Can Population Genetic Structure Be Predicted from Life-History Traits?

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abstract: Population genetic structure is a key parameter in evolutionary biology. Earlier comparative studies have shown that genetic structure depends on species ecological attributes and life-history traits, but species phylogenetic relatedness had not been accounted for. Here we reevaluate the relationships between genetic structure and species traits in seed plants. Each species is characterized by a set of life-history and ecological features as well as by its geographic range size, its heterozygote deficit, and its genetic structure at nuclear and organelle markers to distinguish between pollen- and seed-mediated gene flow. We use both a conventional regression approach and a method that controls for phylogenetic relationships. Once phylogenetic conservatism and covariation among traits are taken into account, genetic structure is shown to be related with only a few synthetic traits, such as mating system for nuclear markers and seed dispersal mode or geographic range size for organelle markers. Along with other studies on invasiveness or rarity, our work illustrates the fact that predicting the fate of species across a broad taxonomic assemblage on the basis of simple traits is rarely possible, a testimony of the highly contingent nature of evolution.

Keywords: comparative method, chloroplast markers, independent contrasts, nuclear markers, pollen dispersal, seed dispersal.

Investigations of population genetic structure are a prerequisite for the understanding of species evolution, because they help in assessing to what extent distinct populations have embarked on separate evolutionary trajectories or remain linked by gene flow; whereas weak genetic structure points to species cohesion, the contrary can imply incipient speciation. As a consequence, genetic structure has been investigated and its causes discussed in thousands of studies involving virtually any type of organism. Both population history and species-specific characteristics have been considered to shape genetic structure. For instance, it is now well documented that past climatic variations have strongly affected the current geographic distribution of genetic lineages (Hewitt 2000; Petit et al. 2003, 2005*a*). Genetic structure should also be influenced by life-history traits (LHT), species distribution, and other ecological features of species that are more or less directly related to gene dispersal (hereafter collectively referred to as LHT). However, evaluating the relative dispersal ability of distantly related species on the basis of the assessment of specific traits is not straightforward. For instance, an increase in seed mass is unlikely to have the same consequence on seed dispersal in orchids (whose tiny seeds are dispersed by wind) and in oaks (whose acorns are cached by animals).

It is therefore surprising that previous cross-species analyses of the plant population genetics literature have found such strong associations between measures of the organization of genetic diversity (such as G_{ST}, which measures the proportion of total genetic variation that resides among populations) and various characteristics of the species. In particular, mating system, life form, and, to a lesser

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extent, mode of pollen and seed dispersal and geographic range have been considered to be predictors of G_{ST} in surveys of the isozyme literature (Loveless and Hamrick 1984; Hamrick and Godt 1989; Hamrick et al. 1992; Hamrick and Godt 1996), and similar conclusions have been reached in recent reviews based on nuclear DNA markers (Nybom and Bartish 2000; Nybom 2004). These reviews and meta-analyses have generated much interest and continue to motivate theoretical or empirical research in the field. For instance, Austerlitz et al. (2000) justify their theoretical work on the effects of colonization process in trees versus annual plants by the empirical evidence of a lower G_{ST} in trees than in herbs. Similarly, Pacheco and Simonetti (2000, p. 1767) introduce their study of a mimosoid tree deprived of its seed disperser by recalling that "species that are biotically dispersed generally show less population differentiation than those abiotically dispersed." More recently, Moyle (2006, p. 1068) recalled that "broad-scale comparisons among endemic versus widespread … species have shown contrasting and distinctive patterns of genetic variation among populations in these groups."

The implicit assumption behind these widely accepted tenets is that an evolutionary correlation exists between ecological traits and G_{ST} across species, resulting in similar G_{ST} values for species sharing similar LHT. However, there are two potential pitfalls when attempting to interpret the relationships between G_{ST} and LHT using cross-species analyses: nonindependence of the taxa and nonindependence of the LHT themselves.

First, most published studies have treated species as independent data points without attempting to account for phylogenetic nonindependence (but see Gitzendanner and Soltis 2000 and Aguinagalde et al. 2005 for plants or Bohonak 1999 for animals). Such direct cross-species comparisons have been dubbed TIPs because they compare the extant species at the tips of the phylogeny (Martins and Garland 1991). However, LHT often present a strong phylogenetic inertia, that is, a tendency to resist evolutionary change despite environmental changes (Morales 2000). Biologically, this means that patterns of shared ancestry, not adaptation to the changing environment, are driving variation in LHT across species. Statistically, this results in nonindependence of data in cross-species analyses and hence in an increase in the Type I error rate (the risk of incorrectly rejecting the null hypothesis of no relationship among traits; Garland et al. 2005). An important aspect of this problem, which is not yet widely appreciated, is that this lack of independence between species cannot be compensated for by increasing sample size (Ackerly 2000). This is because the critical values for significance testing decline rapidly with increasing sample sizes, whereas the number of truly independent comparisons increases only slowly, so more of the outcomes are judged significant when standard statistical criteria based on the usual assumption of independence are used. Fortunately, different methods have been developed to deal with this problem, and they are increasingly used in comparative studies (e.g., Felsenstein 1985; Martins and Garland 1991; Paradis and Claude 2002; Housworth et al. 2004).

Second, LHT are often correlated with each other, thereby confounding the relationships with G_{ST}. Examples of associations between traits that have been detected in cross-species comparisons include those between breeding system (i.e., gender variation), pollen dispersal, and growth form of the species (Renner and Ricklefs 1995); between animal-mediated dispersal and fruit diameter (Jordano 1995); between seed mass, dispersal mode, and growth form (Westoby et al. 1996); between breeding system, plant distribution, growth form, and pollen dispersal (Vamosi et al. 2003); between seed mass and growth form (Moles et al. 2005); between longevity and mating system (Barrett et al. 1996); and between mating system and pollen dispersal (Vogler and Kalisz 2001). Hence, we need to account for phylogenetic effects and to cope for trait interactions when assessing the evolutionary relationships between G_{ST} and LHT.

Previous comparative studies could not take advantage of the complementary information provided by different types of DNA markers, because the bulk of the literature on organelle DNA variation in plants is very recent (Petit et al. 2005*b*; Petit and Vendramin 2006). Plants have three distinct intracellular genomes characterized by a contrasted mode of inheritance (Petit et al. 2005*b*). In seed plants, the rule is that organelle DNA is inherited maternally (except chloroplast DNA in conifers, which is predominantly paternally inherited). In contrast, the nuclear genome is biparentally inherited. Hence, whereas nuclear markers are transmitted via pollen and seeds, maternally inherited markers are transmitted via seeds only. Accordingly, LHT could differentially affect genetic structure at biparentally inherited markers (hereafter G_{STb}) and at maternally inherited markers (hereafter G_{STm}), and the inclusion of both fixation indexes (G_{STb} and G_{STm}) should help distinguish between the consequences of pollen- and seed-mediated gene flow on genetic structure.

Here we test the influence of a set of LHT on G_{STb} and G_{STm} in seed plants. Traits that have been reported to directly or indirectly influence gene flow through pollen or seeds were investigated (growth form, plant size, perenniality, seed dispersal mode, seed mass, reproduction type, and geographic range for both G_{STb} and G_{STm}; pollination mode, mating system, and breeding system for G_{STb} only). We also consider the relationship between G_{STb} and the within-population inbreeding coefficient F_{IS} (Wright 1951). We use both TIPs and Felsenstein's method based

on phylogenetically independent contrasts (PICs) to investigate whether previous studies (based on TIPs) have resulted in robust inferences. We also examine whether the identified relationships persist when other traits are used as covariates in the analyses.

Material and Methods

List of Studied Taxa

Of the 164 studies of the distribution of genetic diversity within and among plant populations based on maternally inherited organelle DNA markers compiled previously (Petit et al. 2005*b*), we discarded those dealing with aquatic species (insufficiently represented) and those studies that had first pooled individuals for screening variation, because this seemed to result in some bias in the estimate of G_{STm} (Petit et al. 2005*b*). Altogether 141 species were retained. When a species had been studied with both chloroplast and mitochondrial markers, the mean between the two G_{STm} estimates was used if both genomes were similarly maternally inherited (there were eight species in that case), because G_{STm} estimated with markers from either genome closely co-vary (Petit et al. 2005*b*). The molecular techniques employed in the different genetic diversity studies were as described by Petit et al. (2005*b*). The set of species covers all five continents and all climatic zones, although Northern Hemisphere species are overrepresented. The same database was used to investigate the genetic structure at nuclear markers (G_{STb}). A total of 112 species were available for this purpose, including 103 common with the previous set of 141 species (150 distinct species in total).

List of Plant Species Characters

For each species, a set of LHT was compiled (see app. A in the online edition of the *American Naturalist*). The information was obtained from various sources, including the original articles used to compile genetic structure (listed in Petit et al. 2005*b*), standard works such as floras and peer-reviewed publications identified with Isi Web of Science, and direct contact with the authors of the original articles.

We considered a widely used list of plant features in order to maximize the comparability of our results with former work. We merged some of the categories used by previous authors in order to obtain a sufficient sample size. Categories were as follows.

Taxonomic status of the species. Each species has been classified at five taxonomic levels (plant group, subclass, order, family, genus) according to the classification used on the NCBI taxonomy browser Web site (http://www.ncbi.nlm.nih.gov/Taxonomy/). The first level (termed plant group) defines whether the species is a gymnosperm, a eumagnoliid, or a eudicot. Then each species is characterized by its subclass, order, family, and genus. Six subclasses were represented (Asteridae, Caryophyllidae, Coniferopsida, Liliidae, Magnoliidae, and Rosidae), as well as 25 orders, 45 families, and 86 genera (see app. A).

Growth form. Herbaceous: forb + graminoid, vine, shrub, tree. A shrub was defined as a woody plant, usually smaller than a tree, that produces several stems rather than a single trunk from the base. A tree was defined as a perennial plant that grows from the ground with a single, normally tall, woody, self-supporting trunk or stem and an elevated crown of branches and foliage. Because only two species (*Hedera helix* and *Vitis vinifera*) were vines in our data set, this category was not included in the analysis of relationships between G_{ST} and growth form.

Perenniality. Annual, biennial, short-lived perennial, long-lived perennial.

Seed dispersal. Wind, animal ingested, animal attached, animal cached, gravity. The corresponding botanical names are anemochorous, endozoochorous, epizoochorous, diszoochorous, and barochorous, respectively, but for the sake of clarity, we stick to the simpler terms in the text. Assignment to these categories was based either on particular anatomic features that hint at specific modes of dispersal or on published field observations.

Pollen dispersal. Anemophilous, zoophilous.

Mating system. Selfed, mixed, outcrossed.

Heterozygote deficit (F_{IS}). Data were taken directly from studies on nuclear diversity based on codominant genetic markers. Sometimes other publications than the article that provided the G_{ST} estimate had to be consulted.

Breeding system. Hermaphrodite/monoecious, gynodioecious, dioecious. The distribution of sexes is considered at the level of the plant, not at the level of the flower. Hence, hermaphrodite plants (male and female function both present in the same flowers) were pooled with monoecious plants (male and female function in separate flowers of the same individual).

Reproduction. Both sexual and vegetative, sexual only.

Geographic range. Endemic, narrow, regional, and widespread. Following previous surveys, we used a threshold of 50,000 km^2 to define endemic species. A species' geographic range size was considered narrow if it occupies <25% of its continent, regional if it is distributed over >25% but <50%, and widespread if it is distributed over >50%.

Seed mass and plant size. We used estimates of dry seed mass (mg $seed^{-1}$) and plant height (m).

Data Analysis

Transformation of the Variables. To improve normality, G_{ST} and F_{IS} estimates were arcsine–square root transformed,

and seed mass and plant size were log transformed. The remaining variables are either binary (pollination mode, reproductive type) or multiple-state categorical variables. Among the latter, all but one (mode of seed dispersal) could be ranked to yield semiquantitative variables. The following notations were used: for growth form, herbaceous = 1, shrub = 2, tree = 3; for perenniality, annual = 1, biennial = 2, short-lived perennial = 3, long-lived perennial = 4; for pollination mode, anemophilous = 0, zoophilous = 1; for reproductive type, sexual and vegetative = 0, sexual only = 1; for mating system, selfed = 1, mixed = 2, outcrossed = 3; for breeding system, monoecious = 1, gynodioecious = 2, dioecious = 3; for geographic range, endemic = 1, narrow = 2, regional = 3, widespread = 4. Each of the five seed dispersal categories was transformed into a 0, 1 dummy variable because we could not think of an objective way to rank them to yield a semiquantitative variable.

Taxonomic Effects. For the nested ANOVA, we specified the taxonomic levels (plant group, subclass, order, family, genus) as nested random effects within each higher level. We estimated the variance components for the sequential Type I sum of squares because the results were consistent with those obtained with Type III sum of squares for our unbalanced design (Bell 1989). A PROC GLM procedure was used to fit the nested ANOVA model with SAS software (ver. 9.1 for Windows 2004; SAS Institute, Cary, NC). Computations of Abouheif's (1999) test for serial dependence were carried out using R (ver. 2.0.1; Ihaka and Gentleman 1996) with the ade4 package (available at http://www.r-project.org/). Phylogenetic signal was measured for each continuous or ranked variable: seed mass, plant size, perenniality, growth form, breeding system, range size, pollen dispersal, reproduction type, F_{IS}, G_{STm}, and G_{STb}.

Conventional Comparisons (TIPs). Simple linear regressions and one-way ANOVAs with the GLM procedure were performed with SYSTAT, version 10.2.05 (SYSTAT 2002). To facilitate comparisons between TIPs and PICs approaches, the conventional (TIPs) approach was based on regressions rather than on ANOVAs. However, we also performed ANOVAs, and the conclusions were identical (results not shown).

Phylogenetically Independent Contrasts (PICs). The reference plant phylogeny used is that of Soltis et al. (2000). Because not all studied species were present in this phylogeny, missing species were grafted according to information available in other phylogenetic studies (Rieseberg 1991; Wang and Szmidt 1993; Schilling and Linder 1998; Hedren 2001; Hedren et al. 2001; Soltis et al. 2001; A. Wolfe, personal communication). Either intragenus phylogenetic relationships were reconstructed following Arduino et al. (1996), Liston et al. (1999), Manos et al. (1999), and http://www.fmnh.helsinki.fi/users/haaramo/Plantae/Coniferophyta/Pinaceae/Abies.htm, or they were left as soft polytomies when the infragenus relationships could not be resolved with the available information (in the case of *Betula* sp., *Helianthus* sp., *Sorbus* sp., *Senecio* sp., *Packera* sp.). The phylogenetic supertree used for the analyses is presented in appendix B in the online edition of the American Naturalist. All branch lengths were assigned a value of 1. With Felsenstein's (1985) method of independent contrasts, one assumption is that characters evolve following a Brownian motion model and that branch lengths are expressed in units of expected amount of character change. However, this method generally performs well when information on branch lengths is missing (Martins and Garland 1991). Considering all branches equal signifies that the characters investigated are assumed to follow a model of a punctuational evolution, with changes taking place only at speciation events (Martins and Garland 1991). A standard procedure to ascertain that the punctuational model of evolution assumptions leads to adequately standardized independent contrasts was proposed by Garland et al. (1992). The verification procedure consists of plotting the absolute value of each standardized independent contrast as a function of its standard deviation. Any significant trend in the plot indicates that the contrasts are not adequately standardized and that phenotypic data or branch lengths have to be transformed. All regressions had a slope close to 0 (data not shown), indicating that the assumption of equal branch lengths is not biasing the results (app. C in the online edition of the *American Naturalist*).

Independent contrasts (Felsenstein 1985) were estimated with CAIC, version 2.6 (Purvis and Rambaud 1995). When dealing with categorical data, the Brunch option was used (Purvis and Rambaud 1995).

Partial Regressions. To check whether observed relationships between given LHT traits and G_{STb} could be the result of correlations between predictor LHT variables, partial regressions were performed on the independent contrasts using SYSTAT, version 10.2.05 (SYSTAT 2002). Regressions were forced through the origin (Felsenstein 1985).

Results

Phylogenetic Signal

A first logical step in comparative approaches is to test whether there is a phylogenetic signal in the data (Freckleton et al. 2002). Nested ANOVAs (Bell 1989) and tests for serial dependence (Abouheif 1999) were used for this

Table 1: Nested ANOVA and variance component estimations for population genetic structure indexes based on biparentally (G_{STb}) and maternally inherited markers (G_{STm})

	G_{STb}					G_{STm}				
Level	df	SS	*F*	*P*	Variance component (%)	df	SS	*F*	*P*	Variance component (%)
Plant group	2	.194	2.76	.079	2.48	2	.314	3.25	**.046**	2.30
Subclass	3	.297	2.82	.054	3.80	3	.061	.42	.737	.45
Order	14	1.881	3.83	**<.001**	24.06	19	4.267	4.65	**<.001**	31.30
Family	11	1.403	3.63	**.002**	17.94	19	2.273	2.48	**.005**	16.68
Genus	26	2.921	3.20	**.001**	37.35	40	4.061	2.1	**.005**	29.79
Error term	32	1.124	…	…	14.37	55	2.655	…	…	19.48

Note: SS = sum of squares. Significant *P* values in bold.

purpose. Nested ANOVAs were performed to detect the proportion of variance present at each taxonomic level for the variables G_{STb} and G_{STm}. They demonstrate that taxonomically related species partition genetic diversity in a similar way across populations: phylogenetic effects up to order level explain 79% (G_{STb}) and 77% (G_{STm}) of the total variance of these variables (table 1). Similarly, many of the predictor LHT variables present a significant phylogenetic signal according to Abouheif's (1999) test for serial dependence, with the exception of breeding system, mating system, and reproductive type (fig. 1).

Relationships between LHT and G_{STb}

Both conventional regressions (TIPs) and regressions based on PICs were carried out with each data set. The G_{STb} presents multiple dependences on LHT when using TIPs analysis. In particular, plant growth form, plant size, perenniality, seed dispersal mode, seed mass, pollination mode, mating system, and F_{IS} are all related to G_{STb} (table 2; app. D in the online edition of the *American Naturalist*). However, several of these relationships disappear when using PICs. Only four remain: species that are perennial, dioecious, or outcrossed present lower G_{STb}, as do species characterized by a low heterozygote deficit (F_{IS}; table 3; app. E in the online edition of the *American Naturalist*).

Interactions between Predictor Variables

To check whether the observed relationships between specific traits and G_{STb} could be affected by interactions between predictor variables (i.e., result from indirect effects of another predictor variable), a correlation analysis based on PICs was performed. Mating system is correlated with both sexual type and perenniality, with outcrossing plants being more often perennial and dioecious, whereas lower F_{IS} values are typically observed in dioecious, outcrossed perennial species (fig. 2). To take these interactions into account in subsequent analyses, partial regressions based on PICs were used. The fixation index F_{IS} appears to be the best predictor variable of G_{STb}, because G_{STb} still depends significantly on F_{IS} when perenniality, sexual type, or mating system are controlled for, whereas the opposite does not hold (table 4).

Relationships between LHT and G_{STm}

According to TIPs analyses, G_{STm} depends on seed dispersal mode, reproduction type, and seed mass (table 2). Some of these relationships disappear when tested on PICs (table 3). One seed dispersal mode (gravity) and reproduction type remain significant, whereas geographic range size becomes significant in PICs analyses. Specifically, (i) species with gravity-dispersed seeds present larger G_{STm} values compared with species with other dispersal modes, (ii) species capable of vegetative reproduction have lower G_{STm}

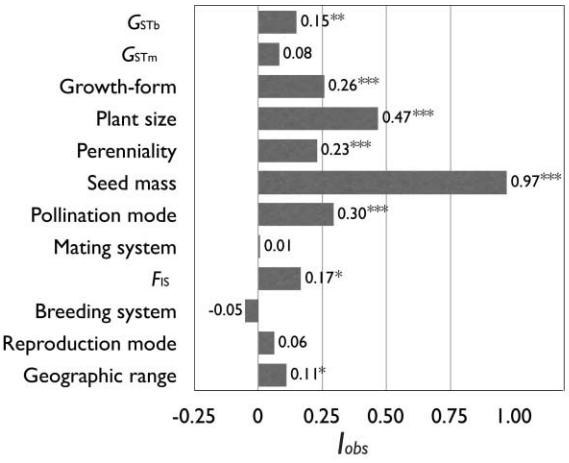

Figure 1: Estimation of phylogenetic signal for G_{ST} values and life-history traits according to Abouheif's (1999) method. Asterisks indicate the significance of the signal (*one asterisk*, $.05 > P > .01$; *two asterisks*, $.01 > P > .001$; *three asterisks*, $P < .001$).

Table 2: Conventional regressions (TIPs) between G_{STb} or G_{STm} and independent life-history trait variables

	G_{STb}				G_{STm}			
Variable	*N*	Sign	R^2	*P*	*N*	Sign	R^2	*P*
Growth form	115	−	.15	**<.001**	139	+	.01	.258
Plant size	110	−	.14	**<.001**	132	+	.01	.207
Perenniality	116	−	.10	**<.001**	141	+	.01	.203
Seed dispersal mode:								
Wind	109		.00	.808	134		.00	.712
Gravity	109	−	.02	.114	134	−	.01	.181
Animal attached	109	−	.02	.133	134	+	.01	.264
Animal ingested	109		.00	.658	134	+	.04	**.029**
Animal cached	109	+	.08	**.003**	134	−	.04	**.015**
Seed mass	112	−	.04	**.030**	136	+	.06	**.005**
Pollination mode	108	+	.13	**<.001**	…		…	…
Mating system	112	−	.16	**<.001**	…		…	…
F_{IS}	69	+	.31	**<.001**	…		…	…
Breeding system	116		.00	.948	141		.00	.567
Reproduction type	103		.00	.684	102	−	.15	**<.001**
Geographic range	116		.00	.669	140	−	.02	.074

Note: *N* indicates number of species (number of TIPs). The sign refers to the slope of the regression. Ellipses indicate relations that were not tested. Significant *P* values in bold.

values than species with pure sexual reproduction (marginally; cf. the small R^2), and (iii) species with large range size tend to have low G_{STm} values.

Discussion

Related species tend to partition genetic diversity in similar ways within and among populations: nested ANOVAs and, to a lesser extent, tests for serial dependence indicate that much of the variation in G_{ST} at both nuclear and organelle markers is accounted for by the phylogenetic (or taxonomic) affinity of the species. Earlier studies had already demonstrated that G_{STb} tends to be similar in species belonging to the same family (e.g., Hamrick and Godt 1996), but this effect had not been further tested and quantified. Taxonomic affinity and phylogenetic relationships are not completely equivalent, which might explain some differences observed between nested ANOVAs and tests of serial dependence. Because closely related species tend to have similar ecological attributes and traits, it is a priori not surprising that they partition genetic diversity similarly within and among populations.

Using the conventional TIP approach, we confirmed many of the relationships identified previously between LHT and G_{STb} (Hamrick and Godt 1989, 1996), even though our data set is more limited. However, the existence of a strong phylogenetic signal supports our contention that the dependency of G_{ST} on LHT cannot be inferred from simple conventional comparisons across species. Accordingly, the results based on PICs reveal far fewer significant relations than those based on TIPs. In addition, most of the remaining relationships vanish when we consider the interactions among different LHT: only the relation of mating system with nuclear genetic structure remains significant. Hence, our results suggest that previously identified relationships between genetic structure and LHT need to be reevaluated within an explicit evolutionary context.

Mating System

The mating system seems to represent the only factor that directly affects genetic structure at nuclear genes (G_{STb}) across most seed plants. According to Charlesworth (2003, p. 1052), "[The mating system is] probably among the factors with major effects on variability, clear enough to be discernible even in the presence of other factors." Our results fully support this view. Other factors such as perenniality or breeding system are also suitable predictors of G_{STb}, but direct causal relationships seem unlikely because the effects of these factors are no longer significant when controlling for variation in mating system. We attribute this to the fact that perenniality and breeding system are strongly correlated with the mating system. For instance, all dioecious species are necessarily allogamous, and no predominantly selfing tree species is known (Barrett 1998).

Table 3: Phylogenetic regressions between G_{STb} or G_{STm} and independent life-history trait variables

	G_{STb}				G_{STm}			
Variable	*N*	Sign	R^2	*P*	*N*	Sign	R^2	*P*
Growth form	89	−	.02	.196	109	−	.01	.328
Plant size	85	−	.02	.276	103	−	.01	.520
Perenniality	90	−	.05	**.031**	111	−	.01	.353
Seed dispersal mode:								
Wind	19	−	.04	.207	23	+	.00	.773
Gravity	9	+	.06	.482	13	−	.41	**.013**
Animal attached	6	+	.05	.320	7		.00	.986
Animal ingested	13	−	.03	.533	16	+	.20	.070
Animal cached	3	+	.61	.221	4	+	.03	.768
Seed mass	87	−	.00	.303	106	−	.00	.520
Pollination mode	8	+	.27	.346	…	…	…	…
Mating system	88	−	.11	**.002**	…	…	…	…
F_{IS}	57	+	.35	**<.001**	…	…	…	…
Breeding system	90	−	.13	**<.001**	111	+	.02	.177
Reproduction type	12	−	.22	.404	14	−	.03	**.035**
Geographic range	90	−	.00	.667	110	−	.06	**.010**

Note: *N* indicates phylogenetically independent contrasts. The sign refers to the slope of the regression. Ellipses indicate relations that were not tested. Significant *P* values in bold.

Heterozygote Deficit

The G_{STb} showed a stronger relationship with F_{IS} than with mating system. At least two factors could account for this difference. First, according to Wright (1965), F_{IS} provides an indirect but quantitative estimate of the outcrossing rate *t*, assuming that (1) the outcrossing rate (*t*) has been constant for a sufficient number of generations, (2) the population is in inbreeding equilibrium, and (3) selfing is the major cause of departure from Hardy-Weinberg frequencies. Under these assumptions, we have $F_{IS} = (1 - t)/(1 + t)$. Hence, F_{IS} could reflect mating system more accurately than the three categories used to classify mating system, possibly resulting in a stronger relation with G_{STb}. Second, heterozygote deficit is affected not only by mating system but also by genetic substructure within population (Wahlund 1928). Such a substructure could be caused by reduced seed or pollen gene flow. As a consequence, F_{IS} provides information on both mating system and gene dispersal distances within populations. This could explain why it shows a stronger relationship with G_{STb} than does mating system itself.

Seed Dispersal Mode

In TIP analyses, we found that species whose seeds are cached by animals had significantly lower G_{STb} than species with other dispersal modes. Earlier studies (all based on TIPs) have also identified differences in nuclear genetic structure as a function of seed dispersal categories (Hamrick et al. 1993; Hamrick and Godt 1989, 1996; Nybom 2004). However, Hamrick and Nason (1996) have warned that rates of pollen flow could obscure the effects of seed dispersal mechanisms on nuclear genetic structure. A recent survey has confirmed that postfertilization gene flow (by seeds) accounts for a very limited fraction of overall nuclear gene flow (Petit et al. 2005*b*). Hence, our finding that the relationship between modes of seed dispersal and G_{STb} no longer holds when using PICs makes biological sense. Moreover, the lack of correspondence between G_{STb}

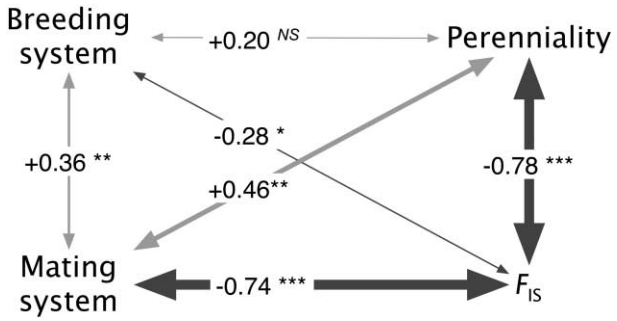

Figure 2: Correlations between life-history trait variables based on phylogenetically independent contrasts. Mating system is coded as a function of increasing allogamy (selfed, mixed, outcrossed) and breeding system as a function of increasing dicliny (hermaphroditic/monoecious, gynodioecious, dioecious). The values and significance of the Pearson correlations between contrasts when forced through the origin are indicated on arrows. *Light gray lines*, positive correlations; *dark gray lines*, negative correlations; arrow thickness is proportional to the *r* value (*one asterisk*, $.05 > P > .01$; *two asterisks*, $.01 > P > .001$; *three asterisks*, $P < .001$; *NS*, not significant).

Table 4: Partial regression coefficients based on phylogenetically independent contrasts for G_{STb} as a function of perenniality, breeding system, mating system, and heterozygote deficit (F_{IS})

Relation between G_{STb} and	Controlled variable	b_{st}	R^2_{part}	P
Perenniality	Mating system	−.116	.013	.396
Breeding system	Mating system	−.182	.033	.179
F_{IS}	Mating system	.292	.085	**.029**
Perenniality	F_{IS}	.106	.011	.435
Breeding system	F_{IS}	−.106	.011	.437
Mating system	F_{IS}	.029	.001	.830
Mating system	Perenniality	−.169	.029	.214
F_{IS}	Perenniality	.289	.083	**.031**
Mating system	Breeding system	−.273	.075	**.042**
F_{IS}	Breeding system	.447	.200	**.001**

Note: The standardized partial regression coefficients (b_{st}), the partial R^2 (R^2_{part}), and the associated P values measure the effect of one variable after accounting for the effects of the other controlled variable; $N = 55$ species for all regressions. Significant P values in bold.

and G_{STm} across modes of seed dispersal indicates that inferences of seed movements based on biparentally inherited markers (G_{STb}) can be completely misleading.

In contrast, a straightforward relationship is expected between genetic structure at maternally inherited markers (G_{STm}) and those LHT that affect seed dispersal. In particular, species lacking specialized features for seed dispersal (gravity-dispersed seeds) should be characterized by high values of G_{STm} in comparison with species characterized by more specialized biotic or abiotic seed dispersal modes. In agreement with this prediction, we found that species with gravity-dispersed seeds had significantly higher G_{STm} in PICs analyses. No significant relationships were identified between G_{STm} and the other modes of seed dispersal, although species with animal-ingested seeds had a rather low G_{STm}. These results might be due to the difficulties in evaluating seed dispersal ability. First, many species have mixed seed dispersal strategies (e.g., Chambers and MacMahon 1994; Greene and Johnson 1995; Hampe 2004), reducing the relevance of the categories used. Second, the categories might be too broad. For instance, large differences in dispersal ability certainly exist among species with wind-dispersed seeds, depending on seed mass or on the actual anatomical adaptations (gliders, parachutes, helicopters, spinners, cottony seeds, etc.). Whereas tiny cottoneous, plumose, or dust seeds can be carried regularly over large distances, heavy samaras should be typically less effectively dispersed. Third, seed dispersal alone does not fully describe realized seed-mediated gene flow, that is, the successful final establishment of a dispersed propagule; fruit/seed removal, seed delivery, seed predation, seed bank dynamics, germination, and seedling establishment might be equally important factors (Wang and Smith 2002).

Similarly, the lack of relationships between G_{STm} and seed mass is not that surprising. An increase in seed mass is unlikely to have the same consequence for plants having very different seed dispersal modes. Whereas light seeds should favor dispersal for most anemochorous plants, this is not necessarily the case for species whose seeds are dispersed by animals (e.g., Bossema 1979). Moreover, larger seeds might favor seedling establishment success and competitive ability (especially in closed forest vegetation; Eriksson et al. 2000). Finally, the classical trade-off between seed mass and seed number in plants (Rees et al. 2001) could obscure the effect of seed mass on genetic structure, since seed number can affect the likelihood that a given seed is deposited in a suitable habitat.

Despite these potential difficulties, Aguinagalde et al. (2005) have described a positive relationship between G_{STm} and seed mass using the same analytical approach. However, their study was based on data from a more homogeneous sample (forest trees and shrubs) and region (Europe), increasing the comparability of the results. Altogether, the large number of factors involved helps us understand why generalizations of the effect of seed characteristics on population genetic structure at maternally inherited markers remain difficult, even if the relation is a priori much more direct than for nuclear markers.

Geographical Range

Although some studies have identified a relationship between geographic range and G_{STb} (Loveless and Hamrick 1984; Hamrick et al. 1992), most have not (Hamrick and Godt 1989; Nybom and Bartish 2000; Nybom 2004). Paired comparisons of G_{STb} in widespread and endemic species were not significant (Gitzendanner and Soltis 2000; Cole 2003). Here, G_{STb} was independent of range size regardless of the method used (TIPs and PICs analyses). However, results based on maternally inherited markers were different. Species with more restricted ranges (narrow and regional) are characterized by larger G_{STm} than widespread ones in PICs analyses, in line with the findings of Aguinagalde et al. (2005), who reported that European woody plant species with broad boreal-temperate distribution had smaller G_{STm} than more temperate species. The explanation that had been put forward to account for the relationship between G_{ST} and geographic range size is that species with large ranges must necessarily have high colonization abilities (i.e., by seeds); otherwise, they would never have achieved such a broad distribution (e.g., Loveless and Hamrick 1984). Furthermore, the degree of range fragmentation often co-varies negatively with species range sizes (Higgins et al. 2003), since processes that move seeds may break down in disjunct populations. This could further contribute to increasing G_{STm} in narrowly distributed

species. In any case, the fact that a relation with geographic range size was found for G_{STm} but not for G_{STb} makes sense, given the overwhelming importance of seed dispersal on range expansion. However, this relation does not hold for species with particularly small ranges (i.e., belonging to the endemic category), thus restricting the generality of this finding.

Conclusions

Few direct relations between genetic structure and LHT were supported by our analyses when explicitly testing for correlated evolution within a phylogenetic framework. The G_{STm} is weakly related with geographic range size and with reproduction type. The only other factors that we found to be related with genetic structure are mating system (selfing vs. outcrossing) for nuclear markers and seed dispersal mode (gravity vs. the other categories) for maternally inherited markers. These two cases correspond to the most trivial distinctions in terms of dispersal of pollen and seeds: selfing represents the case of total lack of pollen gene flow, whereas the category gravity corresponds in fact to the absence of adaptation for seed dispersal. Although some LHT such as perenniality can still be used to predict the partitioning of genetic diversity at nuclear genes, we showed that their association with genetic structure is only indirect, mediated by evolutionary covariation with the mating system.

On the contrary, related species generally have similar levels of genetic structure at both maternally and biparentally inherited markers, to the extent that 77%–79% of all variation in G_{ST} is accounted for by species' taxonomic classification. However, it is difficult to imagine that genetic structure itself could be directly inherited across species following speciation. Rather, phenotypic traits affecting gene flow appear to be the most likely causes of this marked similarity in the organization of genetic structure of closely related taxa. Nevertheless, genetic structure did not show evolutionary correlations with most LHT in our study of seed plants: only a few LHT such as mating system (for nuclear markers) and seed dispersal mode or geographic range (for organelle markers) had explanatory power for interspecific variation in genetic structure within an explicit evolutionary scenario. This paradox can be explained if we consider that LHT do affect genetic structure but in ways that depend largely on the particular context (historical, ecological, and especially taxonomical). These contingencies have been previously emphasized to explain why there are so few traits consistently affecting the diversification of plant lineages (de Queiroz 2002).

Efforts by ecologists to identify traits that can help predict the fate of a species (e.g., whether it will become invasive or will remain rare and whether it will diversify by speciation or become extinct) have also been met with relatively little success. For instance, Stebbins (1965) was unable to find attributes common to plants that have become weeds in California. Subsequently, several authors have shown little optimism that single organisms' features may indicate their potential of invasiveness and have attributed this to the idiosyncrasy of each invasion (e.g., Goodwin et al. 1999; Muth and Pigliucci 2006). Other researchers remain optimistic regarding the possibility to predict invasions but stress the need to better specify the context where this will apply (e.g., Hamilton et al. 2005). The difficulty to identify universal constraints on basic species properties such as invasiveness or genetic structure should probably not come as a surprise. It simply illustrates the numerous strategies that exist for the successful expansion and diversification of species on Earth.

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Appendix A from J. Duminil et al., "Can Population Genetic Structure Be Predicted from Life-History Traits?"

(Am. Nat., vol. 169, no. 5, p. 662)

Table A1
Life-history traits and genetic structure for all species studied

Species	Taxonomic status	Subclass	Order	Family	Perenniality	Growth form	Breeding system	Pollination mode	Seed dispersal mode	Reproduction type	Mating system	Geographic range	Seed mass (mg seed^{-1})	Size (m)	G_{STm}	G_{STb}	F_{IS}
Abies alba	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	W	76.800	45	.92	.09	.05
Abies firma	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	E	40.290	45	.86		
Abies homolepis	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	E	15.500	24	.47		
Abies sachalinensis	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	E	9.320	25	.56	.02	.09
Acacia acuminata	D	*Rosidae*	*Fabales*	*Fabaceae*	LP	S	H	E	…	…	O	R	16.200	5	.40	.10	.33
Acer campestre	D	*Rosidae*	*Sapindales*	*Aceraceae*	LP	T	H	EA	W	S	O	W	111.000	15	.70		
Acer pseudoplatanus	D	*Rosidae*	*Sapindales*	*Aceraceae*	LP	T	H	EA	AI	S	O	W	109.600	30	.67		
Allium vineale	M	*Liliidae*	*Asparagales*	*Alliaceae*	SP	G	H	E	G	V	O	W	1.000	1	.76	.39	
Alnus cordata	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	T	H	A	W	S	O	N	6.800	18	1.00	.12	
Alnus glutinosa	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	T	H	A	W	S	O	W	2.100	18	.87	.20	.10
Alyssum bertolonii	D	*Rosidae*	*Brassicales*	*Brassicaceae*	SP	F	H	A	G	…	…	E	.559	.25	.21		
Anacamptis palustris	M	*Liliidae*	*Asparagales*	*Orchidaceae*	SP	F	H	E	W	V	O	…	.001	1.35	.87	.18	.00
Aquilegia chrysantha	D	*Magnoliidae*	*Ranunculales*	*Ranunculaceae*	SP	F	H	E	G	S	OS	N	1.037	.61	.87		
Aquilegia longissima	D	*Magnoliidae*	*Ranunculales*	*Ranunculaceae*	SP	F	H	E	G	S	OS	N	1.037	.61	.89		
Arabidopsis thaliana	D	*Rosidae*	*Brassicales*	*Brassicaceae*	A	F	H	E	G	S	S	W	.020	.3	.97	.62	.99
Arabis holboellii	D	*Rosidae*	*Brassicales*	*Brassicaceae*	SP	F	H	E	G	V	OS	R	.213	1	.61		
Argania spinosa	D	*Asteridae*	*Ericales*	*Sapotaceae*	LP	T	H	E	AI	S	O	N	3,000.000	10	.60	.18	.10
Aucoumea klaineana	D	*Rosidae*	*Sapindales*	*Burseraceae*	LP	T	D	E	W	…	O	N	98.000	45	.60	.14	.15
Beta vulgaris	D	*Caryophyllidae*	*Caryophyllales*	*Chenopodiaceae*	B	F	G	A	W	S	O	W	5.000	2	.49	.10	.22
Betula nana	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	S	H	A	W	S	…	W	.200	1	.54		
Betula pendula	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	T	H	A	W	S	O	W	.250	24	.41	.03	
Betula pubescens	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	T	H	A	W	S	O	W	.200	20	.30		
Caesalpinia echinata	D	*Rosidae*	*Fabales*	*Fabaceae*	LP	T	H	E	G	…	O	W	303.000	15	.91	.58	
Calluna vulgaris	D	*Asteridae*	*Ericales*	*Ericaceae*	LP	S	H	EA	…	V	OS	W	.030	.8	.47	.05	.06

Table A1 (*Continued*)

Species	Taxonomic status	Subclass	Order	Family	Perenniality	Growth form	Breeding system	Pollination mode	Seed dispersal mode	Reproduction type	Mating system	Geographic range	Seed mass (mg seed^{-1})	Size (m)	G_{STm}	G_{STb}	F_{IS}
Carpinus betulus	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	T	H	A	W	S	O	W	35.500	20	.97	.07	
Carpinus orientalis	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	S	H	A	W	S	O	W	20.938	8	1.00		
Caryocar brasiliense	D	*Rosidae*	*Malpighiales*	*Caryocaraceae*	LP	T	H	Z	G	…	O	R	50.270	10	.88	.29	.04
Castanea sativa	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	EA	AC	S	O	W	9,944.000	35	.43	.20	.21
Cedrela odorata	D	*Rosidae*	*Sapindales*	*Meliaceae*	LP	T	H	E	W	S	O	R	17.000	30	.96	.55	.00
Corallorhiza maculata	M	*Liliidae*	*Orchidales*	*Orchidaceae*	SP	F	H	E	W	V	O	W	.003	.5	.27		
Coreopsis grandiflora	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	W	…	O	R	2.580	91	.64	.07	.00
Coreopsis nuecensis	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	W	…	O	N	1.221	…	.78	.10	.00
Corylus avellana	D	*Rosidae*	*Fagales*	*Betulaceae*	LP	S	H	A	AI	S	O	W	1,262.400	4.5	.90	.20	.03
Corythophora alta	D	*Asteridae*	*Ericales*	*Lecythidaceae*	LP	T	H	E	AC	…	O	R	…	…	.96		
Crataegus laevigata	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	S	H	E	AI	S	O	W	60.100	6	.34		
Crataegus monogyna	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	S	H	E	AI	S	O	W	66.000	8	.24		
Cytisus scoparius	D	*Rosidae*	*Fabales*	*Fabaceae*	LP	S	H	E	G	S	O	W	8.300	2	.57		
Dactylis glomerata	M	*Liliidae*	*Poales*	*Poaceae*	SP	G	D	A	G	V	O	W	.850	1.2	1.00	.23	.00
Dactylorhiza incarnata/ maculata	M	*Liliidae*	*Asparagales*	*Orchidaceae*	SP	F	H	E	W	V	O	W	.001	.7	.66	.10	
Dicorynia guianensis	D	*Rosidae*	*Fabales*	*Fabaceae*	LP	T	H	E	W	S	OS	E	500.000	50	.41	.04	−.18
Draba aizoides	D	*Rosidae*	*Brassicales*	*Brassicaceae*	SP	F	H	E	G	…	O	R	.058	.1	.29		
Dryas integrifolia	D	*Rosidae*	*Rosales*	*Rosaceae*	SP	F	H	E	W	V	O	W	.400	.15	.44		
Dunnia sinensis	D	*Asteridae*	*Gentianales*	*Rubiaceae*	LP	S	H	E	W	…	O	E	…	…	.65		
Epipactis helleborine	M	*Liliidae*	*Orchidales*	*Orchidaceae*	SP	F	H	E	W	V	OS	W	.003	.8	.44		
Eritrichium nanum	D	*Asteridae*	*Lamiales*	*Boraginaceae*	SP	F	H	E	G	…	OS	E	…	.08	1.00	.19	
Eucalyptus angustissima complex	D	*Rosidae*	*Myrtales*	*Myrtaceae*	LP	T	H	E	G	S	O	E	1.500	8	.98	.11	.04
Eucalyptus brownii/ populnea complex	D	*Rosidae*	*Myrtales*	*Myrtaceae*	LP	T	H	EZ	W	S	O	E	.560	12	.35	.05	.30
Eucalyptus kochii	D	*Rosidae*	*Myrtales*	*Myrtaceae*	LP	T	H	E	W	S	O	E	2.220	5	.66	.05	.08
Eucalyptus nitens	D	*Rosidae*	*Myrtales*	*Myrtaceae*	LP	T	H	EZ	W	S	O	N	2.800	36	.62	.30	.31
Eugenia uniflora	D	*Rosidae*	*Myrtales*	*Myrtaceae*	LP	T	H	E	…	V	O	E	4.000	10	.26	.21	
Fagus crenata	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	N	178.570	40	.97	.04	.03
Fagus sylvatica	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	W	274.100	35	.83	.06	.02
Frangula alnus	D	*Rosidae*	*Rosales*	*Rhamnaceae*	LP	S	H	E	AI	S	O	W	17.500	5	.79		
Fraxinus angustifolia	D	*Asteridae*	*Lamiales*	*Oleaceae*	LP	T	D	A	W	S		W	53.400	25	.94		
Fraxinus excelsior	D	*Asteridae*	*Lamiales*	*Oleaceae*	LP	T	D	A	W	S	O	W	76.300	35	.85	.09	.01
Gliricidia sepium	D	*Rosidae*	*Fabales*	*Fabaceae*	LP	T	H	E	G	…	O	R	103.000	12	.69	.17	.02
Glycine soja	D	*Rosidae*	*Fabales*	*Fabaceae*	A	F	H	E	AI	S	S	R	48.019	…	.52	.48	1.00
Gymnadenia conopsea	M	*Liliidae*	*Orchidales*	*Orchidaceae*	SP	F	H	E	W	V	O	W	.008	.65	.33	.45	.73
Hedera helix s.l.	D	*Asteridae*	*Apiales*	*Araliaceae*	LP	V	H	E	AI	V	O	W	21.600	30	.64		

Table A1 (*Continued*)

Species	Taxonomic status	Subclass	Order	Family	Perenniality	Growth form	Breeding system	Pollination mode	Seed dispersal mode	Reproduction type	Mating system	Geographic range	Seed mass (mg seed^{-1})	Size (m)	G_{STm}	G_{STb}	F_{IS}
Helianthus annuus	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	AA	S	O	R	44.500	3.5	.76	.16	
Helianthus deserticola	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	AA	S	O	R	5.300	.4	.73	.25	
Helianthus petiolaris	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	AA	S	O	W	2.000	1	.49	.19	
Hieracium pilosella agg.	D	*Asteridae*	*Asterales*	*Asteraceae*	SP	F	H	E	W	V	…	R	.220	.3	.33		
Hordeum vulgare	M	*Liliidae*	*Poales*	*Poaceae*	A	G	H	A	AA	V	S	W	41.900	1.3	.75	.48	1.00
Ilex aquifolium	D	*Rosidae*	*Aquifoliales*	*Aquifoliaceae*	LP	T	D	E	AI	V	O	W	103.000	15	.60		
Ipomopsis aggregata complex	D	*Asteridae*	*Ericales*	*Polemoniaceae*	SP	F	H	Z	AI	…	O	R	2.071	.4	1.00	.15	.06
Kandelia candel	D	*Rosidae*	*Malpighiales*	*Rhizophoraceae*	LP	T	H	E	…	…	OS	R	…	8	.42	.06	.02
Lambertia orbifolia	D	*Rosidae*	*Proteales*	*Proteaceae*	LP	S	H	Z	AA	…	OS	N	20.000	5	.84	.44	.32
Larix olgensis	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	W	6.650	30	.55		
Larix sibirica	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	W	9.600	25	.59	.08	
Lolium perenne	M	*Liliidae*	*Poales*	*Poaceae*	SP	G	H	A	G	V	O	W	1.790	.9	.38	.11	.04
Lolium rigidum	M	*Liliidae*	*Poales*	*Poaceae*	SP	G	H	A	G	V	O	W	2.280	.5	.41	.17	.09
Lupinus texensis	D	*Rosidae*	*Fabales*	*Fabaceae*	A	F	H	E	G	…	OS	N	32.200	.45	.86		
Melaleuca alternifolia	D	*Rosidae*	*Myrtales*	*Myrtaceae*	LP	T	H	E	W	…	O	E	.590	…	.91	.12	.04
Michelia formosana	D	*Magnoliidae*	*Magnoliales*	*Magnoliaceae*	LP	T	H	E	AI	…	…	E	119.183	20	.40	.47	
Nothofagus nervosa	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	W	S	O	R	16.460	40	1.00	.08	.00
Olea europaea	D	*Asteridae*	*Lamiales*	*Oleaceae*	LP	T	H	E	AI	S	OS	W	221.000	12	.55	.25	.00
Packera cana	D	*Asteridae*	*Asterales*	*Asteraceae*	SP	F	H	E	AA	…	O	R	.004	.2	.26		
Packera contermina	D	*Asteridae*	*Asterales*	*Asteraceae*	SP	F	H	E	AA	…	O	N	.004	.1	.36		
Packera pseudaurea	D	*Asteridae*	*Asterales*	*Asteraceae*	SP	F	H	E	AA	…	O	R	.004	.4	.11		
Packera sanguisorboides	D	*Asteridae*	*Asterales*	*Asteraceae*	B	F	H	E	W	…	O	E	.004	…	.69		
Packera subnuda	D	*Asteridae*	*Asterales*	*Asteraceae*	SP	F	H	E	AA	…	O	R	.004	.1	1.00		
Parnassia palustris	D	*Rosidae*	*Saxifragales*	*Saxifragaceae*	SP	F	H	E	…	…	OS	W	.030	.2	.74	.16	.05
Pedicularis chamissonis	D	*Asteridae*	*Lamiales*	*Scrophulariaceae*	SP	F	H	E	AA	…	O	N	.716	.6	.91		
Phacelia dubia	D	*Asteridae*	*Solanales*	*Hydrophyllaceae*	A	F	H	E	AI	S	O	R	.800	.4	.61	.02	.22
Picea abies	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	W	7.443	60	.68	.05	.07
Picea mariana	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	V	O	W	1.300	18	.54	.06	−.07
Pinus albicaulis	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	AC	S	OS	R	147.800	18	.84	.06	.35
Pinus chiapensis	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	…	S	O	E	42.800	50	.89	.23	
Pinus contorta	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	N	4.400	33	.72	.09	
Pinus densata	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	N	42.800	23	.91	.09	.07
Pinus flexilis	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	AC	S	O	W	81.600	15	.77	.09	.11
Pinus muricata	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	E	13.680	25	.75	.45	
Pinus parviflora	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	AC	S	O	R	94.700	20	.89	.04	.12
Pinus pinaster	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	R	53.520	30	1.00	.17	.00
Pinus ponderosa	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	W	38.000	33	.97	.02	.00

Table A1 (*Continued*)

Species	Taxonomic status	Subclass	Order	Family	Perenniality	Growth form	Breeding system	Pollination mode	Seed dispersal mode	Reproduction type	Mating system	Geographic range	Seed mass (mg seed^{-1})	Size (m)	G_{STm}	G_{STb}	F_{IS}
Pinus radiata	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	E	31.900	35	.74	.16	.01
Pinus sylvestris	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	W	6.000	30	.88	.03	−.01
Piriqueta caroliniana	D	*Rosidae*	*Malpighiales*	*Turneraceae*	SP	F	H	E	AC	V	O	W	…	…	.67		
Platanthera aquilonis	M	*Liliidae*	*Asparagales*	*Orchidaceae*	SP	F	H	E	W	V	S	W	.001	.8	.84		
Platanthera dilatata	M	*Liliidae*	*Asparagales*	*Orchidaceae*	SP	F	H	E	W	V	O	W	.001	.9	.68		
Platanthera huronensis	M	*Liliidae*	*Asparagales*	*Orchidaceae*	SP	F	H	E	W	V	O	W	.001	1	.61		
Populus tremula	D	*Rosidae*	*Malpighiales*	*Salicaceae*	LP	T	D	A	W	V	O	W	.110	18	.11		
Primula cuneifolia	D	*Asteridae*	*Ericales*	*Primulaceae*	SP	F	H	E	G	S	OS	N	24.320	.15	1.00		
Prunus avium	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	T	H	E	AI	V	O	W	118.200	20	.29	.05	.11
Prunus spinosa	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	S	H	E	AI	V	O	W	148.500	7	.34		
Pseudotsuga menziesii	G	*Coniferopsida*	*Coniferales*	*Pinaceae*	LP	T	H	A	W	S	O	R	11.000	100	.74	.23	
Quercus alba complex	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	…	O	W	3,173.000	24	.87	.03	.00
Quercus faginea	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	…	O	R	2,560.056	20	.95		
Quercus frainetto	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	R	2,560.056	30	.83		
Quercus glauca	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	E	AC	…	O	R	526.320	15	.56		
Quercus ilex	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	W	2,311.000	20	.92	.10	.05
Quercus petraea	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	W	2,577.200	35	.86	.03	.05
Quercus pubescens	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	R	2,560.056	20	.90	.03	
Quercus pyrenaica	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	V	O	R	2,560.056	25	.96		
Quercus robur	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	W	3,817.000	35	.78	.02	.20
Quercus rubra	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	E	2,981.000	40	.47	.09	.10
Quercus suber	D	*Rosidae*	*Fagales*	*Fagaceae*	LP	T	H	A	AC	S	O	R	2,609.000	25	.84	.11	−.01
Raphanus sativus	D	*Rosidae*	*Brassicales*	*Brassicaceae*	B	F	G	E	G	S	O	W	10.750	1	.55	.03	
Rubus fruticosus s.l.	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	S	H	E	AI	V	O	W	2.490	3	.31		
Rumex nivalis	D	*Caryophyllidae*	*Caryophyllales*	*Polygonaceae*	SP	F	D	A	G	…	O	R	1.000	…	.58	.21	
Salix caprea	D	*Rosidae*	*Malpighiales*	*Salicaceae*	LP	T	D	EA	W	S	O	W	.090	10	.09		
Santalum spicatum	D		*Santalales*	*Santalaceae*	LP	S	H	E	AI	…	…	N	234.000	4	.94	.09	−.03
Saxifraga oppositifolia	D	*Rosidae*	*Saxifragales*	*Saxifragaceae*	SP	F	H	E	W	…	OS	W	.089	.3	.82	.15	
Senecio gallicus	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	AA	…	O	R	.446	.4	.57	.15	.11
Senecio glaucus	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	AA	…	O	W	.446	.5	.42	.12	.12
Senecio leucanthemifolius	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	W	…	O	E	.446	.4	.12	.30	
Senecio vernalis	D	*Asteridae*	*Asterales*	*Asteraceae*	A	F	H	E	AA	…	O	W	.446	.5	.05	.04	.12
Silene hifacensis	D	*Caryophyllidae*	*Caryophyllales*	*Caryophyllaceae*	SP	F	D	E	…	S	O	E	.500	…	1.00	.58	
Solanum acaule	D	*Asteridae*	*Solanales*	*Solanaceae*	A	F	H	E	G	…	S	W	2.105	.1	.53		
Sorbus aria	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	T	H	E	AI	V	O	W	169.000	20	.25		
Sorbus aucuparia	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	T	H	E	AI	…	O	W	34.000	15	.31	.06	−.01
Sorbus torminalis	D	*Rosidae*	*Rosales*	*Rosaceae*	LP	T	H	E	AI	V	O	W	5.500	20	.36	.15	.13

Table A1 (*Continued*)

Species	Taxonomic status	Subclass	Order	Family	Perenniality	Growth form	Breeding system	Pollination mode	Seed dispersal mode	Reproduction type	Mating system	Geographic range	Seed mass (mg seed^{-1})	Size (m)	G_{STm}	G_{STb}	F_{IS}
Tabebuia heterophylla	D	*Asteridae*	*Lamiales*	*Bignoniaceae*	LP	T	H	E	W	…	O	W	48.414	25	.58	.36	.00
Tilia cordata	D	*Rosidae*	*Malvales*	*Malvaceae*	LP	T	H	E	W	S	O	W	46.300	23	.57		
Tilia platyphyllos	D	*Rosidae*	*Malvales*	*Malvaceae*	LP	T	H	E	W	S	O	W	87.000	30	.41		
Trillium grandiflorum	M	*Liliidae*	*Liliales*	*Melanthiaceae*	SP	F	H	E	AI	…	O	W	10.700	.45	.95	.35	.29
Ulmus glabra	D	*Rosidae*	*Rosales*	*Ulmaceae*	LP	T	H	A	W	V	O	W	14.100	19.9	.61		
Ulmus minor	D	*Rosidae*	*Rosales*	*Ulmaceae*	LP	T	H	A	W	V	O	W	20.897	25	.47		
Vitis vinifera	D	*Rosidae*	*Vitales*	*Vitaceae*	LP	V	D	A	AI	V	O	W	36.300	35	.19	.14	.34
Vouacapoua americana	D	*Rosidae*	*Fabales*	*Fabaceae*	LP	T	H	E	AA	S	OS	E	6,260.000	40	.89	.08	.08

Note: Ellipses indicate no data.

Appendix B from J. Duminil et al., "Can Population Genetic Structure Be Predicted from Life-History Traits?"

(Am. Nat., vol. 169, no. 5, p. 662)

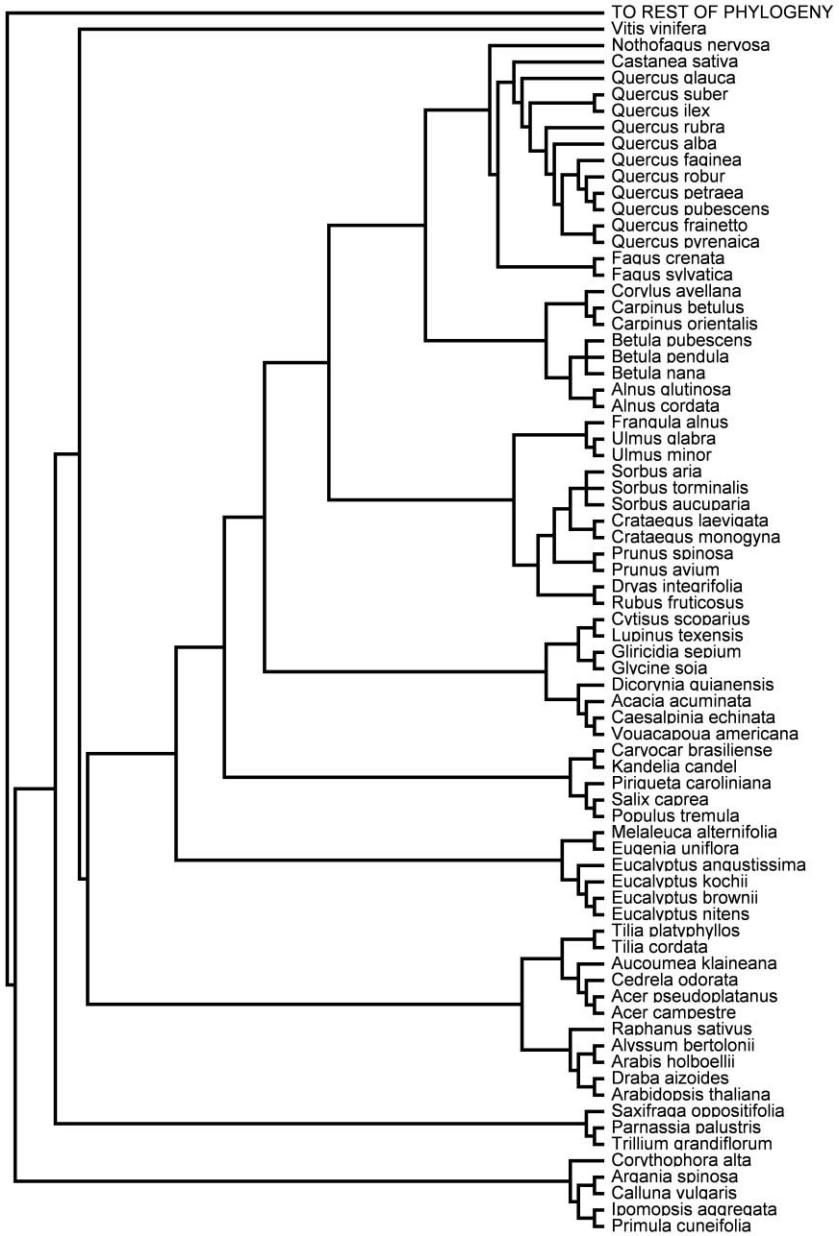

Figure B1: Phylogenetic tree used in the comparative analyses.

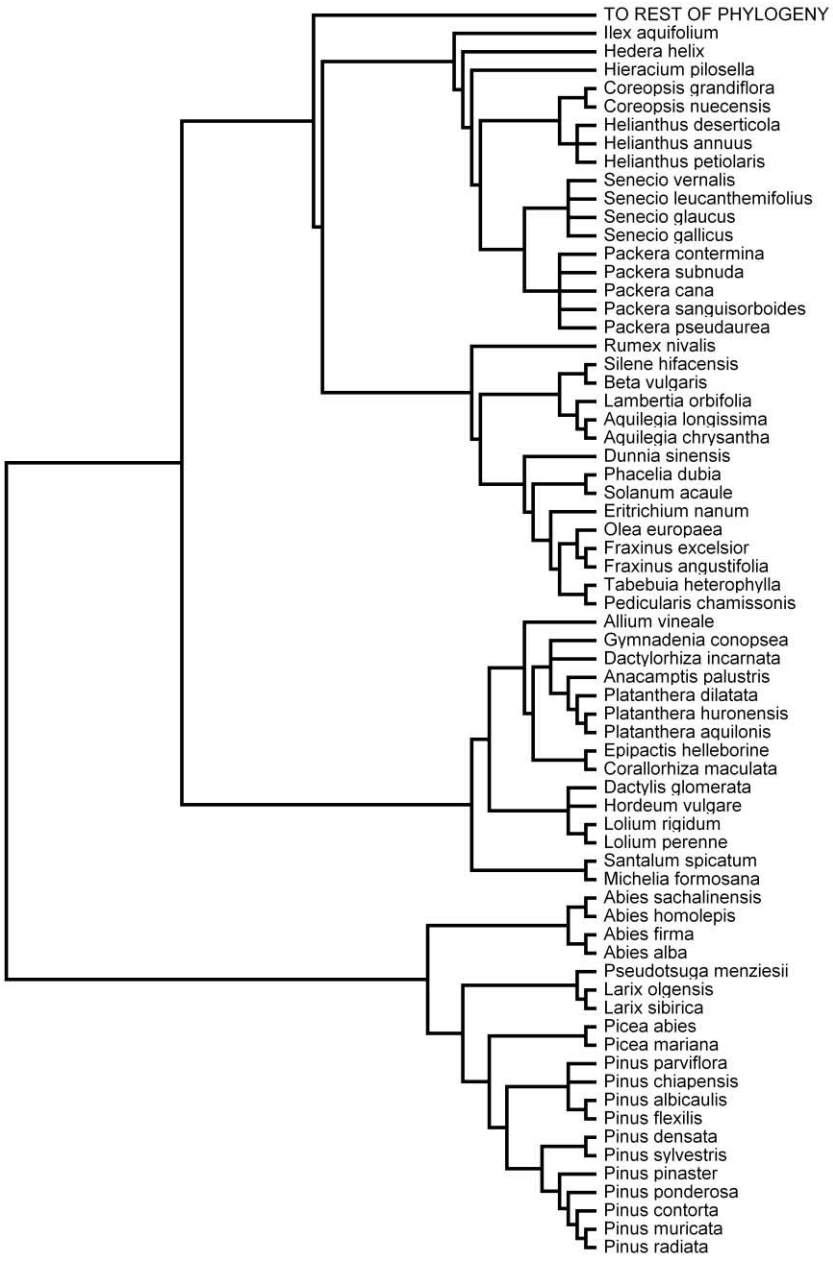

Figure B1 (*Continued*)

Appendix C from J. Duminil et al., "Can Population Genetic Structure Be Predicted from Life-History Traits?"

(Am. Nat., vol. 169, no. 5, p. 662)

Table C1
Garland's test of the effect of branch length

Parameter	Correlation	*N*	*P*
G_{STb}	.05	112	.41
G_{STm}	−.07	141	.60
Plant size	.09	126	.31
Seed weight	−.05	126	.58
F_{IS}	.13	69	.29

Note: For each continuous variable investigated, the correlation between the absolute values of the standardized contrasts and the standard deviations of those contrasts is provided and tested against 0 (after Garland et al. 1992). Results were obtained with the PDAP:PDTree package enclosed in the MESQUITE software (ver. 1.02; http://www.mesquiteproject.org/mesquite/mesquite.html).

Appendix D from J. Duminil et al., "Can Population Genetic Structure Be Predicted from Life-History Traits?"

(Am. Nat., vol. 169, no. 5, p. 662)

Table D1

Comparison of genetic structure across traits categories

Variable	N	G_{STb} mean	N	G_{STm} mean
Taxonomic status:				
Gymnosperms	31	.12 (.11)	20	.76 (.16)
Eumagnoliid	13	.31 (.14)	15	.62 (.24)
Eudicots	72	.16 (.15)	106	.63 (.24)
Growth form:				
Herbaceous	40	.27 (.21)	51	.62 (.26)
Shrub	5	.20 (.16)	14	.59 (.26)
Tree	73	.13 (.13)	76	.68 (.24)
Perenniality:				
Annuals/biennials	20	.27 (.25)	18	.58 (.23)
Short-lived perennials	20	.28 (.17)	33	.64 (.28)
Long-lived perennials	76	.14 (.13)	90	.67 (.25)
Seed dispersal mode:				
Wind	53	.18 (.19)	58	.64 (.24)
Animal ingested	12	.26 (.18)	22	.53 (.25)
Animal attached	12	.25 (.16)	14	.58 (.30)
Animal cached	15	.06 (.04)	19	.75 (.21)
Gravity	17	.20 (.14)	21	.71 (.25)
Pollination mode:				
Anemophilous	54	.12 (.11)	54	.73 (.24)
Zoophilous	53	.24 (.20)	77	.60 (.25)
Mating system:				
Outcrossed	93	.16 (.14)	114	.65 (.25)
Mixed	12	.14 (.12)	16	.73 (.21)
Selfed	6	.56 (.24)	6	.72 (.19)
Breeding system:				
Monoecious	105	.19 (.18)	129	.66 (.25)
Dioecious/gynodioecious	5	.19 (.23)	12	.58 (.33)
Reproduction type:				
Sexual and vegetative	21	.19 (.14)	70	.58 (.26)
Only sexual	82	.18 (.18)	71	.72 (.22)
Geographic range:				
Endemic	19	.18 (.16)	21	.63 (.27)
Narrow	15	.18 (.18)	16	.80 (.18)
Regional	29	.19 (.15)	32	.70 (.25)
Widespread	53	.18 (.19)	72	.60 (.25)

Note: Number of species (N) and mean and average deviation (in parentheses) of G_{STb} and G_{STm} are reported for each category of the variables.

Appendix E from J. Duminil et al., "Can Population Genetic Structure Be Predicted from Life-History Traits?"

(Am. Nat., vol. 169, no. 5, p. 662)

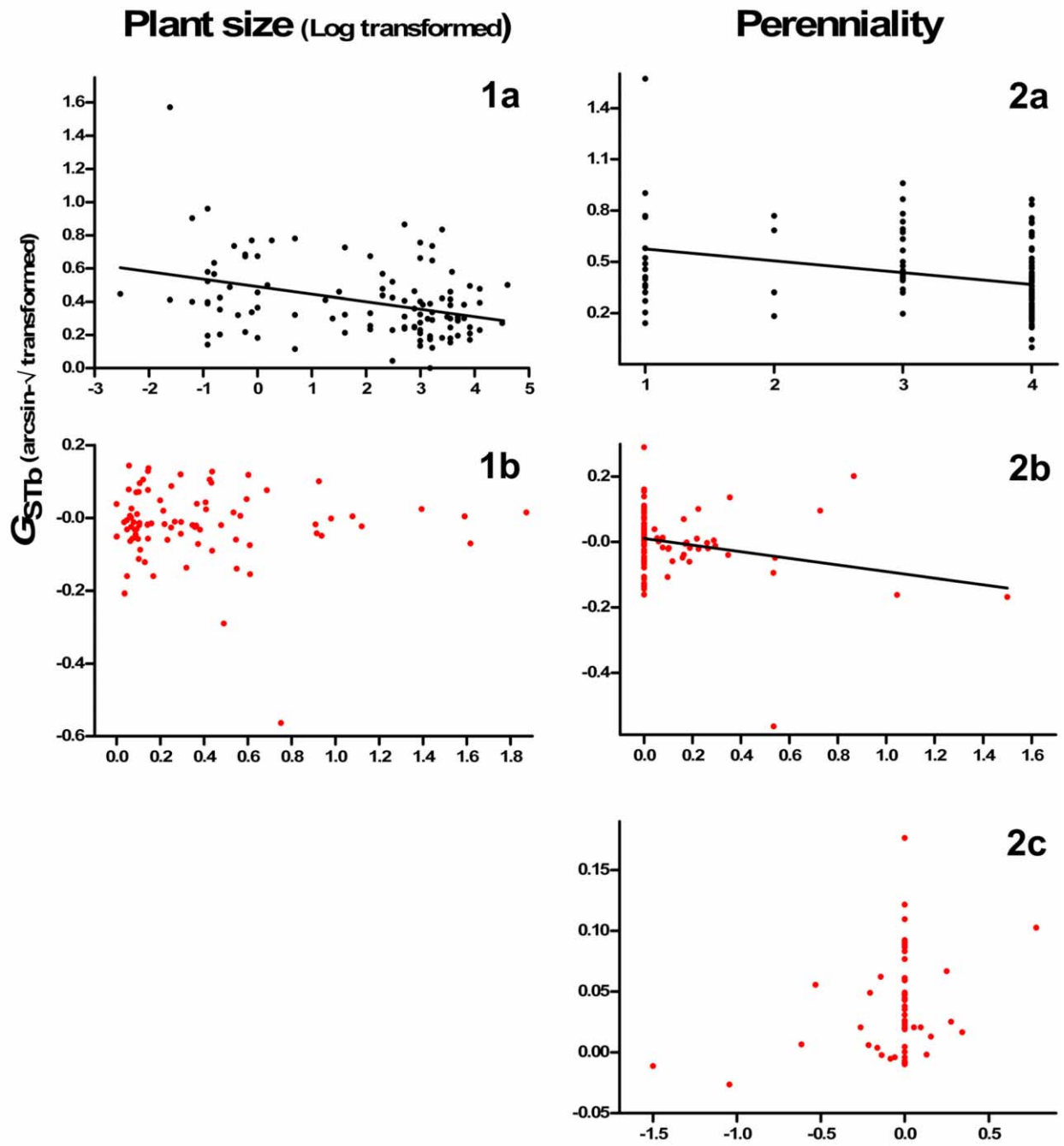

Figure E1: Illustration of the necessity to control for phylogenetic relationships and confounding covariates in cross-species analyses of genetic structure. *1a*, Plot of G_{STb} on plant size (TIPs analysis). *1b*, Plot of the contrasts of G_{STb} on the contrasts of plant size (PICs analysis). The major axis regression line is shown when significant. The relation initially detected is no longer significant when controlling for phylogeny. *2a*, Plot of G_{STb} on perenniality (TIPs analysis). *2b*, Plot of the contrasts of G_{STb} on the contrasts of the perenniality (PICs analysis). *2c*, Plot of the contrasts of G_{STb} on the contrasts of the perenniality (PICs analysis) when F_{IS} is used as a covariate. The major axis regression line is shown when significant. The relation is still significant when controlling for phylogeny but not when including F_{IS} as a covariate.