; Eldredge 1985; Gould 1985; Gould and Eldredge 1986; and references therein). To avoid becoming caught up in this controversy, I use the expression "sorting process" in this article to mean, generically, any process whereby lineages having different attributes acquire different proportional representations in regional species assemblages because of differences in diversification rates, regardless of the mechanism(s) involved.

In recent years, evolutionary ecologists have often examined the influence of phylogeny on interspecific ecological patterns. In contrast, the significance of historical effects and sorting processes has been considered, documented, or discussed much less frequently (but see, e.g., Fowler and MacMahon 1982; Pearson 1982; Lechowicz 1984; Brown and Maurer 1987). The objective of this article is to provide evidence demonstrating that historical effects and sorting processes may be of substantial importance in explaining patterns of covariation among life-history and reproductive features (and associated "character syndromes") observed at the regional plant community level, as illustrated by the woody flora of western Andalusia, in southwestern Spain. The flora of the Mediterranean basin is particularly well suited to an analysis of the influence of historical effects and sorting processes on contemporary patterns, as it represents a complex mixture of taxa with disparate biogeographical affinities, ages of origin, and evolutionary histories (Braun-Blanquet 1937; Raven 1971, 1974; Quézel et al. 1980; Mai 1989; Palamarev 1989). A further advantage is that our current knowledge of basic historical and ecological aspects is reasonably good for some regional floras.

It must be noted that the aim of this article is not to contribute to the literature just one more detailed analysis describing, or attempting to interpret, associations among plant reproductive and life-history traits (see references in the next section). Instead, this subject is treated as a representative example to illustrate some cautions that should be kept in mind by those attempting to interpret ecological patterns on the basis of adaptive arguments alone. Nevertheless, as shown in the next section, most of the plant characters and associations considered in this study have been previously examined for a variety of plant communities, and results obtained here are also subsidiarily relevant to some recent controversies on patterns of covariation among plant life-history and reproductive attributes.

PLANT CHARACTER SYNDROMES

The examination of plant species assemblages ranging in size from local communities to regional or world floras has often led to the identification of nonrandom patterns of covariation across taxa of morphological, life-history, and reproductive traits, sometimes leading to the identification of distinct character syndromes. These include associations among life form, leaf persistence, breeding system, pollinating agent, flower size, and seed dispersal mode (McComb 1966; Opler 1978; Bawa 1980; Conn et al. 1980; Freeman et al. 1980; Givnish 1980; C. M. Herrera 1982*a*, 1985; Sobrevila and Kalin Arroyo 1982; Flores and Schemske 1984; Bullock 1985; Fox 1985; J. Herrera 1987; Arroyo 1988; Steiner 1988; Donoghue 1989; and others). Dioecy, for instance, has been frequently found to be significantly associated with woody habit, wind pollination, small flowers, and seed dispersal by animals (see, e.g., McComb 1966; Bawa 1980; Givnish 1980; Flores and Schemske 1984). Generally, covariation between any two or more life-history and reproductive characters and the syndromes brought about by the nonrandom association of character states across taxa have been interpreted as indicative of adaptations (i.e., as being the consequence of adaptive evolutionary changes experienced by the taxa involved), and evolutionary hypotheses have frequently been advanced to explain them. In addition, some of these associations have provided the basis for formulating evolutionary explanations for the appearance of particular reproductive or life-history traits. The significant association frequently found between dioecy and seed dispersal by animals, for instance, has inspired adaptive hypotheses on the evolution of that breeding system and stirred considerable controversy (Bawa 1980, 1982*a*, 1982*b;* Givnish 1980, 1982; Thomson and Barrett 1981; C. M. Herrera 1982*a*, 1982*b;* Flores and Schemske 1984; Fox 1985; Muenchow 1987; Donoghue 1989; and references therein).

The assumption that contemporary interspecific patterns in plant life-history and reproductive traits are solely the consequence of adaptive processes affecting individual taxa (i.e., the combined importance of phylogenetic constraints, historical effects, and sorting processes is null or negligible) is common to all those adaptive interpretations of character evolution that are based on interspecific patterns of character covariation. Nevertheless, this assumption generally has been neither made explicit nor critically examined. In the few instances in which the importance of phylogenetic constraints has been examined, these have been found to play a prominent role in determining character syndromes in contemporary plant communities (Fox 1985; Muenchow 1987; Donoghue 1989), thus invalidating in part the assumption noted above. Nevertheless, the role of historical effects and sorting processes in determining plant character syndromes has not been previously examined, and this provides justification for the analyses presented here.

GENERAL METHODS

Analyses were conducted on the woody plants (angiosperms and gymnosperms) of western Andalusia, southwestern Spain, a region of 45,000 km^2 homogeneously characterized by a Mediterranean-type climate (Capel Molina 1981). I compiled the list of native woody plant genera according to a comprehensive regional flora (Valdés et al. 1987). From this list (83 genera) I excluded genera represented by a single species with extreme relict distributions in the region and those for which reliable information on the reproductive and life-history traits considered in this study (see below) was unavailable (for genera with geographical distributions extending beyond the Mediterranean region, I attempted to use biological information coming exclusively from studies or observations conducted in Iberian Mediterranean climatic regions; see references below). The final sample used in the analyses consisted of 66 genera belonging to 31 families. The available data on the distribution of character states among excluded genera, although fragmentary, do not suggest the possibility of any significant bias caused by omitting them from the analyses. Choosing genera, instead of species, as the units for the analyses has the advantage of minimizing the influence of a few genera with many species on overall patterns of character covariation (Fox 1985; Muenchow 1987). Similarly, restricting the survey to woody plants (shrubs, trees, and woody vines) reduces the internal heterogeneity of the sample, because life form is often correlated with reproductive traits, as noted earlier.

I scored each genus for 10 simple qualitative characters referred to general habit (deciduousness, spinescence, and sclerophylly), flowering biology (flower size and sexuality, perianth color and degree of reduction, and pollinating agent), and seed dispersal (seed size and dispersal agent). The two criteria used to select the characters were that they had been examined in some previous study of plant character syndromes and that they were readily scored on a qualitative basis. Characters and character states considered were as follows (only two possible character states were recognized for each trait): (1) spinescence: spiny (spines on stems or leaves) versus nonspiny; (2) leaf type: sclerophyllous leaves versus leaves of different characteristics; (3) habit: evergreen versus deciduous (winter or summer-facultative deciduous); (4) flower size: perianth depth times width of less than 25 mm^2 (5 mm × 5 mm) versus more than 25 mm^2; (5) flower sexuality: hermaphroditic versus unisexual flowers; (6) perianth color: brownish or greenish versus a different color; (7) perianth reduction: perianth with at least one verticil (petals or sepals) absent or much reduced versus complete perianth; (8) pollinator type: wind pollination versus insect pollination; (9) seed size: seed length times width of less than 2.25 mm^2 (1.5 mm × 1.5 mm) versus more than 2.25 mm^2; and (10) seed dispersal: animal dispersed (endozoochory) versus otherwise. For character 7, gymnosperms (lacking a perianth) were all scored as if they had a reduced perianth. For characters 4 and 9, cut points used to separate the "small" and "large" categories were chosen a priori, representing a subjective assessment (based on my familiarity with the regional flora) of the median values of regional distributions of flower and seed size.

A complete list of genera and character states for these qualitative variables is presented in Appendix A. Scoring of plant genera with respect to variables 1, 2, 3, 5, 6, and 7 above was mainly based on Valdés et al. (1987), with complementary information obtained from Hutchinson (1964, 1967), Ruiz de la Torre (1971), and Mabberley (1987). For characters 4, 8, 9, and 10, I relied largely on Catalán Bachiller (1978), J. Herrera (1982, 1985, 1988), C. M. Herrera (1984*a*, 1987, 1989), Jordano (1984), Bosch (1986), and Obeso (1986), but I also used my own unpublished observations for those genera not treated in these studies. Almost all genera were internally homogeneous with respect to all characters. In the few cases in which a genus was internally heterogeneous with regard to any variable (e.g., spinescence in *Juniperus* and flower sexuality in *Asparagus*), the rule of thumb

TABLE 1

Covariation of Life-History and Reproductive Characters among Extant Genera of Western Andalusian Woody Plants

Character	LT	HA	FS	FSE	PC	PR	PT	SS	SD
Spinescence (SP):									
All	...	...	...	...	...	...	...	...	...
Young	...	...	...	...	...	...	...	...	...
Old	...	...	...	...	...	...	...	...	...
Leaf type (LT):									
All		*	*	*	*	*	...	...	...
Young		...	...	...	...	...	...	...	...
Old		*	*	...	...	...	...	...	...
Habit (HA):									
All			...	...	...	...	...	...	...
Young			...	...	...	...	...	...	...
Old			...	...	...	...	...	...	...
Flower size (FS):									
All				*	*	*	*	...	*
Young				...	...	...	...	...	...
Old				*	*	*	*	...	...
Flower sexuality (FSE):									
All					*	*	...	...	...
Young					...	...	...	...	...
Old					*	*	...	...	...
Perianth color (PC):									
All						*	*	...	...
Young						...	...	...	...
Old						*	*	...	...
Perianth reduction (PR):									
All							*	...	...
Young							...	...	...
Old							*	...	...
Pollinator type (PT):									
All								...	...
Young								...	...
Old								...	...
Seed size (SS):									
All									*
Young									...
Old									...
Seed dispersal (SD):									
All									
Young									
Old									

Note.—Pairs of characters marked with asterisks co-vary nonrandomly across genera ($P < .05$). Cells with ellipses denote nonsignificant character associations ($P \geq .05$). Analyses were conducted on the whole sample ("all," $N = 66$) and separately for genera having either contemporary intercontinental range disjunctions or Pliocene fossil records, on one hand ("old," $N = 46$), and for those lacking both features, on the other ("young," $N = 20$). For each pair of characters, a two-way contingency table was obtained, and its significance tested with a two-tailed Fisher exact probability test. In each of the three separate association tables, significance levels were adjusted by the sequential Bonferroni method (Rice 1989). Adjusted tablewide α levels for a nominal $\alpha = 0.05$ were 0.0017, 0.0012, and 0.0014 for the "all," "young," and "old" values, respectively.

used was to score it as a function of the character state prevailing among western Andalusian species.

ANALYSES AND RESULTS

Covariation of Characters

Covariation of characters across genera was first examined by constructing all possible two-way contingency tables for character pairs and testing these for significance with two-tailed Fisher exact probability tests (Zar 1984). Because many simultaneous tests were carried out, significance levels of individual tests were adjusted for increased Type I error by the sequential Bonferroni method (Rice 1989). Sixteen significant character associations were found (table 1). Spinescence was the single character for which no significant association was found, and flower size and leaf type were those exhibiting the largest number of significant associations with others. Significant associations between character pairs found among western Andalusian plant genera are analogous to those reported previously for other species assemblages. These include, among others, associations between flower sexuality and perianth coloration, flower size and seed dispersal mode, and leaf type and perianth reduction (table 1).

Analyses of the associations between character pairs are insufficient to describe overall, multivariate patterns of intergeneric variation (Fox 1985). In order to examine whether pairwise associations between characters actually reflect one or more multivariate gradients of variation, or character syndromes, a similarity matrix between pairs of genera, based on the 10 characters examined, was constructed with a simple matching coefficient. Pairs of genera similar in all characters had a similarity of one, whereas those not sharing any character state had a similarity of zero. All characters were weighted similarly in computing the similarity coefficient. Nonmetric multidimensional scaling (NMDS; Kruskal 1964; du Toit et al. 1986) was performed on the 66 × 66 symmetrical similarity matrix, according to procedure MDS in SYSTAT, the Kruskal algorithm, and monotonic regression (Wilkinson 1986). This geometric method determines the configuration of objects (plant genera in the present instance) in one Euclidean space of minimal dimensions that best represents the original object distances.

Models ranging from one to five dimensions yielded stress values (a measure of the correspondence between original distances and those obtained after dimensionality reduction; Kruskal 1964) of 0.15, 0.08, 0.05, 0.03, and 0.01, respectively. According to the criteria outlined by Kruskal (1964), these figures suggest that a configuration in two dimensions describes satisfactorily the relationships between plant genera on the basis of their similarities in the 10 characters considered here. The distribution of genera on the plane defined by the two dimensions is shown in figure 1 (see App. A for coordinates of individual genera). Most intergeneric variation occurs along dimension 1, and a discernible gap exists in the distribution of points along it. Genera fall into two discrete clusters, each exemplifying a characteristic association of character states, or syndrome. The group on the left side of figure 1 (Cluster I hereafter) is made up predominantly of genera with sclerophyllous, evergreen leaves, small, unisexual greenish or brownish flowers

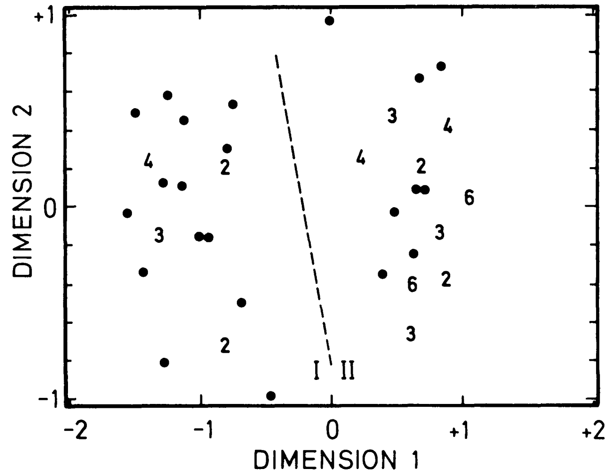

FIG. 1.—Distribution of western Andalusian woody plant genera on the plane defined by dimensions 1 and 2 obtained by nonmetric multidimensional scaling of a similarity matrix of their life-history and reproductive characteristics. *Numerals* indicate the number of tied observations at particular points. The *dashed line* is shown to illustrate the separation of genera into two distinct clusters (I and II), as described in the text.

with a reduced perianth, and large seeds dispersed by animals. Representative examples in this group are *Chamaerops* (Palmae), *Olea* (Oleaceae), *Osyris* (Santalaceae), and *Pistacia* (Anacardiaceae). In contrast, the cluster on the right side (Cluster II) is predominantly characterized by the set of complementary character states (e.g., *Cistus* [Cistaceae], *Genista* [Fabaceae], and *Rosmarinus* [Lamiaceae]).

Historical Effects

To search for evidence of historical effects in the syndromes documented above, I considered paleontological and biogeographical information.

I screened the plant paleontological literature for early Pliocene or pre-Pliocene fossil records (either pollen or macrofossils) of the extant genera of woody plants examined here. I considered only records coming from localities in the Mediterranean basin (including Portugal) and continental western Europe (France, western Germany, and Denmark). The Pliocene was chosen as a cut point for the search because it is generally agreed that current Mediterranean climatic conditions first appeared during the second half of that period (Suc 1984). In this way, extant genera with early Pliocene or pre-Pliocene fossil records are to be considered as descendants of lineages that certainly did not evolve under contemporary, Mediterranean climatic conditions. In contrast, genera failing to provide Pliocene or pre-Pliocene fossil records will more likely represent lineages appearing in the region (by origination or migration) after the beginning of current Mediterranean climatic conditions. The data used here were taken from Depape (1922), Bauzá Rullàn (1961), Pons (1964, 1981), Diniz (1967), Fernández Marrón (1971), Medus

TABLE 2

Effects of Range Disjunctions ("disjunctions") and Occurrence of Pliocene or Pre-Pliocene Fossil Records ("fossils") on DIM1

Effect	df	Mean Square	*F*	*P*
Disjunctions	1	4.0122	6.26	.015
Fossils	1	7.7081	12.02	.001
Disjunctions × fossils	1	.0261	.04	.841
Error	62	.6433		

Note.—A general linear model was fitted to the data according to the GLM procedure (SAS Institute 1988) with Type III sum of squares. Disjunctions and fossils were treated as two-level (presence-absence) categorical variables. Significance of model: $F = 7.83$, df = 3,62, $P = .0002$, $R^2 = 0.275$.

and Pons (1980), van der Burgh (1983), Friis (1985), Vicente i Castells (1988), and Palamarev (1989; see App. A for data used).

Broadly disjunct geographical ranges of plant taxa on the world scale may be brought about through a variety of processes, but they generally attest an old origin for the lineage (Raven and Axelrod 1974; Schuster 1976; Axelrod 1983). I examined the worldwide distributional patterns of all the genera considered here and scored them for broad intercontinental disjunction of geographical range. I considered as disjunct only those geographical ranges falling into the "fragmentary North Temperate," "African-Eurasian," or "pantropical" disjunction categories as defined by Thorne (1972). Biogeographical information was taken from Hutchinson (1964, 1967), Thorne (1972), Quézel et al. (1980), and Mabberley (1987). A total of 25 genera in my sample qualified as having disjunct distributions according to the criteria used (App. A).

Paleontological and biogeographical information was examined by fitting a general linear model to the data according to procedure GLM in SAS (SAS Institute 1988). Position along the life history–reproductive gradient (DIM1), a continuous variable, was entered as the dependent (criterion) variable, and occurrence of Pliocene or pre-Pliocene fossils, and intercontinental disjunctions, as independent (predictor) variables. Results are summarized in table 2. The fitted model was statistically significant, accounting for 27.5% of observed (intergeneric) variance of DIM1. The two independent variables have significant effects on DIM1. Genera with Pliocene or pre-Pliocene fossil records or exhibiting intercontinental range disjunctions tend to score significantly lower on DIM1 than those lacking these characteristics (fig. 2). This pattern is also evidenced by the differential distribution of genera with Pliocene or pre-Pliocene fossils and exhibiting range disjunctions among the two clusters revealed by NMDS. Eighty percent of genera in Cluster I ($N = 25$) yielded Pliocene or pre-Pliocene fossil records, as compared with only 43.9% of genera in Cluster II ($N = 41$) (Fisher test, $P = .003$). Likewise, genera having disjunct distributions were unequally distributed among Clusters I and II (60% and 24.4% of genera in Clusters I and II, respectively; Fisher

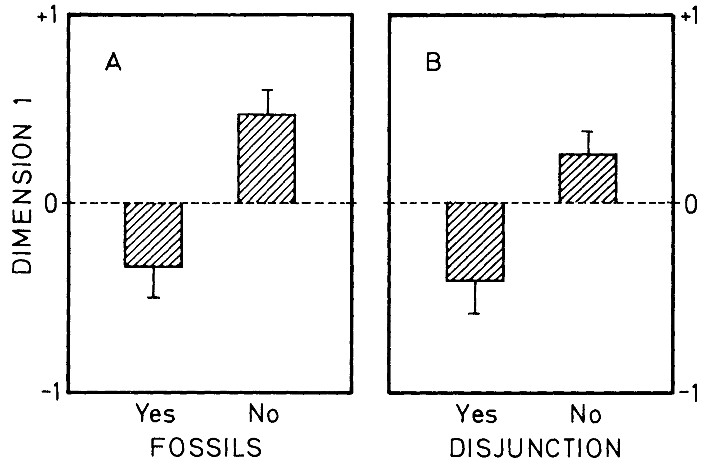

FIG. 2.—Mean location on the first axis from nonmetric scaling (score on dimension 1; fig. 1) of groups of western Andalusian plant genera defined as a function of the occurrence of (*A*) Pliocene or pre-Pliocene fossil records and (*B*) intercontinental range disjunction. Vertical bars extend over 1 SE of the mean. See table 2 for statistical analysis.

test, $P = .008$). At this point, it must be noted that the paleontological and biogeographical data used represent statistically independent lines of evidence, as there is not a significant association between the occurrence of intercontinental disjunctions and that of Pliocene or pre-Pliocene fossils in the sample of genera studied (Fisher test, $P = .21$).

Taken together, therefore, paleontological and biogeographical data show that the heterogeneity of historical origins represented in the set of genera examined has considerable explanatory power in predicting intergeneric variation in life-history and reproductive characters. To what degree are the associations between characters that determine Clusters I and II of genera only an artifact of the heterogeneity of the sample with regard to lineage age? In other words, do associations between characters still persist when the sample of genera is split as a function of presumed lineage age? Genera were split into two groups, namely "old" and "young." Those with either contemporary intercontinental range disjunction *or* Pliocene or pre-Pliocene fossil records were scored as old ($N = 46$), and those lacking both of these features were considered young ($N = 20$). The initial character-association matrix was recomputed separately for each group by the same methods used for the whole sample (table 1). Five of the 16 original significant associations between characters vanished after splitting the sample into the two age-based groups. Of the 11 original associations still remaining in the separate analyses, all occurred in the group of old genera, and none in the group of young ones.

These results suggest that historical effects are directly responsible for some of the character associations found among western Andalusian plant genera. An alternative interpretation, however, could be that modifications in the number of significant character associations are simply a consequence of the reduction in sample size (and so the power of the test) caused by splitting the sample into two smaller subsamples. I examined this possibility using a simulation scheme. The original sample of genera was randomly divided into two subsamples of a size equal to that of the old ($N = 46$) and young ($N = 20$) groups, and the significance of all pairwise character associations was tested separately in each subsample by the same methods as in table 1. This process was iterated 1,000 times, and on each occasion the number of significant character associations found in each random subsample was recorded. Critical probability values were then obtained from the cumulative frequency distributions of the number of significant-associations tests. The probability of obtaining, by chance alone, 11 or fewer significant character associations after splitting the sample of genera into the two age-based subgroups was $P = .006$, and that of failing to record even a single significant character association in the smallest group of genera (young ones) was $P = .020$. It may be concluded, therefore, that the modifications in the patterns of character associations that follow the subdivision of the sample of genera into age-based groups are real and not the consequence of a reduction in the power of statistical tests due to decreased sample size.

In conclusion, therefore, some contemporary character associations (those disappearing after sample subdivision) must be interpreted as a consequence of the historical heterogeneity of the sample of genera, whereas others (those "resistant" to subdivision) are characteristic only of a historically defined, particular subset of genera (the old ones). Examples of correlations that disappear after sample subdivision are those between flower size and seed dispersal mode and between seed size and seed dispersal mode (table 1). When the whole sample of genera is considered, animal dispersal is significantly associated with large seeds and small flowers, but none of these relations hold within each of the two age-based groups of genera. Correlations between flower sexuality, perianth color, and perianth reduction exemplify those found exclusively within the subgroup of old genera (table 1). Unisexual flowers and reduced, brownish or greenish perianths tend to be associated only in that group of genera, and these associations emerge also when the whole sample is considered.

Sorting Processes

As shown in the preceding section, the character syndromes observed among contemporary western Andalusian plant genera are partly explained by the heterogeneity of the sample with regard to historical origin. All character associations that remain after accounting for this effect apply only to the group of genera belonging to old lineages. Not a single significant character association exists within the group of more recent genera (those presumably evolved after the initiation of Mediterranean climatic conditions). Sorting processes may underlie these patterns. First, those character associations that depend exclusively on the heterogeneity of the sample with regard to historical origin may reflect differential levels of recent diversification of lineages as a function of their life-history and reproductive characteristics. Second, those character associations found exclusively within the group of old genera might be a consequence of differential post-Pliocene extinctions of pre-Mediterranean lineages occurring nonrandomly

TABLE 3

EFFECTS OF DIM1 AND GEOLOGICAL AGE OF EXTANT WESTERN ANDALUSIAN WOODY PLANT GENERA ON THE NUMBER OF SPECIES PER GENUS ON BOTH THE WESTERN ANDALUSIAN AND WORLD SCALES

Effect	df	Mean Square	*F*	*P*
A. Andalusian species:*				
DIM1	1	3.5792	6.15	.016
Age	1	.6155	1.06	.31
DIM1 × age	1	1.2643	2.17	.145
Error	62	.5816		
B. World species:†				
DIM1	1	1.0998	.32	.57
Age	1	2.4698	.73	.40
DIM1 × age	1	.8224	.24	.63
Error	62	3.4038		

NOTE.—A general linear model was fitted according to the GLM procedure (SAS Institute 1988) with Type III sum of squares. Dependent variables (number of species per genus) were log-transformed for the analyses.

* Significance of model: $F = 5.84$, df = 3,62, $P = .0014$.

† Significance of model: $F = 0.82$, df = 3,62, $P = .49$.

with respect to life-history and reproductive characteristics. I will consider these two aspects in turn.

Differential diversification.—This aspect can be examined only indirectly in the data set considered in this article. The effect of potential differences in lineage diversification rate on patterns of covariation among characters could be more readily assessed if these patterns had been elucidated with species, instead of genera, as the taxonomical units for the analyses. Nevertheless, indirect evidence supporting a potential role of sorting processes in determining character syndromes could still be found in the sample of extant western Andalusian genera if, after statistically controlling for differential lineage age, (1) the number of extant species of each genus in the study region (net regional diversification, the result of originations minus extinctions) were significantly related to its score on DIM1 *and* (2) this relationship were characteristic of the region concerned, and not simply the regional expression of a pattern occurring on a broader geographical scale.

To test aspects 1 and 2 above, the influence of lineage "age" (young vs. old genera, as defined above) and life-history and reproductive characters (score on DIM1) on net diversification was examined simultaneously by fitting a general linear model to the data. The number of species comprised by each genus in western Andalusia (log transformed; based on Valdés et al. 1987) was used as the criterion variable, and age and score on DIM1 as predictor variables. One further analysis was done with the total number of species in each genus in the world (log transformed; based on Mabberley 1987) as the dependent variable. Results are summarized in table 3.

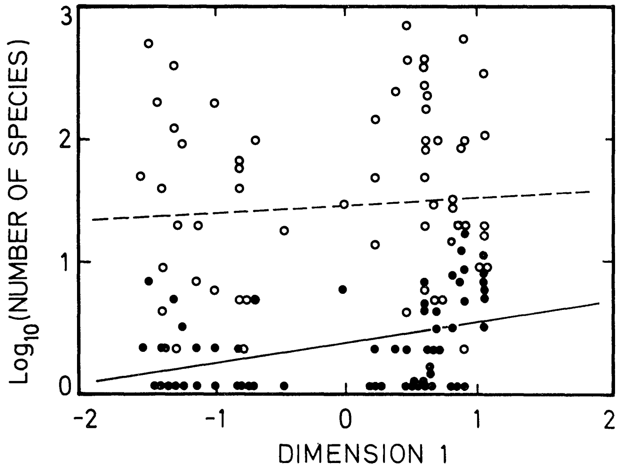

FIG. 3.—Variation in the number of extant species in western Andalusia (*filled circles, solid regression line*) and on a worldwide basis (*open circles, dashed regression line*), for each of the extant western Andalusian woody plant genera. Regression lines were fitted according to the least-squares method. See table 3 for analytical results.

In the sample of genera examined, there is a significant positive relationship between the number of species occurring in western Andalusia and DIM1 (table 3A; fig. 3). Neither the effect of age nor the interaction age × DIM1 is significant, which reveals that the regional species richness of western Andalusian plant genera is independent of lineage age and is best explained in terms of the life-history and reproductive attributes summarized by DIM1. When the total number of species of each genus on a world basis is used as the dependent variable, no significant effect is found for any of the independent variables or the interaction term, and the model fitted is not significant (table 3B; fig. 3). These results indicate that, in western Andalusia, genera at different positions on the life history–reproductive gradient have diversified at different rates and this effect is characteristic of the region concerned and does not merely echo a general diversification pattern of the genera on the world scale. The hypothesis of a role of differential diversification in enhancing character syndromes is, therefore, supported.

Differential extinction.—I compiled the list of woody plant genera (angiosperms and gymnosperms) occurring in southwestern Europe (Iberian Peninsula and southern France) during the Pliocene and mid- to late Miocene (based on information in Depape 1922; Pons 1964; Fernández Marrón 1971; Medus and Pons 1980; Vicente i Castells 1988), exclusive of those that have since become extinct on a world basis. Genera that are not currently represented in western Andalusia but occur elsewhere in the western Mediterranean basin or in west-central Europe were likewise excluded. The sample of genera (N = 83) was divided into extinct (N = 45) and extant (N = 38) in the contemporary western Andalusian flora. Regionally extinct genera were scored for four of the traits examined earlier (flower sexuality, perianth reduction, pollinator type, and seed dispersal), on the

TABLE 4

Covariation of Reproductive Characters among Woody Plant Genera That Occurred in Southwestern Europe in the Pliocene or Mid- to Late Miocene

Character	PR	PT	SD
Flower sexuality (FSE):			
Extinct	*	*	. . .
Extant	*	. . .	. . .
Perianth reduction (PR):			
Extinct		*	. . .
Extant		*	. . .
Pollinator type (PT):			
Extinct			. . .
Extant			. . .
Seed dispersal (SD):			
Extinct			
Extant			

Note.—Pairs of characters marked with asterisks co-vary nonrandomly across genera ($P < .05$). Cells with ellipses denote nonsignificant ($P \geq .05$) character associations. Analyses were conducted separately for genera extant ($N = 38$) and extinct ($N = 45$) in western Andalusia. Methods are as in table 1. Adjusted table-wide α levels for a nominal $\alpha = 0.05$ were 0.008 for the values for extant and extinct genera.

basis of characteristics currently found in extant species of these genera elsewhere (based on information provided by Hutchinson 1964, 1967; Heywood 1978; Cronquist 1981; Mabberley 1987; and Kramer and Green 1990). These four characters were chosen because, among the traits studied, they tend to exhibit the greatest constancy within genera. In this way, scoring for these characteristics of genera extinct in southwestern Europe can confidently be done by reference to the traits of their extant species elsewhere. A list of extinct genera and the data used are shown in Appendix B.

The pattern of association of characters in the sample of extinct genera was compared with that found in genera that occur at present in western Andalusia and for which there are Pliocene or pre-Pliocene fossil records. With a single exception, the pattern of association among the four characters considered is similar in the groups of extinct and extant genera (table 4). The exception concerns the association between flower sexuality and pollinator type, which is significant among extinct genera but not among extant ones (see also table 1). These results support the notion that, with regard to the patterns of covariation of the characters examined, the set of extant woody genera in western Andalusia tends to represent a random sample of the whole set of woody genera present in southwestern Europe in the Pliocene and late Miocene. The hypothesis of a role of differential extinction in determining character syndromes thus is not supported.

DISCUSSION

This article was conceived as an exercise to illustrate that some particular nonadaptive hypotheses deserve more consideration than they have received so far when interspecific ecological patterns have been examined. The particular subject under consideration, plant character syndromes, was chosen only by way of illustration, and for this reason the results that refer specifically to this particular subject will not be discussed here in detail. Instead the discussion will focus mainly on the more general objective of the article, namely, documenting the importance of historical effects and sorting processes as determinants of interspecific ecological patterns.

As is found in many other plant species assemblages elsewhere, life-history and reproductive characters co-vary nonrandomly among western Andalusian plant genera. Nine out of the 10 characters examined exhibited at least one significant association with another. These pairwise character associations represent the manifestation, at the bivariate level of resolution, of a more complex multivariate gradient of variation in life-history and reproductive traits, as is found also in other studies of character syndromes (Fox 1985). In fact, some of the associations between characters found here have been previously reported from other plant assemblages. So far, therefore, this study has revealed nothing essentially different from previous investigations on plant character syndromes. In contrast to previous studies of character associations, however, the present one has shown that character associations and the multivariate syndromes they reflect may largely be explained without resorting to adaptive explanations based on the contemporary ecological conditions faced by the taxa involved.

The syndromes exhibited by contemporary western Andalusian woody plants have a strong historical component. The multivariate life-history and reproductive gradient depicted by NMDS closely reflects differential lineage age, and variables describing the latter are able to explain, despite their admitted crudeness, as much as 27% of intergeneric variation in DIM1. This historical effect is largely the consequence of (1) the internal heterogeneity of the sample with regard to lineage age (some character associations contributing to the syndromes vanish after the sample is split into groups based on presumed lineage age) and (2) the differential patterns of association of life-history and reproductive features found among lineages that originated at different geological times. Obviously, the possibility exists that the paleontological data used here are subject to some indeterminate biases (e.g., differential probability of fossilization associated with the DIM1 gradient). Because of the very nature of the data, no information is available to reject this possibility, but the observation that independent biogeographical evidence confirms the results based on paleontological data tends to suggest that biases, if any, are most likely inconsequential to the results.

All character associations that remained significant after extant genera were split into discrete old and young age groups occurred exclusively within the former category. The occurrence of these character associations in the whole set of extant genera was therefore caused exclusively by the presence within the sample of an important proportion of old, pre-Mediterranean lineages. As this group of genera represents a random subsample of those occurring in southwestern Europe during the mid- to late Miocene and Pliocene (with regard to the association of reproductive features), there is no evidence that the character associations that they exhibit at present have been brought about by post-Pliocene selective extinction processes occurring among pre-Mediterranean lineages as a function of their configuration of reproductive features. The set of character associations found at present among the regionally surviving old genera presumably were already present before the initiation of Mediterranean conditions and have persisted unchanged since the subsequent extinction of a substantial fraction of woody genera. These character associations are probably best seen as ecological phantoms, evolved in temporally and ecologically distant pre-Mediterranean, tropical-like scenarios, and evolutionarily unrelated to present ecological conditions. At this point, it is most instructive to record that those character associations that are restricted to the subset of old genera are virtually identical to those reported from present-day Neotropical forests by Bawa (1980).

In addition to historical effects, sorting processes also partly explain the patterns of covariation among characters found among extant western Andalusian plant genera. Evidence was found of differential diversification rates of genera depending on their life-history and reproductive characteristics (DIM1). After the effect of lineage age was controlled, net diversification rates of individual genera in the study region increased significantly with increasing DIM1 values. If we assume that a similar trend has also occurred at a higher level in the taxonomical hierarchy (differential origination rate of genera), this finding provides support for the idea that differential proliferation of genera along the life history–reproductive gradient has also enhanced character syndromes.

In view of the results discussed above, a parsimonious, nonadaptive explanation for observed contemporary patterns of covariation of life-history and reproductive characters among extant western Andalusian woody plant genera and associated multivariate syndromes may be synthesized as follows. Certain character associations and concomitant syndromes already existed among the set of woody plants present in southwestern Europe before the initiation of Mediterranean climatic conditions in the Pliocene, when the region was under a different, tropical-like climatic regime. Since then, and presumably influenced by the ecological changes brought about by climatic alterations, numerous extinctions and originations of genera have taken place in the area. Extinctions of old lineages occurred randomly with respect to the character associations found in them, and, consequently, the original pre-Mediterranean associations of character states across taxa are still "preserved" as ecological phantoms among those old genera that still survive. While some old lineages were becoming extinct, new ones were becoming superimposed on the surviving remains of the Pliocene species assemblage. These additions, in contrast to extinctions, did not occur randomly with respect to life-history and reproductive characters, but were more abundant on some sectors of the DIM1 gradient, hence enhancing certain associations between characters within the whole sample of extant genera. Within this group of recent genera, however, significant associations between the characters examined here no longer exist.

The contemporary woody flora of the Mediterranean basin represents a historically very heterogeneous assortment of lineages having varied origins in time and space (for details, see, e.g., Braun-Blanquet 1937; Raven 1971, 1974; Axelrod 1975; Pignatti 1978; Quézel et al. 1980; Pons 1981; Palamarev 1989). It might thus be argued that the importance of historical effects documented here is but a singular consequence of the peculiarities of this study system and cannot be readily extrapolated to other plant species assemblages. To variable degrees, however, heterogeneity in the historical background of contemporarily coexisting taxa is most likely the rule, rather than the exception, in present-day plant communities throughout the world, as is illustrated by many paleontological and biogeographical studies (e.g., Axelrod 1958, 1986; Stebbins and Major 1965; Meusel 1971; Davis 1976; Sunding 1979; Tiffney 1985). The generality of this circumstance confers on historical effects and sorting processes a potential explanatory power for a variety of interspecific ecological patterns, particularly when long-duration taxa and characters subject to appreciable phylogenetic constraints are involved. The only other study known to me in which historical effects were explicitly considered as potential determinants of ecological patterns in plant communities also provides support for this view (Lechowicz 1984).

Paying attention to the role of historical effects (or "historical explanations" of Lechowicz [1984]) as explanations of contemporary ecological patterns rests on the assumption that, for whatever reasons (e.g., phylogenetic constraints, weak selective pressures, or insufficient time), the characters under examination have remained essentially unchanged over long time periods in the face of changing ecological conditions. The natural consequence of this assumption is the expectation that contemporary patterns are "contaminated" to variable degrees by traits and trait associations that evolved in the past under different circumstances and that are not adaptations to present-day conditions. The symmetrical assumption (that present-day patterns may be explained without recourse to historical explanations), and its likewise symmetrical consequence (that observed patterns represent adaptations only to contemporary conditions), are a central tenet of the "adaptationist programme" (Gould and Lewontin 1979), and as such they have largely become quintessential features in the practice of plant evolutionary ecology (C. M. Herrera 1986). For practical reasons, it is difficult to document unambiguously the continued phenotypic stability of plant taxa over long time periods. Nevertheless, published evidence shows that the assumption of phenotypic stability that underlies historical explanations of the kind examined in this article is well supported in many instances and for a variety of traits (Stebbins and Day 1967; Goldblatt 1980; Stebbins 1982; Niklas et al. 1985; C. M. Herrera 1986; Liston et al. 1989*a*, 1989*b*; Parks and Wendel 1990; and references therein). For obvious reasons, the stability assumption cannot apply universally to all taxa, but the very fact that it sometimes does provides in itself sufficient justification for considering historical explanations as one valid alternative or at least additional hypothesis to adaptive explanations in plant evolutionary ecology research programs (see also Lechowicz 1984).

Evolutionary ecology has, by definition, many of the ingredients of a historical science, insofar as it attempts to explain contemporary patterns and processes in relation to past events. Rather paradoxically, however, it tends to exhibit in practice certain traits of an ahistorical discipline, insofar as it deliberately tends to confine itself to the examination of what is but a restricted subset of past events (adaptive evolutionary change undergone by species and populations). Apparently, the possibility that the contingencies of history play a prominent role in explaining contemporary ecological patterns has been felt by some ecologists as a threat to the survival of their scientific practice. Westoby (1988, p. 554) wrote, exemplifying what perhaps represents an extreme view, that "if history were all-important, ecologists would have to retreat to natural history. Community and ecosystem study would pass into the hands of paleontologists." These fears not only are unfounded, but also, if unchallenged, may lead to serious misinterpretations in research programs in evolutionary ecology (Gould and Lewontin 1979). Abandoning the assumption that history never has any influence on present-day ecological patterns and that everything we see can always be understood in terms of present-day environments alone does not amount to stating that history is all-important. It implies only that the potential role of historical effects should also be taken into consideration when present-day ecological patterns are interpreted, in addition to the customarily included, often ad hoc adaptive explanations. As an analogy, consider the case of the influence of phylogenetic constraints on present-day ecological patterns. Only after their potential influence on interspecific patterns was recognized by evolutionists were a variety of methods developed that allowed for a dissection of observed interspecific patterns into their potentially adaptive and phylogeny-influenced components (Huey and Bennett 1987; Pagel and Harvey 1988; Bell 1989; Burt 1989; Donoghue 1989; Grafen 1989). Likewise, only after it is recognized that past historical contingencies may often shape contemporary ecological patterns will methods be devised to quantify the relative influence of these historical effects and identify plausible adaptive hypotheses in relation to present-day environments alone. In the case of the character syndromes of western Andalusian woody plants documented here, for instance, consideration of historical effects suggests that genera falling near the right extreme of the DIM1 gradient are probably those for which adaptive explanations related to present-day environments are both most straightforward and best justified. In contrast, adaptive hypotheses and expectations would less likely apply for old genera falling near the left extreme of the DIM1 gradient. This prediction is upheld by the results of field studies on the seed dispersal ecology of species in the old, pre-Mediterranean genera *Pistacia* (Jordano 1988, 1989), *Olea* (Jordano 1987), and *Osyris* (C. M. Herrera 1984*b*, 1988) in southwestern Spain, which found little support for interpreting many of their reproductive features as adaptations to present-day Mediterranean climatic environments.

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APPENDIX A

TABLE A1

EXTANT WESTERN ANDALUSIAN WOODY PLANT GENERA CONSIDERED IN THIS STUDY, AND SUMMARY OF LIFE-HISTORY, REPRODUCTIVE, PALEONTOLOGICAL, AND BIOGEOGRAPHICAL DATA USED IN THE ANALYSES

Genus	SP	LT	HA	FS	FSE	PC	PR	PT	SS	SD	PLI	DIS	DIM1	DIM2
Adenocarpus	0	0	1	1	0	1	1	1	1	0	0	1	.82	−.14
Amelanchier	0	0	1	1	0	1	1	1	1	1	0	1	.61	−.41
Arbutus	0	1	0	1	0	1	1	1	1	1	1	1	.23	.24
Asparagus	1	0	0	0	1	0	1	1	1	1	0	1	−.68	−.50
Berberis	1	0	1	1	0	1	1	1	1	1	0	0	.61	−.67
Calicotome	1	0	0	1	0	1	1	1	1	0	0	0	.67	.09
Calluna	0	0	0	1	0	1	1	0	0	0	1	0	.84	.73
Celtis	0	0	1	0	1	0	0	1	1	1	1	1	−.80	−.73
Ceratonia	0	1	0	0	1	0	0	0	1	1	1	0	−1.39	.23
Chamaerops	1	1	0	0	1	0	0	1	1	1	1	0	−1.30	−.15
Cistus	0	0	1	1	0	1	1	1	0	0	0	0	1.06	.04
Clematis	0	0	1	1	0	0	1	1	1	0	0	1	.63	−.25
Colutea	0	0	1	1	0	1	1	1	1	0	1	0	.82	−.14
Corema	0	0	0	0	1	0	0	0	1	1	0	1	−1.28	.12
Coriaria	0	1	0	0	0	0	1	0	1	1	1	1	−.74	.53
Coronilla	0	0	0	1	0	1	1	1	0	0	0	0	.91	.41
Cotoneaster	0	0	1	1	0	1	1	1	1	1	1	0	.61	−.41
Crataegus	1	0	1	1	0	1	1	1	1	1	1	0	.61	−.67
Cytisus	0	0	1	1	0	1	1	1	1	0	0	0	.82	−.14
Daphne	0	1	0	1	0	1	1	1	1	1	1	0	.23	.24
Dorycnium	0	0	0	1	0	1	1	1	1	0	0	0	.70	.20
Ephedra	0	1	0	0	1	0	0	0	1	1	1	1	−1.39	.23
Erica	0	0	0	1	0	1	1	1	0	0	0	1	.91	.41
Fumana	0	0	1	1	0	1	1	1	0	0	0	0	1.06	.04
Genista	1	0	1	1	0	1	1	1	1	0	0	0	.88	−.38
Halimium	0	0	1	1	0	1	1	1	0	0	0	1	1.06	.04
Hedera	0	1	0	0	0	0	0	1	1	1	1	0	−.80	.22
Helianthemum	0	0	1	1	0	1	1	1	0	0	0	0	1.06	.04
Ilex	1	1	0	0	1	0	0	1	1	1	1	1	−1.30	−.15
Jasminum	0	0	0	1	0	1	1	1	1	1	1	1	.48	−.03
Juniperus	1	1	0	0	1	0	0	0	1	1	1	1	−1.55	−.03
Laurus	0	1	0	1	1	0	0	1	1	1	1	0	−.79	.30
Lavandula	0	0	1	1	0	1	1	1	0	0	0	0	1.06	.04
Lonicera	0	0	1	1	0	1	1	1	1	1	1	1	.61	−.41
Myrtus	0	1	0	1	0	1	1	1	1	1	1	1	.23	.24
Nerium	0	1	0	1	0	1	1	1	1	0	1	0	.47	.47
Olea	0	1	0	0	0	0	0	0	1	1	1	1	−1.12	.45
Osyris	0	1	0	0	1	0	0	1	1	1	0	1	−1.13	.11
Phillyrea	0	1	0	0	1	0	0	0	1	1	1	0	−1.39	.23
Phlomis	0	0	0	1	0	1	1	1	1	0	0	0	.70	.20
Pinus	0	1	0	0	1	0	0	0	1	0	1	0	−1.24	.58
Pistacia	0	1	0	0	1	0	0	0	1	1	1	1	−1.39	.23
Prunus	0	0	1	1	0	1	1	1	1	1	1	0	.61	−.41
Pyrus	0	0	1	1	0	1	1	1	1	1	1	0	.61	−.41
Quercus	1	1	0	0	1	0	0	0	1	0	1	0	−1.49	.49
Retama	0	1	0	1	0	1	1	1	1	0	0	0	.47	.47
Rhamnus	1	1	0	0	1	0	0	1	1	1	1	1	−1.30	−.15
Rhododendron	0	1	0	1	0	1	1	1	1	0	1	1	.47	.47

(*continued*)

TABLE A1 (*Continued*)

Genus	SP	LT	HA	FS	FSE	PC	PR	PT	SS	SD	PLI	DIS	DIM1	DIM2
Rhus	0	1	1	0	1	0	0	0	1	1	1	1	−1.43	−.34
Rosa	1	0	1	1	0	1	1	1	1	1	1	0	.61	−.67
Rosmarinus	0	0	0	1	0	1	1	1	0	0	0	0	.91	.41
Rubia	0	1	0	0	0	0	0	1	1	1	0	0	−.80	.22
Rubus	1	0	0	1	0	1	1	1	1	1	1	0	.39	−.35
Ruscus	1	1	0	0	1	0	1	1	1	1	1	0	−.99	−.16
Satureja	0	1	0	1	0	1	1	1	0	0	0	0	.68	.67
Securinega	1	1	1	0	1	0	0	1	0	0	0	0	−1.27	−.81
Smilax	1	1	0	0	1	0	1	1	1	1	1	1	−.99	−.16
Sorbus	0	0	1	1	0	1	1	1	1	1	1	0	.61	−.41
Stauracanthus	1	0	0	1	0	1	1	1	1	0	0	0	.67	.09
Teucrium	0	0	0	1	0	1	1	1	0	0	1	0	.91	.41
Thymelaea	0	1	0	1	1	0	1	1	0	0	0	0	−.01	.97
Thymus	0	0	1	1	0	1	1	1	0	0	0	0	1.06	.04
Ulex	1	0	1	1	0	1	1	1	1	0	0	0	.88	−.38
Ulmus	0	0	1	0	0	0	0	0	1	0	1	1	−.46	−.99
Viburnum	0	1	0	1	0	1	1	1	1	1	1	0	.23	.24
Vitis	0	0	1	0	1	0	0	1	1	1	1	1	−.80	−.73

NOTE.—Symbols for characters, and codes for character states, are as follows: SP, spinescence (1, spiny; 0, nonspiny); LT, leaf type (1, sclerophyllous; 0, nonsclerophyllous); HA, habit (1, winter or summer-facultative deciduous; 0, evergreen); FS, flower size (1, perianth depth × width < 25 mm^2; 0, perianth length × width > 25 mm^2); FSE, flower sexuality (1, unisexual flowers; 0, hermaphroditic flowers); PC, perianth color (1, colored; 0, brownish or greenish); PR, perianth reduction (1, perianth complete; 0, at least one verticil absent or much reduced); PT, pollinator type (1, insect pollinated; 0, wind pollinated); SS, seed size (1, length × width > 2.25 mm^2; 0, length × width < 2.25 mm^2); SD, seed dispersal mode (1, endozoochorous; 0, nonendozoochorous); PLI, occurrence of Pliocene or pre-Pliocene fossil records (1, occurrence; 0, absence); DIS, intercontinental range disjunction (1, occurrence; 0, absence). DIM1 and DIM2, coordinates on the first and second dimensions generated by nonmetric multidimensional scaling of the similarity matrix of life-history and reproductive characters.

APPENDIX B

TABLE B1

WOODY PLANT GENERA THAT WERE PRESENT IN SOUTHWESTERN EUROPE IN THE PLIOCENE OR MID- TO LATE MIOCENE AND SUBSEQUENTLY BECAME EXTINCT THERE, BUT ARE STILL SURVIVING ELSEWHERE

Genus	FSE	PR	PT	SD
Acanthopanax	1	1	1	1
Ailanthus	1	0	1	0
Aralia	1	1	1	1
Bumelia	0	1	1	1
Caesalpinia	0	1	1	0
Calycanthus	0	1	1	1
Carya	1	0	0	0
Cassia	0	1	1	0
Celastrus	0	1	1	1
Chrysophyllum	0	1	1	1
Cinnamomum	0	0	1	1
Clethra	0	1	1	0
Dalbergia	0	1	1	0
Diospyros	1	1	1	1
Empetrum	1	0	0	1
Engelhardtia	1	0	0	0
Euclea	1	1	1	1
Eucommia	1	0	0	0
Ginkgo	1	0	0	1
Glyptostrobus	1	0	0	0
Lindera	1	0	1	1
Liquidambar	1	0	0	0
Liriodendron	0	1	1	0
Magnolia	0	1	1	1
Myrica	1	0	0	1
Myrsine	1	0	1	1
Nyssa	1	0	1	1
Ocotea	1	1	1	1
Persea	0	0	1	1
Phoebe	0	1	1	1
Pisonia	1	1	1	1
Platanus	1	0	0	0
Podocarpus	1	0	0	1
Pterocarya	1	0	0	0
Robinia	0	1	1	0
Sabal	1	0	1	1
Sapindus	1	1	1	1
Sassafras	1	0	1	1
Sequoia	1	0	0	0
Symplocos	0	1	1	1
Taxodium	1	0	0	0
Torreya	1	0	0	1
Tsuga	1	0	0	0
Weinmannia	0	1	1	0
Zanthoxylum	0	1	1	1

NOTE.—Characters and codes for character states are as described in App. A. See text for literature sources used.

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