Trait evolution and the coexistence of a species swarm in the tropical forest understorey

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Summary

1. A small number of species-rich plant genera make a substantial contribution to the α diversity of tropical forests. These 'species swarms' (Gentry 1982) challenge a view of community assembly that maintains that niche overlap, and hence, the likelihood of competitive exclusion should increase with phylogenetic affinity. Related species may, however, occupy different microhabitats within a forest stand or, alternatively, differ ecologically in ways that allow them to coexist syntopically.

2. To explore the relationship between phylogenetic history and niche differentiation among sympatric, congeneric species, we performed phylogenetic analyses of microhabitat preferences, photosynthetic and hydraulic traits, and experimental responses to light and water availability for 20 species of *Psychotria* (Rubiaceae) from Barro Colorado Island (BCI), Panama.

3. The *Psychotria* present in small (3-m radius), circular plots were more closely related than expected by chance. Photosynthetic and hydraulic traits were both associated with species habitat distributions, but only hydraulic traits were conserved phylogenetically. Experimental responses to water availability were also conserved phylogenetically. Functional trait analyses revealed little or no evidence of niche partitioning within sites.

4. We conclude that *Psychotria* species' responses to both light and moisture availability determine their microhabitat distributions on BCI and that evolutionarily conserved hydraulic traits lead to phylogenetic clustering of co-occurring species.

5. *Synthesis*. The evolutionary conservation of hydraulic traits related to soil moisture tolerance largely explains phylogenetic clustering in the local assembly of the hyperdiverse genus *Psychotria*. We suggest that close relatives are unlikely to exclude one another from shared habitats because resource availability is determined largely by asymmetric competition with the overstorey, rather than by competition with neighbouring understorey plants. In light of the recent biogeographic admixture in central Panama, the phylogenetic niche conservatism exhibited by *Psychotria* on BCI raises the possibility of an association between local microhabitats and the ancestral climatic regimes under which major *Psychotria* lineages evolved before arriving in sympatry.

Key-words: Barro Colorado Island, community assembly, determinants of plant community diversity and structure, phylogenetic community structure, phylogenetic signal, *Psychotria*

Introduction

A handful of species-rich genera contribute disproportionately to the species diversity of woody plants in tropical forests. For example, the five largest of *c.* 500 woody plant genera comprise 22% of the species of trees and shrubs on Barro Colorado Island (BCI), Panama (Foster & Hubbell 1990). Gentry (1982, 1989) marvelled at the local species diversity and apparent ecological similarity within 'species swarms' of *Miconia* (Melastomataceae), *Piper* (Piperaceae), *Psychotria* (Rubiaceae), and

other understorey genera in southern Central America and northwestern South America, but the phenomenon is not limited to the understorey. A 1-ha plot in Ecuador harboured 22 species of canopy trees in the genus *Pouteria* (Sapotaceae), while just 0.16 ha contained the same number of species of *Inga* (Mimosoideae) (Valencia, Balslev & Mino 1994).

How large numbers of woody plant species coexist in the face of intense competition for resources remains a fundamental challenge to community ecology (Wright 2002; Silvertown 2004). All plants require CO_2, light, water, and a common set of nutrients, which seemingly limits the number of niche dimensions along which species can evolve to avoid

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competition (Silvertown 2004). Plants also compete for the services of mutualists, such as pollinators, seed dispersers, and mycorrhizal fungi, and for enemy-free space as they interact with pests and pathogens (apparent competition; Holt 1977). Classical ecological theory maintains that for competing species to coexist stably, they must occupy distinct niches, broadly defined by the way they interact with the abiotic environment and all other species (Gause 1934; Hutchinson 1959; MacArthur & Levins 1967). While niche differences with respect to light intensity, soil moisture and regeneration have been identified, they rarely explain the coexistence of more than a small fraction of the plant species in tropical forests (Wright 2002). What is more, coexisting species often must pass through habitat filters that select for physiological similarity (Weiher & Keddy 1995; Baraloto *et al.* 2012), further limiting the scope for differentiation among syntopic species, or those that co-occur in a habitat (Rivas 1964).

Locally diverse genera such as Gentry's (1982, 1989) species swarms further challenge our understanding of coexistence, since phylogenetically related species share recent common ancestry and therefore a recent ancestral niche. For closely related species to coexist stably, they must either have diverged from their ancestral niche in some important way that allows them to partition niche space syntopically or else have diverged with respect to traits that allow them to exploit distinct environments. Species differences in both of these niche dimensions may distinguish populations that are broadly sympatric (Rivas 1964) and thereby facilitate their coexistence. Do phylogenetic lineages tend to diversify over environmental gradients or retain habitat preferences over time? Which niche axes play a role in the coexistence of sympatric congeners? Community-level patterns of trait and phylogenetic structure depend on the answers to these questions.

If tropical species swarms behave similarly to temperate genera, three studies may provide particular insight. Closely related *Quercus* trees (Cavender-Bares *et al.* 2004) and *Ceanothus* shrubs (Ackerly, Schwilk & Webb 2006) were found to exploit distinct habitats defined by fire frequency and soil moisture and by temperature and elevation, respectively. In both of these cases and in a study of South African sedges (Slingsby & Verboom 2006), syntopic assemblages were composed of relatively distantly related species derived from separate early diverging clades within the genus, indicating evolutionary convergence of habitat preference and phylogenetic evenness (i.e. overdispersion sensu Cavender-Bares *et al.* 2004) of coexisting species.

Similar patterns might apply to Gentry's species swarms, with closely related species having diverged functionally to replace one another over fine-scale environmental gradients and more distantly related congeners having converged functionally to coexist syntopically. On the other hand, closely related species might coexist syntopically despite their functional similarity, if they occur in environments where the potential for competitive exclusion is limited (Hubbell 2001; Adler, HilleRisLambers & Levine 2007). This would result in phylogenetically clustered local communities. Phylogenetic clustering might also occur if species differences that do not

reflect habitat preferences are evolutionarily labile and effectively stabilize coexistence (Silvertown 2004; Adler, HilleRisLambers & Levine 2007; Kursar *et al.* 2009a). Examining the evolution of ecologically important traits and their distributions among sympatric congeners may thus help elucidate the processes that generate and maintain tree diversity in tropical forests.

In this study, we investigate the influence of trait evolution on the coexistence of 20 woody species in the genus *Psychotria* (Rubiaceae) on BCI, Panama. In addition to distributional and functional trait data, we take advantage of a factorial transplant experiment performed during a severe El Niño year (1993–94; previously unpubl. data) to investigate species' microhabitat niches and responses to potential environmental filters. Through a phylogenetic analysis of traits, habitat distributions, and experimental responses to light and moisture availability, we address the following questions: (i) Are species assemblages of *Psychotria* at small (3-m radius) spatial scales non-random with respect to phylogeny? (ii) Is there evidence of environmental filtering among the 20 congeneric *Psychotria* species with respect to light and moisture availability? (iii) Is there evidence that functional traits are evenly distributed among species with similar microhabitat preferences, such as might indicate within-site niche differences? (iv) Do those traits that are associated with microhabitat or within-site niche differences exhibit phylogenetic signal? Finally, we ask how the distributions and phylogeny of the *Psychotria* of BCI inform our understanding of the role of trait evolution in the diversification of the genus and coexistence in species-dense local communities.

Materials and methods

STUDY SITE

Barro Colorado Island (9°9′N, 79°51′W) has a tropical monsoon climate under the Köppen system of climatic classification and supports semi-deciduous tropical forest with a mature canopy height of 35 m. Mean monthly temperatures are 27 °C in April and 26 °C otherwise. Annual rainfall averages 2600 mm. A 4-month dry season begins in December or occasionally November and ends in April or occasionally May. Median rainfall is 84 mm over 90 days between 1 January and 31 March. Croat (1978), Windsor, Rand & Rand (1990) and Leigh (1999) provide further descriptions of BCI.

Unusually long and severe dry seasons are sometimes associated with El Niño events on BCI (Leigh *et al.* 1990). This was the case during the dry season of 1991–92 when just 71.7 mm of rain fell over 140 consecutive days. Gravimetric soil water content and plant water status were evaluated during this harsh dry season.

PSYCHOTRIA

Psychotria is globally one of the largest plant genera with some 1650 species distributed throughout the tropics and subtropics (Taylor 1996). The genus is comprised almost exclusively of shrubs and small trees of the forest understorey. Along with several other species-rich genera, *Psychotria* inspired Gentry (1982, 1989) to coin the term 'species swarm' to describe genera comprised of seemingly ecologically undifferentiated species contributing to high alpha diversity. Because

of the Andean-centred distribution of such genera, Gentry (1989) suggested that topographic heterogeneity associated with the Andean uplift may have caused their allopatric divergence (and subsequent remixing) without notable ecological differentiation. Sympatric *Psychotria* are indeed similar with regard to pollinators (Sakai & Wright 2008), seed dispersers (Poulin *et al.* 1999) and growth form. In this study, we more carefully examine microhabitat differences.

Psychotria are exceptionally abundant on BCI. Mean density summed over all *Psychotria* was 0.66 stems m^{-2} in this study (methods described below). Extrapolating from this figure, 15.9 km^2 BCI supports *c.* 10 000 000 *Psychotria* stems. BCI is home to 19 species in two well-defined subgenera, *Psychotria* subgenus *Psychotria* (nine species on BCI) and *Psychotria* subgenus *Heteropsychotria* (10 species on BCI), as well as *Carapichea ipecacuanha* (formerly *Psychotria ipecacuanha*). The two subgenera diverged *c.* 40 Ma (Paul *et al.* 2009).

MICROHABITAT DISTRIBUTIONS

All *Psychotria* stems were identified, measured (diameter at 5 and 20 cm heights), and tagged in 134 circular plots (3 m radius; 28.3 m^2 area) between 18 June and 9 August 1992. Plots were located 20 m to the south of permanent 100-m trail markers along a 6.2-km transect (62 plots) and arbitrarily along eight streams (52 plots) and in a seasonally inundated area (20 plots). Soils at the latter sites remain relatively moist through the dry season.

Moisture and light availability were determined for each of the 134 plots. Canopy photographs were used to calculate incident global radiation, and gravimetric soil moisture was measured during the final 7 weeks of the El Niño dry season. A canonical correspondence analysis (CCA) was performed using the R package 'VEGAN' (R Development Core Team 2006; Oksanen *et al.* 2009) to relate *Psychotria* species composition to the two environmental variables. Soils at 40-cm depth in the seasonal swamp were obviously wet late in the 1992 dry season, yet gravimetric soil water content was indistinguishable for plots in the swamp (0.242 ± 0.031; mean ± SD) and along the 6.2-km transect (0.255 ± 0.035). Consequently, the analysis was restricted to the 15 *Psychotria* species represented by a total of 20 or more stems in the 114 well-drained plots.

PHYSIOLOGICAL MEASUREMENTS

Photosynthetic properties

Leaf traits vary on a global axis thought to reflect strategies that extend from leaves that are long-lived and tolerant to leaves that are highly productive but unprotected and short-lived (Wright *et al.* 2004). We measured leaf respiration rates, light compensation points (LCP), quantum yields and light saturated photosynthetic rates (A_{max}) using an oxygen electrode (Hansatech, Norfolk, UK). Leaf absorptance was determined using an LI-1800 radiometer (Li-Cor, Lincoln, NE, USA).

Hydraulic traits

Tolerance of low leaf water potential is a strong determinant of drought performance and distributions among tropical woody plants (Kursar *et al.* 2009b), whereas stem conductivity exhibits a trade-off with susceptibility to xylem cavitation and hence drought performance (Markesteijn *et al.* 2011). Leaf water potentials (ψ) were measured in March 1992 with a portable pressure chamber (Model 1000; PMS Instruments, Corvallis, OR, USA) and a steady-state porometer

(Model 1600; Li-Cor), respectively. Pressure-volume curves were constructed to determine turgor-loss point water potentials (Koide & Schreiner 1992). Leaf-specific native stem conductivity (K_l) was assessed for 17 species in November 2010. Turgor-loss leaf water potential (ψ_t) and K_l were used in subsequent analyses. Specific leaf area (SLA) reflects a trade-off between thin leaves with high metabolic rates per unit mass, on the one hand, and thick leaves with enhanced nutrient and water-use efficiency on the other (Wright *et al.* 2004; Ackerly & Cornwell 2007) and exhibits a strong negative association with rainfall globally (Wright *et al.* 2004). Here, we consider SLA among hydraulic traits.

COMMON GARDEN EXPERIMENT

A factorial experiment conducted in 1993–94 assessed responses to light environment (recent tree fall gaps vs. shaded understorey) and dry-season moisture availability (irrigated vs. control) for 17 *Psychotria* species. Seedlings were germinated under high- and low-light conditions and were transplanted into 20 naturally occurring gaps and 20 arbitrarily chosen understorey sites, respectively, in square grids at 25-cm intervals. Ten randomly selected plots from each light environment were irrigated weekly with water from oligotrophic Gatun Lake. Survival and stem height were measured in April, August and December 1994. Because of the high rates of survival in the irrigated gap plots (see Table S3 in Supporting Information), we did not use a fully factorial calculation of performance in the experiment. Drought performance in shade ($P_{drought}$) was calculated as 1 minus the difference between the fraction surviving in control understorey plots and in irrigated understorey plots. Shade performance without irrigation (P_{shade}) was 1 minus the difference between survivorship in control understorey relative to control gap plots.

PHYLOGENETIC RECONSTRUCTION

The nuclear internal transcribed spacer region (ITS) and the chloroplast *psbA-trnH* spacer region were chosen for use as phylogenetic markers because of their variability and ease of amplification in the study species (laboratory methods provided in Appendix S1). After a partition homogeneity test conducted in PAUP* 4.10b (Swofford 2002) confirmed that the gene sequences could be combined for phylogenetic analysis (Farris *et al.* 1994), the ITS and *psbA-trnH* data sets were concatenated and analysed through 6 million MCMC generations in MRBAYES 3.1.2 (Huelsenbeck & Ronquist 2001) under a mixed model with independent estimation of parameters for the GTR + I model of DNA sequence evolution as selected by a likelihood ratio test implemented in MRMODELTEST 2.3 (Nylander 2004). The two-locus Bayesian consensus tree was pruned to include only those species representing the BCI species pool. This community phylogeny (Fig. 1) was used in subsequent analyses of community structure.

Phylogenetic signal in the evolution of physiological traits and responses to experimental treatments was evaluated using the R package 'PICANTE' (R Development Core Team 2006; Kembel *et al.* 2008), which calculates Blomberg's *K* statistic of phylogenetic signal using generalized least squares (Blomberg, Garland & Ives 2003). Because Blomberg's test loses power below about 20 taxa (Blomberg, Garland & Ives 2003), this test was corroborated by a Mantel test of the correlation between the phylogenetic distance matrix and the pairwise Euclidean distance matrix for each trait (implemented in R; R Development Core Team 2006).

Revell (2010) has shown that phylogenetic generalized least squares (PGLS) linear regression is unnecessary when the residual error of the
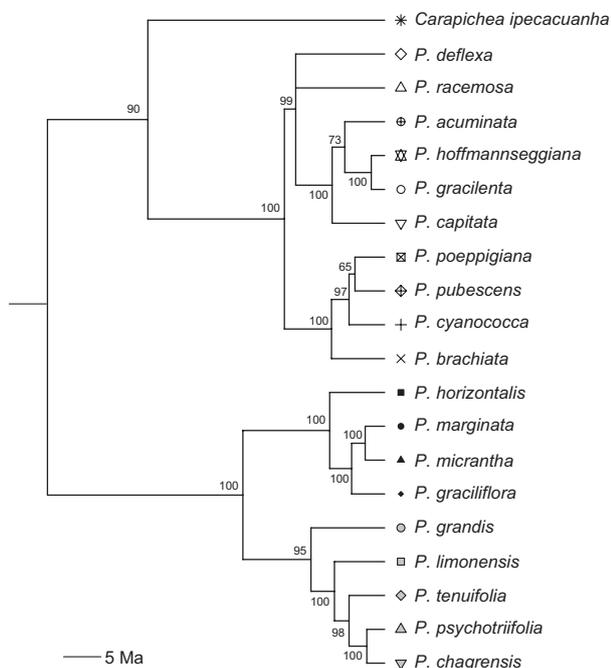
Fig. 1. Community Phylogeny of the Barro Colorado Island (BCI) *Psychotria*. A phylogram of 20 *Psychotria* representing the BCI community was pruned from a Bayesian consensus tree constructed from 25 *Psychotria* of central Panama as well as the outgroups *Coussarea curvigemmia* and *Faramea occidentalis*. Concatenated and partitioned nuclear internal transcribed spacer region and cp *psbA-trnH* spacer DNA sequence was analysed in MRBAYES 3.1.2 (Huelsenbeck & Ronquist 2001). The pruned community phylogeny shown here was used in subsequent analyses. Taxon bipartition labels represent Bayesian posterior probabilities. Species symbols relate to Figs 2, 4 and 5. Filled black and grey symbols indicate *Psychotria* subgenus *Psychotria*.

regression model does not exhibit phylogenetic signal, even if the independent variable does show signal, and furthermore that ordinary least squares (OLS) linear regression outperforms PGLS in those circumstances. Because residual errors did not exhibit phylogenetic signal in any of our regression models (Figs 4 and 5), we examined the relationships between species distributions, functional traits and experimental responses using OLS linear regression. Phylogenetic signal and linear regression analyses were conducted on species means.

COMMUNITY STRUCTURE

Phylogenetic community structure was measured by calculating the mean phylogenetic distance (MPD) and mean nearest-taxon distance (MNTD; Webb 2000) between *Psychotria* species surviving in experimental plots as well as those within natural communities sampled by the 104 census plots with two or more species present. MPD represents the mean phylogenetic branch length measured between every pairwise combination of species found in a local community or census plot, while MNTD includes only the branch lengths between each species and the most closely related species with which it co-occurs and thus represents community structure at a more terminal phylogenetic scale. The MPD and MNTD metrics were then calculated for 9999 null communities generated using an independent swap algorithm in which the number of species per community sample and the frequency of occurrence of each species across samples were held constant

while the particular species that co-occur in each sample was randomized (Gotelli & Entsminger 2003). Finally, we calculated two standardized effect size metrics. The net-relatedness index (NRI) and nearest-taxon index (NTI) equal the difference between observed and mean simulated values of MPD and MNTD, respectively, standardized by the standard deviation of phylogenetic distances in simulated null communities (Webb *et al.* 2002). Significance was tested using a Wilcoxon rank sum test.

To evaluate potential differences in phylogenetic structure between habitats, NRI and NTI were calculated for subsets of plots located in the seasonal swamp ($n = 17$ plots with ≥ 2 spp.) as well as for plots within the upper 30% quantile ($n = 32$) and lower 30% quantile ($n = 25$) of non-swamp plots with respect to soil moisture. All community phylogenetic metrics were calculated using 'PICANTE' (Kembel *et al.* 2008).

In addition to phylogenetic structure, we also measured four metrics of the functional trait structure of local communities relative to the BCI species pool following Kraft & Ackerly (2010). The range and variance of trait values are sensitive to trait clustering caused by habitat filtering (Kraft & Ackerly 2010). The standard deviation of neighbour (SDND) and nearest-neighbour (SDNN) trait distances can be used to test for a signature of limiting similarity, such as that caused by within-site niche differentiation or competitive exclusion, when compared with a null model of community assembly (Ricklefs & Travis 1980). Dividing SDND and SDNN by the trait range within each sample may allow these metrics to detect within-site trait evenness even against a background of habitat filtering (Kraft & Ackerly 2010). Standardized effect sizes were calculated by comparing trait range, variance, SDNNr and SDNDr to their distributions for 999 null communities assembled by choosing *Psychotria* species at random, but weighted by their occurrence frequency in the pool of census plots (Table 1).

Results

MICROHABITAT DISTRIBUTIONS

Microhabitat differences among species contributed to the near ubiquity of the genus on BCI (Fig. 2). There were 2553 stems of potential reproductive size (total area sampled = 0.38 ha) and at least one species was present in 128 of 134 small 3-m radius permanent plots (Fig. S1). Levels of habitat overlap and coexistence were exceptionally high, with ≥ 5 *Psychotria* species present in 12% of the plots (Fig. S1). Two plots contained nine species, whereas just six plots lacked *Psychotria*.

Most plots were in the shaded understorey. Median global radiation estimated from hemispheric canopy photographs was 0.64 ± 0.31 Mjoules m^{-2} day^{-1} (mean $\pm$ 1 SD), and global radiation exceeded 1 Mjoule m^{-2} day^{-1} in just 14% of the plots. Global radiation and gravimetric soil water content were uncorrelated ($R^2 = 0.018, n = 134$).

The first CCA axis was defined by gravimetric soil water content (canonical coefficients, axis 1: soil moisture 0.986, light intensity -0.159), and the second by global radiation (canonical coefficients, axis 2: soil moisture 0.167, light intensity 0.987). Eigenvalues were 0.219 and 0.077 and species-environment correlation coefficients were 0.610 and 0.412 for axes 1 and 2, respectively (Fig. 2).

Table 1. Trait community structure and phylogenetic signal. For each community structure metric, we report the mean standardized effect size (SES) ± 1 standard deviation. *P*-values < 0.05 are shown in boldface. Significance is indicated by asterisks (*P < 0.05; **P < 0.01). Traits are: maximum photosynthetic capacity (A_{max}), leaf respiration, light compensation point (LCP), leaf water potential at turgor loss (ψ_t), leaf-specific stem conductivity (K_l), and specific leaf area (SLA). Experimental shade and drought performance are included

	Trait clustering		Trait evenness		Phylogenetic signal	
	Range	Variance	SDNNr	SDNDr	*K*	Mantel
A_{max}	0.09 ± 0.99	**0.04 ± 0.99***	−0.04 ± 0.94	−0.02 ± 0.89	0.2332	−0.0271
Respiration	0.09 ± 0.89	0.03 ± 0.93	−0.01 ± 1.05	−0.10 ± 0.64	0.2494	−0.0242
LCP	**0.14 ± 0.92***	0.09 ± 0.91	−0.01 ± 0.85	0.05 ± 0.68	0.1771	−0.0070
P_{shade}	−	−	−	−	0.2388	0.0601
ψ_t	−0.13 ± 0.95	**−0.20 ± 0.85****	−0.04 ± 1.01	−0.05 ± 1.12	**0.4360***	0.1187
K_l	**−0.21 ± 0.78****	**−0.19 ± 0.74****	−0.16 ± 1.09	−0.07 ± 0.78	0.3261	**0.2823****
SLA	**−0.05 ± 0.93***	**−0.05 ± 1.00****	0.05 ± 0.88	**−0.07 ± 1.37****	0.4020	0.0640
$P_{drought}$	−	−	−	−	**0.3735***	0.1743

SDNDr, standard deviation of neighbor distances divided by range; SDNNr, standard deviation of nearest-neighbor distances divided by range.
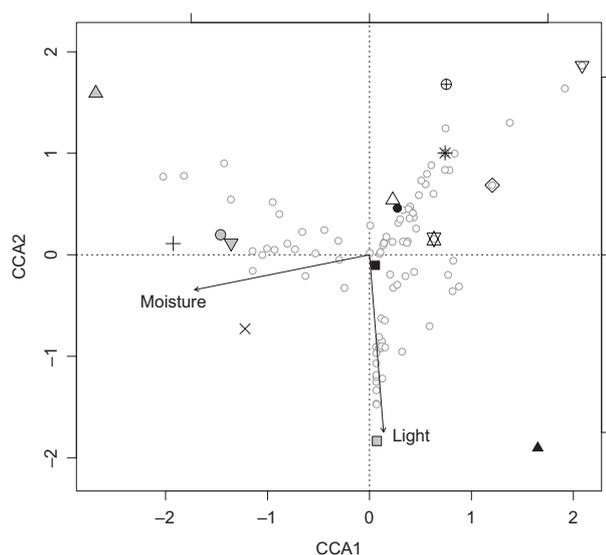

Fig. 2. Ordination diagram representing the distributions of 15 *Psychotria* species along gradients of moisture and light availability on Barro Colorado Island. Arrows represent environmental variables. Species symbols relate to Fig. 1. Filled black and grey symbols indicate *Psychotria* subgenus *Psychotria*.

The *Psychotria* include two widespread species (*P. horizontalis*, *P. marginata*) found in 94 and 61 of the 134 sites, respectively, one drought-tolerant species (*P. capitata*) whose distribution is restricted to the driest parts of BCI, five moisture-sensitive species (*P. brachiata*, *P. chagrensis*, *P. cyanococca*, *P. grandis*, and *P. psychotriifolia*) whose distributions are limited to moisture-retaining microsites, and two light-demanding species with greater abundance (*P. limonensis*) or largely limited (*P. micrantha*) to microsites with relatively large values of global radiation (Fig. 2). The two widespread species, *P. horizontalis* and *P. marginata*, are relatively closely related (Fig. 1). The five moisture-sensitive species comprise two sets of closely related taxa. Within the subgenus *Psychotria*, *P. chagrensis* and *P. psychotriifolia* are nearest relatives and

also share a close relationship with *P. grandis* (Fig. 1). Among the *Heteropsychotria*, *P. brachiata* and *P. cyanococca* are closely related, while their other closest relatives, *P. poeppigiana* and *P. pubescens*, are rare gap specialists and thus do not contribute strongly to the community pattern (Fig. 1). The two remaining light-demanding, gap-dependent species, *P. limonensis* and *P. micrantha*, are in the subgenus *Psychotria*, but are not closely related to one another (Figs 1 and 2).

PHYLOGENETIC STRUCTURE OF SYNTOPIC SPECIES

The phylogenetic structure of syntopic *Psychotria* was significantly more clustered than were null communities generated using an independent swap algorithm (Gotelli & Entsminger 2003), whether measured in terms of MPD (mean −NRI = −0.2273, *P* < 0.02) or MNTD (mean −NTI = −0.3358, *P* < 0.0001; Fig. 3).

Phylogenetic structure varied with soil moisture. Figure 3 displays the phylogenetic structure of all 134 plots relative to subsets of plots located in the seasonal swamp (*n* = 17 plots with ≥2 spp.) and the wettest and driest 30% of the remaining well-drained plots. Phylogenetic clustering was significant for plots located in the seasonal swamp (mean −NRI = −0.5819, *P* < 0.01) and in the wettest 30% of plots (mean −NRI = −0.4019, *P* < 0.005) but not for the driest 30% (mean −NRI = 0.0414, *P* = 0.69; Fig. 3a). The closest relative of each species in each plot was also more closely related than by chance in swamp (mean −NTI = −0.7559, *P* < 0.002) and wet (mean −NTI = −0.4764, *P* < 0.001) plots, but not significantly so in dry plots (mean −NTI = −0.1756, *P* = 0.27; all one-sided Wilcoxon rank sum tests; Fig. 3b).

In the common garden experiment, non-random mortality led to phylogenetic clustering when measured in terms of NRI (mean −NRI = −0.6687, *P* < 0.01; mean −NTI = 0.0015, *P* = 0.52, one-sided Wilcoxon rank sum test). The eight most strongly phylogenetically clustered plots were in the understorey; five were irrigated and three were control plots.
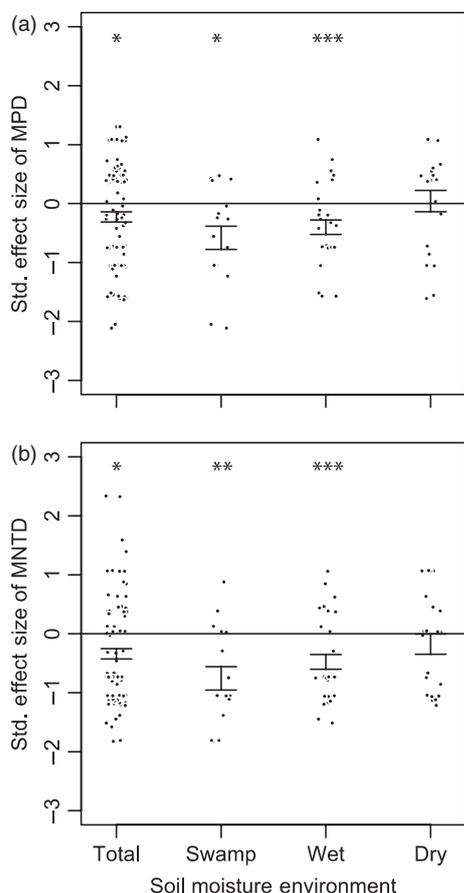
Fig. 3. Phylogenetic structure of Barro Colorado Island *Psychotria* communities sampled in 3-m radius census plots. Points represent the standardized effect size of the mean phylogenetic distance (MPD) or the mean nearest-taxon distance (MNTD). Bars indicate the mean ± 1 standard error. Values presented here have the opposite sign of Webb's (2000) net-relatedness index (NRI) and nearest-taxon index (NTI), such that positive values indicate phylogenetic evenness, and negative values indicate phylogenetic clustering. Deviation from the null was tested using one-sided Wilcoxon rank sum tests (*P < 0.02; **P < 0.01; ***P < 0.005). MPD and MNTD are shown with respect to all plots ($n = 104 \geq 2$ spp.) and subsets of plots located in the seasonal swamp ($n = 17$), and the wettest and driest 30% of the remaining well-drained plots. All analyses are limited to the 104 plots with two or more species.

PHOTOSYNTHETIC TRAITS, PERFORMANCE AND DISTRIBUTION

There was no evidence for phylogenetic signal among the photosynthetic traits or for performance in shade (P_{shade}) in the common garden experiment (Table 1). Both A_{max} and LCP exhibited significant trait clustering in the 134 small, circular plots with respect to one of the two metrics used, but no photosynthetic traits exhibited evidence of trait evenness (Table 1).

The positions of species along the light intensity gradient are represented by the perpendicular projection of each species onto the light intensity axis in the ordination. A_{max} showed a weak but not significant correlation with position along the light intensity gradient (Fig. 4a). In the common garden experiment, shade performance (P_{shade}) was significantly associated

with A_{max} (Fig. 4e). Despite demonstrating the greatest shade tolerance of all the species analysed, *P. limonensis* was surprisingly abundant in high-light environments (Fig. 4d; grey square). The relationship between P_{shade} and species positions on the light intensity gradient was significant when *P. limonensis* was excluded ($R^2 = 0.44$, $P < 0.02$), but insignificant otherwise (Fig. 4d).

HYDRAULIC TRAITS, PERFORMANCE AND DISTRIBUTION

One of the two metrics employed for each of the three hydraulic traits showed significant phylogenetic signal. In the common garden experiment, there was also significant phylogenetic signal for drought performance in understorey plots (Table 1).

The range and variance of traits observed for syntopic species within the 134 small, circular plots provided evidence of significant trait clustering for all three hydraulic traits (Table 1). Only SLA revealed significantly non-random SDNDr, suggesting that SLA of co-occurring species was not as similar as it might be (Kraft & Ackerly 2010). Neither ψ_t nor K_l exhibited trait evenness (Table 1).

The positions of species along the soil moisture gradient are represented by species' perpendicular projections onto the soil moisture axis in the ordination (Fig. 2). *Psychotria* species that tolerated lower ψ_t were associated with drier microhabitats (Fig. 5a), as were species with lower K_l (Fig. 5b). SLA, however, was not significantly related to species distributions relative to soil moisture. Despite the associations between ψ_t and K_l and species native distributions, none of the hydraulic traits exhibited a significant relationship with $P_{drought}$ as assessed in the common garden experiment. $P_{drought}$ was also unrelated to the position of a species along the soil moisture gradient (Fig. 5d).

Tolerance of low leaf and stem water potentials is thought to involve a trade-off with hydraulic efficiency, resulting in a negative correlation between drought performance and ψ_t or K_l (Kursar *et al.* 2009b; Markesteijn *et al.* 2010). However, the ratio of species mortality in control versus irrigation treatments in our experiment was not clearly related to either hydraulic traits (Fig. 5e–g) or soil moisture habitat distribution (Fig. 5d). Indeed, rather than suffering high mortality in control plots during the dry El Niño year, moisture-loving species exhibited high survivorship across treatments, while species found in dry microsites in the forest tended to die in the irrigated treatment (Table S3).

Discussion

The phylogenetic structure of communities, when combined with analyses of trait evolution and community trait composition, can reveal which aspects of the niche have differentiated over the course of a clade's evolutionary history. Several genera of temperate plants appear to have diversified with respect to traits that determine climatic and environmental tolerances, such that close relatives exploit distinct habitats and replace each other over environmental gradients (Cavender-Bares
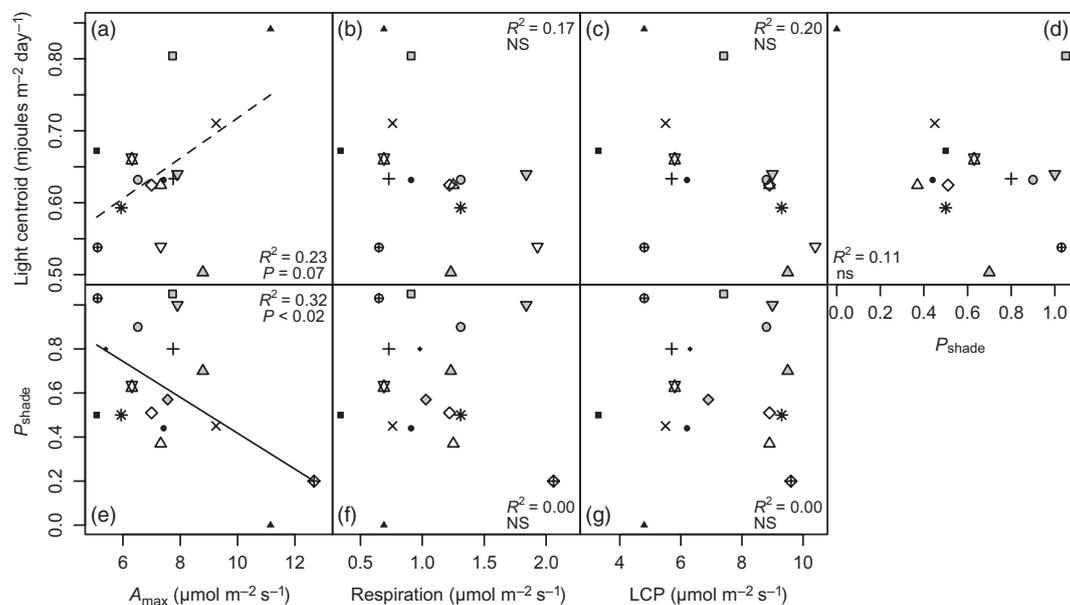
Fig. 4. Scatter plots of species distributions (panels a–d) and experimental responses to gap and understorey environments (panels e–g) versus photosynthetic traits. Significant and marginally significant linear regressions are represented by solid and dashed lines, respectively. R^2 values and significance levels are given for each pairwise relationship (ns = not significant). The relationship in panel d is significant with the exclusion of *Psychotria limonensis* ($R^2 = 0.44$, $P < 0.02$). Light centroid is the least squares estimate of each species weighted average distribution with respect to light intensity (Oksanen *et al.* 2009). Species symbols can be found in Fig. 1.
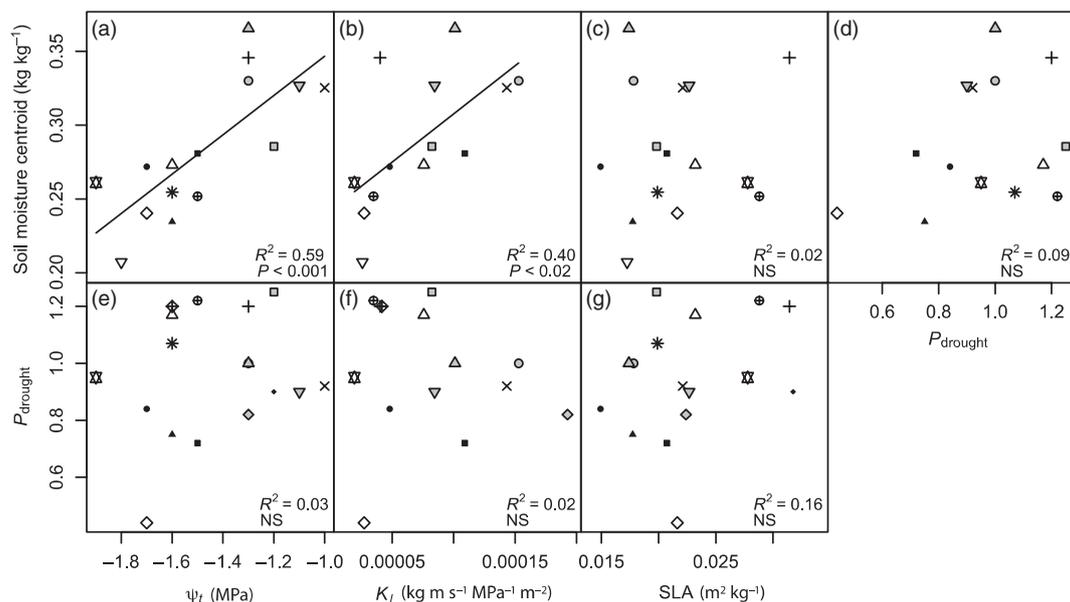

Fig. 5. Scatter plots of species distributions (panels a–d), and experimental responses to control and irrigation treatments (panels e–g) versus hydraulic traits. Significant linear regressions are represented by solid lines. R^2 and significance levels are given for each linear relationship (ns = not significant). Soil moisture centroid is the least squares estimate of each species weighted average distribution with respect to soil moisture (Oksanen *et al.* 2009). Species symbols can be found in Fig. 1.

et al. 2004; Ackerly, Schwilk & Webb 2006; Slingsby & Verboom 2006). Is there evidence that a similar history of evolutionary diversification with respect to understorey light and moisture environments might characterize *Psychotria* and thereby facilitate the maintenance of high local species richness?

Community assembly of the *Psychotria* was clearly influenced by light availability. Photosynthetic rate (A_{max}) was associated with species distributions relative to light intensity in the understorey (Fig. 4a) and exhibited lower than expected variance in census plots (Table 1). Furthermore, species responses to gap and understorey environments in the

common garden experiment were concordant with their photosynthetic capacities (A_{max}; Fig. 4e) and their microhabitat distributions with the exception of one species (Fig. 4d). The absence of phylogenetic signal among photosynthetic traits (Table 1) means that the contribution of habitat filtering along this axis to the observed community phylogenetic structure was probably minimal. In addition, these findings suggest that responses to light environments are evolutionarily labile among these understorey plants.

A consideration of species soil moisture distributions with respect to hydraulic traits supports a role for habitat filtering along the soil moisture environmental gradient. Leaf water potential at turgor loss (ψ_t) and leaf-specific stem conductivity (K_l) were both correlated with species distributions along the soil moisture gradient (Fig. 5a,b) and displayed evidence of trait clustering within census plots (Table 1). Unlike the photosynthetic traits measured, both ψ_t and K_l displayed phylogenetic signal (Table 1). The retention of phylogenetic signal among hydraulic traits and the influence of soil moisture environment on the degree of phylogenetic clustering (Fig. 3b) indicate that soil moisture environments are a strong abiotic filter for physiologically similar and closely related species of *Psychotria*.

Species' performances in experimental drought treatments were not consistent with habitat preferences in the forest (Fig. 5d) or with measured physiological traits (Fig. 5e–g). Despite the implementation of the experiment during a strong El Niño, the control, non-irrigated plots did not prove intolerable to species that, based on hydraulic traits and distributions, would be expected to suffer higher mortality in that treatment. Indeed, moisture-loving species exhibited high survivorship across treatments, while species found in dry microsites in the forest tended to die in the irrigated treatment, suggesting a correlation between moisture and pathogen load may have played a role (Givnish 1999). However, despite the ambiguity concerning the relationship between drought performance and hydraulic traits, drought performance itself exhibited phylogenetic signal (Table 1) and mortality in common garden plots resulted in phylogenetically clustered species assemblages. The common garden experiment showed that subjecting unbiased species assemblages of seedlings to different light and moisture environments was sufficient to generate phylogenetically clustered assemblages. On the other hand, the ambiguous relationship between $P_{drought}$ and either species hydraulic traits or habitat distributions suggests that seedling survival during a harsh El Niño year cannot be extrapolated to adult habitat distributions in the field.

The contribution of phylogeny to community ecology is illustrated by comparing the present study to those of Cavender-Bares *et al.* (2004) and Ackerly, Schwilk & Webb (2006). In all three studies, trait clustering and trait associations with abiotic habitats suggested that environmental filtering influenced species composition at the scales of analysis. Local communities of *Quercus* exhibited functional traits associated with local soil moisture and fire regimes (Cavender-Bares *et al.* 2004), while syntopic *Ceanothus* exhibited functional similarities related to temperature and elevation (Ackerly, Schwilk &

Webb 2006). *Psychotria* likewise showed evidence of environmental filtering mediated by both photosynthetic and hydraulic traits. Only by examining the three genera with respect to phylogeny does one come to the conclusion that the environmental gradients in question were important axes of relatively recent evolutionary differentiation among closely related oaks (Cavender-Bares *et al.* 2004) and *Ceanothus* shrubs (Ackerly, Schwilk & Webb 2006). In contrast, our results suggest that species distributions are phylogenetically conserved with respect to soil moisture, and therefore, that differentiation along this niche axis has not played a strong role in the recent diversification of the genus, despite the fact that soil moisture is an important determinant of species distributions in tropical forests generally (Engelbrecht *et al.* 2007) and with respect to *Psychotria* in particular (Figs 2 and 5a).

One Neotropical species swarm, the rain forest tree genus *Inga*, varies in its community phylogenetic structure in Panama and Peru (Kursar *et al.* 2009a). Yet in both locations, nearby individuals are significantly less similar with respect to secondary chemistry than by chance (Kursar *et al.* 2009a), suggesting that trophic interactions may distinguish close relatives in ways that allow them to coexist. The name *Psychotria* belies its potent secondary compounds (some species yield hallucinogenic, or psychotropic, compounds), yet it remains unclear whether co-occurring or closely related *Psychotria* differ in ways that limit the extent to which they share natural enemies.

ASSEMBLY OF TROPICAL FOREST UNDERSTOREYS

That the community structure of *Psychotria* understorey shrubs contrasts with that of genera in temperate forest and chaparral communities may not be incidental. Several features of tropical forest understorey plants may act to reduce resource competition. These include: (i) low population densities, (ii) dispersal limitation, and (iii) stochasticity imposed by sunflecks and canopy gaps.

Understorey plants, unlike canopy trees, may not compete with each other directly for light, water and soil nutrients if their densities are low enough that their crowns and root systems (i.e. zones of influence of resource use) do not overlap (Wright 2002; Paine *et al.* 2008; Svenning, Fabbro & Wright 2008). There is evidence that the low stem densities of understorey shrubs may be caused by asymmetrical competition with the overstorey and by herbivore pressure. Experimental trenching experiments that eliminate root competition with overstorey trees lead to increased growth rates in the understorey (Coomes & Grubb 1998, 2000; Lewis & Tanner 2000; Barberis & Tanner 2005; Tanner & Barberis 2007), and even shade-tolerant species typically perform better in full sunlight (Barberis & Tanner 2005; this study). Understorey plants have been found to respond with increased growth when protected from mammalian (Dirzo & Miranda 1991; Terborgh & Wright 1994) and insect (Sagers & Coley 1995) herbivores. In contrast, understorey removal and competition experiments have consistently failed to find a measurable effect on performance (Marquis, Young & Braker 1986; Brown & Whitmore 1992; Paine *et al.* 2008; Svenning, Fabbro & Wright 2008). The

growth of understorey plants is clearly limited by the availability of light and water. However, the limits on the availability of these resources imposed by other understorey plants pales in comparison with the burden imposed by the forest overstorey. From a resource perspective, membership in the understorey appears to be largely determined by environmental tolerance to understorey conditions rather than competitive trade-offs in resource utilization.

A species is said to be dispersal-limited if its propagules fail to arrive at suitable sites in sufficient numbers to become established (Nathan & Muller-Landau 2000). Seed-addition experiments and studies using seed traps on BCI have found dispersal limitation to be nearly ubiquitous for canopy trees (Hubbell *et al.* 1999; Wright *et al.* 2003; Svenning & Wright 2005; Muller-Landau *et al.* 2008) and it may be even more acute among understorey plants because of their reduced fecundity and their dependence on low density populations of understorey birds for seed dispersal (Givnish 1999). In addition to the effects of small size and limited physical resources on fecundity, the heterostylous *Psychotria* are all obligate outcrossing species. If the relatively small floral displays are not effective at attracting pollinators, then their fecundity may also be pollen limited (Sakai & Wright 2008). Fecundity and dispersal limitation can limit the potential for direct competitive interactions.

Chance variation in light is critical to the success of understorey plants. Sunflecks contribute from 32% to 65% of the daily carbon gain of understorey plants in closed canopy forests (Chazdon & Pearcy 1991). In addition, treefalls temporarily release understorey plants from light limitation by opening gaps in the forest canopy. The elevated resources available in such gaps may be critical to the reproductive success even of shade-tolerant understorey species (Levey 1988; Denslow *et al.* 1990; Dirzo *et al.* 1992; Schnitzer, Mascaro & Carson 2008). The chance, ephemeral nature of both sunflecks and treefall gaps imposes stochasticity on the success of understorey plants that may further mitigate against competitive exclusion.

In sum, the overstorey and herbivore suppression, stochasticity imposed by gaps and sunflecks, and dispersal limitation common to tropical forest understoreys may facilitate unstable coexistence by slowing the rate of competitive exclusion relative to random drift (Hubbell 2001) or regional assembly processes (Ricklefs 2004). These considerations may apply to a large proportion of tropical forest plant diversity. Nearly 70% of the free-standing woody plant species of central Panama attain a maximum height below that of the canopy (King, Wright & Connell 2006). While many of those species are substantially larger than *Psychotria*, they most likely face many of the same factors that attenuate competitive exclusion in the understorey.

BROADER BIOGEOGRAPHIC PERSPECTIVES

The Isthmus of Panama is a zone of biogeographic interchange wherein lineages from Mesoamerica, South America and the Caribbean contribute to local floras (Croat &

Busey 1975). Within the Isthmus, BCI is situated in the centre of a north–south precipitation gradient, which varies from < 2000 mm year^{-1} on the Pacific coast to > 3000 mm year^{-1} near the Caribbean (Pyke *et al.* 2001). This gradient influences tree species distributions (Engelbrecht *et al.* 2007) and results in greater species turnover (β diversity) in Central Panama than across much greater distances in Amazonia (Condit *et al.* 2002). BCI contains rain forest species that are generally restricted to the Caribbean slope, as well as dry forest species more characteristic of the Pacific coast (Pyke *et al.* 2001; Condit *et al.* 2002). Because of its location in the path of the Great American Biotic Interchange and its intermediate level of rainfall with microsite variation in soil moisture, BCI is a zone of historical and regional floristic admixture, both of which may contribute to the local pattern of community assembly.

If clades of *Psychotria* that originated in climatically different regions, such as wet and dry forest biomes, are slow to evolve away from the edaphic and soil moisture adaptations of their ancestors, then conserved physiological traits may influence the habitat preferences of members of the clade long after they migrate to new geographic localities. We hypothesize that environmental differences among regional biogeographic centres of speciation contribute to the phylogenetic signal observed in *Psychotria* habitat preferences and ultimately result in the observed phylogenetic clustering as members of the regional species pool filter into local assemblages according to phylogenetically conserved soil moisture niches. This hypothesis linking biogeographic origins and environmental filtering at the stand level can be tested with the aid of an ancestral area analysis (Ronquist 1997) across a more intensively sampled *Psychotria* phylogeny.

Phylogenetic niche conservatism has been found to characterize the assembly of continental and regional biotas (Wiens & Donoghue 2004; Donoghue 2008; Ricklefs & Renner 2012). Here, we show that niche conservatism may influence local community assembly as species filter into distinct microhabitats. Although competitive interactions are expected to be most severe between relatives with similar niches, the absence of resource competition among understorey dwellers described above may allow habitat preferences derived from shared biogeographic histories to be retained at fine spatial scales.

Conclusion

Psychotria is one of a handful of genera that contribute disproportionately to the species richness of tropical forests. Phylogenetic signal among physiological traits and along environmental gradients within these genera would suggest that niche evolution has occurred along trait axes not quantified in our study, such as defensive traits related to herbivory (Ehrlich & Raven 1964). The role of environmental filters and the reduced importance of resource competition in the understorey may have important implications for community assembly of Gentry's (1982, 1989) Neotropical 'species swarms', and even for canopy trees as they pass through life-history stages in the understorey.

Acknowledgements

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Supporting Information

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

Appendix S1. Phylogenetic methods.

Figure S1. Species density of *Psychotria* on BCI.

Table S1. Photosynthetic traits measured for 18 *Psychotria* species of BCI.

Table S2. Hydraulic traits measured for 20 BCI *Psychotria*.

Table S3. Survival in four factorial experimental treatments.

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