



The likelihood of sympatric speciation and morphological divergence in plants

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Sympatric speciation is considered rare, but oceanic *Howea* palms, crater lake cichlids, and parasitic indigobirds provide compelling evidence that it occurs. Still, the frequency of sympatric speciation and its relationship to morphological divergence in plants remains poorly understood, especially in plants. Here, we analyze the geographic distributions, traits, and divergence times of palm and conifer sister species (740 species from 108 genera) to determine the dominant geographic mode and role of morphological divergence in plant speciation. We show that allopatric speciation is dominant, and while frequent sympatric speciation cannot be discounted, the most likely scenario is that zero (conifers) or 10% (palms) of speciation events occur in sympatry. Our models show that the incidence of sympatry among sister pairs rises rapidly within the first million years after speciation and then declines, suggesting that species failing to attain sympatry early tend to remain allopatric. Finally, we find no evidence for morphological divergence in allopatric or sympatric palms. Our findings question the link between speciation and morphological divergence and suggest that while plants and animals share similar modes of speciation, plants exhibit a complex spatiotemporal dynamic, challenging the typical vertebrate pattern of steadily increasing sympatry.

biogeography | diversification | ecological speciation | geographical speciation | phylogenetics

Speciation is often assumed to involve geographical isolation and trait divergence between sister species. The first assumption has been better studied in animals than plants and the consensus is that geographical isolation is the main speciation mode in vertebrates (1). By contrast, the few available studies on plants hint toward a shared role of speciation with geographical isolation (hereafter allopatric) and speciation without geographical isolation (sympatric) (2–11). Sympatric speciation in plants can arise through ecological divergence (3, 4) or through nonecological mechanisms such as hybridization and polyploidy (2, 5–7). Regarding morphological divergence, a recent study revealed that most allopatric sister species of birds, mammals, and amphibians have evolved toward similar rather than divergent forms (12). Similar studies combining the geographical and morphological context of divergent species are rare in plants and usually limited to single genera.

Here, we address two key questions relevant to the speciation process: first, whether species originate solely through geographical isolation, and second, whether speciation involves morphological divergence. Concerning the first question, we find that young sister pairs in both conifers and palms show substantial range overlap, which slightly declines with age (Fig. 1 *A* and *B*). A similar pattern occurs in *Calochortus* (Liliaceae) (7) and in species from 12 families in the California Floristic Province (8). These patterns are, however, difficult to interpret without explicitly modeling the speciation process and subsequent geographic range dynamics. To address this, we use a biogeographic model that infers speciation modes while accounting for postspeciation transitions between allopatry and sympatry and their variation over time (*SI Appendix*). We find that allopatric speciation is likely the dominant mode in both conifers and palms, accounting for 100% of events in conifers (Fig. 1 *C*) and 90% in palms (Fig. 1 *D*). Broad confidence intervals, however, prevent ruling out higher sympatric speciation rates—of up to 30% in conifers and 50% in palms.

Our analyses also reveal a rise and subsequent decline in the incidence of sympatry with sister species age (Fig. 1 *E* and *F*). This pattern is best explained by a model where the rate of transition to sympatry slows down with time since divergence. This suggests that sister pairs initially separated by relatively permeable geographic barriers attain sympatry rapidly following speciation (i.e., within ~1 Ma). In contrast, those divided by impassable barriers such as seaways or deep valleys remain indefinitely allopatric. Such complex spatiotemporal dynamics differs from the monotonic trend toward greater sympatry seen in vertebrates.

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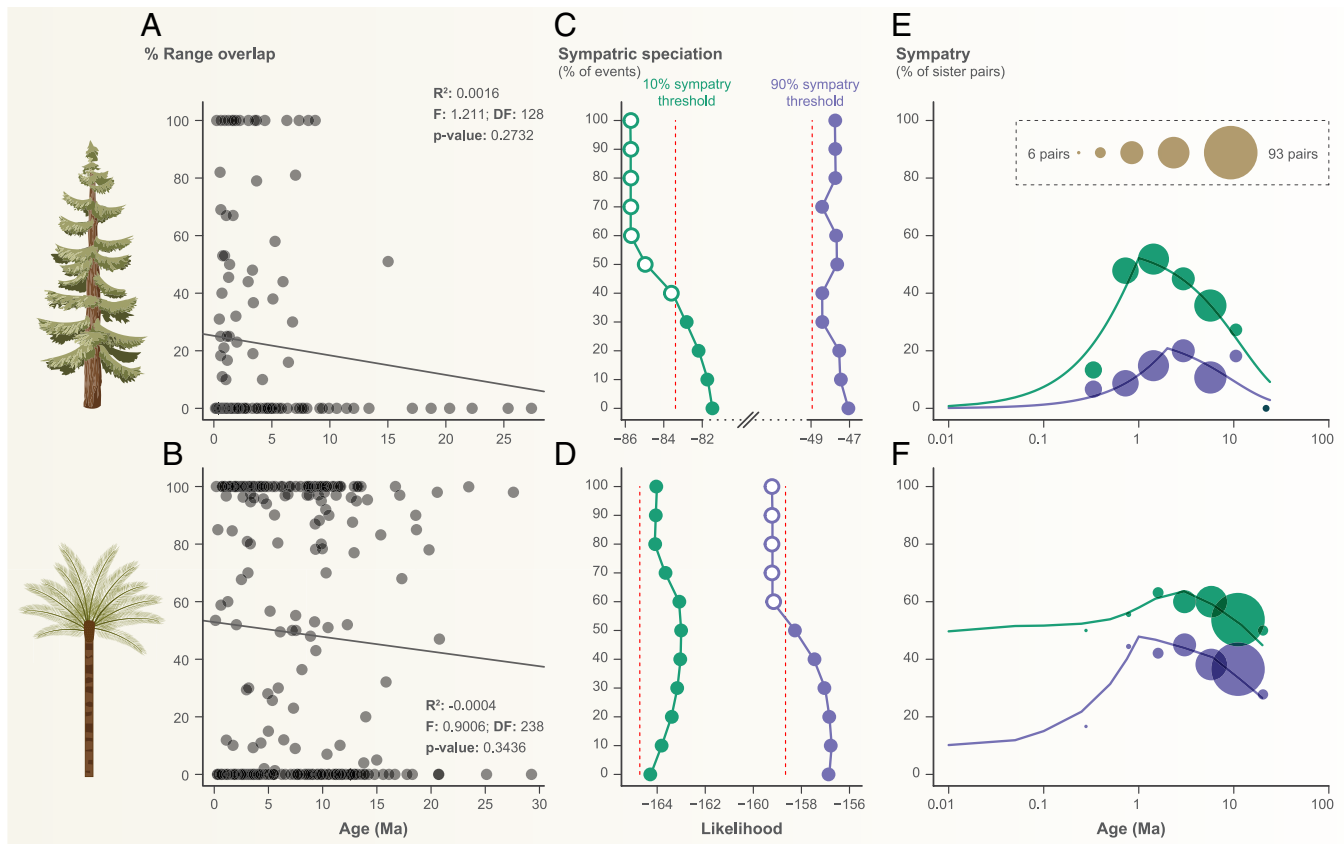


Fig. 1. The likelihood and temporal dynamics of sympatric speciation in palms and conifers. (A and B) Weak negative relationships between percentage of current range overlap and time since divergence (million years ago, Ma) for conifer (A) and palm sister pairs (B). (C and D) Likelihood of a biogeographic model assuming varying degrees of sympatric speciation (0 to 100%, in 10% intervals) for conifers (C) and palms (D) under a relaxed (10% of the smaller range overlap, in green) or conservative (90%, in purple) definition of sympatry. Higher values (to the Right) indicate more likely models. Filled points do not differ significantly from the best model. Red dashed line indicates 1.92 log-likelihood units from the best model. (E and F) Best-fitting model predicted proportions of sister pairs in sympatry over time (log-scale) under the 10% (green) and 90% (purple) overlap thresholds for conifers (E) and palms (F). Bubbles represent observed data. Bubble size is proportional to the number of species pairs in each time bin.

We hypothesize that the higher incidence of sympatric speciation in palms may be due to the greater permeability of geographical barriers in the lowlands, where they mostly diversified. While Amazonian rivers are geographic barriers for birds (13) and primates (14), population-level analyses of the shrub *Amphirrhox longifolia* (Violaceae) in the Rio Branco (9) and the trees *Caryocar villosum* and *C. microcarpum* (Caryocaraceae) in the Rio Negro (10) show that most rivers are largely permeable to plants. The mechanisms of sympatric speciation in palms might also differ from those in *Calochortus* (6, 7) and other plants (2, 8) in which polyploidy is frequent. The influence of polyploidy in our studied groups is small because changes in chromosome number are rare—occurring in 4 of 330 palms (15) and in 14 of 512 conifer species (16). Instead, sympatric speciation in palms may be due to drivers like assortative mating, ecological divergence associated with pleiotropic effects, or to nonecological drivers like genetic drift, founder effects, or bottlenecks.

We now turn to the second question of whether speciation necessarily involves morphological divergence. Recent genomic, ecological, and experimental research has confirmed that *Howea* palms diverged in sympatry (3, 4). In *Howea*, trait differences are a strong example of divergent evolution. But how common is this in plants? To answer this, we modeled trait divergence over time as in Anderson et al.'s study (12) using morphological traits for 84 pairs of palm species with zero and complete range overlap. We find no evidence for a divergence model for species with zero or complete overlap (Fig. 2). Instead, our results demonstrate that sister palm species have repeatedly evolved toward similar forms. Sister species might converge onto similar solutions when exposed to comparable

conditions. The cryptic radiation of Andean *Geonoma* palms (11) exemplifies such morphological convergence in genetically independent groups. Thus, as in vertebrates (12), morphological convergence seems to be common also among palm sister species.

In conclusion, our results indicate that allopatric speciation is the predominant mode of speciation in palms and conifers. Yet, sympatric speciation in palms—and possibly in other plant groups with similar diversification strategies—is not confined to exceptional cases. Speciation in palms with or without geographical isolation does not seem to be the result of a morphologically divergent process, but rather, of a process leading to convergent morphologies. Future research is needed to determine whether morphological convergence represents parallel ecological evolution (17) or to determine to what degree palm sister pairs differ in yet unmeasured traits, like phenology or habitat preferences (8). Furthermore, ecological divergence in sympatric pairs may be uneven across the range of species and only detectable at the local scales where populations of both species co-occur. Finally, to confirm cases of sympatric speciation, further studies would need to investigate the degree of reproductive isolation and the probability of an allopatric phase during speciation (18).

Materials and Methods

Biogeographic Models. We estimated the relative frequency of sympatric vs. allopatric speciation by fitting a nonhomogeneous Markov model to sister species data. Species pairs originate in allopatry or sympatry and may transition between states. Using sister pair ages (Ma) and current range overlap, we estimated via

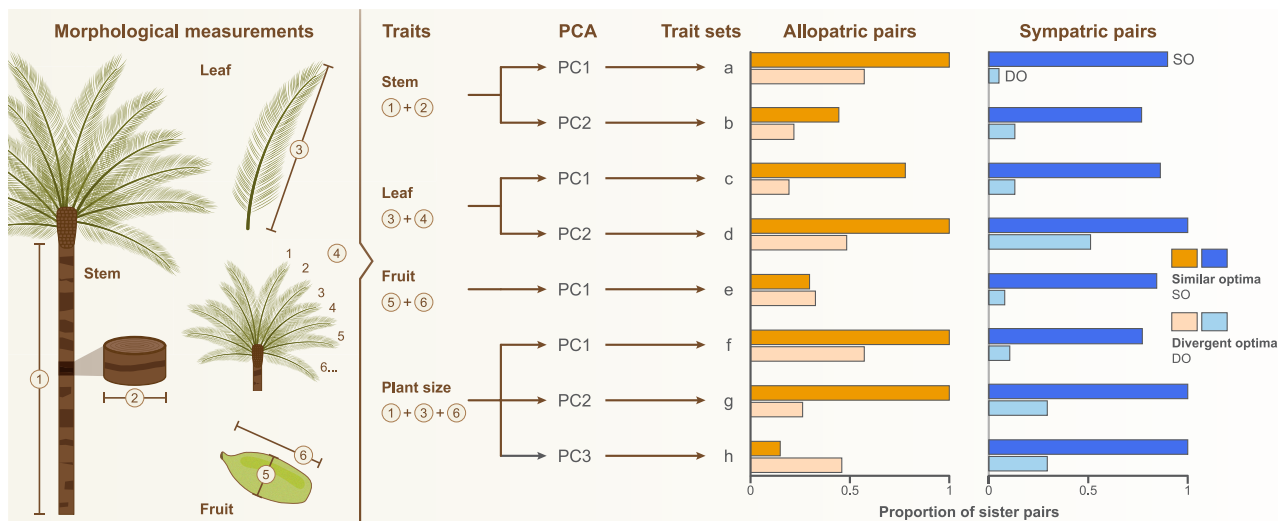


Fig. 2. Speciation frequently leads to similar morphologies. Illustrations represent morphological measurements: 1) stem length, 2) stem diameter, 3) leaf length, 4) number of leaves, 5) fruit width, and 6) fruit length. The panel “Traits” shows the combination of measurements included in the principal component analyses (PCA) to provide a score for each sister species and trait. A “trait-set” is a set of differences in the PCA scores for a given trait for all the sister pairs having information on that trait. Bar-plots indicate the estimated proportion of sister pairs in a trait-set whose divergence conforms to an evolutionary model of divergent optima (DO) or toward the same optimum as the sister species (SO).

maximum likelihood: γ = allopatric speciation frequency, σ = transition rate to sympatry, and ϵ = transition rate to allopatry. Range overlap was treated as binary, using both relaxed ($\geq 10\%$) and conservative ($\geq 90\%$) sympatry thresholds. Only sister pairs with support ≥ 0.5 were included. Initial data exploration revealed a rise and fall in the incidence of sympatry with sister age, so we used a piece-wise model allowing σ to vary before and after an estimated breakpoint (0, 1, or 2 Ma). For each, we performed a profile-likelihood search across γ values from 0% to 100% allopatry in 10% intervals.

Trait Evolution Models. We analyzed four groups of traits that include measurements of the stem, leaves, and fruits. In these models, the response variable is the absolute difference in a continuous trait between sisters, i.e., the change in the statistical distribution of the difference over time. The resulting distributions were then fit to models whose shapes are expected to differ depending on whether lineages generally evolved through a combination of the following

models: a) toward the same optimum as the sister species (SO), b) toward a different or divergent optimum (DO), or c) under unconstrained random walk-like processes (RW) (*SI Appendix*).

Data, Materials, and Software Availability. All data and scripts have been deposited on Zenodo (19). Extended methods and references to previously published data used in this study are available in the *SI Appendix*.

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