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# Soil-based habitat partitioning in understorey palms in lower montane tropical forests

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## ABSTRACT

**Aim** Dispersal assembly and niche assembly are two competing theories proposed to explain the maintenance of species diversity in tropical forests. Dispersal theory emphasizes the role of chance colonization events and distance-limited seed dispersal in explaining species abundance and distribution, whereas niche theory emphasizes differences among species in requirements for potentially limiting resources. Species distribution patterns in tropical forests often correlate with geology and topography, but tests of the relative importance of dispersal and niche partitioning have been hampered by an inadequate characterization of resource availability. The aim of this study was to explore how soil chemical and physical properties, climate, and geographic distance affect understorey palm communities in lower montane forests.

**Location** Fortuna Forest Reserve, Chiriquí Province, and Palo Seco Forest Reserve, Bocas del Toro Province, in western Panama.

**Methods** Understorey palms and soil nutrient concentrations were surveyed within 10 sites on different soil types across a 13-km transect. Variation in palm community composition was examined in relation to spatial and environmental variables.

**Results** The 25 understorey palm species recorded in the study were non-randomly distributed among forests differing in soil nutrient availability. In support of dispersal theory, floristic similarity decreased predictably with increasing geographic distance. However, environmental and soil variables were also correlated with geographic distance. Floristic similarity was also highly associated with a subset of environmental variables. Variation in palm community similarity was most strongly correlated with inorganic nitrogen availability and cation concentration. A subset of soil variables had a stronger relationship with floristic similarity when geographic distance was controlled for than did geographic distance when differences in soils were controlled for.

**Main conclusions** Both dispersal and niche processes affect palm species distribution patterns. Although spatially limited dispersal may influence species distribution patterns, soil-based habitat associations, particularly with respect to soil nitrogen, cation availability and aluminium concentrations, remain important factors influencing palm community composition at the mesoscale level in this tropical montane forest.

## Keywords

**Arecaceae, base cations, community assembly, floristic similarity, habitat associations, nitrogen, Panama.**

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## INTRODUCTION

Gaining an understanding of the mechanisms responsible for the maintenance of high levels of plant diversity is a central issue in tropical plant ecology. At present, there is debate over whether the composition of plant communities is governed primarily by ‘dispersal assembly’ or by ‘niche assembly’ processes. According to the dispersal assembly view, local community composition is a consequence of chance colonization and distance-limited dispersal, with species abundances undergoing random drift (Hurtt & Pacala, 1995; Hubbell, 2001). Neutral models, based on S. P. Hubbell’s neutral theory, can successfully predict certain community attributes such as species relative abundance distributions from dispersal processes (Hubbell, 2001; Volkov *et al.*, 2003). However, current models are less successful in predicting the decay of community similarity across spatial scales (Condit *et al.*, 2002; Costa *et al.*, 2009).

In contrast, the niche assembly view argues that species coexist by partitioning limiting resources through niche differentiation (Hutchinson, 1959; Silvertown, 2004). Habitat specialization may arise when species differ in their requirements for specific resources such as soil nutrients (Cavender-Bares *et al.*, 2004), water (Engelbrecht & Kursar, 2003; Engelbrecht *et al.*, 2007) or light (Brokaw, 1987; Montgomery & Chazdon, 2002). Alternatively, habitat specialization may also be mediated by plant–animal interactions such as differential seed predation in gaps compared to understorey (Schupp & Frost, 1989) or differential costs of herbivory damage according to resource availability (Fine *et al.*, 2004).

Whereas light-gradient partitioning among species has been well established through field experiments with tropical seedlings (Montgomery & Chazdon, 2002; Dalling *et al.*, 2004), belowground resource partitioning has been less commonly studied, particularly in Neotropical systems. The few experimental studies that do examine plant–soil associations provide evidence for growth trade-offs with anti-herbivore defence, biomass allocation and resource use efficiency, but with no consensus on the relative importance of these mechanisms across the tropics (Fine *et al.*, 2004; Palmiotto *et al.*, 2004; Baltzer *et al.*, 2005). Most evidence for habitat specialization of tropical plant species to soil conditions is indirect, based largely on correlative tests of associations between community composition and soil type or topography (Duivenvoorden, 1995; Tuomisto & Poulsen, 1996; John *et al.*, 2007). Recent work conducted in large forest dynamic plots (25–52 ha) and networks of small plots ( $\leq 1$  ha) has documented associations between tree species and soil nutrient distributions (Potts *et al.*, 2002; Palmiotto *et al.*, 2004; Paoli *et al.*, 2006; John *et al.*, 2007). Analysis of tree species distributions in relation to soil chemistry in lowland forests in Amazonian Ecuador and central Panama and at a montane site in southern Colombia showed that between 36% and 51% of species were non-randomly distributed in relation to one or more soil properties (John *et al.*, 2007). However, few studies have conducted detailed analyses of the suite of soil chemical

properties important to plant growth and function in structuring tropical plant communities.

Palms are a dominant component of tropical lowland and lower montane forests, and reports on associations between palm species and soil type and/or topography are relatively common (Kahn & Decastro, 1985; Clark *et al.*, 1995; Vormisto *et al.*, 2004). Most palm community studies show general soil-based habitat associations, but the specific soil properties involved have seldom been examined (although see Poulsen *et al.*, 2006; Roncal, 2006). Soil-based habitat differentiation has been implicated in the maintenance of high levels of palm species diversity through the promotion of both parapatric and sympatric speciation (Svenning, 2001a; Roncal, 2006; Savolainen *et al.*, 2006).

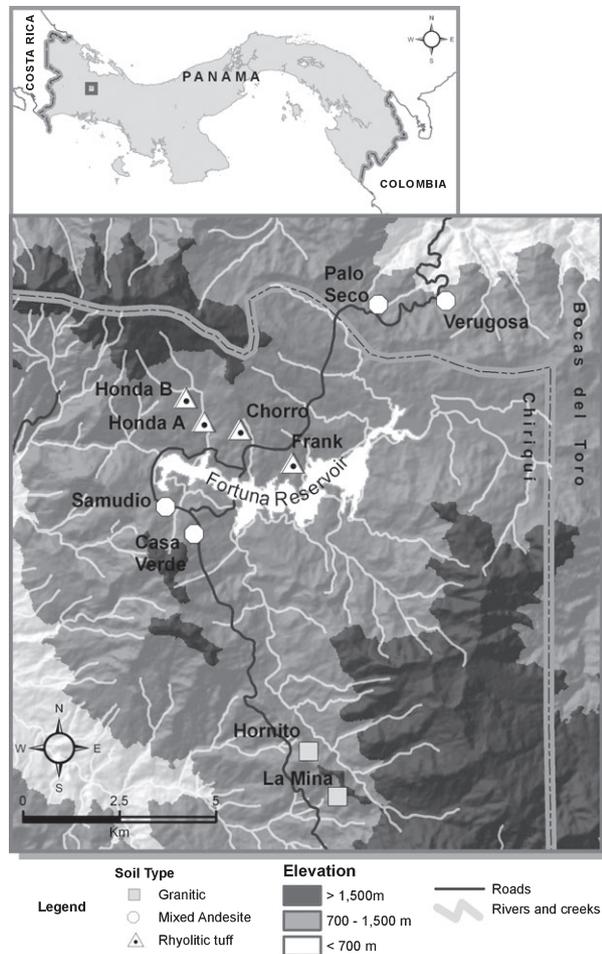
Here we use understorey palms to explore mesoscale (1–100 km<sup>2</sup>) plant distribution patterns in relation to soil properties, light, and climate variables in lower montane forests in western Panama. Our objective was to examine the extent to which dispersal (geographic distance) and niche (habitat association) processes explain variation in the palm community. If species distributions follow dispersal assembly processes, community similarity should decrease predictably with increasing geographic distance. Alternatively, if species distributions follow niche assembly processes, associations should exist between species and soil nutrients independent of geographic distance. Finally, if niche processes influence the palm community, our aim was to identify the specific environmental factors involved.

## MATERIALS AND METHODS

### Study site

Fieldwork was conducted at the Fortuna Forest Reserve (19,500 ha), Chiriqui Province, and at the adjacent Palo Seco Forest Reserve (125,000 ha), Bocas Del Toro Province, along the Central Cordillera of Panama (Fig. 1). The area encompasses lower montane forests ranging between 700 and 1500 m a.s.l. Mean annual rainfall ranges between 1500 and 6800 mm, depending on orographic position (Cavelier *et al.*, 1996). There is seasonality in rainfall, but rainfall in the drier months (January–April) is 100–200 mm month<sup>-1</sup> and exceeds monthly pan-evaporation rates. Mean annual temperature ranges from 19 to 22°C across the study sites (Cavelier *et al.*, 1996).

Within the study region, six permanent and four temporary forest inventory plots have been established (Fig. 1, Table 1). These plots represent some of the only permanent forest inventory plots in highland forests of Central America and encompass critical habitat for several palm species. Sites were selected within mature lower montane forests based on differences in vegetation and soil type. The forests differ in canopy tree species composition (J.W. Dalling, unpublished data). Although most parts of the forest reserves support mixed forest ( $> 80$  species  $\geq 10$  cm d.b.h. ha<sup>-1</sup>), some areas support monodominant forests of *Oreomunnea mexicana*



**Figure 1** The location of the ten 1-ha plots in the Fortuna Forest Reserve (Chiriqui Province) and Palo Seco Reserve (Bocas del Toro Province), Panama.

(Juglandaceae) or of the canopy palm, *Colpotherinax aphanopetala* (Arecaceae).

Soil variation reflects the complex geology, with the Cordillera Central (rhyolitic tuff and andesites) and the Cerro Hornito (granitic outcrops) converging in the Fortuna area (IRHE, 1975). Fine-grained extrusive and coarse-grained intrusive igneous rocks, agglomerates and tuffs ranging in age from early Tertiary to Pleistocene underlie the general study region (IRHE, 1975). Sites can be grouped by three main parent materials: (1) rhyolitic tuff, with organic topsoil supporting stands of *Colpotherinax* (Chorro sites: CH, FRANK) and *Oreomunnea* (Honda sites: HON, HONB) forests; (2) andesite, with mineral topsoil supporting mixed-species forests (Samudio sites: CV, SAM; Palo Seco sites: PS, VER); and (3) granodiorite ('granitics'), with organic topsoil supporting the mixed oak forests of Cerro Hornito (Hornito sites: HRN, LM; Table 1).

Panama is a centre of diversity for several genera of understory palms, making it an ideal setting in which to examine patterns and mechanisms for palm species coexistence. Understory palms are defined as species with average

adult height < 5 m (Svenning, 2001b) and generally have more restricted distribution patterns than do canopy palms (Svenning, 1999; Ruokolainen *et al.*, 2002). This study focuses on a group of taxonomically diverse understory palms in the Arecoideae subfamily with similar life histories. This group of palms is particularly abundant across the study region. *Chamaedorea* (tribe Chamaedoreae) and *Geonoma* (tribe Geonomateae) are the two largest Neotropical genera, with 24 of 77 species of *Chamaedorea* and 12 of 51 species of *Geonoma* occurring in Panama (Henderson *et al.*, 1995). Fruits are presumably dispersed by small mammals and birds (Henderson *et al.*, 1995; Svenning, 2001a). Seeds of the focal species are relatively large (5–20 mm; K.M. Andersen, unpublished data), but per individual seed production is generally low (5–140 fruits per individual per year). Therefore, reproductive and dispersal limitation may strongly influence the spatial structure of palm distributions. By focusing on a closely related group of species with similar growth forms, we limit the effects of phylogeny and life-history traits in determining plant–soil associations.

### Study plots and sampling regime

Within each 1-ha plot, fifteen 5 × 5 m subplots were selected. In each subplot the understory palm community was surveyed, and light and soil conditions were measured. Subplots were located every 20 m along three transects, which were set 30 m apart. The 1-ha plot size was chosen to reduce levels of heterogeneity of local environmental conditions (light, soil, climate) within a site.

### Palm surveys

In each 1-ha plot, all understory palms occurring in fifteen 5 × 5 m subplots were permanently tagged, mapped and identified. Voucher specimens of each species were deposited in the University of Panama (PMA) and the Smithsonian Tropical Research Institute (STRI) herbaria. Nomenclature follows Henderson *et al.* (1995); however, several species in our study have only recently been described. Species treatments for *Calypstrogyne* (Henderson, 2005) and newly identified *Chamaedorea* (Hodel, 1997) were used to provide the most recent taxonomic treatments. Each ramet of clonal and multi-stemmed species was treated as a separate individual, as densities were too high to separate genets accurately in all cases. Life-history stage was noted as seedling, sapling, juvenile, or reproductive adult.

### Soil surveys

Soil from each 1-ha plot was analysed for extractable inorganic nitrogen (NH<sub>4</sub> and NO<sub>3</sub>), extractable phosphorus and cation (Al, Ca, Fe, K, Mg, Zn) concentrations, pH, bulk density, net nitrogen mineralization and nitrification rates. For nitrogen, phosphorus, cation and pH measurements, composite samples for soil chemical properties were collected in each of the fifteen

**Table 1** Site location, palm species diversity, and environmental characteristics of ten 1-ha plots in lower montane forests in western Panama. Plots are paired by watershed and listed in order of increasing soil total inorganic nitrogen. Temperature was estimated using the adiabatic lapse rates in Cavellier *et al.* (1996). Palm species diversity, light and soil variables were measured in fifteen 5 × 5 m subplots within each 1-ha forest plot. Soil bulk density, nitrogen mineralization and nitrification rates are means of five samples, and all other soil chemistry values are means of 15 samples (0–10 cm depth) with standard errors. Values with different letters indicate significantly different means after Bonferroni correction ( $P < 0.05$ ).

	CH		HON		SAM		PS		HRN							
Environmental variables	Chorro (CH)		Frank (Frank)		Honda B (HONB)		Casa Verde (CV)		Palo Seco (PS)		Verugosa (VER)		Hornito (HRN)		La Mina (LM)	
Substrate	Rhyolitic tuff	Rhyolitic tuff	Rhyolitic tuff	Rhyolitic tuff	Rhyolitic tuff	Mixed andesite	Mixed andesite	Mixed andesite	Mixed andesite	Mixed andesite	Mixed andesite	Mixed andesite	Mixed andesite	Granitic	Granitic	
Topsoil	Organic	Organic	Organic	Organic	Organic	Mineral	Mineral	Mineral	Mineral	Mineral	Mineral	Mineral	Mineral	Organic	Organic	
Dominant tree species	<i>Colpothrinax</i>	<i>Colpothrinax</i>	<i>Oreomunnea</i>	<i>Oreomunnea</i>	<i>Oreomunnea</i>	Mixed species	Mixed species	Mixed species	Mixed species	Mixed species	Mixed species	Mixed species	Mixed species	Mixed species/ <i>Quercus</i>	Mixed species/ <i>Quercus</i>	
Latitude (N)	8°44'58"	8°44'29"	8°45'40"	8°45'26"	8°43'30"	8°43'52"	8°43'52"	8°46'43"	8°46'46"	8°46'46"	8°46'46"	8°46'46"	8°46'46"	8°39'49"	8°39'49"	
Longitude (W)	82°13'46"	82°13'06"	82°14'22"	82°14'37"	82°14'29"	82°14'53"	82°14'53"	82°11'53"	82°10'56"	82°10'56"	82°10'56"	82°10'56"	82°12'26"	82°12'26"	82°12'26"	
Elevation (m)	1100	1074	1155	1241	1232	1215	1215	878	947	1330	1330	1330	1379	1379	1379	
Temperature (°C)	20.5	20.7	20.2	19.7	19.7	19.8	19.8	21.8	21.4	19.2	19.2	19.2	18.9	18.9	18.9	
Annual rainfall (mm year <sup>-1</sup> )	4290	—	6059	6153	—	4440	4440	6491	—	5083	—	5083	—	—	—	
Dry season rainfall (mm)	1166	—	1410	1106	—	456	456	1670	—	465	—	465	—	—	—	
Red : Far red	0.51 ± 0.03 <sup>ab</sup>	0.52 ± 0.02 <sup>ab</sup>	0.38 ± 0.03 <sup>bc</sup>	0.34 ± 0.03 <sup>bcd</sup>	0.44 ± 0.04 <sup>ab</sup>	0.53 ± 0.02 <sup>a</sup>	0.53 ± 0.02 <sup>a</sup>	0.27 ± 0.03 <sup>c</sup>	0.42 ± 0.03 <sup>ab</sup>	0.26 ± 0.03 <sup>c</sup>	0.42 ± 0.03 <sup>ab</sup>	0.26 ± 0.03 <sup>c</sup>	0.37 ± 0.03 <sup>c</sup>	0.37 ± 0.03 <sup>c</sup>	0.37 ± 0.03 <sup>c</sup>	
Canopy openness (%)	6.32 ± 0.34 <sup>bc</sup>	6.53 ± 0.33 <sup>b</sup>	4.31 ± 0.25 <sup>d</sup>	5.77 ± 0.25 <sup>bcd</sup>	8.60 ± 0.65 <sup>a</sup>	6.27 ± 0.29 <sup>bc</sup>	6.27 ± 0.29 <sup>bc</sup>	4.85 ± 0.19 <sup>cd</sup>	4.85 ± 0.19 <sup>cd</sup>	5.31 ± 0.24 <sup>bcd</sup>	4.85 ± 0.19 <sup>cd</sup>	4.85 ± 0.19 <sup>cd</sup>	5.59 ± 0.29 <sup>bcd</sup>	5.59 ± 0.29 <sup>bcd</sup>	5.59 ± 0.29 <sup>bcd</sup>	
Palm species	7	5	11	10	11	8	8	14	12	8	12	8	3	3	3	
Palm density (individuals m <sup>-2</sup> )	0.27	0.71	0.45	0.13	0.82	0.66	0.66	2.05	2.54	0.17	2.54	0.17	0.69	0.69	0.69	
Fisher's $\alpha$	1.71	0.87	2.64	3.89	2.23	1.58	1.58	2.64	2.13	2.4	2.13	2.4	0.48	0.48	0.48	
<i>Soil properties</i>																
Bulk density (g cm <sup>-3</sup> )	0.08 ± 0.06 <sup>b</sup>	0.34 ± 0.07 <sup>a</sup>	0.11 ± 0.05 <sup>b</sup>	0.13 ± 0.03 <sup>a</sup>	0.35 ± 0.04 <sup>a</sup>	0.37 ± 0.05 <sup>a</sup>	0.37 ± 0.05 <sup>a</sup>	0.45 ± 0.01 <sup>a</sup>	0.35 ± 0.01 <sup>a</sup>	0.39 ± 0.09 <sup>a</sup>	0.35 ± 0.01 <sup>a</sup>	0.35 ± 0.01 <sup>a</sup>	0.26 ± 0.05 <sup>a</sup>	0.26 ± 0.05 <sup>a</sup>	0.26 ± 0.05 <sup>a</sup>	
pH	3.91 ± 0.07	4.04 ± 0.07	4.63 ± 0.1	3.63 ± 0.03	4.12 ± 0.06	5.06 ± 0.12	5.06 ± 0.12	5.08 ± 0.06	3.97 ± 0.05	5.76 ± 0.12	3.97 ± 0.05	3.97 ± 0.05	4.86 ± 0.13	4.86 ± 0.13	4.86 ± 0.13	
N mineralization (g cm <sup>-3</sup> day <sup>-1</sup> )	0.10 ± 0.04	0.05 ± 0.02	-0.12 ± 0.17	0.15 ± 0.04	0.12 ± 0.05	0.07 ± 0.02	0.07 ± 0.02	0.29 ± 0.36	0.09 ± 0.08	0.04 ± 0.08	0.09 ± 0.08	0.09 ± 0.08	-0.03 ± 0.07	-0.03 ± 0.07	-0.03 ± 0.07	
Nitrification (g cm <sup>-3</sup> day <sup>-1</sup> )	0.00 ± 0.01	0.04 ± 0.02	-0.03 ± 0.11	0.01 ± 0.01	0.12 ± 0.04	0.10 ± 0.02	0.10 ± 0.02	0.29 ± 0.07	0.07 ± 0.05	0.12 ± 0.06	0.07 ± 0.05	0.07 ± 0.05	0.02 ± 0.05	0.02 ± 0.05	0.02 ± 0.05	
NH <sub>4</sub> (g cm <sup>-3</sup> )	0.51 ± 0.05 <sup>d</sup>	0.79 ± 0.08 <sup>cd</sup>	2.08 ± 0.41 <sup>ab</sup>	0.70 ± 0.11 <sup>d</sup>	0.56 ± 0.12 <sup>d</sup>	1.25 ± 0.1 <sup>bc</sup>	1.25 ± 0.1 <sup>bc</sup>	2.63 ± 1.07 <sup>ab</sup>	1.72 ± 0.17 <sup>ab</sup>	2.88 ± 0.35 <sup>a</sup>	1.72 ± 0.17 <sup>ab</sup>	1.72 ± 0.17 <sup>ab</sup>	2.41 ± 0.37 <sup>ab</sup>	2.41 ± 0.37 <sup>ab</sup>	2.41 ± 0.37 <sup>ab</sup>	
NO <sub>3</sub> (g cm <sup>-3</sup> )	0.12 ± 0.02 <sup>cd</sup>	0.05 ± 0.01 <sup>d</sup>	1.32 ± 0.74 <sup>b</sup>	0.11 ± 0.03 <sup>cd</sup>	0.27 ± 0.1 <sup>bc</sup>	0.17 ± 0.02 <sup>bc</sup>	0.17 ± 0.02 <sup>bc</sup>	0.27 ± 0.06 <sup>bc</sup>	0.72 ± 0.17 <sup>b</sup>	1.64 ± 0.95 <sup>b</sup>	0.72 ± 0.17 <sup>b</sup>	0.72 ± 0.17 <sup>b</sup>	5.46 ± 1.72 <sup>a</sup>	5.46 ± 1.72 <sup>a</sup>	5.46 ± 1.72 <sup>a</sup>	
Total inorganic N (g cm <sup>-3</sup> )	0.63 ± 0.06 <sup>e</sup>	0.85 ± 0.09 <sup>de</sup>	3.40 ± 1.13 <sup>bc</sup>	0.80 ± 0.13 <sup>de</sup>	0.84 ± 0.16 <sup>de</sup>	1.42 ± 0.1 <sup>cd</sup>	1.42 ± 0.1 <sup>cd</sup>	2.90 ± 1.09 <sup>bc</sup>	2.44 ± 0.19 <sup>abc</sup>	4.52 ± 0.99 <sup>ab</sup>	2.44 ± 0.19 <sup>abc</sup>	2.44 ± 0.19 <sup>abc</sup>	7.87 ± 1.99 <sup>a</sup>	7.87 ± 1.99 <sup>a</sup>	7.87 ± 1.99 <sup>a</sup>	
N : P	0.25 ± 0.03 <sup>c</sup>	2.33 ± 0.38 <sup>a</sup>	2.27 ± 0.57 <sup>a</sup>	0.36 ± 0.12 <sup>c</sup>	1.17 ± 0.2 <sup>ab</sup>	0.44 ± 0.07 <sup>bc</sup>	0.44 ± 0.07 <sup>bc</sup>	0.87 ± 0.36 <sup>bc</sup>	1.45 ± 0.12 <sup>abc</sup>	0.50 ± 0.1 <sup>bc</sup>	1.45 ± 0.12 <sup>abc</sup>	1.45 ± 0.12 <sup>abc</sup>	1.83 ± 0.31 <sup>ab</sup>	1.83 ± 0.31 <sup>ab</sup>	1.83 ± 0.31 <sup>ab</sup>	
P (g cm <sup>-3</sup> )	2.74 ± 0.23 <sup>bcd</sup>	0.47 ± 0.09 <sup>e</sup>	1.70 ± 0.27 <sup>d</sup>	4.10 ± 0.63 <sup>bc</sup>	0.76 ± 0.09 <sup>e</sup>	3.67 ± 0.3 <sup>b</sup>	3.67 ± 0.3 <sup>b</sup>	3.91 ± 0.41 <sup>b</sup>	1.94 ± 0.28 <sup>cd</sup>	10.92 ± 1.94 <sup>a</sup>	1.94 ± 0.28 <sup>cd</sup>	1.94 ± 0.28 <sup>cd</sup>	4.67 ± 0.74 <sup>ab</sup>	4.67 ± 0.74 <sup>ab</sup>	4.67 ± 0.74 <sup>ab</sup>	
Al (g cm <sup>-3</sup> )	316 ± 48 <sup>e</sup>	531 ± 33 <sup>c</sup>	503 ± 35 <sup>cd</sup>	356 ± 58 <sup>e</sup>	856 ± 34 <sup>b</sup>	1858 ± 65 <sup>b</sup>	1858 ± 65 <sup>b</sup>	1858 ± 53 <sup>a</sup>	913 ± 32 <sup>b</sup>	913 ± 102 <sup>bc</sup>	913 ± 32 <sup>b</sup>	913 ± 32 <sup>b</sup>	304 ± 24 <sup>de</sup>	304 ± 24 <sup>de</sup>	304 ± 24 <sup>de</sup>	
Ca (g cm <sup>-3</sup> )	97 ± 22 <sup>c</sup>	105 ± 21 <sup>c</sup>	82 ± 21 <sup>de</sup>	40 ± 12 <sup>e</sup>	215 ± 34 <sup>bc</sup>	249 ± 36 <sup>b</sup>	249 ± 36 <sup>b</sup>	135 ± 38 <sup>bcd</sup>	144 ± 26 <sup>bcd</sup>	1358 ± 229 <sup>a</sup>	144 ± 26 <sup>bcd</sup>	144 ± 26 <sup>bcd</sup>	1243 ± 165 <sup>a</sup>	1243 ± 165 <sup>a</sup>	1243 ± 165 <sup>a</sup>	
Fe (g cm <sup>-3</sup> )	55 ± 11	—	129 ± 19	108 ± 23	—	176 ± 25	176 ± 25	161 ± 19	—	212 ± 26	—	—	—	—	—	
K (g cm <sup>-3</sup> )	18.8 ± 2.5 <sup>ef</sup>	23.3 ± 2.4 <sup>de</sup>	11.3 ± 1.2 <sup>f</sup>	30.0 ± 5.2 <sup>cde</sup>	39.5 ± 2.7 <sup>bcd</sup>	63.7 ± 15.8 <sup>ab</sup>	63.7 ± 15.8 <sup>ab</sup>	31.4 ± 2.8 <sup>bcd</sup>	45.0 ± 4.6 <sup>bc</sup>	96.1 ± 7.9 <sup>a</sup>	45.0 ± 4.6 <sup>bc</sup>	45.0 ± 4.6 <sup>bc</sup>	92.5 ± 13.5 <sup>a</sup>	92.5 ± 13.5 <sup>a</sup>	92.5 ± 13.5 <sup>a</sup>	
Mg (g cm <sup>-3</sup> )	18.9 ± 3.1 <sup>de</sup>	37.2 ± 5.8 <sup>bcd</sup>	19.8 ± 2.9 <sup>cde</sup>	26.4 ± 7.1 <sup>c</sup>	41.4 ± 5.4 <sup>bcd</sup>	53.2 ± 5.5 <sup>b</sup>	53.2 ± 5.5 <sup>b</sup>	40.3 ± 6.9 <sup>bcd</sup>	46.2 ± 7.3 <sup>bc</sup>	254.0 ± 44.7 <sup>a</sup>	46.2 ± 7.3 <sup>bc</sup>	46.2 ± 7.3 <sup>bc</sup>	170.7 ± 24.0 <sup>a</sup>	170.7 ± 24.0 <sup>a</sup>	170.7 ± 24.0 <sup>a</sup>	
Zn (g cm <sup>-3</sup> )	—	0.38 ± 0.05	—	—	1.38 ± 0.18	—	—	—	0.80 ± 0.09	—	0.80 ± 0.09	0.80 ± 0.09	6.02 ± 1.17	6.02 ± 1.17	6.02 ± 1.17	
CEC (%)	53.3 ± 6.2 <sup>b</sup>	28.1 ± 1.5 <sup>c</sup>	61.4 ± 3.7 <sup>a</sup>	37.5 ± 5.1 <sup>bc</sup>	40.7 ± 1.4 <sup>bc</sup>	63.7 ± 2.2 <sup>a</sup>	63.7 ± 2.2 <sup>a</sup>	50.2 ± 1.5 <sup>b</sup>	41.8 ± 2.2 <sup>b</sup>	52.0 ± 3.1 <sup>b</sup>	41.8 ± 2.2 <sup>b</sup>	41.8 ± 2.2 <sup>b</sup>	92.5 ± 10.0 <sup>a</sup>	92.5 ± 10.0 <sup>a</sup>	92.5 ± 10.0 <sup>a</sup>	
Base saturation (%)	19.4 ± 4.3 <sup>cd</sup>	34.9 ± 3.2 <sup>ab</sup>	8.6 ± 1.8 <sup>dc</sup>	18.4 ± 5.6 <sup>de</sup>	30.8 ± 3.7 <sup>bc</sup>	7.9 ± 0.9 <sup>d</sup>	7.9 ± 0.9 <sup>d</sup>	4.7 ± 1.0 <sup>e</sup>	29.0 ± 3.1 <sup>bc</sup>	43.2 ± 5.9 <sup>ab</sup>	29.0 ± 3.1 <sup>bc</sup>	29.0 ± 3.1 <sup>bc</sup>	80.9 ± 3.6 <sup>a</sup>	80.9 ± 3.6 <sup>a</sup>	80.9 ± 3.6 <sup>a</sup>	

5 × 5 m subplots at each site. Soil samples were taken from the top 10 cm of soil, which represents the main rooting zone in these forests (Cavelier, 1992).

Soil bulk density, nitrogen mineralization and nitrification were measured in only five subplots (centre and four corners) per 1-ha plot. Bulk density was determined by drying a known volume of soil at 105°C. Nitrogen mineralization and nitrification rates were measured *in situ* using PVC incubation tubes at each of the five soil bulk density sampling locations. After 30 days, soil from the tubes was collected and extracted for the determination of inorganic nitrogen.

All nitrogen samples (inorganic nitrogen and incubation samples) were extracted directly in the field by adding 10 mL of soil to bottles containing 50 mL of 2 M KCl. In-field extractions were used because of the marked and rapid changes in extractable inorganic nitrogen in stored samples (Arnold *et al.*, 2008; Turner & Romero, 2009; K.M. Andersen, unpublished data). The solutions were shaken manually and allowed to settle for 18 h. The supernatant was then separated and refrigerated until analysis. Nitrate and ammonium were analysed by automated colorimetry on a Lachat QuikChem 8500 flow injection analyzer (Hach Company, Loveland, CO, USA).

Soil pH was measured in water with a glass electrode in a 1 : 2 dry soil : water solution ratio. Extractable cations and phosphorus were determined by shaking 2.5 g (dry mass equivalent) of fresh soil with 20 mL Mehlich-3 extractant (Mehlich, 1984), and the filtrate was analysed by inductively coupled plasma (ICP) optical-emission spectrometry on an Optima 2100 spectrometer (Perkin Elmer Inc., Shelton, CT, USA). All chemical values are expressed on the basis of oven-dry soil, determined by drying soil at 105°C for 48 h per unit volume. Values are reported in volumetric rather than mass-based units to account for the marked differences in bulk density among the soils.

### Light

Light conditions at each site were measured using coupled red to far-red (R : FR) light ratios and hemispherical photographs. R : FR and a paired photograph were taken at a constant height of 1 m at three points (0, 2.5, 5 m) along the central north–south line of each palm subplot. R : FR is a measure of light quality, an important factor determining physiological processes such as seed germination and stem elongation (Lambers *et al.*, 1998). In addition, R : FR ratios can be used to estimate diffuse light transmittance in tropical forest understories (Capers & Chazdon, 2004). R : FR measurements are more sensitive to heterogeneous light conditions in the understorey, whereas hemispherical photographs estimate the overall light conditions established by the canopy. R : FR measurements were taken using a Skye Instruments SKR 110 sensor (Skye Instruments, Llandrindod Wells, UK), which records the ratio of light in the 660 and 730 nm wavelengths at  $\mu\text{mol s}^{-1}$ . For hemispherical photographs, we used a Nikon 8-mm fisheye lens mounted on a Nikon Coolpix 995 digital

camera (Nikon Inc., Melville, NY, USA). Photographs were taken under uniformly cloudy conditions. Hemispherical photographs were analysed using Gap Light Analyzer software (GLA; <http://www.ecostudies.org/gla/>; accessed January 2008) to calculate canopy openness. Canopy openness is defined as the amount of open sky visible from below the canopy as a percentage of the total area (Frazer *et al.*, 1999).

### Rainfall

At each of the six permanent forest inventory sites, rain gauges were installed in the centre of large gaps to collect rainfall inputs. Accumulated rainwater was measured every 2 weeks from January 2007 to February 2008. Monthly precipitation and dry season (January–April) precipitation were calculated. For sites where rain stations were not established, rainfall estimates from nearby sites (< 2 km away) were used.

### Data analysis

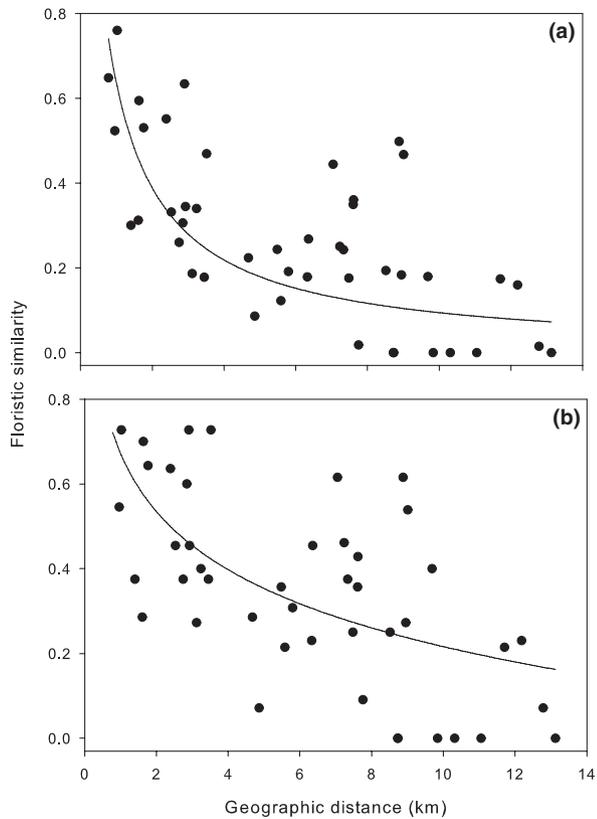
Multivariate analyses of palm communities, soil properties and environmental variables were implemented using the statistical software package VEGAN version 1.8-5 (Oksanen *et al.*, 2007) in the R programming environment version 2.4.1 (R Development Core Team, 2007).

### Palm community

Differences in species composition between sites were assessed with floristic dissimilarity matrices for both presence/absence and species abundance data. The Steinhaus dissimilarity matrix was computed using the Bray–Curtis method, double-standardized by species maxima and site totals of square-root-transformed species abundance data for each site. The Sørensen dissimilarity matrix was computed with the same methods but using presence/absence data. All species were included, so that patterns of species diversity could be examined. Dissimilarity matrices were converted to similarity matrices ( $S = 1 - D$ , where  $S$  is the similarity matrix and  $D$  is the dissimilarity matrix) to examine the decay of floristic similarity with geographic distance (Fig. 2). Analysis of similarity (ANOSIM) and hierarchical clustering were used to examine site differences in species composition. ANOSIM is a nonparametric variant of analysis of variance and is often used to test for differences in community data among predefined groups (McCune & Grace, 2002). The  $R$  statistic is based on mean ranks within and among groups, and significance is based on permutation tests. ANOSIM is conceptually related to non-metric multidimensional scaling (NMDS), as both are based on rank order.

### Geographic distance

Three-dimensional geographic distances between sites were calculated using plot Universal Transverse Mercator (UTM)



**Figure 2** Floristic similarity of the palm community for all pairs of ten 1-ha plots in the Fortuna Forest Reserve (Chiriqui Province) and Palo Seco Reserve (Bocas del Toro Province), Panama, as a function of the geographic distance between the pairs. (a) Floristic similarity based on palm species abundances. (b) Floristic similarity based on species presence/absence.

coordinates and altitude. Coordinates were measured with a Magellan GPS 300 (MiTAC International Corporation, USA), and altitude was measured using a Suunto digital altimeter (Suunto USA, Ogden, UT, USA) at the south-west corner of each 1-ha plot. The geographic distance matrix was calculated using an Euclidean index with non-transformed data.

#### *Environmental and soil properties*

Mixed-model two-factor analysis of variance (ANOVA) was used to compare individual light and soil chemical variables among the sites. Nitrogen, cation and phosphorus concentrations were log-transformed prior to analysis to meet the assumptions of ANOVA. Data for pH, aluminium saturation, nitrogen mineralization and nitrification rates were compared using Kruskal–Wallis tests. To examine differences in soil nutrient availability among sites, soil variables were combined using a principal components analysis (PCA). To account for differences in units and value ranges among soil properties, each variable was centred by subtracting the soil variable mean from each value and scaled by dividing the (centred) value by the soil property standard deviation prior to analysis. Euclidean distances were computed for the first three PCA axes for use in Mantel tests.

#### *Mantel tests*

Mantel tests were performed to examine correlations between the palm community and environmental distance matrices, palm and geographic distance matrices, as well as environmental and geographic matrices. All Mantel tests were performed on both species presence/absence and abundance data. Environmental variables were combined into four matrices: (1) an environmental distance matrix (Env PCA), based on the first three axes of a principal components analysis of all environmental variables, (2) a soil distance matrix (Soil PCA), based on the first three axes of the principal components analysis of the soil variables, (3) a light distance matrix (light), based on R : FR and canopy openness measurements, and (4) a rainfall distance matrix (rainfall), based on total annual precipitation and dry season (January 1–April 30) rainfall. Simple Mantel tests were performed on species abundance and presence/absence data to assess the correlation with the combined environmental matrices, with each of the soil variables separately, and with geographic distance. In addition, simple Mantel tests were performed on each environmental variable matrix separately to examine the correlation with geographic distance. Finally, partial Mantel tests were used to examine the correlation between among-site differences in the palm community and environmental variables controlling for geographic distance ('pure environmental') and between among-site differences in the palm community and geographic distance controlling for environmental variables ('pure spatial'). Standardized Mantel statistics are based on Pearson's product-moment correlation coefficients, and significance was assessed using randomization tests with 1000 permutations.

#### *Palm–habitat associations*

To identify how environmental variables were associated with palm community composition, rainfall, light and soil property vectors were fitted onto an NMDS ordination of species abundances. Based on a permutation test, the function finds the direction in ordination space with the most rapid change in the environmental vectors while maximizing the correlations with the ordination (Oksanen, 2008). We specifically used unconstrained ordinations to relate variation in the palm community to that of all possible environmental variables. The palm community ordination was based on the Steinhaus dissimilarity matrix.

## RESULTS

### **Palm communities**

A total of 3175 individuals were recorded in the sampled area, representing 25 understory palm species belonging to seven genera in three tribes within the Arecoideae subfamily: *Prestoea* and *Reinhardtia* (Areceae), *Asterogyne*, *Calyptrogyne*, *Geonoma* and *Pholidostachys* (Geonomateae), and *Chamaedorea* and *Synechanthus* (Chamaedoreae; Table 2). Efforts

**Table 2** Palm species recorded in fifteen 5 × 5 m subplots within ten 1-ha forest inventory plots in lower montane forests in western Panama. Values represent the total number of individuals recorded at each site. Plots are listed in order of increasing site soil inorganic nitrogen concentration, as shown in Table 1.

Tribe	Genus	Species	Site													Total
			Species code	CH	Frank	HON	HON B	CV	SAM	PS	VER	HRN	LM			
Arecaceae	<i>Prestoea</i>	<i>longepetiolata</i> var. <i>roseospadix</i> L. H. Bailey	PL	1	0	2	5	5	0	0	0	0	2	0	15	
	<i>Reinhardtia</i>	<i>gracilis</i> (H. Wendl.) Drude ex Dammer	RG	0	0	0	0	0	0	0	22	0	0	0	22	
	Geonomateae	<i>Asterogyne</i>	<i>martiana</i> (H. Wendl.) H. Wendl. ex Hemsl.	AM	0	0	0	0	0	0	0	11	15	0	0	26
		<i>Galyptogyne</i>	<i>panamensis</i> var. <i>occidentalis</i> Henderson	CaP	0	1	9	2	24	23	13	32	0	0	0	104
		<i>Geonomia</i>	<i>cuneata</i> (H. Wendl. ex Spruce)	GC	0	8	69	4	106	121	394	551	37	0	0	1290
		<i>Geonomia</i>	<i>cuneata</i> var. <i>gracilis</i> (H. Wendl. ex Spruce) Skov	GG	0	0	39	4	16	12	0	2	3	0	0	76
		<i>Geonomia</i>	<i>deversa</i> (Poit.) Kunth	GD	0	0	0	0	0	0	0	104	0	0	0	104
		<i>Geonomia</i>	<i>interrupta</i> (Ruiz & Pav.) Mart.	GI	0	0	0	0	0	0	0	4	0	0	0	4
		<i>Geonomia</i>	sp. 1	GS	9	9	11	12	0	0	0	0	0	0	0	41
		<i>Geonomia</i>	<i>undata</i> Klotzsch	GU	27	0	0	1	1	0	0	0	1	0	0	30
Chamaedoreaceae	<i>Pholidostachys</i>	<i>pulchra</i> H. Wendl. ex Burret	PP	0	0	0	0	0	0	4	0	0	0	0	4	
	<i>Chamaedorea</i>	<i>costaricana</i> Oerst.	CC	0	0	0	0	0	0	0	0	0	0	6	23	
	<i>Chamaedorea</i>	<i>deckeriana</i> (Klotzsch) Hemsl.	CD	0	0	0	0	0	0	0	94	103	0	0	197	
	<i>Chamaedorea</i>	<i>microphylla</i> H. Wendl.	CM	0	0	0	0	0	0	0	0	0	1	0	1	
	<i>Chamaedorea</i>	<i>palmeriana</i> Hodel & Uhl	CPA	6	0	16	2	70	28	0	63	0	0	0	185	
	<i>Chamaedorea</i>	<i>pinnatifrons</i> (Jacq.) Oerst.	CPI	30	19	2	4	23	8	76	17	12	0	0	191	
	<i>Chamaedorea</i>	<i>recurvata</i> Hodel	CRE	24	0	6	3	10	10	0	0	0	0	0	53	
	<i>Chamaedorea</i>	<i>robertii</i> Hodel & Uhl	CRO	0	0	9	0	34	43	49	16	0	0	0	151	
	<i>Chamaedorea</i>	<i>scheryi</i> L. H. Bailey	CSC	0	0	0	0	14	3	9	1	0	0	0	27	
	<i>Chamaedorea</i>	sp. 1	CPY	0	0	0	0	0	0	0	0	0	1	14	15	
	<i>Chamaedorea</i>	<i>sullivanorum</i> Hodel & Uhl	CSU	0	0	0	0	0	0	0	22	27	0	0	49	
	<i>Chamaedorea</i>	<i>tepejilote</i> Liebm.	CT	0	0	0	0	0	0	0	16	0	0	0	16	
	<i>Chamaedorea</i>	<i>verecunda</i> Grayum & Hodel	CV	3	0	2	10	0	0	0	0	0	0	0	15	
	<i>Chamaedorea</i>	<i>woodsoniana</i> L. H. Bailey	CW	0	0	0	0	4	0	7	0	4	220	235		
	<i>Synechanthus</i>	<i>warszewiczianus</i> H. Wendl.	SW	0	230	3	0	0	0	44	18	0	0	0	295	
		Total		100	267	168	47	307	248	765	951	65	257	3175		

were made to identify taxa to at least the species level. However, one morphospecies of *Chamaedorea* and one of *Geonoma* remain unidentified morphospecies and were treated as unique taxa (species) in all analyses. *Chamaedorea* was the most species-rich genus, with 13 species, followed by *Geonoma*, with six species. *Chamaedorea* and *Geonoma* were also the most abundant genera, with one dominant species of *Geonoma* (*Geonoma cuneata*) accounting for 40% of all individuals sampled and present in eight of 10 sites sampled. In contrast, five species were restricted to one site. Of these, one species had a high relative abundance whereas another was a singleton.

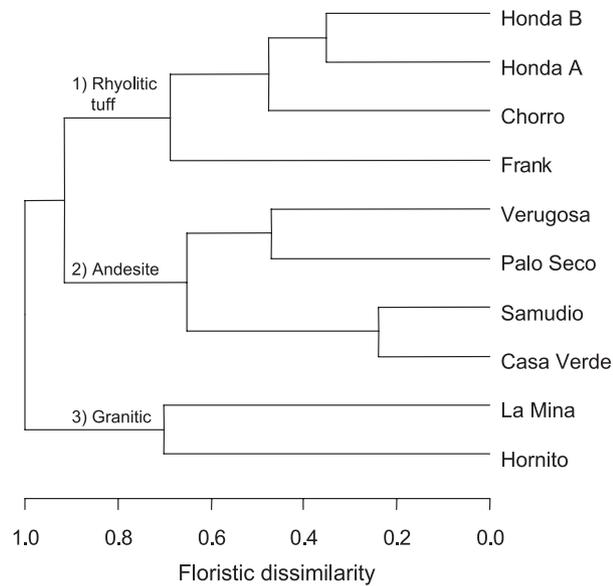
Palm diversity ranged from three to 15 species per site. Overall species richness was highest on andesite soils ( $n = 19$  species total) and lowest on granitic soils ( $n = 8$  species total). Fisher's alpha diversity ranged from 0.48 at a granitic site to 3.89 at a rhyolitic site. In contrast to Fisher's  $\alpha$ , palm density was highest on andesite soils and lowest on rhyolitic (low-nutrient) and granitic (high-nutrient) soils, both with organic topsoils. Palm density ranged from 1250 to > 25,000 individuals per hectare (Table 1).

The floristic similarity of the plots decayed linearly with log geographic distance for both Steinhaus (abundance;  $r^2 = 0.45$ ) and Sørensen (presence/absence;  $r^2 = 0.44$ ) indices (Fig. 2, Table 3). Palm community similarity declined rapidly over the first 4 km, and by 8 km some sites shared no species. However, sites between 6 and 10 km apart varied markedly in floristic similarity, ranging from 0 to > 0.6 based on presence/absence data.

Understorey palm species were non-randomly distributed among the 10 sites (ANOSIM Global  $R = 0.604$ ,  $P < 0.01$ ), reflecting species associations with particular soil types. Species grouped into three clusters identified in both the hierarchical clustering analysis and ordination (Figs 3 & 4). Group one species were associated with rhyolitic soils and were mostly endemics to the Fortuna forest or distinct morphospecies within a larger species complex (i.e. *Geonoma* sp. 1 was referenced as *Geonoma* cf. *cuneata* in the PMA herbarium collection). Group two species were associated with mineral topsoils (andesite substrate) and contained the largest number of species, most with relatively large ranges (latitudinal and altitudinal). *Chamaedorea* species were especially well

**Table 3** Mantel and partial Mantel test results for among-site differences in palm community, environmental properties, and geographic distance matrices. Env PCA includes all environmental variables. The light matrix includes R : FR and canopy openness, and the rainfall matrix includes annual rainfall and total dry season rainfall. Soil PCA includes only soil properties. Simple Mantel tests examined the correlation between the floristic dissimilarity matrix based on the Steinhaus index (abundance) and Sørensen index (presence/absence) and among-site differences in each environmental variable. In addition, correlations between among-site differences in each environmental variable and geographic distance were examined using simple Mantel tests. Partial Mantel tests were used to examine the correlation between the floristic dissimilarity and (1) among-site differences in each environmental variable after partialling out the influence of geographic distance ('pure environmental'), and (2) geographic distance after partialling out the influence of environmental differences ('pure spatial'). Values represent Mantel correlation coefficients ( $r$ ) based on Pearson product–moment correlation coefficients, and significance was examined using Monte Carlo permutation tests ( $***P < 0.001$ ,  $**P < 0.01$ ,  $*P < 0.05$ ).

Environmental variable	Partial Mantel tests						
	Mantel tests			'Pure environmental'		'Pure spatial'	
	Abundance	Pres/abs	Geographic distance	Abundance	Pres/abs	Abundance	Pres/abs
Env PCA	0.63**	0.65**	0.68**	0.32	0.37*	0.42*	0.38*
Light	-0.37	-0.34	-0.15	-0.36	-0.32	0.67***	0.65***
Rainfall	0.02	0.04	0.30*	-0.25	-0.21	0.70**	0.68***
Soil PCA	0.61**	0.70***	0.61**	0.52**	0.50**	0.42*	0.41*
pH	0.13	0.04	0.17	0.02	-0.09	0.66***	0.66***
Ca	0.64**	0.61*	0.76**	0.27	0.23	0.37	0.38
Al	0.12	0.07	-0.07	0.22	0.15	0.68***	0.66***
K	0.51*	0.48*	0.62*	0.16	0.13	0.52**	0.52*
Mg	0.54*	0.50*	0.66*	0.18	0.13	0.49*	0.50*
P	0.17	0.12	0.29	-0.03	-0.09	0.66***	0.65***
NH <sub>4</sub>	0.22	0.22	0.21	0.11	0.12	0.65***	0.64***
NO <sub>3</sub>	0.61*	0.66*	0.54*	0.40	0.48	0.51**	0.48*
Total inorg. N	0.62**	0.66**	0.57**	0.39	0.46*	0.49*	0.46*
N:P	-0.05	0.02	-0.23	0.14	0.23	0.68***	0.68***
CEC	0.44	0.48	0.25	0.39	0.43	0.65***	0.63**
Base saturation	0.61**	0.66**	0.56**	0.37	0.46	0.50**	0.46*
Al saturation	0.66**	0.71***	0.60**	0.43	0.51*	0.45*	0.41*
Bulk density	0.15	0.10	0.08	0.29	0.20	0.69***	0.67***
Geographic distance	0.67***	0.66**					



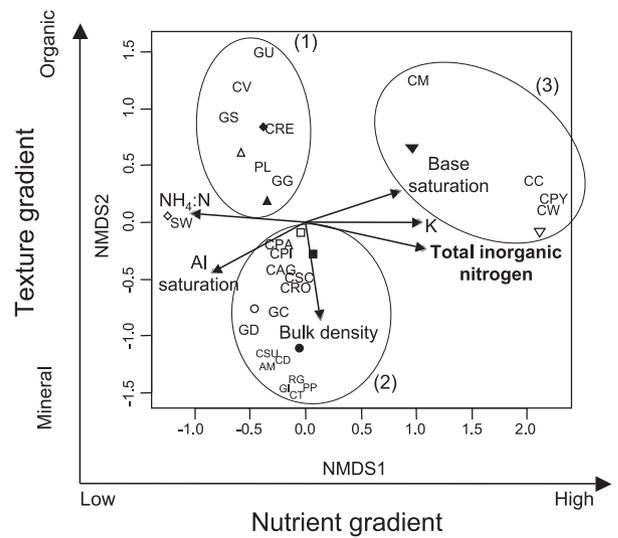
**Figure 3** Cluster diagram of the floristic distance of understory palm communities among ten 1-ha plots in the Fortuna Forest Reserve (Chiriqui Province) and Palo Seco Reserve (Bocas del Toro Province), Panama. Floristic dissimilarity was calculated with the Steinhaus index to include species abundances. Classification was analysed using Ward’s minimum-variance linkage. Palm communities clustered into three groups based on substrate.

represented in group two. Group three species were associated with granitic soils and contained several endemics and montane species within the genus *Chamaedorea*, including the most widespread and largest-statured species, *Chamaedorea woodsoniana*.

**Environmental variables and soil chemistry**

Sites differed in nitrogen, phosphorus and cation concentrations as well as in other physical and chemical soil properties (Table 1). There was a marked difference in total inorganic nitrogen ( $\text{NH}_4 + \text{NO}_3$ ): values ranged from 0.6 g N  $\text{cm}^{-3}$  dry soil at a rhyolitic site to 7.9 g N  $\text{cm}^{-3}$  dry soil at a granitic site. As total extractable inorganic nitrogen increased across sites, so too did the relative contribution of nitrate to the soil nitrogen pool. In contrast, nitrogen mineralization rates were consistently low across all sites, from  $-0.12 \mu\text{g N cm}^{-3} \text{ day}^{-1}$  (i.e. overall net nitrogen immobilization) at both a rhyolitic and a granitic site to  $0.29 \mu\text{g N cm}^{-3} \text{ day}^{-1}$  at a slightly lower-elevation andesitic site. Nitrification rates varied from net immobilization at a rhyolitic site to  $0.29 \mu\text{g N cm}^{-3} \text{ day}^{-1}$  at an andesitic site.

Cation and phosphorus concentrations generally followed the same trend as nitrogen, increasing from the nutrient-poor rhyolitic soils to the relatively nutrient-rich granitic soils. In particular, there were large differences in calcium ( $40\text{--}1350 \mu\text{g cm}^{-3}$ ), magnesium ( $20\text{--}250 \mu\text{g cm}^{-3}$ ) and potassium ( $10\text{--}100 \mu\text{g cm}^{-3}$ ). These differences corresponded to differences in pH, which ranged from  $< 4$  at sites with low cation



**Figure 4** Palm–soil associations defined by non-metric multi-dimensional scaling (NMS) ordination and fitted soil vectors for the ten 1-ha plots in the Fortuna Forest Reserve (Chiriqui Province) and Palo Seco Reserve (Bocas del Toro Province), Panama. Species abundances were used to compute ordinations. Species and subplot scores for the first two dimensions are plotted. Mean concentrations of soil nutrients were fitted to the ordinations to test for correlations between the palm community and soil nutrient availability. The direction of the arrow indicates the most rapid change in that soil chemical variable. The length of the arrow is proportional to the correlation with palm community ordination. (1) Rhyolitic tuff (low nutrient, organic topsoil) sites: (◆) Chorro (◇) Frank (▲) Honda (△) Honda B; (2) Mixed andesite (moderate nutrient, mineral soils) sites: (□) Casa Verde (■) Samudio (●) Palo Seco (○) Verugosa; (3) Granitic (nutrient-rich, organic topsoil) sites: (▼) Hornito (▽) La Mina. Overlapping species codes in group 2 were shrunk and offset slightly for clarity.

concentrations to  $\geq 5$  at sites with high cation concentrations. In addition, the granitic site contained soils with the highest nutrient availability and base saturation, whereas the andesitic sites contained soils with low base saturation (Table 1).

In the PCA of all soils data, each of the first three PC axes accounted for  $\geq 10\%$  of the variation, all three together accounting for a cumulative proportion of 83% of the variation. All cations (except aluminium), CEC, base saturation and total inorganic nitrogen loaded negatively and aluminium saturation loaded positively on PC1. Aluminium concentration, pH, bulk density and nitrogen mineralization and nitrification rates loaded negatively on PC2. Phosphorus concentrations loaded positively and N : P ratios loaded negatively on PC3. In addition, soil properties changed with geographic distance (Soil PCA:  $r = 0.61, P < 0.01$ ; Table 3).

*Light conditions*

Similarly, light conditions also differed among the sites (Table 1). Site mean R : FR values ranged from 0.26 to 0.53 and differed significantly among the sites ( $F_{9,121} = 10.82$ ,

$P < 0.0001$ ). Canopy openness ranged from 4.3% to 8.6% and differed among the sites ( $F_{9, 121} = 13.05$ ,  $P < 0.0001$ ). However, there was not a significant correlation between R : FR and canopy openness. The two rhyolitic Chorro sites (Table 1) had the most open canopies and the highest R : FR, whereas an andesitic and granitic site both had lower canopy openness and lower R : FR ratios than the other sites.

### Palm habitat associations

Results from the Mantel tests using species abundance were similar to the results from presence/absence data. Mantel tests confirmed correlations between floristic similarity and among-site geographic distance and differences in soil variables (Table 3). Palm community similarity was significantly correlated with variation in the environmental and soils-only PCA matrices, calcium, potassium, magnesium (presence/absence only), nitrate, total inorganic nitrogen, base saturation and aluminium saturation among sites. Among-site differences in rainfall, environmental and soil PCA matrices, calcium, potassium, magnesium, nitrate, total inorganic nitrogen, base saturation and aluminium saturation were also correlated with geographic distance. After taking geographic distance into account, the soil PCA matrix was still significantly correlated with palm community similarity for both abundance and presence/absence, whereas the environmental PCA matrix, total inorganic nitrogen, and aluminium saturation were significantly correlated only with species presence/absence. There were no significant correlations between palm community similarity and similarity in light, rainfall, pH, aluminium, phosphorus, or ammonium concentrations, nitrogen to phosphorus ratio (N:P), cation exchange capacity (CEC) or bulk density.

In addition, unconstrained ordinations were performed to examine *how* individual environmental variables were correlated with the palm community ordination. Total inorganic nitrogen concentration was most strongly correlated with floristic similarity followed by (in order) CEC, ammonium as the proportion of total inorganic nitrogen, aluminium saturation, magnesium, bulk density and base saturation (Fig. 4). NMDS axis 1 represents inorganic nitrogen and nutrient availability and aluminium saturation gradients, whereas NMDS axis 2 can be interpreted as a gradient in topsoil properties from mineral soils with high bulk density to soils high in organic matter with a low bulk density.

## DISCUSSION

### Palm community

The palm community at Fortuna represents a diverse assemblage of species from genera common in the lower montane forests of Central America (Hodel, 1992; Henderson *et al.*, 1995). Despite the palm survey in this study being restricted to focal taxa in the Arecoideae subfamily, the palm diversity found here is comparable to that reported in studies in Amazonia that surveyed the entire palm community (Vorm-

isto *et al.*, 2004; Poulsen *et al.*, 2006; Costa *et al.*, 2009). For example, the species richness of understorey palms is similar to that in Ecuador and Peru, with *c.* 20 sympatric species recorded within a 1- to 25-ha plot area (Svenning, 1999; Poulsen *et al.*, 2006).

In addition to a high palm diversity, Fortuna forests have an extraordinarily high density of understorey palms. The species *G. cuneata* alone attained densities of over 14,500 plants ha<sup>-1</sup> at the site with the highest overall understorey palm density. A recent study examining mesoscale variation in palm communities at Reserva Forestal Aldolpho Ducke, Brazil, reported densities of  $0.16 \pm 0.05$  individuals m<sup>-2</sup> (Costa *et al.*, 2009), comparable to the low range of palm densities in the Fortuna forests. High densities of understorey palms probably influence overall forest structure and inhibit the recruitment success of other species by intercepting seed fall, creating dark microsites for seedling recruitment, and causing damage from falling senescent palm leaves (Farris-Lopez *et al.*, 2004; Montgomery, 2004; Wang & Augspurger, 2004).

### Environmental variables

#### Soil properties

Soils at Fortuna vary markedly across relatively short distances. Values for soil nutrients span the range recorded elsewhere for lower montane forests (Vitousek & Sanford, 1986; Marrs *et al.*, 1988; Cavelier, 1992). The rhyolitic sites are acidic and poor in nutrients, whereas the granitic sites are relatively nutrient-rich. Studies of nutrient cycling in tropical montane forests suggest that nitrogen is commonly the most limiting nutrient to plant growth at high elevation (Marrs *et al.*, 1988; Vitousek & Matson, 1988; Sollins, 1998; Tanner *et al.*, 1998). In this study, the major soil nutrient gradients across sites were in extractable inorganic nitrogen and base cation concentration. Within the Fortuna area, local climate and geologic history are likely to explain the large ranges in soil nutrient concentrations.

#### Light and forest structure

Light levels in the Fortuna forests are low, but typical for tropical forests (Nicotra *et al.*, 1999; Capers & Chazdon, 2004). Light availability is probably an important factor in determining individual performance and has been found to be a significant factor correlated with palm species distributions on local (< 1 km) scales (Chazdon, 1986; Svenning, 2002). In Costa Rica, three species of Geonomeae palms were found to partition light gradients along forest-gap edges by differing in their photosynthetic capacities and height (Chazdon, 1986). Similarly, in Ecuador, population dynamics of *Geonoma macrostachys* were found to be influenced by light availability (Svenning, 2002). In both of these studies, light positively affected growth and overall performance, although light conditions within closed canopy forests are dynamic and may not influence distribution patterns over larger spatial and temporal scales. Studies examining distribution patterns of

*Geonoma* taxa across landscapes in relation to environmental factors found that light was not a significant factor explaining distribution patterns (Souza & Martins, 2005; Roncal, 2006). Furthermore, in studies where light was not found to be an important factor in determining species distribution patterns, including the present study, various soil properties were correlated with *Geonoma* and other understorey palm taxa distribution patterns.

### Dispersal versus niche processes

Palm communities in the lower montane forests of Fortuna are shaped by both spatially limited dispersal and niche processes. The 'pure environmental' effect of soil nutrients, particularly with respect to soil inorganic nitrogen and aluminium saturation, was strongly correlated with floristic similarity. The strength of the relationship between soil variables and floristic similarity was comparable to that of floristic similarity and the 'pure spatial' effect. A mesoscale study of the entire palm community at Reserva Forestal Aldolpho Ducke, in the Brazilian Amazon, revealed that geographic distance had little influence on floristic similarity, but that soil variables explained the majority of variation in the palm community (Costa *et al.*, 2009). Geographic distance was found to be only marginally important in determining the presence/absence of understorey palms and had no effect on the presence/absence of canopy palms or the variation of palm communities based on species abundance for either understorey or canopy palms (Costa *et al.*, 2009). In western Amazonia, environmental and geographic distance together explained 70–85% of the landscape-scale variation in palm community similarity, with the remainder of the floristic variation unexplained (Vormisto *et al.*, 2004). However, in western Amazonia, geographic distance was more important than environmental variables in determining floristic similarity, in contrast to the findings from the Brazilian Amazon or the present study. Thus, differences in scale (landscape versus mesoscale), focal taxa (all palms including trees  $\geq 10$  cm diameter versus understorey palms) and/or habitat (lowland tierra firme versus lower montane forests) may influence the relative importance of geographic distance on palm communities.

#### *Spatially limited dispersal*

Floristic similarity declined linearly with log-distance, as predicted by dispersal limitation theory (Condit *et al.*, 2002). The strength of the floristic decay was similar for species abundance and presence/absence matrices, indicating that, in sites with similar species assemblages, the shared species had similar relative abundances. This pattern is probably driven by the most widespread and common species, *G. cuneata* var. *cuneata*, which tended to have similar abundances at sites with similar species assemblages, and also by locally abundant species with restricted distributions (i.e. *Chamaedorea deckeriana*). Understorey palms have relatively large fruits borne in the lower strata of the forest (0–5 m above the forest floor)

that are dispersed by birds and small mammals (Zona & Henderson, 1989). Communities of understorey herbs and trees with animal-dispersed seeds tend to have higher rates of floristic decay with geographic distance than plants in different strata of the forest and with different dispersal modes (Clark *et al.*, 1999; Nekola & White, 1999; but see Tuomisto *et al.*, 2003). Several studies examining the community assembly of palms in various forest types have found strong spatial signals in palm community composition at various scales (Svenning, 2001b; Svenning *et al.*, 2009; Vormisto *et al.*, 2004; Normand *et al.*, 2006), indicating that distance-limited dispersal may be an important component in the structuring of palm communities.

Although our results support the idea that understorey palm communities are limited by dispersal, it is difficult to fully dissect the relative importance of geographic distance and most environmental variables owing to spatial autocorrelation. In particular, the environmental variables correlated with floristic similarity are also highly correlated with geographic distance. Andesitic sites had high floristic similarity despite distances of 8 km between groups of sites, suggesting that either long-distance dispersal (Kessler, 2000), or specific environmental variables associated with andesitic soils are important in structuring palm communities in the Fortuna forests.

#### *Niche partitioning*

We have identified specific soil properties that influence palm species distribution patterns: soil exchangeable nutrient availability and degree of organic matter accumulation. Previous studies examining the influence of soil nutrients on palm communities most commonly reported that variations in base cation availability and soil texture were correlated with variation in floristic similarity (Vormisto *et al.*, 2004; Poulsen *et al.*, 2006; Costa *et al.*, 2009). In the current study, we also found a strong correlation between variation in base saturation and floristic similarity. However, inorganic nitrogen was the soil nutrient most strongly and consistently correlated with the palm community composition across all analyses in the current study. To our knowledge, this is the first report of the influence of soil nitrogen availability on palm community composition. Previous studies examining floristic comparisons of palm communities were based in lowland tropical forests, where phosphorus is assumed to be the most limiting soil nutrient, and did not measure soil nitrogen availability (Vormisto *et al.*, 2004; Poulsen *et al.*, 2006; Roncal, 2006). However, Tanner *et al.* (1998) suggested that, in tropical montane forests, plant productivity is most limited by soil nitrogen availability. In a study examining plant–soil associations in large-scale forest dynamic plots, nitrogen, in addition to phosphorus, was one of the most important nutrients associated with tree species soil-niche breadths at the single montane plot at La Planada, Colombia (John *et al.*, 2007). Nitrogen availability is relatively high at La Planada, whereas the large gradient in nitrogen availability found across the

Fortuna sites is more likely to influence species distributions. Thus, the relative importance of specific soil nutrients in influencing plant communities is probably dependent on the relative abundance of soil nutrients (i.e. nutrient ratios) and the strength of soil nutrient gradients (Costa *et al.*, 2009).

In the present study we used bulk density as a proxy measure for mineral versus high-organic-matter topsoils. Mineral soils with a high clay or sand content have higher bulk densities than soils with a high organic content (Brady & Weil, 2002). Andesitic sites had mineral soils with low organic matter content, high bulk density and high aluminium concentrations. Studies that have quantified soil texture in association with palm communities have found correlations between species distributions and soil texture and/or aluminium concentration (Vormisto *et al.*, 2004; Poulsen *et al.*, 2006; Roncal, 2006). Soil texture and aluminium concentrations are likely to be correlated with other factors such as soil moisture regimes that may influence species performance (Kursar *et al.*, 2005; Baillie *et al.*, 2006). For example, although the andesitic soil sites have high aluminium saturation values, these sites also tend to have higher nitrogen mineralization and nitrification rates. The high density and diversity of palms at sites with andesitic soils high in aluminium may reflect both the tolerance of palms for high aluminium concentrations and the competitive ability of palms in high-nitrogen-turnover environments over other understorey plants with lower aluminium tolerance (Sollins, 1998). Slow growth and low mortality rates of understorey palms (K.M. Andersen, unpublished data) may give palms a competitive advantage at these sites (Sollins, 1998). Whether the low growth requirements of palms provide them with an advantage at sites with high levels of aluminium or whether they have specific mechanisms to tolerate aluminium has not been examined.

### Palm–soil associations

We have identified three palm–soil association groups: species associated with (1) nutrient-poor, organic topsoils (rhyolitic soils), (2) moderately nutrient-rich, mineral topsoils (andesitic soils), and (3) nutrient-rich, with organic topsoil (granitic soils). Rare species are associated with sites with organic topsoils, groups (1) and (3). Species associated with (1) rhyolitic and (3) granitic soils are either recently described endemics or distinct morphospecies generally lumped in large species complexes (Hodel, 1992). For example, *Chamaedorea recurvata*, *Chamaedorea verecunda* and *Geonoma* sp. 1 are restricted to rhyolitic soils, and *G. cuneata* var. *gracilis* is associated with low-nitrogen sites, whereas the abundant *G. cuneata* is common in all but the extremes of the nitrogen gradient. Distinctive morphotypes or potentially separate species within a large species complex are often found on distinct soil types. In central Panama, multivariate analyses of morphological characters separated populations of widespread understorey palm species occurring on distinct old volcanic soils from surrounding populations (Henderson, 2005; Thomas *et al.*, 2006), suggesting that these may represent

unique taxa (Hodel, 1992). Recent population genetics studies show that *Chamaedorea alternans*, which has been generally considered to represent morphologically distinct populations of *Chamaedorea tepejilote* occurring on limestone soils in Mexico, is also genetically distinct and should be reclassified as a separate species (Bacon & Bailey, 2006; Cuenca & Asmussen-Lange, 2007). In Peru, however, sympatric varieties of *G. macrostachys* show clear habitat differentiation based on soil texture and potassium availability, but there was little genetic differentiation between the two varieties examined (Roncal *et al.*, 2005; Roncal, 2006). Clearly, localized associations to specific soil types allow for increased diversity from molecular to community levels.

Soil heterogeneity plays an important role in maintaining the high species diversity of understorey palms in the lower montane forests in this study. Andesitic sites had both the highest palm diversity and the highest density. The andesitic sites examined here occur at intermediate elevations (800–1000 m a.s.l.) or adjacent to sites with rhyolitic soils. The high diversity at andesitic sites may be influenced by mass effects, or by the continued dispersal of species with affinities to different elevations and soil types (*sensu* Shmida & Wilson, 1985). In a study of Andean palm communities, upslope-directed mass effects contributed to local species richness at higher elevations (Kessler, 2000). However, we recorded reproductive adults and seedlings of all species at all sites, indicating that the palm species present at each site are able to maintain viable populations. Nonetheless, the mixture of species with lowland and/or montane distributions, in addition to species with rhyolitic associations, probably contributes to the high levels of diversity at the andesitic sites.

At the other extreme, species diversity and density were lowest at the high-nutrient granitic sites. Species occurring on organic-rich soils at granitic sites may be susceptible to occasional dry spells. Although the granitic sites received > 5 m of rain in 2007, dry season rainfall (January–April) was < 0.5 m, with frequent dry spells (< 5 cm in a 2-week period). In comparison, andesitic sites received 1.5 m of rain over the dry season with no dry spells. Results from seedling transplant experiments indicate that infrequent dry spells decreased survival rates of drought-sensitive species (K.M. Andersen, unpublished data), and it seems likely that the relatively small and shallow rooting systems of understorey palms may not be able to compete with larger shrub or tree root systems for water during dry periods. Studies in seasonal lowland forests in Panama have linked species distribution patterns with species' drought tolerance (Engelbrecht & Kursar, 2003). Understorey palm species that are found in both Fortuna and the lowlands of Barro Colorado Island in central Panama had increased mortality rates during drought years (Condit *et al.*, 1995), indicating that water availability may be important in shaping palm distributions.

In summary, we found evidence for both dispersal-limited and soil-mediated distribution patterns of understorey palms in a lower montane forest in Panama. Soil variables remained strongly correlated with palm communities after controlling

for geographic distance, suggesting that both dispersal limitation and soil-based habitat partitioning structure the palm community examined here. Inorganic nitrogen and aluminium concentration were the main soil chemical properties correlated with floristic variation. Whereas the majority of the species occurred on andesite soils with intermediate nutrient availability, soils at the high and low ends of the nutrient gradient maintain rare and endemic species. Thus, dispersal limitation may filter species potential distribution patterns, and soil-based habitat associations further influence species realized distribution patterns.

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