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Evolutionary Time for Dispersal Limits the Extent but Not the Occupancy of Species' Potential Ranges in the Tropical Plant Genus *Psychotria* (Rubiaceae)

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ABSTRACT: Explaining the diversity in geographic range sizes among species is a central goal of ecological and evolutionary studies. We tested species age as an explanation of range size variation within a group of understory shrubs in the Neotropics (*Psychotria* subgenus *Psychotria*, Rubiaceae). We distinguish between range occupancy (filling an occupied area) and range extent (maximum distances dispersed). We used Bayesian relaxed-clock dating of molecular sequence data to estimate the relative age of species, and we used species distribution modeling to predict species' potential ranges. If the range sizes of species are limited by time for dispersal, we hypothesize that older species should have (1) larger realized range occupancies and realized range extents than younger species, (2) filled a greater proportion of their potential range occupancies, and (3) colonized a greater proportion of their potential range extents. We found (1) a significant but weak positive relationship between species age versus both realized range occupancy and realized range extent, (2) no relationship between species age and filling of potential range occupancies, but (3) that older species had colonized a significantly greater proportion of their potential range extents than younger species. Our results indicate that a time-for-dispersal effect can limit the extent of ranges of species but not necessarily their occupancies.

Keywords: dispersal limitation, divergence time, geographic range, phylogeny, species age, Neotropical.

Introduction

Even among closely related species, geographic range size can vary over many orders of magnitude (Brown et al. 1996; Gaston 2003). Understanding what factors best explain variation in geographic range size among species is a central question at the interface of ecology and evolution. Range expansions are driven by dispersal, so variation in

dispersal ability has been predicted to explain much of the variation in range sizes among species (Hanski et al. 1993; Gaston 2003), with a general expectation that species with superior dispersal abilities attain larger range sizes more quickly (Hanski et al. 1993; Brown et al. 1996). Despite the perceived importance of dispersal, only limited empirical evidence supports this conjecture, and a recent review even suggests that dispersal ability may not be particularly important in driving range size variation in many species (Lester et al. 2007). Dispersal ability, however, is only one side of the coin, because dispersal that expands a species' range is not an instantaneous process; the time available for dispersal can also play a central role in explaining range size variation. For example, even a species with very poor dispersal abilities may attain a large geographic range size given sufficient time. Similarly, species that show little variation in dispersal ability may have drastically different range sizes simply because the time that has been available for dispersal differs among the species. Hence, when attempting to explain the variation in range size among species, time may be a critical limiting factor, particularly if the species of interest show no obvious differences in their dispersal potentials.

Temporal dispersal limitation, although not explicitly stated as such, forms the underpinning of theory that predicts a positive relationship between species age and range size (e.g., Willis 1922). If species start with small population sizes and restricted geographic ranges, many of those with restricted geographic ranges could simply be young species. This was one of the key predictions of Willis's age and area hypothesis (1922), and a similar prediction is made by Hubbell's neutral theory (2001), a dispersal-assembly theory. The premise is simple and built on three key assumptions: (1) new species have restricted geographic ranges, (2) species with small geographic ranges are extinction prone (and thus most young species never attain either older ages or larger ranges), and (3) species

with large geographic ranges are buffered from extinction (Johnson 1998; Payne and Finnegan 2007). When these assumptions are met, there is a general expectation that, on average, young species will have smaller ranges than old species (Paul and Tonsor 2008). The majority of studies of the age and area relationship have simply tested whether there is a positive linear relationship between some metric of species age and range size (although other species age and range size relationships, such as a unimodal one, may be expected; see Webb and Gaston 2000). These tests have been largely equivocal (Jones et al. 2005). Evidence of a positive relationship between species age and range size has been found for some mollusk species (Jablonski 1987; Miller 1997), but only early in their evolutionary history, after which time ranges appear to stabilize in size. In Cenozoic mollusks, species occupancy of fossil assemblages (the proportion of collections in which a species is present) shows a hump-shaped distribution, with species attaining their maximum occupancies for a brief time in the approximate middle of their species lifetimes (Foote et al. 2007). Studies on large diverse groups of taxa, such as across New World bird species (Gaston and Blackburn 1997) or mammals or carnivores (Jones et al. 2005), find no consistent relationship between species age and range size. These tests used taxa in which the species have diverse and broadly different ecological niches. When species with more similar ecological requirements have been compared, for example, in six clades of birds (Webb and Gaston 2000), the relationship between species age and range size is variable and clade specific. In the case of the *Sylvia* warblers (Böhning-Gaese et al. 2006), age is a significant factor explaining variation in range size (although age was strongly correlated with dispersal ability). Likewise, Paul and Tonsor (2008) examined a genus of ecologically similar tropical plants (*Piper*) and found that species age explained 25% of the variation in range size in this group, with young species having smaller ranges than old species.

Two important components have been missing from previous tests of age and area. The first is accounting for the fact that all species have limitations as to where their populations can be expected to persist because of each species' specific physiological and ecological requirements. As a result, previous tests of age and area have not accounted for one major potential driver of range size variation, the ecological tolerances of species. Better tests would evaluate the area that a species could occupy given its ecological constraints (termed its potential range; Gaston 1994*b*, 2003) relative to its realized range (current observed range). The ratio of the realized range (R) to the potential range (P) can be used to assess to what degree species occupy their potential ranges ("range filling"; Gaston 2003; Svenning and Skov 2004). Species distribution modeling (i.e., Elith et al. 2006) provides a method to estimate the potential range of a given species (in the absence of dispersal limitation) on the basis of a set of biologically relevant variables and georeferenced records of presence localities.

The second component that has not been adequately addressed in previous studies is that both realized and potential range sizes can be measured in two general ways, as the area of occupancy (the number of locations with a presence record for a species) or as the extent of occurrence (the maximum linear distance between locations with a presence record for a species; Gaston 1994*a*). Although these measures can be correlated, they can also be decoupled (Gaston 1994*a*). For many applications of range size data, such as studies regarding conservation biology, the area of occupancy is the preferred measure because it gives a better idea of where specifically on the landscape a species is likely to be found. Only area of occupancy measures have been used for previous tests of age and area (e.g., Webb and Gaston 2000; Jones et al. 2005). However, if the predictions of age and area are viewed as a result of the process of temporal dispersal limitation, then an extent of occurrence measure may be more appropriate. The time available for dispersal could limit how far a species has colonized into its potential range but have little impact on its occupancy within its range. For example, a species that is a poor competitor but that has superior dispersal abilities could have a large range extent but only limited occupancy within its range. Interestingly, the only study to date incorporating species age as a factor in range filling (Schurr et al. 2007) found no evidence of an effect on the area of occupancy of potential ranges in South African Proteaceae species (extent of occurrence was not measured).

To address these two limitations of previous studies, we developed range size metrics that specifically incorporate species' potential ranges as well as areas of occupancy and the extent of occurrence measures. We define species' realized range occupancy (R_O) as the number of occupied locations (e.g., grid cells) and the realized range extent (R_E) as the maximum linear distance between the locations of records of occurrence. Potential range occupancy (P_O) and potential range extent (P_E) are defined in the same way as realized ranges, except modeled potential locations are used (fig. 1). We define the degree to which species occupy their potential ranges as the ratio of realized range occupancy to potential range occupancy (range occupancy ratio, R_O/P_O), and we define the degree to which they have colonized their potential range extents as the ratio of realized range extent to potential range extent (range extent ratio, R_E/P_E).

We tested the general hypothesis of a positive relationship between species age and these four metrics of geographic range size: (1) realized range occupancy (R_O), (2) realized range extent (R_E), (3) range occupancy ratio
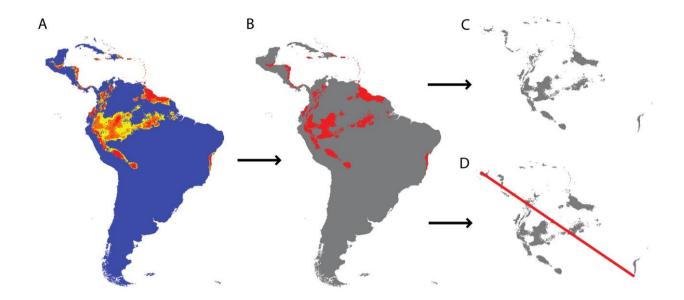
Figure 1: Measuring species' predicted and realized range occupancy and range extent. *A*, Potential distribution is modeled using a maximum entropy approach. *B*, High probability areas are extracted. *C*, Potential range occupancy (P_O; number of pixels predicted to be occupied). *D*, Potential range extent (P_E; maximum linear extent between predicted occupied pixels, shown by red line) are measured. For realized ranges, only steps *C* and *D* are used, with the realized range occupancy (R_O) given by the number of occupied pixels (collection records) and the realized range extent (R_E) given by the maximum linear extent between collections.

(R_O/P_O), and (4) range extent ratio (R_E/P_E). We examined the impact of temporal dispersal limitation on range size variation in a clade of closely related, ecologically similar species of tropical understory shrubs in the genus *Psychotria* (Rubiaceae). We predicted that older species have greater realized range occupancies and extents, greater range occupancy ratios, and greater range extent ratios. We used species distribution modeling (using Maxent; Phillips et al. 2006) to estimate the potential ranges of species and Bayesian relaxed-clock dating (with uncorrelated rates as implemented in BEAST; Drummond and Rambaut 2007) to estimate the "tip ages" (sensu Roy and Goldberg 2007) of species. We focused on species in one clade within *Psychotria* (subgenus *Psychotria*) in one biogeographic region (Mesoamerica) that has been well collected and in which the taxonomic work has been recently updated (C. M. Taylor, unpublished manuscript). Mesoamerican *Psychotria* subgenus *Psychotria* is a valuable model group because the species therein vary by over three orders of magnitude in their range sizes, yet they appear to be broadly ecologically similar.

Methods

Study Taxa

Psychotria (Rubiaceae) is one of the most speciose angiosperm genera, consisting of approximately 1,600 species

(Hamilton 1989). *Psychotria* species are primarily found pantropically in wet to seasonal forests, with a few species occupying dryer habitats. *Psychotria* species vary markedly in both their range sizes and local abundances (J. Paul, unpublished data), and they make up a significant proportion of species and stems in the understories of many tropical forests (Gentry 1990). The majority of *Psychotria* species are similar in their general growth forms (small trees and shrubs), most are obligate outcrossing species pollinated by insects (e.g., Stone 1995), and the seeds of most are dispersed by frugivorous birds (e.g., Loiselle et al. 1995). Molecular phylogenetic work by Nepokroeff et al. (1999) and Andersson (2002) has largely confirmed the systematic relationships outlined by Taylor (1996). There are 78 recognized *Psychotria* subgenus *Psychotria* taxa in Mesoamerica (C. M. Taylor, unpublished manuscript). In this article, we use *Psychotria* to refer to *Psychotria* subgenus *Psychotria*.

Realized and Potential Geographic Range Estimates

Collection Records. We used the Missouri Botanical Garden's (MBG) Tropicos database of collection records (http://www.tropicos.org) to estimate the range sizes of species. We queried the database on September 9, 2006, to find all collection records of the Mesoamerican *Psychotria* subgenus *Psychotria* species (including records

from South America). Species determinations in *Psychotria*, like many Rubiaceae taxa, can be challenging. All species determinations at MBG have been made or checked by one of us (C.M.T.), thus affording a high degree of consistency to the species identifications. Furthermore, MBG has one of the largest and most extensive collections of Rubiaceae from Mesoamerica. Therefore, we chose to limit our geographic estimates to the MBG database in order to preserve the consistency of the species identifications.

Species Distribution Modeling. To model the potential geographic range sizes of species, we used the program Maxent 3.1.2 (Phillips et al. 2006). Species distribution modeling uses presence-only data and a set of environmental variables to predict the probability of a species' occurrence across a landscape. Maxent uses a maximum entropy approach to species distribution modeling (Phillips et al. 2004), and it has been shown to perform better than many other species distribution modeling programs (Elith et al. 2006), particularly for species with a small number of collection records (Hernandez et al. 2006; Pearson et al. 2007). For each species, georeferenced collection records were input in Maxent along with 20 environmental variables (from the WorldClim database, http://www.worldclim.org; see app. A in the online edition of the *American Naturalist* for the list). We also ran analyses with a reduced number of environmental variables (11) to account for potential overfitting of relationships by Maxent (Peterson et al. 2007). Analyses were first run using 70% training and 30% testing data to assess model performance. The analyses were then run with all collections used for training to project species' potential distributions. The results of these projections were used to calculate the potential range size measures. Details on our species distribution modeling are presented in appendix A, and the number of collection records used and model assessment statistics are presented in appendix B.

Geographic Range Size Estimates. Range occupancy, for the R_O and R_O/P_O analyses, was calculated as the number of occupied (or predicted to be occupied) grid cells (fig. 1). Range extent, for the R_E and R_E/P_E analyses, was calculated as Feret's diameter in ImageJ (Rasband 1997), that is, the largest distance between two occupied (or predicted to be occupied) grid cells (fig. 1). We calculated R_O and R_E for all species and R_O/P_O and R_E/P_E for all species with sufficient collection records ($\geq$6 unique collection localities). Details of our methods used to assess range sizes are presented in appendix A.

Molecular Methods

We used both field-collected samples and herbarium sheets as the basis for our DNA extractions. Leaf samples for DNA extraction (stored in 15-mL centrifuge tubes with silica gel) and corresponding voucher specimens were collected in 2005 in Costa Rica. Vouchers were field identified by J.R.P., and C.M.T. and J.R.P. made final determinations of the specimens at MBG. Vouchers were deposited at MBG, the Carnegie Museum of Natural History Herbarium (CM), and the Universidad de Costa Rica Herbarium (USJ). To sequence many of the rare and endemic *Psychotria* species for which collecting was unfeasible, specimens of 73 of the 78 recognized taxa of Mesoamerican *Psychotria* subgenus *Psychotria* were loaned from MBG to C.M. at CM. We extracted DNA from leaf material. Some specimens yielded only highly degraded DNA, resulting in partial or missing sequence data for some species (table C1 in the online edition of the *American Naturalist*). We used nuclear ribosomal internal transcribed spacer sequences (ITS) and chloroplast *psbA-trnH* intron sequences for phylogenetic inference. The ITS locus is one of the most extensively used loci for species-level phylogenetic work in angiosperms (Mort et al. 2007). We also used the chloroplast intron *psbA-trnH* to attain an estimate of phylogenetic relationships within *Psychotria* from plastid DNA. This intron was tested in three species of *Heteropsychotria* by Kress et al. (2005), and it showed considerable variation at the species level. Details of laboratory techniques and protocols and justification of our molecular marker choices are provided in appendix A.

Phylogenetic Inference and Divergence Time Estimation

We used a Bayesian relaxed-clock approach as implemented in the program BEAST v. 1.4.8 (Drummond and Rambaut 2007) to concurrently estimate the phylogenetic relationships of species and their divergence times (Renner 2005; Drummond et al. 2006). Details of alternative phylogenetic methods that we used to analyze the data are presented in appendix A. For our purposes, relative ages of species are sufficient, but we used fossil evidence to guide a prior distribution on the root age of the tree in order to make the ages more easily interpretable. Details of our calibration of absolute ages using fossil data are presented in appendix A. We included Hawaiian *Psychotria* species in our analyses (Nepokroeff et al. 2003), and we used the crown age of these species to assess the plausibility of our absolute age estimates. The outgroup species and non-Mesoamerican *Psychotria* subgenus *Psychotria* species used in this study (including GenBank accession numbers) are listed in table D1 in the online edition of the *American*

Naturalist. The pairwise node ages found in ITS-only and combined ITS-*psbA* analyses were strongly correlated ($r = 0.96$), so we took a total evidence approach using the analyses on the combined ITS-*psbA* data set (including all taxa with some missing data) for our age estimates. See appendix A for a further discussion of using a combined or partitioned data set. Analyses including missing data can be robust, and at times they can help to break up long branches that would exist without including taxa with only partial data (Wiens 2006). A summary of the priors and model parameters for the BEAST analyses is given in table 1. We used the combined results of three independent runs (see app. A) to determine the maximum clade credibility tree (MCC tree; the tree that maximizes the product of clade probabilities). This tree and its divergence time estimates were used for all further analyses. We defined species age as time since divergence from its sister taxon in our data set. For consistency, in cases where two sequences of a given species did not group together, we always used the older divergence time estimate for a given species as the species' age.

Statistical Analysis

We performed least squares linear regression analyses and one-way ANOVAs using SAS 8.2 (SAS Institute 2001). Variables were checked for normality using the SAS protocol univariate and transformed as necessary to meet the assumptions of regression and ANOVA. Phylogenetic analyses revealed a strongly supported basal divergence within our study clade that was relevant to interpretation of the results. As a result, we conducted range size analyses on both the total set of species (termed all species) and the two clades separately (termed clades 1 and 2). Regression was used to examine relationships between species age and R_O, R_E, R_O/P_O, and R_E/P_E, as well as between species age and the morphological characters of fruit volume and plant height (estimated from descriptions of flora). We used ANOVA to compare means of R_O, R_E, R_O/P_O, R_E/P_E, fruit volume, plant height, species age, median latitudinal position, elevation range, and elevation midpoint between species in clades 1 and 2. To assess whether modeling species with few collection records was biasing our results, we also reran significant species age and range-size ratio regressions after eliminating all species with $N < 20$ collection records.

Results

Phylogenetic Relationships and Divergence Times

Mesoamerican *Psychotria* species have primarily diversified in the last 16 million years (Ma; fig. 2), with most lineages diversifying within the last 12 Ma. The crown age of the Hawaiian *Psychotria* species is estimated to be 9.76 Ma (95% highest posterior density [HPD], 5.72–14.08). The Bayesian MCC tree had a highly supported split of Mesoamerican *Psychotria* subgenus *Psychotria* species into two distinct clades (labeled clades 1 and 2; fig. 2). These clades had not been identified previously on the basis of any morphological, biogeographic, or ecological characters, but they were also recovered in parsimony and maximum likelihood searches of the full ITS and ITS-*psbA* data sets (results not shown). Our analysis estimates the divergence of these two clades at 15.13 Ma (95% HPD, 10.21–20.28 Ma) with a posterior probability of 0.99. Clade 1 includes 28 taxa and clade 2 includes 34 taxa.

Species Age and Geographic Range Size Metrics

When we analyzed all species, we found a significant, positive relationship between both species age and R_O ($R^2 = 0.07$, $P = .03$, df $= 64$; fig. 3*A*) and species age and R_E ($R^2 = 0.08$, $P = .02$, df $= 64$; fig. 3*B*). Using 20 environmental layers for the modeling of species distri-

Table 1: Prior parameter values for the Bayesian ITS-*psbA* relaxed-clock analysis

Parameter	Distribution	Lower bound	Upper bound
Root height	Gamma	39.7[a]	58.9[a]
GTR substitutions	Uniform	0	100
Gamma shape	Uniform	0	100
Proportion of invariant sites	Uniform	0	1
Lognormal relaxed-clock mean	Uniform	0	100
Lognormal relaxed-clock standard deviation	Uniform	0	10
Yule speciation process birth rate	Uniform	0	1^{-6}
Mean rate of evolution across tree	Uniform	…	…
Variation in rate of evolution across tree	Uniform	…	…
Covariation in lineage-ancestral lineage rates	Uniform	…	…

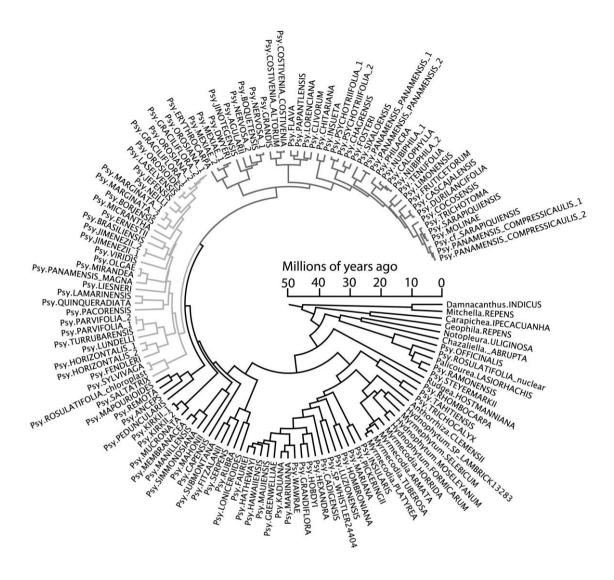[a] Lower and upper 2.5% quantiles of distribution.

Figure 2: Bayesian relaxed-clock ITS-*psbA* maximum clade credibility circle chronogram. Scale gives time in millions of years. *Light gray branches*, clade 1; *dark gray branches*, clade 2 (see text for explanation).

butions, we found no significant relationship between species age and R_O/P_O (fig. 3C), but we did find a significant, positive relationship between species age and R_E/P_E ($R^2 = 0.17$, $P < .01$, df = 48; fig. 3D). When analyzing clades 1 and 2 separately, there was a significant, positive relationship between species age and R_E/P_E for clade 1 ($R^2 = 0.28$, $P = .02$, df = 20; fig. 3E) but not for clade 2 (fig. 3F). Neither clade had significant relationships between species age and R_O, R_E, or R_O/P_O. Using 11 environmental layers for modeling species distributions did not change these results, nor did excluding species with few collection records (see app. E in the online edition of the *American Naturalist* for results of these analyses).

Potential Explanatory Differences between Clade 1 and Clade 2

Species in clade 1 and clade 2 did not significantly differ in their average stature, fruit volume, elevation range size, elevation range midpoint, or average R_O, R_E, P_O, P_E, R_O/P_O, or R_E/P_E values (table 2). The median latitude for realized range occupancies of species in clade 1 was significantly more southern than it was for species in clade 2 ($8°2'24''$ vs. $12°56'60''$; $F = 11.61$, $P = .001$). Species in clade 1 were marginally significantly older (back-transformed mean = 2.68, SD = 2.55) than species in clade 2 (mean = 1.77, SD = 2.08; $F = 3.52$, df = 1, 54, $P =$
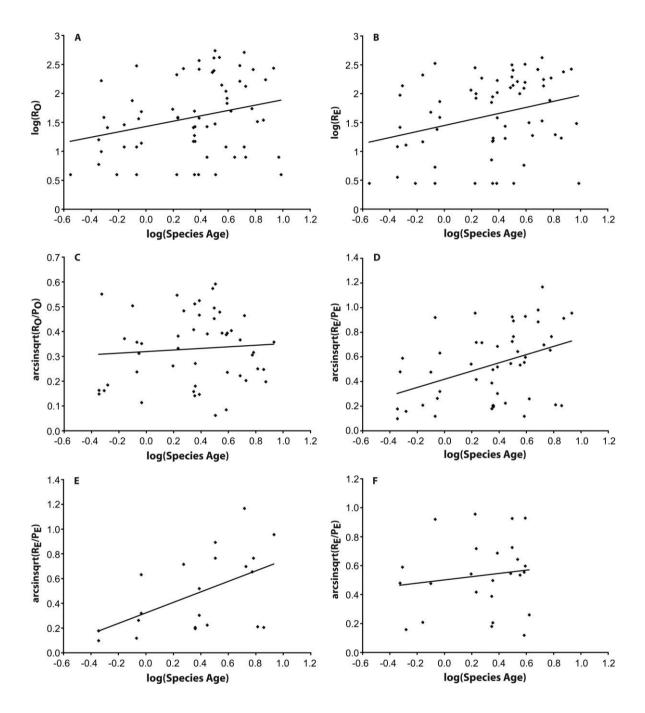
Figure 3: Relationship between species age and range size metrics in *Psychotria* subgenus *Psychotria* species in Mesoamerica. *A*, Regression of species age and realized range occupancy for all species (R_O; $y = 0.4625x + 1.4269$, $R^2 = 0.07$, $P = .03$, df $= 64$). *B*, Regression of species age and realized range extent for all species (R_E; $y = 0.5217x + 1.4485$, $R^2 = 0.08$, $P = .02$, df $= 64$). *C*, Regression of species age and range occupancy ratio for all species (R_O/P_O; $y = 0.0318x + 0.3194$, $R^2 = 0.01$, $P = .59$, df $= 48$). *D*, Regression of species age and range extent ratio for all species (R_E/P_E; $y = 0.3332x + 0.4191$, $R^2 = 0.17$, $P < .01$, df $= 48$). *E*, Regression of species age and range extent ratio for clade 1 species (R_E/P_E; $y = 0.4245x + 0.3226$, $R^2 = 0.28$, $P = .02$, df $= 20$). *F*, Regression of species age and range extent ratio for clade 2 species (R_E/P_E; $y = 0.1117x + 0.5013$, $R^2 = 0.0189$, $P = .51$, df $= 24$).

Table 2: One-way ANOVA results for morphological and geographic character comparisons between clades 1 and 2

Variable, source	df	SS	MS	F	Pr > F	R^2
Fruit volume:[a]						
Model	1	.26	.26	3.41	.07	.06
Error	53	3.99	.17			
Plant stature:[a]						
Model	1	.10	.10	1.09	.30	.02
Error	55	4.85	.09			
Elevation range:						
Model	1	429,773.70	429,773.70	.97	.33	.02
Error	55	24,475,047.35	445,000.86			
Elevation midpoint:						
Model	1	3,558.74	3,558.74	.01	.90	.00
Error	55	13,080,075.47	237,819.55			
Latitude midpoint:						
Model	1	359.79	359.79	11.61	.001	.17
Error	57	1,795.39	31.50			
R_O:[a]						
Model	1	.08	.08	.18	.67	.00
Error	60	26.08	.44			
R_E:[a]						
Model	1	.09	.09	.18	.67	.00
Error	60	28.59	.48			
P_O:[a]						
Model	1	.08	.08	.50	.48	.01
Error	44	6.87	.16			
P_E:[a]						
Model	1	.02	.02	2.00	.16	.04
Error	44	.47	.01			
R_O/P_O:[b]						
Model	1	.07	.07	3.47	.07	.07
Error	44	.88	.02			
R_E/P_E:[b]						
Model	1	.03	.03	.35	.56	.01
Error	44	3.52	.08			

[a] Analyses of log-transformed data.

[b] Analyses of arcsine-square-root-transformed data.

.065). Within clade 2, older species had significantly smaller fruit volume ($R^2 = 0.27$, $P = .003$, df = 30) than did young species. No significant relationships with age were found in clade 1 for fruit volume or stature.

Discussion

Species Age and Geographic Range Size Metrics

Our results provide evidence of a positive relationship between species age and various measures of range size, supporting the central prediction of the age and area hypothesis. The strength of this relationship, while significant, was weak when either R_O or R_E were used for the analyses, explaining only a small fraction of the variances in range sizes. When we took into account species' potential ranges, the explanatory power of species age doubled in the R_E/P_E analysis (explaining 17% of the variance), but there was no relationship with R_O/P_O. Because some species had too few collections to accurately model potential ranges, the analyses using potential ranges had smaller samples sizes and less power. This may explain why the weak relationship found between species age and R_O was not recovered in the R_O/P_O analysis or, alternatively, it suggests that range occupancy may not be influenced by species age as much as range extent. In contrast, the importance of accounting for potential range extent was clear, because the R_E/P_E relationship with species age was stronger despite the smaller sample size. We know of only one other study that has looked for a relationship between species age and the occupancy of species' potential ranges. Schurr et al. (2007) found that species age had no effect

on the proportion of species' potential ranges that were filled in a clade of South African Proteaceae (equivalent to our R_O/P_O metric, but no range extent metric was examined). They argue that processes acting on ecological timescales are largely responsible for the degree that species fill their potential ranges.

Our results suggest that time for dispersal may be an important factor limiting how far individuals disperse and colonize within species' potential ranges, but that it may not limit the density of occupancy of a geographic area when colonizing populations have been established. In a 45-year experiment in Belgium (van der Veken et al. 2007), transplanted populations of the forest herb *Hyacinthoides non-scripta* (Hyacinthaceae) have remained established but have grown very slowly. As a result, much of this species' potential range may remain unoccupied, despite the persistence of small populations far from the source population. The geographic spread of this slowly dispersing forest herb may exhibit properties similar to *Psychotria* species, which are primarily dispersed by understory birds (Nepokroeff et al. 2003). Rare long-distance dispersal events could establish distant populations intermittently, with species that have more time for dispersal (older species) colonizing farther into their potential ranges. But if average population spread is slow, these species will fail to occupy large portions of their potential ranges. Another study, however, did find a relationship between the time for immigration since glacial retreat and the occupancy of species' ranges (Svenning et al. 2008). Alternatively, the lack of a relationship between species age and range occupancy may be driven by the difficulty of accurately estimating occupancy from collection records. Accurate estimates of occupancy likely require intensive collecting throughout the range of a species, and uneven sampling among species may introduce considerable variance into comparative analyses.

Species Age Estimates and Potential Explanatory Differences between Clade 1 and Clade 2

Mesoamerican *Psychotria* subgenus *Psychotria* species consist of two well-supported clades that diverged in approximately the last 15 Ma. Although these two clades have not been identified previously on the basis of their morphology or ecology, the genetic data clearly indicate they have had separate evolutionary trajectories. Clade 1 species had significantly more southern ranges and were on average older than clade 2 species. The species in these two clades did not differ in their average realized range occupancies or extents or in their average range occupancy or extent ratios. Furthermore, species in the two clades did not differ in the average sizes of their elevation ranges

(minimum to maximum difference) or in their average elevation midpoint. It is striking that two groups of species that are so superficially similar could be so divergent in the impact of species age on their current range size distributions. Species age explained over one-quarter of the variance in range extent ratio (R_E/P_E) of clade 1 species, but was not significant in clade 2. The morphological character examined that was directly related to dispersal, fruit volume, also did not differ significantly between the clades. However, within clade 2, younger species had significantly larger fruits than older species. Interestingly, clade 2 species did not show a significant relationship between species age and R_E/P_E. This could indicate that younger species in clade 2 have, on average, greater dispersal ability, and as a result they have been able to colonize farther into their potential range extents than expected if dispersal ability were a neutral character within the clade. Additional evidence would need to be garnered to address this hypothesis, but it is interesting to note that, for species with animal-dispersed seeds, larger fruit size can correlate with seed dispersal by larger-bodied frugivores (Wheelwright 1985; Jordano 1995), who often have larger home ranges and greater average dispersal distances (Howe and Smallwood 1982; Holbrook and Smith 2000).

Robustness of Results

Our crown age estimates of ∼10 Ma (95% confidence interval [CI], 5.6–14.1 Ma) for the Hawaiian *Psychotria* species indicate that species ages may predate the present islands, and they suggest that our absolute age estimates are plausible. The absolute ages estimated here are less important than the ages relative to one another in terms of the comparative tests for which we used them. Our geographic range estimates are conservative in that we limited our data to collections where we have confidence in the species identifications. We also concentrated on Mesoamerica as a biogeographic region because of the relatively high collection intensity for a tropical genus like *Psychotria*. Our predicted range sizes took into account many environmental variables; however, the inclusion of other types of data such as edaphic factors would likely strengthen the predictions. Furthermore, our study did not include data on species interactions, a dimension that is missing from most studies that use ecological niche modeling (Phillips et al. 2006). Clearly, biotic interactions can limit species' distributions, and the incorporation of maps of other species' presences and absences, if geographically accurate data could be amassed, could refine the estimates we make of potential geographic distributions. However, similar to our age estimates, these sources of error should not be biased in their placement or magnitude among species.

Other Factors Impacting Species Age and Range Size Relationships

Ultimately, the utility of species age as a predictor of range size rests on the assumption that various ecological and evolutionary processes (Gaston 1998) do not obscure the simple pattern predicted if species start with small range sizes, are prone to extinction, and transform their ranges at a relatively equal rate (e.g., Hubbell 2001, 2003; Hubbell and Lake 2003). A general positive age and area relationship may not be found if young species attain large geographic range sizes quickly or if old species maintain small geographic range sizes. For example, old species that once had large range sizes could decline in range size by failing to adapt to changing environmental or ecological conditions (Murray and Hose 2005). On the other hand, the process of speciation could generate young species that start their existence with large ranges. Because speciation is predicted to split range sizes under many models of geographic speciation, new species that are derived from ancestral species with large ranges have some probability of starting their existence with a large range size. This probability will relate to the nature of the geographic speciation event for a given species, specifically how asymmetrical it is (e.g., Waldron 2007). In clades where asymmetrical range splitting at speciation is commonplace, the set of new species would include species starting with both relatively large and small range sizes (Paul and Tonsor 2008). However, as demonstrated in the analysis of R_E/P_E and particularly for clade 1 species, species age clearly impacts range extents of these species. The results of our study, in conjunction with an analysis of age and area in Neotropical *Piper* species (Paul and Tonsor 2008), suggest that the impact of species age may be particularly noticeable in species that have limited dispersal abilities and relatively homogeneous habitats. Indeed, it was on the tropical island of Ceylon (now Sri Lanka) that Willis first made his observations leading to the age and area hypothesis. Despite observations of tropical flora providing inspiration for the hypothesis, *Psychotria* and *Piper* are the only two tropical plant genera in which the age and area hypothesis has been tested. Notably, both support Willis's conjecture.

Conclusions

In summary, species age can be a significant predictor of range size variation in plant species. Our results indicate that a time-for-dispersal effect may limit the extent, but not necessarily the occupancy, of species' potential ranges. Although range expansions can occur rapidly in some cases (e.g., Clark et al. 1998), our results demonstrate that time can be a limiting factor to dispersal, a result also found for forest plant species in Europe (Svenning et al. 2008). Time may be an important factor limiting the range sizes of many groups of species, particularly among taxa that have limited dispersal potential. We expect that the effects of species age on range size variation will be as clade specific as we found here and as has been demonstrated elsewhere (Webb and Gaston 2000). Future studies that integrate phylogenetic analyses, species distribution modeling, and ecological data will provide rich insight into the factors that drive the variation in abundance and distribution of species.

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