Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest

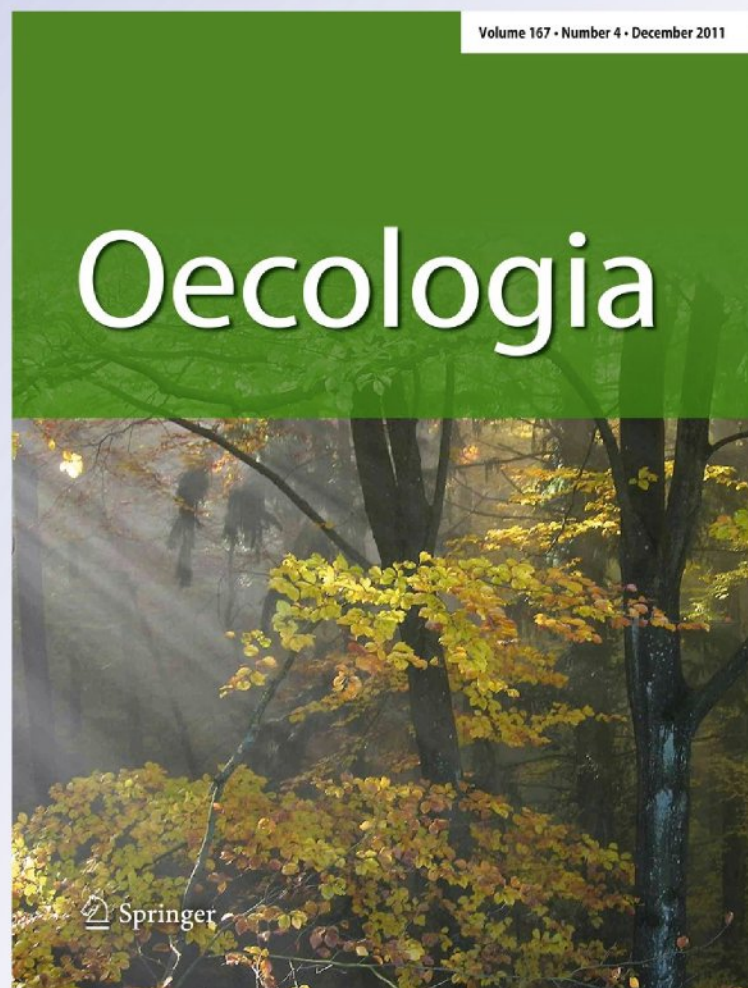## Kelly M. Andersen, Maria Jose Endara, Benjamin L. Turner & James W. Dalling

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Trait-based community assembly of understory palms along a soil nutrient gradient in a lower montane tropical forest

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Abstract Two opposing niche processes have been shown to shape the relationship between ecological traits and species distribution patterns: habitat filtering and competitive exclusion. Habitat filtering is expected to select for similar traits among coexisting species that share similar habitat conditions, whereas competitive exclusion is expected to limit the ecological similarity of coexisting species leading to trait differentiation. Here, we explore how functional traits vary among 19 understory palm species that differ in their distribution across a gradient of soil resource availability in lower montane forest in western Panama. We found evidence that habitat filtering influences species distribution patterns and shifts community-wide and intraspecific trait values. Differences in trait values among sites were more strongly related to soil nutrient availability than to variation in light or rainfall.

Soil nutrient availability explained a significant amount of variation in site mean trait values for 4 of 15 functional traits. Site mean values of leaf nitrogen and phosphorus increased 37 and 64%, respectively, leaf carbon:nitrogen decreased 38%, and specific leaf area increased 29% with increasing soil nutrient availability. For *Geonoma cuneata*, the only species occurring at all sites, leaf phosphorus increased 34% and nitrogen:phosphorus decreased 42% with increasing soil nutrients. In addition to among-site variation, most morphological and leaf nutrient traits differed among coexisting species within sites, suggesting these traits may be important for niche differentiation. Hence, a combination of habitat filtering due to turnover in species composition and intraspecific variation along a soil nutrient gradient and site-specific niche differentiation among co-occurring species influences understory palm community structure in this lower montane forest.

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Introduction

Tropical montane cloud forests are hotspots for diversity (Myers et al. 2000), yet suffer some of the highest rates of habitat conversion of any tropical ecosystem (Doumenge et al. 1995). In addition, tropical montane forests are expected to be impacted disproportionately by climate change as rising cloud-bases (Pounds et al. 1999; Foster 2001) and increasing nitrogen deposition in tropical latitudes directly affect ecosystem function (Foster 2001; Corre et al. 2010). The use of trait-based studies to explore the mechanisms underlying species distributions along natural environmental gradients can provide a means for

prediction of community-wide shifts with changing climate and nutrient regimes (Diaz and Cabido 1997; Lavorel and Garnier 2002; Sandel et al. 2010). Here, we examine plant functional traits and species distribution patterns in relation to soil nutrient, light, and rainfall gradients in a lower montane forest in western Panama.

Soil-based habitat associations can arise directly from a combination of morphological or physiological functional traits, or indirectly via the effects of herbivores on survivorship or growth (Fine et al. 2004; Palmiotto et al. 2004; Baltzer et al. 2005). Species specializing in low nutrient habitats share a suite of traits such as greater leaf lifespan and leaf toughness, and decreased foliar nutrient concentration, leaf area per unit mass (specific leaf area, SLA), photosynthetic potential and respiration rates (Chapin 1980; Chapin et al. 1993; Aerts and Chapin 2000). Collectively, these traits enhance resource use efficiency by increasing carbon gain per unit of nutrient uptake, which may be advantageous for plants growing on low nutrient soils. In contrast, plants possessing traits that maximize growth may have a competitive advantage on high nutrient soils (Chapin 1980; Aerts and Chapin 2000). Differences in traits related to resource use and acquisition among species may, therefore, influence community composition along soil nutrient gradients.

A major advantage of trait-based approaches to community ecology over traditional species-based approaches is that species and ecosystem functional roles are highlighted, offering insight on plant strategies across environmental gradients (Diaz and Cabido 1997; Lavorel and Garnier 2002; McGill et al. 2006). Trait-based approaches have linked community structure and ecosystem function along various resource gradients (Reich et al. 2003), particularly light (Poorter 1999; Poorter and Bongers 2006) and water (Wright et al. 2001; Engelbrecht et al. 2007; Sandel et al. 2010) and to lesser extent soil nutrient (Wright et al. 2001; Cavender-Bares et al. 2004) gradients. Furthermore, the examination of leaf functional traits along resource gradients has led to hypotheses regarding plant strategies on local to global scales (Reich et al. 2003; Lavorel and Garnier 2002) and to insights into processes generating community structure (Keddy 1992; Kraft et al. 2008; Ackerly and Cornwell 2007).

Recent trait-based assessments of plant communities have identified two levels of niche processes influencing community structure: (1) 'habitat' or environmental filtering, whereby convergent trait values are expected for co-occurring species due to environmental trait selection, and (2) niche differentiation, whereby divergent trait values are expected due to interspecific competition among co-occurring species (Cavender-Bares et al. 2004; Ackerly and Cornwell 2007; Kraft et al. 2008). While these two niche processes represent opposing constraints on community structure, they can also act simultaneously (Weiher et al.

1998; Kraft et al. 2008; Cornwell and Ackerly 2010). For example, SLA, a key plant functional trait, has been found to differ among environmentally defined habitats. At the same time, SLA values within habitats have been found to be more evenly dispersed, or divergent, than expected from null models in a variety of ecosystems (Kraft et al. 2008; Cornwell and Ackerly 2009; Jung et al. 2010). Thus, multiple processes may frequently shape trait distributions in diverse plant communities.

Habitat filtering can lead to changes in trait composition along environmental gradients as a result of either turnover in species composition or differences in species abundance (Keddy 1992; Cornwell and Ackerly 2009; Sandel et al. 2010) or intraspecific variation due to plasticity or genetic variation (Cornwell and Ackerly 2009; Hulshof and Swenson 2010; Jung et al. 2010). Whereas most trait-based studies focus on species mean trait values, recent work has incorporated intraspecific variation to trait-based frameworks, adding a greater power to detect trait–environment linkages (Cornwell and Ackerly 2009; Hulshof and Swenson 2010; Jung et al. 2010). Furthermore, the incorporation of intraspecific variation allows a mechanistic approach to predicting species losses due to environmental change and its impact on ecosystem function (Hooper et al. 2005; Jung et al. 2010).

We used a trait-based approach to examine community structure of understory palms in a lower montane tropical forest in Panama. Palms (Arecaceae) are a group of plants common in tropical forests that can show morphological, phenological and genetic divergences among closely related species along resource gradients (Henderson et al. 1995; Svenning 2001; Savolainen et al. 2006). The lower montane forests examined here are a hotspot of diversity for understory palms, which comprise a major component of the understory and have the potential to alter regeneration patterns of woody seedlings (Farris-Lopez et al. 2004; Harms et al. 2004; Wang and Augspurger 2004). In a previous study, understory palm species composition was related to soil nutrients, particularly available nitrogen and cations (Andersen et al. 2010a). Here, we expand on that study to examine community assembly from a trait-based perspective to gain insight on the mechanisms influencing understory palm community structure. We were interested in examining the extent to which trait variation was related to (1) habitat filtering (shifts in site mean trait values) and (2) niche differentiation (within-site variation among species). In addition, we examined the extent to which (3) species turnover and (4) trait plasticity (within-species variation among sites) were related to shifts in trait values along environmental gradients. We measured a series of morphological, physiological and biochemical traits to identify key functional traits related to palm community structure across soil, light, and rainfall gradients.

Materials and methods

Study site and species

The study was conducted in the Fortuna and adjacent Palo Seco Forest Reserves located along the Continental Divide in western Panama. These forests are classified as lower montane forests in the Holdridge life zone system and range from 700 to 1,500 m a.s.l. A network of forest plots has been established across the reserves to assess community composition, forest growth and dynamics in relation to soil type, anthropogenic nitrogen deposition, and climate (Dalling, unpublished; Corre et al. 2010). Three contrasting soil types occur in the study area and are associated with differing plant communities ranging from *Colpothrinax* (Arecaceae)- and *Oreomunnea* (Juglandaceae)-dominated stands on rhyolitic soil to mixed species stands on andesitic soils to mixed *Quercus* (Fagaceae), Lauraceae, and Sapotaceae stands on dacitic soils (Dalling, unpublished). Nutrient availability increases from soils formed on rhyolite, characterized by an organic surface horizon and low nutrient availability, to soils formed on andesite, characterized by mineral soils of intermediate nutrient availability, to soils formed on porphyritic dacite, characterized by an organic surface horizon and high nutrient availability (Andersen et al. 2010a; Table 1). Note that dacite replaces the previous granodiorite in Andersen et al. (2010a), following a more detailed geological investigation of the area. Annual rainfall from 2007 to 2009 ranged from 4 to nearly 12 m, with up to 3 months with <100 mm of rain during the dry season (Andersen et al. 2010a; Table 1). Mean annual temperature ranges from 19 to 22°C across the reserves (Cavelier et al. 1996).

Vegetation and environmental survey data

Floristic and environmental surveys were conducted in a subset of the 1-ha plots included in Andersen et al. (2010a), in which understory palm species and environmental variables were surveyed as part of parallel studies (Andersen 2009; Andersen et al. 2010a). Briefly, all understory palms were identified and red:far red (R:FR), canopy openness, and soil nutrient availability were measured every 20 m along three parallel 100-m transects spaced 30 m apart within five 1-ha plots. Palms were a major component of the understory, ranging from 7 to 14 species ha^{-1} and 1,700–20,500 individuals ha^{-1} in the plot included here (Andersen et al. 2010a). Soil inorganic nitrogen was extracted in situ with 2M KCl and analyzed by automated colorimetry on a Lachat QuikChem 8500 flow injection analyzer (Hach, Loveland, CO, USA). Soil cations and phosphorus were extracted with Mehlich-3 solution and analyzed by inductively-coupled plasma (ICP) optical-emission spectrometry on an Optima 2100

spectrometer (Perkin Elmer, Shelton, CT, USA). Soil moisture was measured bi-monthly from February 2006 through September 2007 in areas along the perimeter of the 1-ha plots as part of separate seedling transplant experiments (Andersen 2009). Volumetric soil moisture was determined as the amount of water per unit volume dry soil calculated from soil bulk density and gravimetric soil water content measurements.

Measurement of functional traits

In September 2006 (wet season), we conducted a survey of morphological and physiological traits of adult palms occurring naturally in the five 1-ha plots to examine variation in leaf functional traits. At each site, we chose 3–5 individuals of each species present to measure morphological, biochemical and physiological traits. Individuals were selected along a central transect within a plot and individuals of the same species were at least 10 m apart. A total of 19 species were sampled in this study (Table 2). Species distributions and abundances differed among the sites, so the number of species and individuals per species varied among the sites. Some species occurred at multiple sites and on multiple soil types; however, species abundances were edaphically aggregated across the sites (Andersen et al. 2010a).

We measured photosynthetic rate (A_{max}; μmol m^{-2} s^{-1}), stomatal conductance (g_s; mmol m^{-2} s^{-1}), transpiration rate (E; mmol m^{-2} s^{-1}) and dark respiration rate (R_d; μmol m^{-2} s^{-1}) using a portable gas exchange system (LI-6400; Li-Cor). Maximum photosynthetic rate was measured at 400 μmol m^{-2} s^{-1} on the youngest, fully expanded leaf of adult individuals in the field. Previous gas exchange measurements indicated that maximum photosynthetic rates were achieved at 400 μmol m^{-2} s^{-1} (Andersen 2009). The environment within the leaf cuvette was maintained at conditions similar to the ambient environment (ca. 75% RH, 20–25°C, and 400 ppm CO_2). We measured specific leaf area (SLA; cm^{-2} g^{-1}) from dried leaf discs of known area, the number of leaves per plant, the rachis length, and maximum leaf height (vertical distance from the ground). Leaf height was a better indicator than stem height of the leaf-level light availability of the plant since many species had decumbent or acaulescent stems, some with long petioles and leaves.

Gas exchange leaves were collected, dried at 60°C and ground to a fine powder using a ball mill. Nutrient analyses were conducted in the Soils Laboratory of the Smithsonian Tropical Research Institute, Panama. Foliar P concentration was determined by ignition at 550°C and extraction in 1 M H_2SO_4, with P detected by molybdate colorimetry using a flow injection analyzer (Latchat QuikChem 8500; Hach). Foliar nitrogen (N) and carbon (C) concentrations and stable

Table 1 Environmental characteristics of five sites occurring on three soil types across a nutrient availability gradient at the Fortuna Reserve, western Panama (data from Andersen et al. 2010a)

Environmental variables	Rhyolite		Andesite		Dacite
	Low nutrient		Intermediate nutrient		High nutrient
	Chorro	Honda	Samudio	Palo Seco	Hornito
Soil variables					
Inorganic nitrogen ($\mu g\ cm^{-3}$)	0.63	3.40	1.42	2.90	4.52
P ($\mu g\ cm^{-3}$)	2.74	1.70	3.67	3.91	10.92
Soil pH	3.91	4.63	5.06	5.08	5.76
Nitrification rate ($\mu g\ N\ cm^{-3}\ day^{-1}$)	0.00	−0.03	0.10	0.29	0.12
$NH_4:NO_3$	5.47	4.65	7.09	10.30	10.08
Soil bulk density ($g\ cm^{-3}$)	0.08	0.11	0.37	0.45	0.39
Rainfall variables					
Mean annual rainfall (m)	4.76	8.98	4.93	6.82	5.79
Mean monthly dry season rainfall (January–April; mm)	291	338	176	434	187
Light variables					
Red:far red	0.51	0.34	0.53	0.27	0.26
Canopy openness (%)	6.32	5.77	6.27	4.85	5.31
Principal component axes values					
Soil PCA 1	−2.15	−1.49	−0.08	1.47	2.25
Soil PCA 2	0.82	−1.34	0.35	0.77	−0.60
Soil PCA 3	0.51	−0.51	0.17	−0.92	0.76
Light PCA	1.37	−0.96	1.44	−1.09	−0.76
Rainfall PCA	−0.44	1.10	−1.38	1.56	−0.84

Soil PCA 1 is related to $NH_4:NO_3$ and pH, *Soil PCA 2* is related to nitrification rates and negatively related to 2M KCl extractable inorganic N, and *Soil PCA 3* is related to Mehlich-3 extractable P, *Light PCA* values are a combination of canopy openness and R:FR values, and *Rainfall PCA* values are a combination of annual precipitation and total dry season (January–April) precipitation data for 2007–2009

isotope ratios were determined using an elemental analyzer (Flash HT) with a continuous flow interface (ConFlo III) and a Delta-V Advantage isotope ratio mass spectrometer (CF-IRMS; Thermo Scientific, Bremen, Germany). The $\delta^{15}N$ ratio of plant leaves generally represents the $\delta^{15}N$ ratio of the soil source the plant takes up, with nitrate having a lower $\delta^{15}N$ ratio than ammonium in most cases (Hogberg 1997; but see Houlton 2007). Carbon isotope ratios have been used to represent integrated water-use efficiency over the leaf lifespan (Farquhar et al. 1989; Baltzer et al. 2005; Cernusak et al. 2007). Leaf $\delta^{13}C$ ratios arise from differences in the diffusivity of ^{12}C and ^{13}C in air and through the stomatal pathway, as well as from the enzymatic discrimination of the isotopes. Plants that use water more efficiently exhibit less negative $\delta^{13}C$ ratios (Farquhar et al. 1989; Baltzer et al. 2005; Cernusak et al. 2007). Instantaneous water use efficiency (WUE) was calculated from $A_{max\ (area)}$ and transpiration according to Lambers et al. (1998): WUE = $A_{max\ (area)}/E$; where $A_{max\ (area)}$ = area-based photosynthetic rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and E = transpiration rate (mol $H_2O\ m^{-2}\ s^{-1}$). Water use efficiency represents the μmol C gained per mole water lost. Photosynthetic nutrient use efficiency (PNUE) was calculated from $A_{max\ (area)}$ and area-based foliar nutrient concentrations, following the calculations of Lambers et al. (1998): PNUE = $A_{max\ (area)}/N_{area}$; where $A_{max\ (area)}$ = area-based photosynthetic rate ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$) and N_{area} = area-based leaf N content ($g\ N\ cm^{-2}$). Photosynthetic N use efficiency quantifies the amount of C gained per unit N invested in leaf material.

Data analysis

Linking species trait values and distribution patterns

To link shifts in species trait values with distribution patterns across the study area, we used the species abundance and environmental data from Andersen et al. (2010a) for the five 1-ha plots examined here to conduct a constrained correspondence analysis (CCA). A previous analysis using non-metric multidimensional scaling ordination to examine the palm community structure found that soil nutrients were related to shifts in species composition among the sites (Andersen et al. 2010a, b). Here, we were interested in defining species habitat associations as peak abundance constrained by environmental variables, and examining

Table 2 Understory palm species and sample sizes (*n*) for functional trait measurements in five 1-ha plots in the Fortuna Forest Reserve, western Panama

Genus	Species	Species code	Chorro	Honda	Samudio	Palo Seco	Hornito	*n*
Rhyolitic species								
Chamaedorea	*palmeriana* Hodel and Uhl	CPA	2	1	3	–	–	6
Chamaedorea	*recurvata* Hodel[a]	CRE	3	1	–	–	–	4
Geonoma	*hugonis* Grayum and de Nevers[b]	GG	3	4	2	–	1	10
Geonoma	*lehmannii* subsp. *corrugata* Henderson[c]	GS	3	2	–	–	–	5
Prestoea	*longepetiolata* var. *roseospadix* L.H. Bailey	PL	1	–	–	–	–	1
Andesitic species								
Chamaedorea	*deckeriana* (Klotzsch) Hemsl.	CD	–	–	–	5	–	5
Chamaedorea	*pinnatifrons* (Jacq.) Oerst.	CPI	2	–	2	3	3	10
Chamaedorea	*robertii* Hodel and Uhl	CRO	–	2	3	2	–	7
Chamaedorea	*scheryi* L.H. Bailey	CSC	–	–	2	2	–	4
Chamaedorea	*sullivaniorum* Hodel and Uhl	CSU	–	–	–	1	–	1
Chamaedorea	*tepejilote* Liebm.	CT	–	–	–	2	–	2
Calyptrogyne	*panamensis* var. occidentalis Henderson[d]	CAG	–	2	2	2	–	6
Geonoma	*cuneata* subsp. *cuneata* H. Wendl. ex Spruce	GCU	2	3	2	3	4	14
Dacitic species								
Chamaedorea	*costaricana* Oerst.	CC	–	–	–	–	3	3
Chamaedorea	*microphylla* H. Wendl.	CM	–	–	–	–	1	1
Chamaedorea	sp 1	CSP	–	–	–	–	4	4
Chamaedorea	*woodsoniana* L.H. Bailey	CW	–	–	–	1	1	2
Geonoma	*jussieuana* Mart.	GJ	–	–	–	–	1	1
Geonoma	*undata* Klotzsch	GU	–	–	–	–	3	3
		Total	16	15	16	21	21	89

Nomenclature follows Henderson et al. (1995) unless otherwise noted. Species are grouped by soil association following Andersen et al. (2010a)

[a] Hodel (1995)

[b] de Nevers and Grayum (1998)

[c] Henderson (2011)

[d] Henderson (2005)

how species mean trait values shifted with distribution along the environmental gradient. Two sites on rhyolitic tuff, two sites on andesite, and one site on dacite were included (Table 1). Species abundances were log-transformed prior to analysis. To reduce the number of environmental parameters included in the full CCA model, three separate principal component analyses (PCA) were conducted on log-transformed light (canopy openness and R:FR), rainfall (mean annual and total dry season), and soil variables (available phosphate and inorganic nitrogen concentrations, pH, nitrification and $NH_4:NO_3$). These soil variables were selected as they were either highly correlated with other soil variables or represented independent soil gradients. We used an automated stepwise model building procedure to select environmental PCA axes to retain in the final CCA model. Permutation tests (using 9,999 permutations) were used to assess significance of the final model and the parameters retained in the model. The

CCA model, therefore, examines the variation in species abundances among the sites as a function of the environmental variables.

To test for habitat filtering, we used linear regression models to compare log_{10}-transformed species mean trait values to their distribution patterns along the soil nutrient gradient, as determined by CCA scores for axis 1 values. Species mean trait values were calculated using all values for a given species, regardless of site. In addition, we conducted a PCA of the species mean trait values (log_{10}-transformed) to examine the correlation between the extracted trait PCA axis 1 scores and species CCA scores. A significant relationship between single and multivariate (trait PCA axis 1) trait values and CCA scores suggested that species turnover was to habitat filtering along the soil nutrient gradient was important in structuring understory palm communities across the sites examined.

Shifts in functional traits along environmental gradients

We conducted correlation tests and linear regression to examine trait divergence along environmental gradients. We used the multivariate environmental variables from the separate PCA analyses for soil, light and rainfall data as described above. Population mean trait values were calculated as the site-specific mean trait value of a given species and were used to calculate the community-wide mean trait values (equivalent to site means) for the regression models. We also examined the relative strength and direction of the correlation between the environmental PCA variables and site mean trait values.

Within species variation in functional traits in Geonoma cuneata

Geonoma cuneata was the only species that occurred at all sites. To examine within-species trait plasticity in *G. cuneata* among the sites, we conducted a one-way ANOVA, with site as a fixed factor. For traits that significantly differed among sites for *G. cuneata*, we used linear regression models to detect relationships between trait values and environmental gradients across the sites.

Within-community variation in functional traits

To examine within-community variation; we used linear mixed models with species as a fixed factor. For each trait, sites were modeled separately to test for differences among co-occurring species. If niche differentiation is important for species coexistence at a given site, we expected that trait values would be significantly different among co-existing species. Alternatively, if environmental filtering alone structures palm communities, we expected that trait values would be similar among co-existing species, but differ among sites. All statistical analyses were conducted in R 2.11.1 (R Development Core Team 2010).

Results

Linking species trait values and distribution patterns

The CCA model explained 65% ($P < 0.05$) of the variation in species abundances among the five 1-ha plots and was constrained by soil PCA 1 and soil PCA 3 (Fig. 1). Soil pH and NH_4:NO_3 loaded positively on soil PCA 1, accounting for >70% of the variation in the soil properties included in the analysis. Soil PCA 1 was positively correlated with all soil nutrients, and represents the major soil nutrient gradient among the sites (Table S1). KCl extractable inorganic nitrogen content loaded negatively on soil PCA 2 and

accounted for 18% of the variation in soil properties among sites. Mehlich 3-extractable soil P loaded positively on soil PCA 3 and accounted for 10% of the variation in soil properties among sites. The first CCA axis explained the majority of the variation in species distributions (42%, $P < 0.05$) and was related positively to soil PCA 1 ($P < 0.05$). The second CCA axis explained an additional 24% of the variation in species distributions ($P < 0.30$) and was related positively to soil PCA 3 ($P < 0.15$).

Species mean values for leaf N, SLA, $A_{max(mass)}$, rachis length, leaf $\delta^{15}N$, PNUE, leaf P were significantly and positively related to species scores for the first axis of the CCA ordination (Fig. 2a–g). Species mean leaf C:N ratio was significantly and negatively related with CCA1 (Fig. 2h). In addition, the first axis of the species mean trait values PCA was positively related to CCA 1 (Fig. 2i). Species trait PCA 1 represented a combination of leaf N, P, and C:N, $A_{max(mass)}$, SLA, rachis length, and number of leaves, accounting for 34% of the variation among species. Species WUE was the only trait correlated with the second axis of the CCA ordination (Pearson's $r = 0.73$, $P < 0.001$).

Community-wide variation in functional traits along resource gradients

Site mean trait values, calculated from the population mean of the species occurring at that site, shifted with at least one environmental parameter for most traits. Soil PCA 1 was the most important environmental variable related to changes in
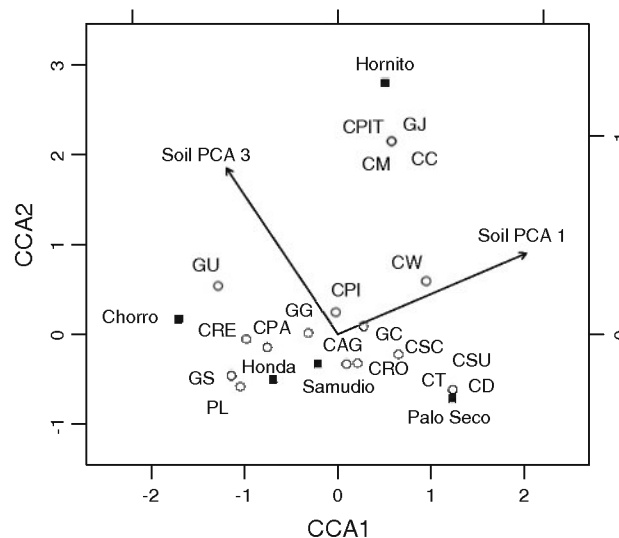

Fig. 1 Canonical correspondence analysis (CCA) of species abundances in five 1-ha plots in western Panama. The CCA ordination was constrained by two soil principal component axes related to NH_4:NO_3 and pH (*Soil PCA 1*) and soil P (*Soil PCA 3*). *CCA 1* explained 42% ($P < 0.05$) and *CCA 2* explained 24% ($P > 0.1$) of the variation in species abundances
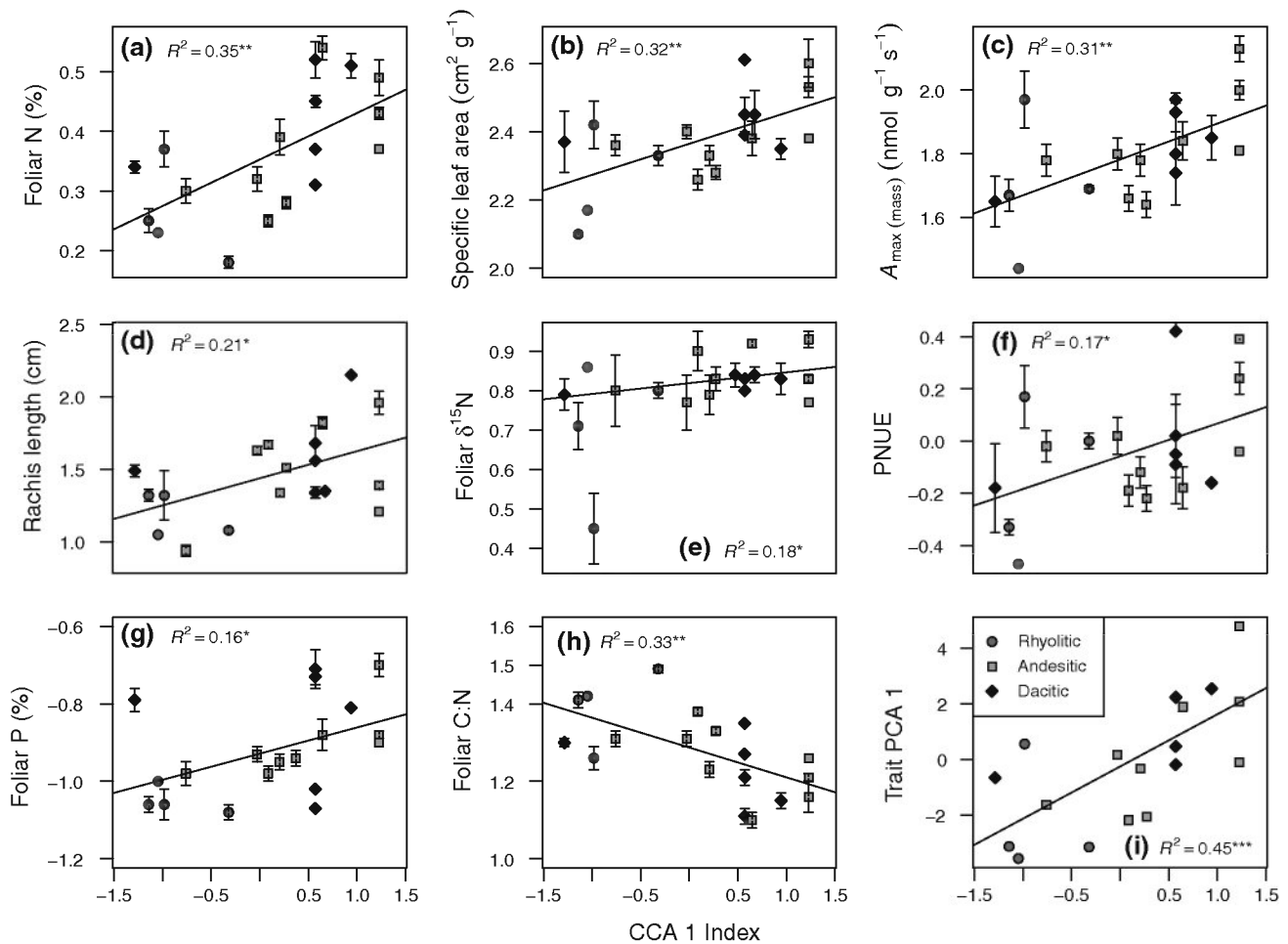
Fig. 2 Correlation between species mean leaf trait values (±SE) and abundance-weighted distribution (based on CCA axis 1 scores) along a soil nutrient gradient for five 1 ha plots in the lower montane forests of the Fortuna Reserve, western Panama. *Symbols* represent mean trait values ($n = 1$–14) for 19 understory palm species and are *shaded* by habitat association based on soil type. Log_{10} *y*-axes for all *panels*. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$

mean trait values (Table S2). Foliar N, P, and SLA increased with soil PCA 1, whereas foliar C:N decreased with soil PCA 1 (Fig. 3). Area-based photosynthetic rates were positively related to soil PCA 2 ($R^2 = 0.82$, $P < 0.05$). Photosynthetic nutrient use efficiency increased ($R^2 = 0.77$, $P < 0.05$) and number of leaves decreased ($R^2 = 0.93$, $P < 0.001$) with soil PCA 3. Leaf N:P ($R^2 = 0.74$, $P < 0.05$) and $\delta^{13}C$ values ($R^2 = 0.83$, $P < 0.05$) increased with increasing light availability (light PCA 1). There were no shifts in site-mean leaf $\delta^{15}N$, $A_{max(mass)}$, g_s, WUE, rachis length or leaf height related to any environmental variables and no site mean trait values were related to the rainfall PCA (Table S2).

### Within species variation in functional traits in *G. cuneata*

Six out of the 15 functional traits measured varied significantly among sites for *G. cuneata*, the only species

occurring at all sites examined (Table S3). Leaf P (%) increased ($R^2 = 0.96$, $P < 0.01$) and leaf N:P decreased with increasing soil PCA 1 values ($R^2 = 0.99$, $P < 0.01$; Fig. 4) and were the only trait variables shifting with soil PCA1. However, the remaining four trait variables were correlated with related soil and climate variables. Rachis length decreased with increasing KCl extractable soil N values ($R^2 = 0.68$, $P < 0.05$; Fig. 4a) and leaf $\delta^{15}N$ values were positively related to soil nitrification rates ($R^2 = 0.79$, $P < 0.05$; Fig. 4c). Water use efficiency decreased with increasing total dry season rainfall ($R^2 = 0.76$, $P < 0.05$; Fig. 4b) and g_s increased with increasing dry season soil water content ($R^2 = 0.84$, $P < 0.05$; Fig. 4d).

Within-community variation in functional traits

Differences in species population mean trait values within a given site were consistent with niche differentiation

Fig. 3 Shifts in leaf traits with changes in soil nutrient status of five sites and within-community trait variation. *Symbols* represent species means at a given site ($n = 1$–4 individuals). *Soil PC1* is a multivariate soil fertility gradient based on pH, NH_4:NO_3, Mehlich-3 extracted P, nitrification rates, and inorganic N. Regression lines and R^2_{adj} values are based on site mean values. Log_{10} y-axes for all panels. *Asterisks* site-specific species differences: $*P < 0.05$, $**P < 0.01$, $***P < 0.001$
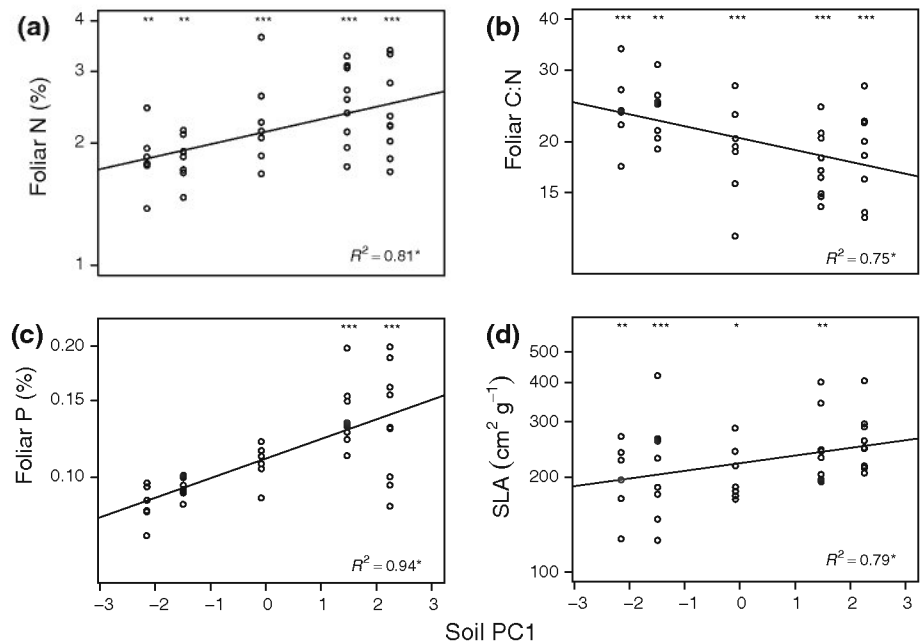
among co-occurring species. All morphological traits varied among co-occurring species for all sites, except for leaf height at the lowest nutrient site, Chorro (Table 3; Fig. 3d, e). Foliar nutrients also varied among co-occurring species in all cases except for leaf P at low nutrient sites (Chorro, Honda and Samudio), leaf $\delta^{15}N$ at the highest nutrient site (Hornito), and leaf $\delta^{13}C$ at sites with intermediate nutrient availability (Honda, Samudio, and Palo Seco; Table 3; Fig. 3a–c). Physiological traits showed less variation among co-occurring species, with no differences among species at Chorro or Samudio for any physiological trait examined here (Table 3). Area-based photosynthetic rates did not differ among co-occurring species for any site, whereas mass-based photosynthesis and PNUE varied among co-occurring species at Honda and Palo Seco. Stomatal conductance and WUE varied among co-occurring species at Honda, Palo Seco, and Hornito.

Discussion

This study used a trait-based approach to examine understory palm community assembly in low elevation cloud forests in western Panama. An earlier study at the same sites showed that palm species distribution patterns were related to soil nutrient availability (Andersen et al. 2010a). Here, we explored the extent to which these community patterns were the consequence of (1) habitat filtering, selecting for similar trait values among co-occurring species and shifts in community-wide trait values with

resource availability, or (2) competitive interactions, restricting similar trait values among co-occurring species. We found several lines of evidence indicating that both habitat filtering and limiting similarity influence trait values and, therefore, impact understory palm community structure. Furthermore, soil nutrient gradients had a greater influence on trait values than light availability or rainfall, corroborating the findings of the species-based approach that soil nutrients were the dominant factor influencing community assembly of understory palms in these lower montane forests.

Habitat filtering can affect mean trait values through differences in (1) species composition, (2) species abundance, and (3) phenotypic plasticity (Weiher et al. 1998; Cornwell and Ackerly 2009). In this study, site means of key morphological and physiological functional trait values changed along a multivariate soil gradient based on increasing extractable soil nutrient concentrations. Species mean trait values were related to their distribution pattern along the soil gradient, thus shifts in site mean trait values were driven in large part by species turnover along this soil gradient. However, trait variation for *G. cuneata,* the species occurring at all sites, along the soil gradient indicated that trait plasticity also contributes to shifts in site mean trait values. At the same time, within-community trait values varied among co-occurring species for most morphological and leaf nutrient traits at most sites examined. Hence, a combination of habitat filtering along a soil nutrient gradient and site-specific niche differentiation among co-occurring species influenced understory palm community structure.
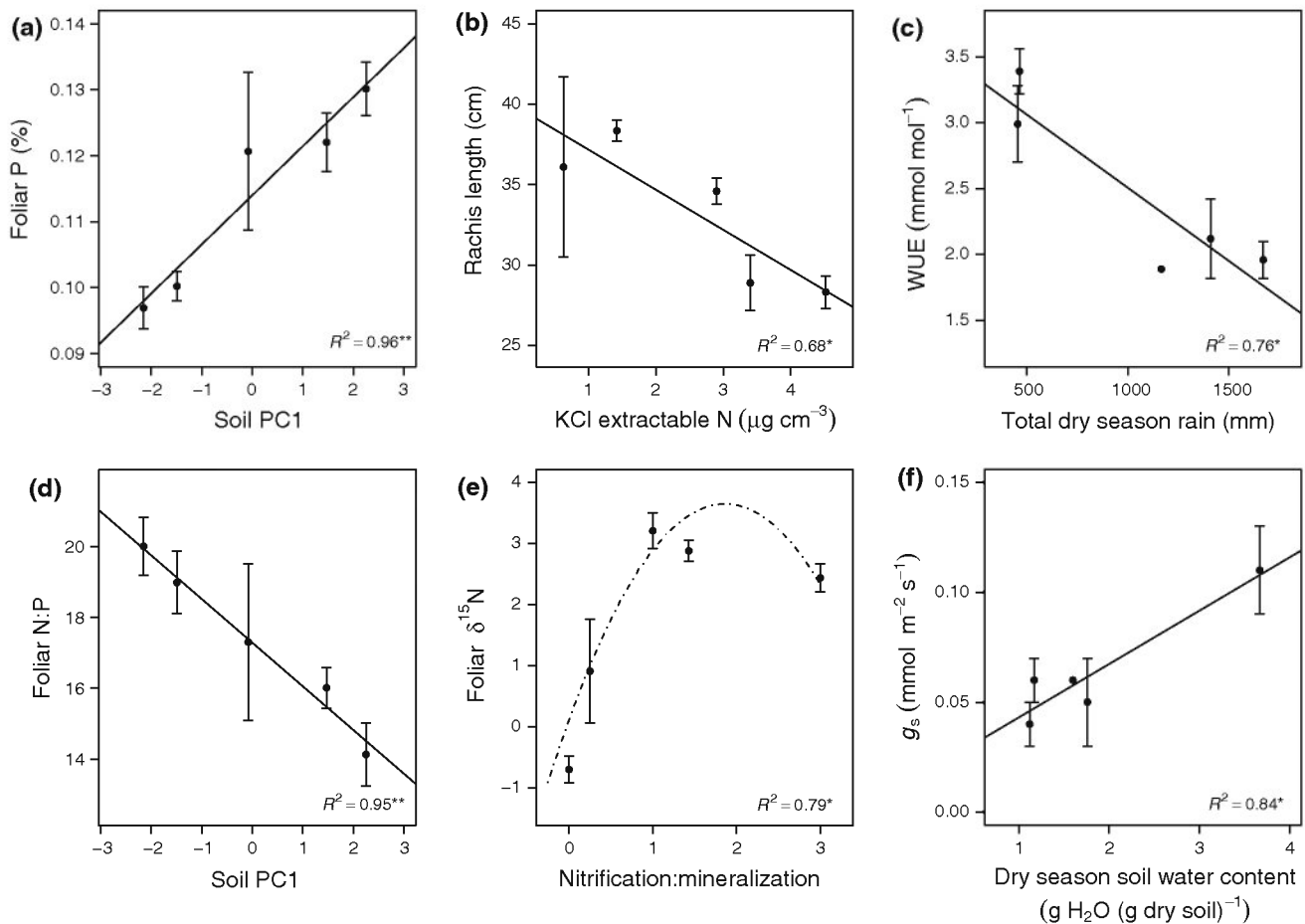
Fig. 4 Variation in leaf functional traits in *Geonoma cuneata* occurring at five sites in lower montane forests in western Panama in relation to site soil (**a**, **b**, **d**, **e**) and climate (**c**, **f**) properties. *Symbols* represent population means ($n = 2–4$) with standard *error bars*. $*P < 0.05$, $**P < 0.01$, $***P < 0.001$

Linking functional traits and species distribution patterns

Previous studies have shown soil-based habitat partitioning among palm species using species distribution data coupled with soil data (Savolainen et al. 2006; Andersen et al. 2010a). Here, we show not only that species distribution patterns were linked to soil nutrient availability but also that species mean trait values shifted with distribution patterns along the soil nutrient gradient. This suggests that palm species sorting along the soil nutrient gradient via habitat filtering (sensu Diaz et al. 1998) promotes species diversity at the mesoscale in the lower montane forests of western Panama. Furthermore, the shifts in species mean trait values with species distribution along the soil gradient included a suite of traits, including morphological, physiological and biochemical traits, indicating that coordinated shifts in species mean trait values reflect overall changes in ecological 'strategies' with soil nutrient availability (Bazzaz 1991; Reich et al. 2003).

Trait–environment linkages were related to resource-use efficiency, suggesting differences in ecological strategies among understory palm species. Leaf N, leaf P, leaf δ^{15}N, rachis length, SLA, $A_{\text{max(mass)}}$, PNUE, and a multivariate combination of all measured traits increased, and leaf C:N decreased, with species distribution along a gradient of increasing soil nutrient availability. Leaf size and quality have also been found to increase with soil nutrient availability in other studies (Reich et al. 2003; Cavender-Bares et al. 2004; Ordoñez et al. 2009). Reciprocal transplant experiments comparing species performance in high and low nutrient soils have shown that differences in resource-use efficiency (Baltzer et al. 2005) and trade-offs between growth and herbivore defense (Cunningham et al. 1999; Fine et al. 2004) are important in maintaining soil-based habitat associations in other tropical forests. Thus, resource-use strategies may influence community structure of understory palms in the lower montane forests of western Panama by promoting species turnover along soil nutrient gradients.

Table 3 Site means (±1SE) and ranges of population means of co-occurring species at the given site for functional traits measured for understory palm species in the lower montane forests of western Panama

Trait	Chorro Mean (SE)	Chorro Range	Honda Mean (SE)	Honda Range	Samudio Mean (SE)	Samudio Range	Palo Seco Mean (SE)	Palo Seco Range	Hormito Mean (SE)	Hormito Range
Morphological traits										
Number of leaves	6 (1)	4–10*	8 (1)	2–14***	8 (1)	4–16**	7 (1)	3–20***	6 (1)	2–16***
Canopy height (cm)	91 (16)	54–130	83 (6)	22–165***	97 (13)	46–149**	136 (14)	46–258***	107 (16)	21–255***
Rachis length (cm)	24.6 (2.4)	11–36***	18.2 (1.8)	6.3–40.5***	33.9 (2.6)	8.1–56.3***	56.4 (4.2)	16.4–147***	42.8 (6.0)	13.2–136**
SLA (cm² g⁻¹)	205 (11)	127–270***	226 (19)	126–420*	208 (17)	170–287*	255 (24)	193–401***	265 (40)	206–405
Foliar nutrients										
Leaf N (%)	1.86 (0.10)	1.38–2.44**	1.85 (0.07)	1.47–2.15***	2.32 (0.11)	1.68–3.64***	2.54 (0.12)	1.75–3.27***	2.42 (0.12)	1.7–3.38***
Leaf P (%)	0.087 (0.005)	0.07–0.10	0.095 (0.003)	0.09–0.10	0.109 (0.009)	0.09–0.12	0.140 (0.008)	0.11–0.20***	0.138 (0.010)	0.09–0.20***
Leaf N:P	22 (1.3)	19–30*	19 (0.9)	17–22	21 (1.1)	17–32***	18 (1.0)	16–22*	18 (1.2)	14–27*
Leaf C:N	25 (1.3)	17–34**	24 (0.8)	19–31***	20 (0.7)	12–27***	18 (0.6)	14–24***	19 (1.0)	13–27***
Leaf δ^{15}N	−1.33 (0.46)	−2.62 to +0.61*	0.95 (0.64)	−0.94 to +2.27*	2.72 (0.27)	+1.85 to +3.33*	2.90 (0.33)	+0.86 to +5.03**	1.67 (0.46)	+1.11 to +2.44
Leaf δ^{13}C	−35.1 (0.33)	−36.4 to −33.7*	−35.9 (0.87)	−37.5 to −33.6	−35.5 (0.82)	−37.1 to −33.9	−36.0 (0.35)	−37.7 to −34.5	−35.9 (0.51)	−38.4 to −32.4**
Physiological traits										
$A_{max(area)}$ (µmol m⁻² s⁻¹)	3.19 (0.61)	2.22–4.32	2.41 (0.36)	1.40–4.36	3.05 (0.48)	2.43–3.96	2.83 (0.41)	2.31–3.63	2.51 (0.26)	1.88–4.06
$A_{max(mass)}$ (nmol g⁻¹ s⁻¹)	64 (11)	44–95	52 (6)	28–111*	63 (12)	52–75	73 (8)	45–137**	66 (15)	43–94
R_d (µmol m⁻² s⁻¹)	0.23 (0.03)	0.17–0.33	0.32 (0.12)	0.17–0.48	0.24 (0.10)	0.14–0.38	0.17 (0.07)	0.06–0.35	0.24 (0.05)	0.12–0.57
g_s (mmol m⁻² s⁻¹)	0.108 (0.02)	0.07–0.16	0.074 (0.01)	0.05–0.10**	0.088 (0.03)	0.06–0.13	0.081 (0.01)	0.03–0.18***	0.060 (0.01)	0.02–0.11**
WUE (mmol mol⁻¹)	1.89 (0.31)	1.30–2.56	1.82 (0.26)	0.88–2.72**	2.35 (0.45)	1.77–3.13	2.18 (0.45)	1.28–3.40**	3.73 (0.43)	2.53–7.31*
PNUE (mmol mol⁻¹)	1.04 (0.19)	0.44–1.61	0.99 (0.14)	0.34–3.10*	0.82 (0.21)	0.68–1.08	1.08 (0.11)	0.60–2.45**	1.12 (0.36)	0.71–2.65

Asterisks site-specific differences among co-occurring species at the given site: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

Community-wide shifts in trait values along environmental gradients

Although light, water, and soil nutrient availability differed among the sites examined here, shifts in trait values were most strongly related to the soil nutrient gradient. Other studies have shown shifts in trait values with light (Falster and Westoby 2005; Poorter and Bongers 2006), soil moisture (Wright et al. 2002; Cavender-Bares et al. 2004; Cornwell and Ackerly 2009), and soil nutrients (Paoli 2006; Ordoñez et al. 2009). In this study, we did not detect community-wide shifts in any trait with rainfall, suggesting that species sorting along rainfall gradients may be less important in regions with such high rainfall compared to those in lower rainfall regions. We did, however, find higher leaf N:P and $\delta^{13}C$ values at sites with higher light availability. The high light sites in this study were also low in soil nutrients, suggesting that a feedback between soil nutrient availability and canopy openness might have influenced understory plant leaf traits related to nutrient stoichiometry and integrated water use efficiency.

In contrast to light and rainfall gradients, several traits related to nutrient cycling and plant productivity were clearly related to soil nutrient availability. Foliar nutrient content increased and C:N values decreased with increasing soil nutrients, suggesting plant–soil feedbacks may influence nutrient cycling (Wedin and Tilman 1990). Coordinated increases in SLA, foliar nutrient content, and decreases in leaf C:N ratios may also reflect trade-offs in allocation to defense and growth with soil nutrient availability, whereby the cost of leaf area lost to herbivory decreases with increasing soil nutrients (Coley et al. 1985; Fine et al. 2006). Andersen et al. (2010b) showed that, among a subset of the species examined here, increased foliar nutrient content resulted in higher leaf tissue loss to herbivory, but not to changes in overall seedling growth rates, with soil nutrient supply. Thus, increased foliar quality with nutrient supply may be important for maintaining increases in productivity, whereas decreased foliar quality with decreasing nutrient availability may represent a conservative nutrient use strategy and herbivore-defense mechanism.

Trait plasticity in *G. cuneata*

The importance of intraspecific variation in determining trait–environmental relationships and trait-based community assembly is becoming increasingly recognized (Ashton et al. 2010; Jung et al. 2010; Sandel et al. 2010). We examined trait plasticity in *G. cuneata*, which occurred across all sites examined here and was also the most abundant species at most sites (Andersen et al. 2010a). In *G. cuneata*, variation in foliar P followed the community-wide trend for increasing leaf P content with soil P availability, but variation in foliar N contrasted with the community-wide trend for increasing leaf N content with soil N availability. This suggests that intraspecific variability in *G. cuneata* is simultaneously driven by convergence in leaf P values through habitat filtering and divergence in leaf N values through niche differentiation. Furthermore, we also found a suite of traits for *G. cuneata* that were related to additional environmental gradients, highlighting the influence of multiple factors on intraspecific variation and trait plasticity. Rachis length, foliar $\delta^{15}N$, WUE and g_s differed among sites in *G. cuneata* and were related to soil nutrient and water availability variables. Several studies have linked species distribution patterns with drought tolerance along rainfall or edaphic gradients (Baltzer et al. 2005; Engelbrecht et al. 2007) and leaf economics strategies with soil nutrient gradients (Craine et al. 2002; Paoli 2006; Baltzer and Thomas 2010). Thus, plasticity along multiple trait axes may be important in allowing *G. cuneata* to persist at high densities at multiple sites despite strong environmental filters. This suggests that trait plasticity is an important influence on the understory palm community structure and may allow this species to occupy and dominate the sites examined here.

Within-site niche differentiation

We found differences among co-occurring understory palm species in most morphological and leaf nutrient traits despite small sample sizes ($n < 5$ individuals per site), but not for physiological traits. Recent trait-based community studies have suggested that sample sizes >10 are necessary to detect species differentiation among similar species on local scales, whereas smaller sample sizes can be used when comparing among divergent species or at larger scales (Baraloto et al. 2010; Hulshof and Swenson 2010). When comparing across species mean trait values in this study, we found differences for most physiological traits as well as for morphological and biochemical traits among the species, indicating that our sampling regime, a compromise between the number of species, traits, and sites, was able to detect differences in trait means at all but the smallest scales (within site) for conserved traits. For example, coefficient of variation of the nearest neighbor trait values (CV_NND; trait values more evenly spaced) has been developed as a measure of niche differentiation of trait values among coexisting species (Stubbs and Wilson 2004; Kraft et al. 2008; Jung et al. 2010). We were unable to detect significantly lower CV_NND than expected under a null model (following Jung et al. 2010) with the limited sample sizes in this study (data not shown). Regardless, our results suggest that divergence in morphological and biochemical traits may promote species co-existence on local

scales, whereas habitat filtering for physiological traits of understory palm species may be more important in selecting species occupancy at a given site.

Our results show that the suite of traits important for species co-existence varies among the sites. For example, leaf $\delta^{15}N$ and SLA varied among coexisting species at all sites except for the highest nutrient site. Thus, these traits may reflect that competitive interactions at low nutrient sites have selected for species with divergent trait values, whereas trait values converge to an optimal value at higher nutrient sites. For example, leaf $\delta^{15}N$, which represents the chemical form of nitrogen taken up, has been found to vary among coexisting species in low nitrogen arctic tundra habitats (McKane et al. 2002; Ashton et al. 2010), but showed community-wide convergence in tropical habitats where nitrogen may be relatively more available (Houlton et al. 2007). By contrast, leaf P values were highly conserved among coexisting species at low soil nutrient sites, yet were highly variable among co-occurring species at higher soil nutrient sites (Fig. 3c; Table 3). This suggests that ecological filtering of species able to maintain low leaf P values was important for sorting species at lower soil nutrient sites, whereas limiting similarity in leaf P values was more important for co-existence at high nutrient sites. Hence, as has been found in other trait-based studies (Cornwell and Ackerly 2009; Jung et al. 2010), we found evidence for both trait convergence due to habitat filtering and trait divergence due to niche differentiation, indicating that both mechanisms simultaneously influence plant community assembly across various taxonomic groups and ecosystems.

Using a trait-based approach, we have shown that understory palm communities are structured by habitat filtering along soil nutrient gradients and may also be influenced by niche differentiation within soil-based habitats. Thus, niche-based processes may be acting on multiple scales, contributing to the remarkably high palm density and species richness in the lower montane forests of western Panama. Furthermore, if the larger plant community follows similar ecological strategies across multiple environmental gradients, we predict that niche-processes play a strong role in determining community assembly in these forest reserves.

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