ORIGINAL ARTICLE

Breeding systems and phylogenetic diversity of seed plants along a large-scale elevational gradient

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ABSTRACT

Aim The factors affecting the distribution of dioecious species have received surprisingly little attention and, as a consequence, are poorly understood. For example, there is a well-documented negative association between dioecy and latitude, for which we have no candidate mechanisms. Conversely, it has been suggested that the relative proportion of dioecious species should be positively correlated with changes in elevation.

Location Costa Rica, Central America.

Methods We made use of data on the distribution of 175 seed plant species from a series of plots along a transect in Costa Rica that ranged from 30 to 2600 m a.s.l. to test the prediction that dioecy is correlated with elevation. Specifically, we examined relationships between the proportion of dioecy, at the species and individual levels, and the elevation, species richness, number of individuals, and phylogenetic diversity (PD) of plots. For comparison, we repeated all analyses with monoecious species, which also have unisexual flowers but do not suffer from reduced mate assurance and the seed shadow effect that may be the outcomes of having spatially separated sexes.

Results The relative proportions of dioecious species and individuals displayed a unimodal relationship with elevation, both peaking at 750 m a.s.l. In contrast, the relative proportions of monoecious species and individuals displayed negative associations with elevation. In addition, the proportion of dioecious species was significantly positively associated with species richness and with the PD of plots. The proportion of monoecious species was not associated with species richness and was weakly positively associated with the PD of plots.

Main conclusions Our results suggest that the selection pressure of elevation on the pollinators and life-history strategy of dioecious species is much less than expected, and is overshadowed by the as-yet unexplained correlation of dioecy with species richness. Additional studies of the ecology of cosexual and unisexual (i.e. dioecious and monoecious) species along large environmental gradients are needed.

Keywords

Breeding systems, community phylogenetics, Costa Rica, dioecy, elevational gradient, monoecy, phylogenetic diversity, species richness.

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INTRODUCTION

Dioecy is a relatively uncommon breeding system in flowering plants but is widely distributed both phylogenetically and geographically, occurring in many angiosperm families (Ren-ner & Ricklefs, 1995) and in most terrestrial ecosystems (Sakai & Weller, 1999). The evolution of dioecy is a key issue in biology (Charlesworth & Charlesworth, 1978; Charnov, 1982; Thomson & Brunet, 1990), and many studies have examined the ecological correlates (Darwin, 1877; Bawa, 1980; Vamosi

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et al., 2003; Vamosi & Vamosi, 2004, and below). However, surprisingly little consideration has been given to factors affecting the present-day abundance and distribution of dioecious species, and, as a consequence, these factors are poorly understood.

Many authors have commented on the correlations of dioecy with, for example, a woody growth form (Fox, 1985); zoophilous (Bawa & Opler, 1975; Bawa, 1980) or abiotic (Renner & Ricklefs, 1995; Sakai et al., 1995) pollination; small, inconspicuous, pale-coloured flowers (Bawa & Opler, 1975; Bawa, 1980); and fleshy fruits (Muenchow, 1987). Other authors have examined factors affecting the distribution of species along environmental gradients (Kitayama, 1992; Nakashizuka et al., 1992; Kitayama & Mueller-Dombois, 1994; Lieberman et al., 1996; Vázquez & Givnish, 1998), but few authors have investigated the geographical or ecological distribution and abundance of species' breeding systems (Jacquemyn et al., 2005). Tropical ecosystems are known to contain a high proportion of dioecious species (Baker, 1959; Carlquist, 1974; Bawa & Opler, 1975; Bawa, 1980; Baker & Cox, 1984; Queenborough et al., 2007; Vamosi et al., 2008), but the possibility of variation in dioecy with change in elevation has received comparatively little attention (e.g. Arroyo & Squeo, 1990). Indeed, a search for the terms '(dioecy OR dioecism) AND (altitudinal OR elevational)' in ISI Web of Science (data: 1900–2009) produced only seven papers, the majority of which focused on within-species gender differences.

Two factors would seem to lead to an increase or decrease in the number of dioecious species at high elevations. First, insect pollinator abundance decreases dramatically with increasing elevation (Mani, 1962; Arroyo et al., 1982, 1983). As dioecious species are obligate outcrossers and many rely on insect pollinators, a decrease in the number of these vectors should lead to a decrease in the likelihood of dioecy persisting in such depauperate systems. We note, however, three potential modifiers to this expectation. First, dioecy is also correlated with anemophily in certain systems (Bullock, 1994), which may increase at high elevation (Regal, 1982; Whitehead, 1983; Berry & Calvo, 1989). Second, although insect abundance is negatively correlated with elevation, major insect groups are differentially affected (Warren et al., 1988). Hymenopterans are typically the dominant pollinators at lower-elevation sites, whereas dipterans become dominant at high elevations. Dioecious species, which have been argued to rely on relatively unspecialized pollinators (Bawa & Opler, 1975; but see Renner & Feil, 1993), may thus be less affected by pollinator reductions than cosexual species. Finally, the abundance of pollinators does not necessarily correlate with pollination success (Arroyo et al., 1985).

The second factor is that, conversely, harsh environments tend to select for longevity of life-form (e.g. Morris & Doak, 1998; Forbis & Doak, 2004; Petit & Hampe, 2006) and dioecy is associated with long-lived (woody) growth forms (Fox, 1985; Vamosi et al., 2003, 2008; Vamosi & Vamosi, 2004). One would therefore predict an increase in the proportion of

dioecious species with increasing elevation, or minimally a shift in the relative proportion of long-lived, wind-pollinated dioecious species. Indeed, increased longevity may compensate for the reduced mate assurance that accompanies dioecy (Pannell & Barrett, 1998), thereby potentially mitigating the negative effects of the reduced abundance of biotic pollen vectors expected at higher elevations (Arroyo & Squeo, 1990).

Several studies of montane vegetation have commented on the elevated number of dioecious species compared with that in lowland forest (Sobrevila & Arroyo, 1982; Tanner, 1982; Griffiths & Lawes, 2006; but see Chen & Li, 2008), but only two studies have specifically investigated the relationship between dioecy and elevation. Baker & Cox (1984) found that islands with higher mountains had a greater proportion of dioecious species than those with lower mountains. However, this may be an artefact because islands with high mountains were forested whereas lower islands supported only littoral vegetation. Hence, the increase in dioecy resulted from a greater number of trees at higher elevations. Comparing similar vegetation types, Arroyo & Squeo (1990) showed that the percentage of dioecious species increased over increasing elevation at a small range of sites in Chilean Patagonia. Concurrently, insect pollinators decreased over this gradient (Arroyo et al., 1985), and so they surmised that habitat harshness was the key factor influencing dioecy through selection for longevity.

In this study we investigate the distribution of dioecious tree species in a series of plots along an elevational gradient from 30 to 2600 m a.s.l. in forests of Costa Rica (Lieberman et al., 1996). Although we are interested primarily in the responses of dioecious species along an elevational gradient, we also present comparable analyses conducted with monoecious species as a contrast and control for patterns observed in dioecious species. For example, the observation that dioecy and monoecy are often phylogenetically associated (occurring in the same families and/or in closely related families; Renner & Ricklefs, 1995) acts a control if the relative representation of one breeding system but not the other is positively associated with the phylogenetic diversity of plots. Note that, because the third breeding system (hermaphroditism) was the most prevalent in all plots, an increase in the relative representation in dioecy was not invariably accompanied by a decrease in the relative representation of monoecy. Insofar as elevational gradients mirror latitudinal ones (Körner, 2007), our expectations are based largely on the negative association between latitude and the relative representation of dioecy. Tropical forests, which are typically characterized by high species richness and phylogenetic diversity, are also noted for their relatively high proportion of dioecy (e.g. Bawa, 1980; Vamosi & Vamosi, 2004).

Based on the weight of related observations regarding the distribution of dioecious and monoecious species, we made the following predictions. First, we predicted that the relative representation of dioecy should be negatively associated with elevation, and positively associated with the total number of individuals, species richness and phylogenetic diversity. In

contrast, we expected no significant associations between the relative representation of monoecy and these variables. These expectations are based on weak, or non-existent, associations between latitude and the relative representation of monoecy. For example, monoecious species account for 12.4% of the flowering plant species at La Selva, Costa Rica (Kress & Beach, 1994) and for c. 9% of the indigenous flowering plant species of New Zealand (Godley, 1979). Partly because almost all aspects of the ecology and evolution of monoecy have been understudied in relation to their counterparts for dioecy, we are unaware of any data that would allow us to make directional predictions regarding associations between environmental gradients (or their correlates, such as species richness) and the relative representation of monoecy.

The main aims of the study were: (1) to explore the general trends in species richness, total abundance (i.e. number of individuals) and phylogenetic diversity along the elevational gradient; (2) to test the predictions mentioned above with regard to associations between each of the two breeding systems and elevation, species richness, total number of individuals and phylogenetic diversity of plots; and (3) to assess potential mechanisms for these relationships in relation to different pollination systems along the elevational gradient.

MATERIALS AND METHODS

Distribution data for seed plants in 15 permanent 1-ha plots along the elevational gradient were obtained from Appendix 1 of Lieberman *et al.* (1996), and mean annual rainfall and temperature data were obtained from Hartshorn & Peralta (1988) and Watkins *et al.* (2006). The table from Lieberman *et al.* (1996) included all species ($n = 181$) with a total of 10 or more tagged individuals along the entire gradient. Because we were interested in correlates of breeding system in seed plants, we excluded six species of ferns in the family Cyatheaceae from all analyses (for a full analysis of ferns along the same gradient, see Watkins *et al.*, 2006). Ferns accounted for only 3.3% and 9% of the initial species diversity and number of individuals, respectively, so we expect our conclusions to be robust to their exclusion.

Breeding systems for the remaining seed plant species, of which only one was a gymnosperm (*Podocarpus oleifolius* D. Don), were researched using a variety of sources, in particular Croat's (1978) treatment of the flora of Barro Colorado Island, Panama, a number of family treatments in the Flora of Panama series (e.g. Woodson *et al.*, 1970; see Woodson & Schery, 1980; for an overview), and volumes of the Families and Genera of Vascular Plants series (e.g. Kubitzki *et al.*, 1993). Additional references for breeding system designations can be found in Vamosi *et al.* (2008) and Queenborough *et al.* (2009). We were unable to assign breeding systems for eight species, which fell into three groups. First, one species ['*Unidentified* (8203)'] had not been assigned to either a family or a genus by Lieberman *et al.* (1996). Second, four species were identified only to the family level, and the two families in question, Rubiaceae and Lauraceae, contain dioecious and cosexual

species. Finally, three species were identified to genus but not to species level; again, these genera contain among-species variation in breeding system. For example, Pennington (1990) describes dioecious, monoecious and hermaphroditic species in the genus *Pouteria*, precluding a definitive breeding system for '*Pouteria* sp. (6711)' in Lieberman *et al.* (1996). These eight species constituted only 3.1% of the total number of remaining individuals (i.e. after excluding ferns), resulting in 167 species retained for further analyses (see Appendix S1 in Supporting Information).

We conducted three sets of a priori analyses. First, we were interested in describing general patterns of log-transformed species richness and total number of individuals in plots along the elevational gradient. A consideration of phylogenetic community structure along elevational gradients is in its infancy (Hardy & Senterre, 2007; Bryant *et al.*, 2008; Vamosi *et al.*, 2009). Therefore, we also calculated the phylogenetic diversity (PD; Faith, 1992) in each plot. To do this we used PHYLOMATIC (Webb & Donoghue, 2005) to construct a hypothesized phylogeny for all of the seed plant species in our sample (see Appendix S2). We used the maximally resolved seed plant tree designated 'R20040202' (see also Vamosi *et al.*, 2008; Queenborough *et al.*, 2009). Estimated branch lengths were generated using the 'bladj' (branch length adjuster) utility (Webb & Donoghue, 2005). This utility fixes nodes for which age estimates are available (Wikstrom *et al.*, 2001), and sets all other branch lengths by placing the nodes evenly between dated nodes, and between dated nodes and terminals (age 0). To remove the effect of species richness on PD, we also examined residual PD along the elevational gradient. Following other studies (e.g. Bhattarai & Vetaas, 2006), we used generalized linear models (GLMs) with quasi-Poisson errors to examine the relationships between elevation and species richness and total number of individuals. For the relationships between elevation and PD and residual PD, we used simple linear models. In all four cases we carried out polynomial regression, comparing the model with only the first-order term (i.e. elevation) with one including the second-order term (i.e. elevation^2). We used *F*-tests to determine the best-fit model of each pair (see also Bhattarai & Vetaas, 2006). Because the number of plots was relatively low, we did not test for the significance of higher-order terms (e.g. elevation^3). These analyses were conducted using R 2.7.0 (R Development Core Team, 2008).

Second, we examined the relative representation of dioecious and monoecious species along the elevational gradient. Specifically, we calculated the proportion of species that were dioecious or monoecious, and the proportion of all individuals that belonged to dioecious or monoecious species, in each plot. For each of the two breeding systems, we also examined patterns in the difference between the two measures [i.e. proportion of dioecious (monoecious) species – proportion of dioecious (monoecious) individuals]. Positive values of this difference suggest that there are fewer individuals with a given breeding system than predicted by the number of species with that breeding system in a given plot, whereas the converse is

true for negative values (see also Vamosi, 2006). We applied GLMs with binomial errors for analysing the relationship between elevation and proportion of dioecious (monoecious) species, and GLMs with quasi-binomial errors for analysing the relationship between elevation and proportion dioecious (monoecious) individuals. We specified quasi-binomial errors in the latter two analyses because the initial models with binomial errors were over-dispersed. Finally, for the analyses of the relationships between elevation and the differences, we applied simple linear models. We again applied polynomial regression in all six analyses to compare the models with and without higher-order terms. We used chi-square tests to determine the best-fit model of each pair for the first two model pairs (i.e. those with binomial errors), and F-tests for the remaining pairs of models.

Third, we examined the association between the relative representation of the two breeding systems and the species diversity and total number of individuals (rather than elevation) of each plot. We tested whether the proportion of dioecious (monoecious) species was associated with species richness or PD, and also whether the proportion of dioecious (monoecious) individuals was associated with the total number of individuals. Because plots situated close to one another may have similar species richness or numbers of individuals, it is important to test for spatial autocorrelation, and to account for it if it exists. Distances between plots were calculated by digitizing the profile diagram of the study area presented in Lieberman *et al.* (1996, p. 138). Correlograms calculated using the 'spatial' package in R, following Crawley (2007, p. 776), revealed positive spatial autocorrelation in species richness, stem density and PD at small scales. Thus, we applied t-tests of the Pearson correlation coefficient between these variables correcting for spatial autocorrelation, following the methods outlined by Dutilleul (1993). These analyses were implemented using the free program 'Mod_t_test' (Legendre, 2000). Based on our a priori predictions, we applied one-tailed tests for dioecious analyses and two-tailed tests for monoecious analyses.

Finally, in order to examine a potential mechanism for the relationships described above, we investigated whether differences in pollinator systems among breeding systems were associated with the resulting patterns. Data on pollination systems for the majority of species were obtained from two sources (Kress & Beach, 1994; Chazdon *et al.*, 2003). We consulted a number of other sources for other species (e.g. Bullock *et al.*, 1983; Koptur, 1983; Tschapka, 2004; W.S. Alverson, Field Museum, Chicago, unpublished data). Detailed data on pollination systems are difficult to obtain (e.g. Anderson *et al.*, 2001) and, unsurprisingly, lacking for many Neotropical species. Furthermore, available data are skewed in favour of herbs and shrubs (e.g. Kress & Beach, 1994; Freitas & Sazima, 2006), whereas the majority of species surveyed by Lieberman *et al.* (1996) were trees (78%) and palms (15%), because only those individuals that had stems ≥10 cm d.b.h. were considered. We were unable to find any data for 27 species, and inferred insect pollination for 13 species that

belonged to families or genera with apparently little variation in pollination system. For example, Neotropical Myrtaceae species appear to be pollinated predominantly by bees (Lughadha & Proença, 1996; and references therein). Similarly, we classified *Macrohasseltia macrotherantha* (Standl. & L. O. Williams) L. O. Williams with reference to the observation that 'all genera [of Salicaceae] are predominantly insect-pollinated except the wind-pollinated *Populus*' (Cronk, 2005, p. 41). In total, we assigned 140 species as relying on bat, hummingbird, insect or wind pollination. We assessed whether there were differences among the three breeding systems in major pollinator classes with a chi-square test, and compared the relative reliance on insect pollination between dioecious and monoecious species with a Fisher exact test. Low sample sizes prevented a similar comparison for wind pollination. Finally, we carried out a preliminary analysis of the relative representation of wind-pollinated dioecious (D) species [i.e. $D_{wind}/(D_{insect} + D_{wind})$] along the elevational gradient. We followed the same methods as for the second set of models described above, using polynomial regression to compare models (GLM, binomial errors) with and without higher-order terms and a chi-square test to determine the best-fit model of the pair.

RESULTS

Overall, the proportions of the three breeding systems [dioecious: 30.5%, hermaphroditic (H): 61.1%, monoecious (M): 8.4%] were quite similar to those in two recent investigations of associations between dioecy and ecological traits (Vamosi *et al.*, 2008; Queenborough *et al.*, 2009). In a sample of 800 woody species in Tambopata, Peru, Vamosi *et al.* (2008) found D: 26%, H: 63.5%, M: 10.5%, and in a sample of 647 species from Yasuní, Ecuador, Queenborough *et al.* (2009) found D: 29.2%, H: 59.2%, M: 11.6%. In all three instances the high local incidence of dioecy, compared with its global representation of 6% (Renner & Ricklefs, 1995), is probably the consequence of the samples being (1) restricted to woody species, and (2) from forests located at tropical latitudes.

Mean annual rainfall demonstrated a unimodal relationship with elevation (Fig. 1a), whereas mean annual temperature declined linearly with elevation (Fig. 1b). Species richness, number of individuals (abundance), PD and residual PD all demonstrated significant unimodal relationships with elevation (Fig. 1c–f). For all four variables, the regression model with the second-order term was found to fit the data significantly better than the simpler model with only the first-order term (Table 1). Species richness (Fig. 1c) and PD (Fig. 1e) exhibited significant, and superficially similar, associations with elevation (Table 1). Both measures of diversity peaked at elevations slightly lower than intermediate. Although abundance was found to vary with elevation, the number of individuals in plots located ≤2300 m fluctuated rather unpredictably between 300 and 450 stems (Fig. 1d). The single plot at 2600 m, accordingly, had high leverage. Finally, residual PD was highest in plots located at intermediate elevations, and
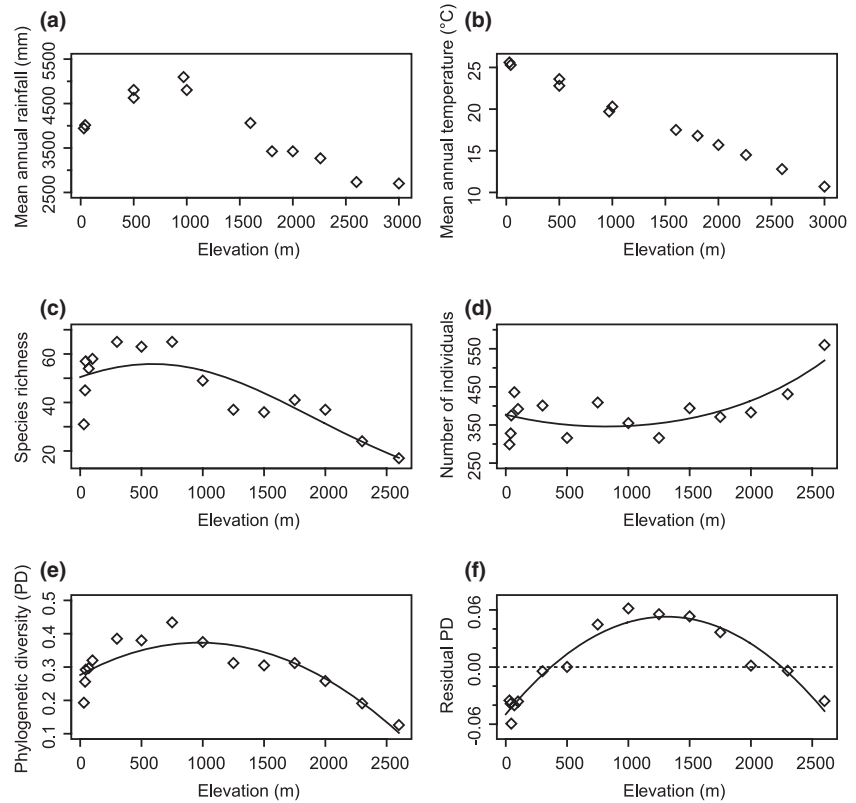
Figure 1 Relationships between elevation (m a.s.l.) and (a) mean annual rainfall, (b) mean annual temperature, (c) species richness, (d) number of individuals, (e) phylogenetic diversity, and (f) phylogenetic diversity corrected for species richness for 167 species of seed plants along the La Selva–Volcán Barva transect in Costa Rica. Lines represent significant relationships derived with generalized linear models (Table 1).

Table 1 Summary of regression statistics for tests of associations between elevation and species richness (SR), number of individuals per plot (NI), phylogenetic diversity (PD) and residual PD (RPD) for 167 species of seed plants from Costa Rica. Polynomial (1) first- and (2) second-order models were tested against one another; P-values are from F-tests comparing the fit of the two models, with significant values (i.e. $P < 0.05$) indicating a better fit for the model containing the second-order term (i.e. elevation^2).

Response variable	d.f.	Polynomial order	Residual deviance	Percentage deviance explained	P-value of model	P-value of comparison
SR	13	1	37.97	49.6	0.003	0.010
	12	**2**	**22.06**	**70.7**	**0.0005**	
NI	13	1	102.15	28.6	0.041	0.029
	12	**2**	**67.49**	**52.9**	**0.011**	
PD	13	1	0.078	18.4	0.11	0.0002
	12	**2**	**0.023**	**75.7**	**0.0002**	
RPD	13	1	0.020	14.5	0.16	<0.0001
	12	**2**	**0.002**	**93.2**	**<0.0001**	

For each pair, the model that was a better fit is highlighted in bold.

exhibited a nearly symmetrical decrease at elevations below and above this range (Fig. 1f).

Patterns in the relative representation of dioecy along the elevational gradient contrasted with those observed for monoecy (Fig. 2). Models with the second-order term were never chosen for analyses with monoecious species, whereas they provided a better fit for two analyses with dioecious species (Table 2). There were unimodal relationships between elevation and the proportion of dioecious species (Fig. 2a), and between elevation and the proportion of dioecious individuals (Fig. 2c), with both values peaking at 700 m a.s.l. In addition, there was a significant negative linear relationship between the species versus individuals difference for dioecy and elevation (Table 2). There were fewer dioecious individuals than

predicted by the proportion of dioecious species at low elevations, whereas the converse was true at high elevations (Fig. 2e). In contrast, the proportion of monoecious species (Fig. 2b) and individuals (Fig. 2d) generally declined with elevation, except that the proportion of monoecious individuals in the plots located at 750 and 1000 m a.s.l. was comparable to values observed at the lowest elevations. There was only one monoecious species, the Red-listed *Quercus tonduzii* Seemen, present at 2300 m a.s.l., and no monoecious species present at 2600 m a.s.l. There was a significant positive linear relationship between the species versus individuals difference for monoecy and elevation (Table 2). At elevations ≤1000 m, there tended to be more monoecious individuals than predicted by the proportion of species with a monoecious
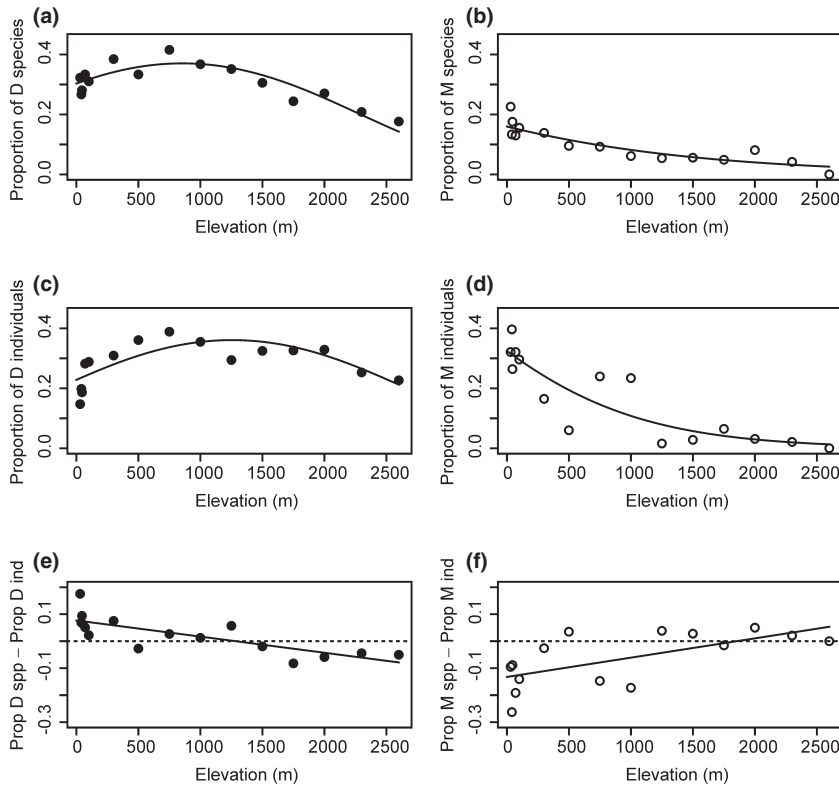
Figure 2 Relationships between elevation (m a.s.l.) and proportion of (a) dioecious (D) and (b) monoecious (M) species, and proportion of (c) dioecious (D) and (d) monoecious (M) individuals for 167 species of seed plants along the La Selva–Volcán Barva transect in Costa Rica. Panel (e) represents the difference between panels (a) and (c), and panel (f) represents the difference between panels (b) and (d). Lines represent significant relationships derived with generalized linear models (Table 2). Scales on the ordinate axis are the same in matched panels to facilitate comparisons in the trends in dioecious and monoecious species.

Table 2 Summary of regression statistics for tests of associations between elevation and proportion of dioecious species (DS), proportion of dioecious individuals (DI), DS – DI (DD), proportion of monoecious species (MS), proportion of monoecious individuals (MI), and MS – MI (MD) for 167 species of seed plants from Costa Rica. For DS and DI, the model with the second-order term (i.e. elevation^2) fit significantly better (indicated with bold highlighting) than the one with the first-order term (i.e. elevation); *P*-values from a chi-square test (DS) or *F*-test (DI) comparing the fit of the models are shown. For the remaining variables, regression statistics are shown only for the model with the first-order term.

Response variable	d.f.	Polynomial order	Residual deviance	Percentage deviance explained	*P*-value of model	*P*-value of comparison
DS	13	1	8.64	17.7	0.17	0.017
DS	**12**	**2**	**2.94**	**72.0**	**0.023**	
DI	13	1	122.33	1.3	0.68	0.001
DI	**12**	**2**	**49.61**	**60.0**	**0.004**	
DD	13	1	0.027	60.4	0.0006	—
MS	13	1	4.56	76.9	0.0001	—
MI	13	1	198.47	77.6	<0.0001	—
MD	13	1	0.081	41.8	0.009	—

breeding system (Fig. 2f). Above this elevation, the two proportions were quite similar to one another, with the proportion of monoecious species in a plot roughly matching the proportion of monoecious individuals in the same plot.

The proportion of species in each plot that were dioecious or monoecious was usually positively correlated with species richness and PD. The proportion of dioecious species per plot exhibited a significant positive relationship with species richness (spatially corrected Pearson correlation: $r = 0.78$, $P = 0.025$; Fig. 3a) and with PD ($r = 0.84$, $P = 0.034$; Fig. 3c).

The proportion of monoecious species was not correlated with the species richness of plots ($r = 0.73$, $P = 0.057$; Fig. 3b), but was positively associated with the PD of plots ($r = 0.50$, $P = 0.045$; Fig. 3d). Interestingly, neither the proportion of dioecious ($r = 0.11$, $P = 0.36$; Fig. 3e) nor that of monoecious ($r = -0.56$, $P = 0.095$; Fig. 3f) individuals (as opposed to the proportion of species) was associated with the total number of stems per plot. The proportion of individuals per plot in each breeding system spanned approximately the same range for both dioecious and monoecious species (D: range: 0.15–0.39;
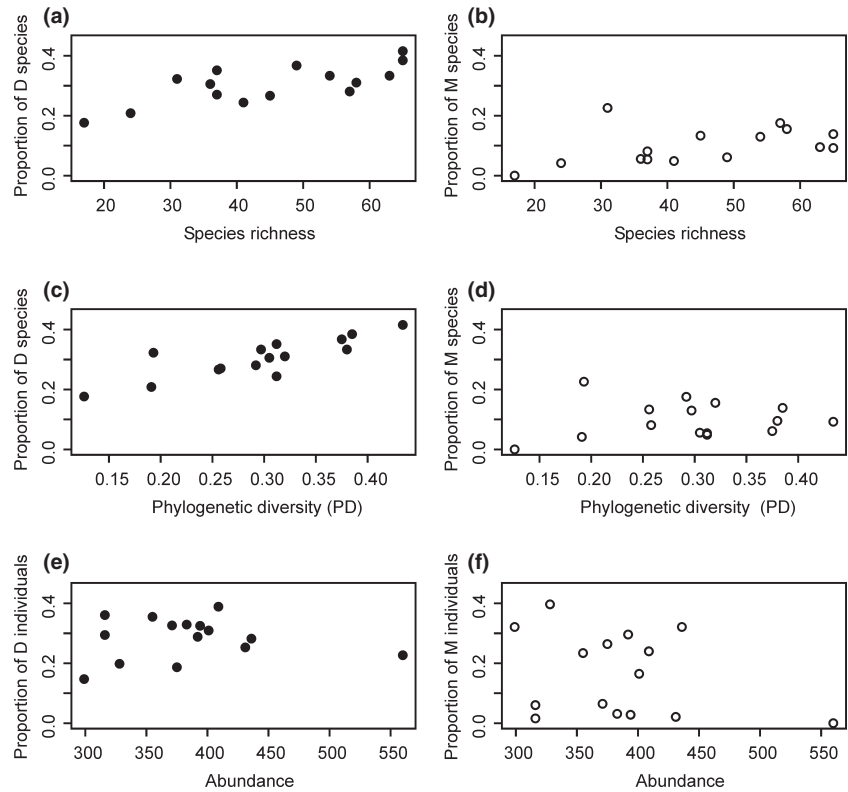
Figure 3 Correlations between species richness of plots and proportion of (a) dioecious (D) and (b) monoecious (M) species; between phylogenetic diversity of plots and proportion of (c) dioecious (D) and (d) monoecious (M) species; and between number of individuals in plots and proportion of (e) dioecious (D) and (f) monoecious (M) individuals for 167 species of seed plants along the La Selva–Volcán Barva transect in Costa Rica.

M: 0–0.40). However, the distribution of these proportions was highly skewed and opposite for the two breeding systems: the proportion of monoecious individuals per plot was <0.2 in eight plots (53%), whereas the proportion of dioecious individuals was >0.2 in 12 plots (80%). Again, we note that the plot at 2600 m a.s.l., which had the lowest species richness ($n = 17$) and associated lowest PD (0.13), and the highest number of individuals ($n = 560$), had high leverage for analyses involving monoecious species (Fig. 3b, d, f).

Finally, our post hoc consideration of potential associations between pollination systems and breeding systems revealed two patterns that largely corroborate previous findings in comparable study systems, but gave little insight into potential mechanisms underlying the different patterns in the representation of dioecious versus monoecious species along the elevational gradient. First, the majority of species for which pollination system could be assigned (94.3%) relied on biotic pollination (Table 3). Within this category, pollination by insects was by far the most common mode (93.9%), followed by hummingbird (3.8%) and bat (2.3%) pollination. Second, certain pollinator × breeding system combinations appeared to be more common than others, although we note that sample sizes were quite low in most categories. Specifically, all bat- and hummingbird-pollinated species were hermaphroditic, whereas the converse was true for wind-pollinated species (Table 3). However, within the large group of species that were insect-pollinated, the proportions of the three breeding systems did not differ from their representation in our sample of 167 species (chi-square test: $\chi^2_2 = 0.024$, $P = 0.99$). Our data suggest comparable reliance on insect pollination in

Table 3 Mean elevation (m a.s.l.) of various pollination systems, and their representation among three breeding systems (dioecious, hermaphroditic and monoecious), for 167 species of seed plants from Costa Rica.

Pollinator	Mean elevation (m)	Number of species Dioecious	Hermaphroditic	Monoecious
Bat	173.3	0	3	0
Hummingbird	546.7	0	5	0
Insect	994.2	38	75	11
Wind	1163.5	6	0	2
Unknown	1107.5	7	19	1

dioecious (86.4%) and monoecious (84.6%) species (Fisher exact test: $P = 1.00$). Finally, the relative representation of wind-pollinated dioecious species did not change along the elevational gradient. Elevation was not a significant predictor in either regression (first-order model: $Z_{1,13} = 0.49$, $P = 0.63$; second-order model: $Z_{1,12} = 0.46$, $P = 0.65$). Furthermore, the regression with the second-order term, which was also not significant ($Z_{1,12} = -0.33$, $P = 0.75$), did not provide a better fit to the data ($P = 0.74$).

DISCUSSION

Environmental gradients are key drivers of beta diversity (e.g. Whittaker, 1965; Harrison *et al.*, 1992; Pyke *et al.*, 2001). In this study we investigated the effect of elevation on the breeding systems of trees present in a series of 1-ha tropical

forest plots in Costa Rica. Based on the global negative association between the relative representation of dioecy and latitude, we predicted that dioecy should decrease with increased elevation, possibly because of a coincident decline in pollinator abundance with elevation. However, we did not find evidence in support of this hypothesis, nor for a linear increase in dioecy as might be predicted because of the increased harshness of high-elevation environments selecting for longer life-span, and the correlation of dioecy with life-span. The unimodal relationship between dioecy, at the levels of species and individuals, and elevation paralleled the mid-elevation peaks in species richness and PD. In general, relationships between monoecious species and these variables either were absent or were weaker than in the comparable analyses involving dioecious species. Finally, the relative reliance on insect and wind pollination was comparable for dioecious and monoecious species.

Although other studies have noted a possible higher proportion of dioecious species at higher elevations, only one previous study has investigated this using transect data from comparable vegetation over a range of elevations. In Chilean Patagonia, Arroyo & Squeo (1990) found an increase in the proportion of dioecious species in four transects that ranged from 700 to 1200 or 1500 m a.s.l., a much smaller range (and lower maximum elevation) than in this study. Furthermore, the vegetation was alpine herbs and shrubs, somewhat dissimilar to the tropical forest of Costa Rica. The elevations of other montane forest plots enumerated for breeding systems are also in the mid-elevational range of this study [Venezuela: 1749 m (Sobrevila & Arroyo, 1982); Jamaica: 1550 m (Tanner, 1982); South Africa: 1000–1450 m (Griffiths & Lawes, 2006)] and, as such, the higher incidence of dioecy at 'high' elevations noted by previous authors may be artefactual because they sampled forests at or around the peak of species richness associated with the rise in elevation.

This mid-elevation peak in species richness has been found in numerous studies among a wide variety of species, although other studies find a negative or no relationship with elevation (Rahbek, 2005). However, the scale of the study has important implications for the pattern found (Nogués-Bravo et al., 2008). This relationship (and the correlation between the incidence of dioecy and species richness) appears to override any effects of pollinator or environmental harshness on breeding system. Insofar as elevational gradients may reflect latitudinal gradients, it is interesting that the proportion of dioecious species showed a positive association with species richness and with PD. As mentioned at the outset, the proportion of dioecy is typically highest in the tropics, and decreases towards the poles (Bawa & Opler, 1975; Bawa, 1980; Sakai & Weller, 1999). For example, the proportion of dioecious (including similar breeding systems, e.g. gynodioecious) species is estimated to be 4.3% in the British Isles (Kay & Stevens, 1986) and 3.9% in Alaska (Fox, 1985). In contrast, the proportion of dioecious species was found to be c. 13% and 14% for a tropical deciduous forest in Mexico (Bullock, 1985) and a sandy coastal plain in Brazil (Matallana et al., 2005), respectively (these two

floras were chosen because they included herbs and vines; among tropical trees and shrubs the range is typically 16–28%; Queenborough et al., 2007). The exceptions to this large-scale latitudinal gradient in dioecy may be islands (Bawa, 1980; Sakai et al., 1995; but see Baker & Cox, 1984). For example, New Zealand has a markedly higher proportion of dioecious species (12–13%) than would otherwise be predicted by its latitude (e.g. Sakai et al., 1995).

What mechanism(s) could underlie the unimodal relationship between dioecy and elevation, and the positive association between dioecy and species richness and PD? One possible factor we explored was the influence of different pollination systems on distribution along the elevational gradient. Most species for which we had data were pollinated by insects, in agreement with other studies (Bawa, 1990). Dioecious and monoecious species were both absent among the few other biotic pollinator systems (i.e. bird, bat) and were solely represented among wind-pollinated species. These observations agree with previous assertions regarding negative associations between unisexual flowers and vertebrate pollination (e.g. Renner & Ricklefs, 1995; Chazdon et al., 2003), and possible positive associations with wind pollination (Bullock, 1994). However, our data on pollination systems fail to explain the general patterns for two reasons. First, species with the two breeding systems demonstrated comparable reliance on insect and wind pollination. We are unaware of any hypotheses that predict a differential response of dioecious versus monoecious species to marked reductions in pollinators with increasing elevation, or to shifts in the relative importance of, for example, bee to fly and/or wind pollination. Second, the proportion of dioecious species that relied on wind pollination was relatively low overall (mean ± SE: 11.9% ± 0.02) and did not show any predictable changes with elevation. Therefore, although subtle shifts in the reliance on different pollinators (e.g. bees versus flies) along the elevational gradient are possible, our analyses detected no signal supporting the role of pollinators in producing the contrasting patterns observed for dioecious versus monoecious species.

Focusing instead on proximate climatic conditions, rainfall was highest at mid-elevations, whereas there was a negative linear relationship between temperature and elevation. With regard to soil and litter characteristics, Lieberman et al. (1996) noted that some (e.g. soil moisture content) displayed a positive association with elevation, whereas others (e.g. nitrogen mineralization) decreased with elevation. Therefore, it may be that the unimodal relationship between the relative representation of dioecy and elevation reflects a response to changing rainfall levels, or the net effect of two (or more) contrasting gradients. Any such explanation would, however, need to invoke a difference between monoecious and dioecious species in the response to such gradients. Although this may sound implausible, we note the possible parallels between our community-wide patterns and the observation that monoecious Siparuna species were found to be restricted to the lowlands, whereas dioecious congeners were largely found in the montane Andes (Renner & Won, 2001). Whether dioecious

species consistently have different edaphic or climatic preferences to those of closely related cosexual species is a largely unexplored area, but is worthy of further attention.

Based on two observations, we can rule out exceptional phylogenetic distinctness of dioecious species as the sole source of the associations. First, the association between the proportion of dioecious species and total species richness would hold even if it was found that dioecious species tended to be found on long branches in the phylogeny (i.e. had high phylogenetic distinctness on average), because PD does not enter into these analyses. Second, visual examination of the phylogeny reveals no consistent trend for dioecious species to be on long branches. Indeed, the five monoecious palm species were the only monocots in the tree (acting as an outgroup to the remaining flowering plants), and the number of monoecious species ($n = 1$) in the relatively poorly represented magnoliid clade ($n = 16$), the outgroup to the larger rosid and asterid clades, was not markedly lower than the number of dioecious species ($n = 3$). However, the proportion of monoecious species showed no clear association with either species richness or PD.

To conclude, we have demonstrated a marked association between the incidence of dioecy and species richness and PD of trees over a large-scale elevational gradient, as well as a mid-elevation peak in all three variables. The higher incidence of dioecy observed in montane systems in previous work is possibly the result of these studies being located at or near such a mid-elevation peak. However, as is the case for the observation that dioecious species are more common in the tropics than in temperate regions (e.g. Vamosi & Vamosi, 2004), we have no conclusive explanations at present for the patterns observed in this study. The positive correlations of dioecious species with species richness and PD show intriguing parallels with the latitudinal gradient in biodiversity. It is likely that further investigation of the distribution of breeding systems along elevational gradients will therefore shed light on the mechanisms underlying both patterns.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Distributional and ecological data for 167 seed plant species.
Appendix S2 Phylogeny of 167 seed plant species.

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