Journal of Vegetation Science 12: 553-566, 2001

Floristic composition across a climatic gradient in a neotropical lowland forest

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Abstract. This study deals with the floristic composition of lowland tropical forest in the watershed of the Panama Canal. The floristic composition of large trees in 54 forest plots was analysed with respect to environmental factors, including precipitation, geologic parent material, stand age, topography, and soils. The plots contain 824 species of trees with a diameter at breast height ≥ 10 cm and represent a regional flora with exceptional β-diversity. Plot data indicate that the Panamanian forest is strongly spatially structured at the landscape scale with floristic similarity decreasing rapidly as a function of inter-plot geographic distance, especially for distances < 5 km. The ordinations and patterns of endemism across the study area indicate broad floristic associations well correlated with Holdridge life zones. The results indicate the positive aspects of life zone classification at regional scales, while simultaneously highlighting its inadequacy for finer scales of analysis and resource management. Multivariate gradient analysis techniques (Non-metric Multidimensional Distance Scaling and Detrended Correspondence Analysis) show clear patterns of floristic variability correlated with regional precipitation trends, surficial geology, and local soil attributes. Geologic and edaphic conditions, such as acidic soils or excessively drained limestone substrates, appear to override the effects of precipitation and modify forest composition. We conclude that the Panamanian forest shows clear patterns of spatial organization along environmental gradients, predominantly precipitation. The rapid decline in floristic similarity with distance between stands also suggests a role for dispersal limitation and stochastic events.

Keywords: Gradient analysis; Life zone; Precipitation; Spatial analysis; Tropical lowland forest.

Abbreviations: BCI = Barro Colorado Island; NMDS = Non-metric Multidimensional Distance Scaling.

Introduction

Classic studies from temperate latitudes have illustrated local and regional species-level floristic responses to environmental controls (e.g. Whittaker 1965; Gillison & Brewer 1985; Harrison et al. 1992). Few comparable studies exist for lowland Neotropical forests, with several notable exceptions from investigations in the Amazonian rain forest (Duivenvoorden 1995; Tuomisto et al. 1995; Ruokolainen et al. 1997). The majority of work at the landscape-scale has focused on the description of forest physiognomy (Holdridge & Budowski 1959; Webb et al. 1970; Holdridge et al. 1971; Mackey 1993, 1994), relatively small spatial domains (Clark et al. 1998), subsets of more common species (Williams et al. 1973; Clark et al. 1995), or family-level taxonomy (Terborgh & Andresen 1998). This difference is strongly linked to practical and logistical hurdles facing field workers in tropical forests. Researchers have been overwhelmed by forests containing large numbers of superficially similar tree species, and data analysis is frequently hampered by poorly documented floras and limited reference materials. Information on the soils, geology, and even topography underlying tropical forests is typically difficult to acquire and seldom available at appropriate scales (Sollins 1998).

Decades of research at the Smithsonian Institution's Barro Colorado Island (BCI) field station has provided an exception to these generalizations and a world-class knowledge base about the ecology of the lowland forest (Croat 1978; Leigh 1996). The combination of a well-documented flora, relatively easy access to field sites, and a complex mixture of environmental gradients makes lowland Panama an excellent study area for community analysis at the landscape scale. In this study, the floristic landscape is defined as the 2400 km^2 area (ca. 60 km × 40 km) bordering the Panama Canal. This study area is nested inside a larger, more poorly defined floristic region that extends into landscapes in adjacent areas of lowland forest. On the local scale, the study considers forest composition as it is represented in plots between 1 ha and 50 ha in size.

The detailed analysis of floristic composition at the landscape-scale provides critical data for conservation activities. Work at the physiognomic and bioclimatic level provides valuable information about forest structure and large-scale organization; however, conservation efforts typically use individual species as their basic operational unit (e.g. the US Endangered Species Act of 1973 or IUCN Red List; but see Riddle & Hafner 1999). Consequently, efforts to monitor and inventory biodiversity in temperate latitudes have emphasized the distribution of individual species and associated communities (Kiester et al. 1996; Scott & Jennings 1998). Conservation practitioners cannot draw on similar biogeographic resources for tropical forests, and more research toward mapping, interpreting, and ultimately predicting, the distribution of species and species assemblages is needed.

The research presented in this paper addresses these issues by asking several fundamental questions in tropical landscape ecology: 1. How are species assemblages organized across an environmental gradient in a lowland forest? 2. To what extent is the composition of diverse plant communities controlled by environmental factors such as precipitation and geologic substrate? 3. What role do stochastic factors play in organizing the lowland forest landscape?

Diversity in the watershed of the Panama Canal

The lowland forest across the Panamanian isthmus is dominated by a strong climatic gradient. Average annual precipitation ranges from over 3100 mm/yr on the Caribbean coast to less than 1600 mm/yr in Panama City on the Pacific side of the isthmus (Rand & Rand 1982). Along the Caribbean coast, the precipitation regime is strongly influenced by local topography, and the highest positions on the Santa Rita ridge may receive in excess of 4000 mm/yr. The remaining strip of forest along the Canal provides an excellent transect traversing this strong climatic gradient.

The ecological expression of these climatic parameters across the isthmus is mediated by a diverse set of geologic substrates. The land forms of the Canal watershed are derived from a young and complex geologic terrain composed of either dense, relatively impermeable volcanics or porous, chemically unstable sedimentary rocks and volcanic mudflow deposits (Dietrich et al. 1982). The soils of the watershed have received only cursory investigation, and detailed soil maps do not exist for the majority of the watershed. Dietrich et al. (1982) note that dense volcanic rocks on Barro Colorado Island (BCI) form shallow soils that shift from homogeneous clays on plateaus to stony units on moderately steep slopes.

Botanical work on BCI has identified over 450 species of trees and shrubs (Croat 1978). A computerized flora produced by the Missouri Botanical Garden indicates that the Panama Canal Area contains 855 native species of trees and shrubs, while the entire Republic of Panama (77 000 km^2) contains an estimated 2870 species (Condit et al. 1996c). The United Nations Food and Agriculture Organization commissioned a map of the life zones of Panama, and the resulting work indicates the dominance of tropical moist forest at low elevation in the Canal watershed, flanked by bands of premontane wet forest (Holdridge & Budowski 1959). The Holdridge life zones were generated strictly based on a combination of bioclimatic indices and their theoretical associations with known forest categories.

Recent work on forest composition has centered on the 50-ha Forest Dynamics Plot (FDP) maintained by the Smithsonian Institution's Center for Tropical Forest Science on BCI. The FDP is a prototype for an international network of monitoring plots in more than a dozen tropical countries and has been the subject of intense research since its establishment in 1982 (Hubbell & Foster 1983). Work on BCI has developed a conceptual picture of a complex, dynamic forest with high α-diversity. The composition of the forest appears to respond quickly to climatic forcing, such as drought related to El Niño events (Condit et al. 1995a, 1996b). The relative abundance of individual species has been partially explained through combinations of inter- and intra-specific interactions (Hubbell et al. 1990; Condit et al. 1994; Wills et al. 1997), tree-fall and gap-dynamics (Dalling et al. 1998), habitat specialization (Hubbell & Foster 1983), and dispersal limitation (Harms 1997; Hubbell et al. 1999).

Methods

Floristic data

The data used for the following analyses were collected from 54 plots distributed across the watershed of the Panama Canal (Fig. 1). The plots were anchored around three intensively surveyed sites at Fort Sherman (Caribbean-side of isthmus), BCI (mid-isthmus), and Gamboa (Pacific-side of the isthmus). These locations have large, permanent plots of sizes 6, 50, and 4 ha respectively. All of the plots at Fort Sherman and Cocoli were included in the sample, as well as six 1-ha samples from within the 50-ha Forest Dynamics Plot on BCI. The sample from BCI represents the range variation in soils, topography, and stand age found across the site. An additional 29 1-ha plots were established between

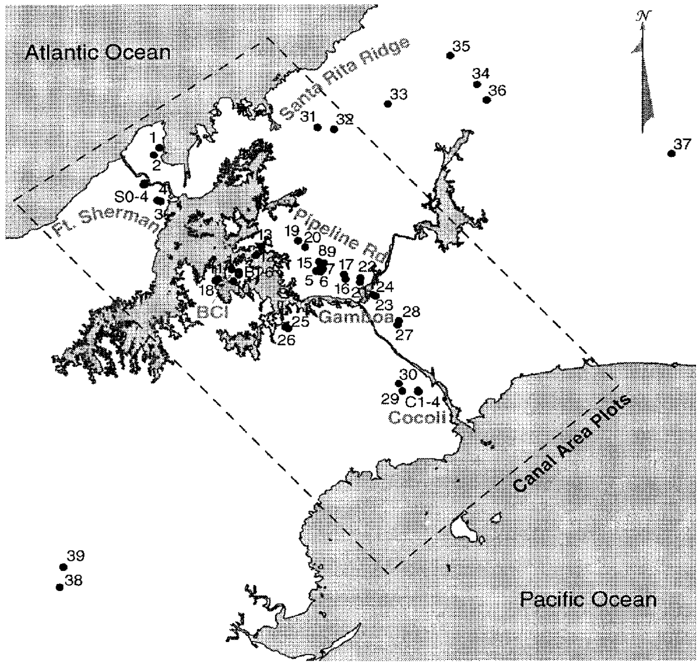

Fig. 1. Extent of the watershed of the Panama Canal and location of 54 inventory plots (Universal Transverse Mercator Zone 17P).

these permanent sites. All the new plots were placed within 5 km of the Panama Canal. Each plot was established as a 100 m × 100 m square with a regular grid of survey markers at 20-m intervals. Nine additional 0.32-ha plots were established farther out in the Canal watershed (> 5 km from the center line of the Canal). These 0.32-ha plots were sampled in the same way as the larger Canal Area plots with the exception of their smaller size. Within each plot, trees ≥ 10 cm diameter at breast height (DBH) were identified to species, tagged, and located with respect to the local grid. Tree specimens from all locations were identified with reference to material maintained by the Smithsonian Tropical Research Institute and the University of Panama. The elevation of each plot was noted and the surrounding terrain was characterized as flat, sloping, or irregular. The age of each stand was inferred from the size of the largest trees and recorded as young, secondary, or old growth. The protocols used for fieldwork and data handling follow those developed for the 50-ha Forest Dynamics Plot on BCI (Condit 1998).

Fisher's alpha and Shannon index of diversity are used to describe the nature of richness in these plots. Fisher's alpha assumes that the abundance of species fits a log-series distribution, and uses this assumption to normalize for sample size and area (Fisher et al. 1943; Rosenzweig 1995; Condit et al. 1998). The Shannon index (H') is based on the proportional abundance of species, and it is related to species richness but it is also influenced by the distribution of species abundance (Magurran 1988). Both indices are provided to facilitate comparisons with other studies.

Environmental data

Each sampling site was characterized with respect to three primary environmental variables: median annual precipitation (mm), cumulative dry season precipitation (mm/December-May), elevation, and geology. A limited set of ancillary data was collected from 23 plots, including pH, depth of A-horizon, color, texture, consistence, and profile morphology. Table 1 summarizes the environmental data available for each plot.

Median annual precipitation was interpolated from meteorological data available from 20 stations within the Panama Canal watershed. A multiple regression model incorporated geographic coordinates (Universal Transverse Mercator, UTM) and plot elevation to predict total annual precipitation:

$$y_{total} = -17543 - 0.006x_1 + 0.023x_2 + 1.378x_3 \qquad (1)$$

Where y_{total} is total annual precipitation in mm per year, x_1 is the UTM Easting, x_2 is UTM Northing, and x_3 is elevation in m; $R^2 = 0.90$. The precipitation interpolation procedure was repeated for a simple index of total dry season precipitation (Eq. 2). The goal was to create a complementary climatic index correlating with the degree of seasonality (i.e., severity of dry season) experienced by each plot. Graphical plots of annual precipitation accumulation (data not presented) indicate that the maximum separation between station observations occurred by integrating rainfall between December and May, even though the dry season typically ends by late April. The model formulation was similar to the total annual precipitation interpolation model, and it obtained

Table 1. Environmental variables and summary statistics for all plots used in the analysis. Topography: 1 = level terrain, 2 = sloping, 3 = irregular. Age: 1 = secondary forest, 2 = mature secondary, 3 = old growth, primary forest. Precipitation (Ppt): annual precipitation estimated from Eq. 1; dry season precipitation estimated from Eq. 2.

Plot Name	Locality (see Fig. 1)	UTM x	UTM y	Size ()	No. of Stems	No. of Species	Fisher's α	Snnon (H')	Topography	Age	Geology	Ppt (mm) dry season	Ppt (mm) annual
B1	BCI	626200	1011800	1.0	400	84	31.41	3.13	2	3	Tb	697	2589
B2	BCI	626200	1011900	1.0	409	90	35.67	3.90	2	3	Tb	696	2586
B3	BCI	626200	1012000	1.0	365	98	40.91	3.82	2	3	Tb	695	2579
B4	BCI	626200	1012100	1.0	450	87	33.92	4.06	2	3	Tb	693	2572
B5	BCI	626200	1012200	1.0	364	93	32.80	3.43	2	3	Tb	697	2594
B5	BCI	626200	1012300	1.0	480	75	22.67	3.62	2	3	Tb	697	2589
C1	Coccoli	651917	993636	1.0	380	50	17.48	3.95	3	1	pT	524	1888
C2	Coccoli	651927	993636	1.0	560	49	17.96	3.54	3	1	pT	525	1890
C3	Coccoli	651937	993636	1.0	503	57	23.57	3.91	3	1	pT	525	1892
C4	Coccoli	651947	993636	1.0	403	58	21.49	3.65	3	1	Tb	524	1887
1	Ft. Sherman	614857	1031786	1.0	449	63	21.02	3.43	1	2	Tct	720	2993
2	Ft. Sherman	628587	1014891	1.0	520	84	32.03	3.33	3	3	Tc	780	3072
3	Ft. Sherman	629529	1015836	1.0	647	74	28.02	2.44	3	1	Tc	811	3007
4	Ft. Sherman	625125	1012545	1.0	381	94	54.76	3.93	3	1	Tc	810	3000
5	Pipeline	637158	1012428	1.0	531	71	26.33	3.75	2	2	Tgo	621	2414
6	Pipeline	637984	1012395	1.0	484	78	26.41	3.55	3	2	Tgo	612	2394
7	Pipeline	638144	1012886	1.0	526	93	39.27	3.81	3	1	Tgo	638	2438
8	Pipeline	637732	1013699	1.0	954	94	32.32	3.06	3	3	pT	635	2456
9	Pipeline	638365	1013754	1.0	424	107	41.60	3.53	3	3	pT	924	2889
10	BCI	637861	1012976	1.0	457	78	28.81	3.89	1	2	Tcm	667	2529
11	BCI	641464	1011328	1.0	467	75	25.73	3.70	3	3	Tcm	647	2516
12	BCI	641108	1011888	1.0	461	74	23.59	3.02	3	2	Tbo	618	2497
13	BCI	622785	1010903	1.0	429	60	16.15	3.89	3	2	Tcm	659	2576
14	BCI	625209	1012640	1.0	519	92	38.53	3.66	1	3	Tcm	652	2535
15	Pipeline	637878	1012775	1.0	534	91	34.13	3.70	1	3	Tgo	646	2455
16	Pipeline	643560	1010755	1.0	405	90	33.17	3.76	3	3	pT	707	2502
17	Pipeline	643599	1011461	1.0	508	63	19.73	3.37	3	3	pT	679	2471
18	Pipeline	645805	1008575	1.0	579	86	32.37	2.70	1	2	Tcm	645	2511
19	Pipeline	645416	1008797	1.0	557	89	30.92	2.95	3	1	pT	743	2688
20	Pipeline	632003	1003751	1.0	593	90	31.01	3.80	3	1	pT	737	2658
21	Gamboa	633322	1003529	1.0	485	78	28.73	3.41	3	1	Tgo	662	2411
22	Gamboa	648907	1004027	1.0	393	75	24.30	3.45	3	1	Tb	722	2514
23	Gamboa	649196	1004697	1.0	408	60	16.82	3.33	3	2	Tlc	585	2248
24	Gamboa	649678	993573	1.0	355	60	17.07	3.33	3	2	Tlc	602	2280
25	Gamboa	632900	1003600	1.0	302	84	26.26	3.16	3	2	pT	641	2334
26	Gamboa	637474	1034700	0.25	466	76	25.30	4.55	3	2	pT	591	2252
27	Gamboa	649003	1003838	0.25	148	61	20.21	4.40	3	1	Tl	681	2305
28	Gamboa	649245	1004503	0.25	191	62	20.35	4.11	3	1	Tl	668	2294
29	Coccoli	649717	993540	0.25	172	65	23.33	3.79	3	1	Tb	568	1969
30	Coccoli	649221	994670	0.25	186	64	24.83	3.98	3	1	Tb	638	2096
31	Santa Rita	637514	1034795	0.25	254	152	48.72	4.06	1	3	pT	*	*
32	Santa Rita	639892	1034555	0.25	257	96	60.14	4.20	3	3	pT	*	*
33	Santa Rita	647620	1038454	0.25	267	86	55.86	4.24	4	3	pT	*	*
34	Outer watershed	660393	1041453	0.25	202	68	34.12	3.78	4	3	pT	*	*
35	Outer watershed	656577	1045987	0.25	288	81	17.48	3.17	3	3	pT	*	*
36	Outer watershed	661790	1039037	0.25	257	89	17.96	2.96	3	3	pT	*	*
37	Outer watershed	688165	1030609	0.25	241	100	23.57	3.29	3	3	pT	*	*
38	Outer watershed	600714	962862	0.25	298	98	21.49	3.24	4	1	pT	*	*
39	Outer watershed	601167	966019	0.25	480	66	31.61	3.83	4	1	pT	*	*
S0	Ft. Sherman	612610	1026067	1.0	409	88	31.61	3.76	3	2	Tc	792	3026
S1	Ft. Sherman	612713	1025857	1.0	408	81	26.63	3.97	3	2	Tc	792	3026
S2	Ft. Sherman	612713	1025957	1.0	407	65	20.20	3.74	3	2	Tc	792	3028
S3	Ft. Sherman	612713	1026057	1.0	526	75	23.92	3.42	3	2	Tc	793	3030
S4	Ft. Sherman	612713	1026157	1.0	597	70	17.40	2.65	3	1	Tc	793	3032

* These values are not available. Interpolated May precipitation and annual precipitation were not considered reliable for plots at the margins of the watershed given the limited distribution of meteorological stations.

an equivalent fit to the input data:

$$y_{dry} = -1464 - 0.0005x_1 + 0.019x_2 + 0.1148x_3 \qquad (2)$$

In this model, y_{dry} is the cumulative dry-season precipitation in mm, and R^2 was 0.90.

These measures of moisture availability were primarily chosen because only a limited data set was available from all rainfall stations (geographic coordinates, elevation, and monthly average precipitation). There are many alternative measures (e.g. days for which evapotranspiration exceeds precipitation, months with less than 100 mm total precipitation, etc.), but all these measures reflect the strength of the dry season and are probably highly correlated with one another (Walsh 1996).

All geologic information was based on a United States Geological Survey map of surficial geology for the Panama Canal and vicinity (Woodring et al. 1980). The map was drawn to a scale of 1:100 000 and digitized

Table 2. The attributes of geologic units described for plots in Table 1. Age given in million years.

Map code	Unit name	Geologic Series	Approximate age (stage) (myr)	Description
Tc	Chagres sandstone	Late Miocene or Early Pliocene	10 (Lower Tortonian) to 3.5 (Upper Zanclean)	Massive, generally fine grained sandstone
Tct	Toro limestone (basal member of Chagres sandstone)	Late Miocene or Early Pliocene	10 (Lower Tortonian) to 3.5 (Upper Zanclean)	Coquina
Tb	Miocene basalt	Middle to Late Miocene	16.2 (Lower Langhian) to 5.0 (Upper Messinian)	Intrusive and extrusive basalt
Tl	La Boca formation	Early Miocene	25.2 (Lower Aquitanian) to 16.2 (Upper Burdigalian)	Siltstone, sandstone, tuff and limestone
Tlc	Las Cascadas formation	Early Miocene	25.2 (Lower Aquitanian) to 16.2 (Upper Burdigalian)	Agglomerate and tuffaceous siltstone, tuff, and foraminiferal limestone
Tcm	Caimito formation	Late Oligocene	30 (Lower Chattan) to 25.2 (Upper Chattan)	Tuffaceous sandstone, tuffaceous siltstone, tuff, and foraminiferal limestone
Tbo	Bohio formation	Early to Late Oligocene	36 (Lower Rupelian) to 25.2 (Upper Chattan)	Conglomerate, principally basaltic and graywacke sandstone
Tgo	Gatuncillo formation	Middle to Late Eocene	54 (Lower Ypresian) to 36 (Upper Priabonian)	Mudstone, siltstone, quartz sandstone, algal and foraminiferal limestone
pT	Pre-Tertiary basalt	Pre-Tertiary	> 66.5 (Mesozoic)	Altered basaltic and andesitic lavas and tuff, includes dioritic and dacitic intrusive rocks

as a part of the US. Agency for International Development/INRENARE Project to Monitor the Watershed of the Panama Canal (Condit et al. subm.). Nine different lithologic units are represented in the 54 monitoring plots (Table 2). Preliminary field data collected for this study suggest regional changes in soil attributes in response to the rainfall gradient. At the watershed scale, soil pH declines with increasing annual rainfall. Deviations from this trend are not predictable from mapped parent lithology or geomorphic position, and they may result from unusual land-use histories. Edaphic conditions across the isthmus remain poorly constrained, and ecological studies at the landscape scale would benefit from a campaign of soil mapping and pedological study.

Multivariate techniques for phytosociology and gradient analysis

Four methods were used to explore floristic structure within large tree assemblages in the watershed of the Panama Canal: (1) indirect, multivariate ordination, including Non-metric Multidimensional Distance Scaling (NMDS) and Detrended Correspondence Analysis (DCA); (2) percentage of species with locally restricted ranges; (3) Mantel tests; (4) semi-variogram analyses of spatial structure. These techniques were implemented using the PC-ORD software package (version 3.18, McCune & Mefford 1999) and the S-plus statistical programming language (version 4.0; Anon. 1997). The Sørensen similarity measure was used for cluster and NMDS analysis. Sørensen similarity is annotated as $2A/(2A+B+C)$, where A is the number of species shared between plots and B and C are the number of species unique to each plot.

An initial NMDS ordination was performed for all 54 plots across the study area. These ordinations clearly showed a floristic gradient for a subset of the study plots, and the analyses were supplemented by a more detailed gradient analysis focused on the 45 1-ha plots adjacent to the Canal. The focused gradient analysis facilitated a more detailed investigation of environmental controls on forest composition, one not possible with the relatively unreliable environmental data available for the outer edges of the watershed. The NMDS gradient analysis was complemented by the use of Detrended Correspondence Analysis (DCA). DCA was used to evaluate relationships between species, genus, and family levels of taxonomic organization and observed patterns of floristic composition across the rainfall gradient. DCA provides eigenvalues that can be used to estimate gradient length (Eilertsen et al. 1990), a feature not available in NMDS. However, analysis of DCA ordination was restricted to only the first ordination axis, as DCA has well-known distortions for higher axes (Hill & Gauch 1980; Gauch. 1982). Mantel tests were also used to examine the relationship between precipi tation and forest composition. The input included Sørensen similarity between plots in the first matrix and differences in annual precipitation in the second matrix. While not providing graphical output, the Mantel tests have the benefit of providing complementary statistical information about relationships in the data. Overall, this ensemble of techniques provides a diverse set of data for assessing community patterns.

The NMDS ordination technique places samples in relative positions in ordination space, rather than fitting axes based on sample eigenvalues or other methods for partitioning sample variance. Previous workers have noted that NMDS performs well in data sets with high beta diversity and noisy environmental information (Prentice 1977, 1980). NMDS analysis is constrained by relatively few assumptions about the nature of data to be analysed. However, this strategy also means that NMDS ordination axes do not have a clear, hierarchical relationship with sample variance. This limitation can be mitigated by processing the raw axis scores with Principal Components Analysis (PCA). PCA was performed on two-dimensional NMDS scores to align axes within the cloud of points and center their values around a mean of zero. Overall, 'centered' NMDS provided the best fit between ordination axis scores and environmental parameters, while DCA supplied eigenvalues indicating relative axis strengths for the subset of 45 Canal Area plots. All analyses used the Sørensen similarity index as a distance measure and considered only species presence or absence.

Levels of endemism were evaluated for floristic groups identified through cluster analysis and ordination. For the purposes of this analysis, tree species were considered endemic if they occurred only within the sub-region in question (e.g., Barro Colorado Island) and nowhere else in the network of sampling plots. The restricted range designation used in this analysis was independent of a species' regional or global distribution.

Mantel tests and semi-variogram analysis were also used to evaluate aspects of the spatial structure of the lowland forest. The Mantel test evaluated two matrices, one providing geographic distances between samples and another providing Sørensen similarity distance. The two distance tables are compared in aggregate to determine the strength and significance of correlations between the matrices. Test output indicates the relative magnitude and direction of the relationship in terms of the distribution of the Student *t* statistic. Semi-variograms provide graphical information about the nature of spatial autocorrelation within a set of measurements in geographic space. Models fit to variogram output can also help define the spatial scale of particular processes of interest, particularly the ranges over which samples in a specific location have predictive power about their surrounding neighborhood. For this project, semi-variograms were prepared for first axis NMDS scores in geographic space using the S-plus Spatial Statistics module (Anon. 1997).

Results

Patterns of diversity

We found high levels of floristic diversity with a rapid turnover of species across the lowland landscape. The 54 plots contained 22 736 individual trees from 824 species. On average, each plot contained 421 stems and 79 species. All forest plots show high diversity by multiple measures, including Fisher's α and the Shannon diversity index H'. In this study area, neither of diversity indices has a simple relationship with precipitation or other available environmental variables. The tropical moist forest and pre-montane forest life zones have contrasting floristic assemblages, and Table 3 illustrates the absence of overlap between the ten most frequent species found in each life zone. Species ranked in Table 4 illustrate the diversity of species composition found *within* three large sites in the tropical moist forest life zone.

Watershed floristic patterns

NMDS ordination produced a dense cluster of plots stretching from the dry sites at Cocoli to the wet Caribbean plots at Fort Sherman (Fig. 2), and a more diffuse group containing the outer watershed plots stretched along a second axis. These floristic divisions are supported by patterns of species accumulation within the watershed. Abrupt increases in species accumulation rates are known to occur when crossing ecotones and boundaries between contrasting floristic areas. The 50-ha forest dynamics plot on Barro Colorado Island contains 229 species of trees ≥ 10 cm DBH, and the addition of 39 ha along the Canal brings the total to 417 species. A further addition of only 2.5 ha (one 1-ha plot and eight 0.32-ha plots) from the outer watershed plots increases the total to 824 species (i.e. 824 species on 41 ha). The restricted local ranges observed for many species further support this relationship (Fig. 3). Species found in the outer watershed plots were not observed in the

Table 3. Most frequently occurring species within plots in the tropical moist forest and premontane forest life zones (*S* = Percent Occupancy in 45 plots within the life zone).

	Tropical moist forest life zone				Premontane wet forest life zone			
Rank	Family	Species	*S* (%)	Total stems	Family	Species	*S* (%)	Total stems
1	*Burseraceae*	*Protium tenuifolium*	84	321	*Rhizoporaceae*	*Cassipourea elliptica*	18	76
2	*Myristicaceae*	*Virola sebifera*	84	356	*Arecaceae*	*Socratea exorrhiza*	18	694
3	*Arecaceae*	*Oenocarpus mapora*	82	568	*Clusiaceae*	*Tovomita longifolia*	18	178
4	*Meliaceae*	*Trichilia tuberculata*	73	283	*Meliaceae*	*Carapa guianensis*	16	54
5	*Olacaceae*	*Heisteria concinna*	71	352	*Araliaceae*	*Dendropanax arboreus (stenodontus)*	16	199
6	*Tiliaceae*	*Luehea seemannii*	67	140	*Arecaceae*	*Iriartea deltoidea*	13	52
7	*Burseraceae*	*Protium panamense*	67	370	*Cecropiaceae*	*Pourouma bicolor (guianensis)*	13	146
8	*Rubiaceae*	*Alseis blackiana*	64	256	*Arecaceae*	*Welfia regia (georgii)*	13	151
9	*Arecaceae*	*Astrocaryum standleyanum*	64	397	*Moraceae*	*Brosimum utile*	11	196
10	*Moraceae*	*Brosimum alicastrum*	64	90	*Ochnaceae*	*Cespedezia macrophylla*	11	66

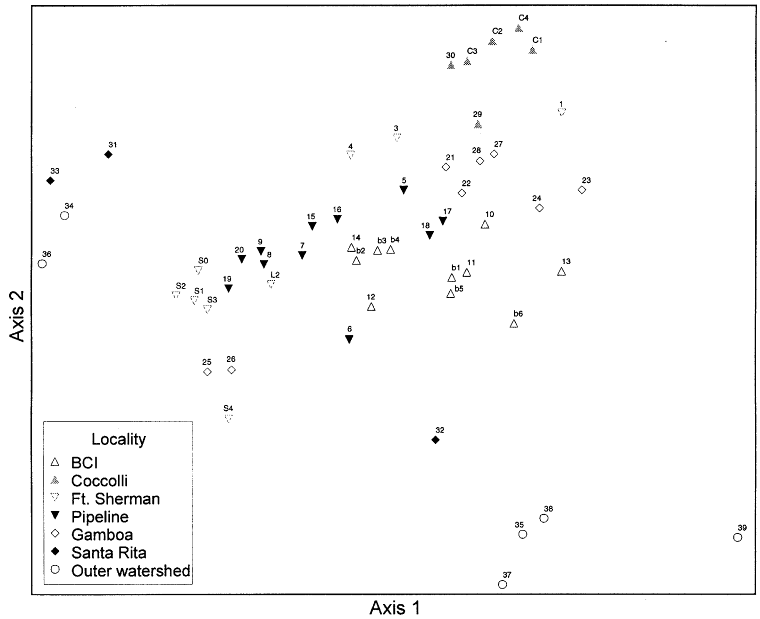

Fig. 2. Non-metric Multidimensional Distance Scaling of 54 1-ha monitoring plots in the Panama Canal watershed. Symbols for reference locations as in Fig. 1. Plots m33 - m39 are in the premontance wet forest/tropical montane wet forest. All plots along the primary wet-dry axis are included in the tropical moist forest life zone (Holdridge & Budowski 1959).

dense set of plots closer to the Canal. This contrasts with the situation along the Canal where, despite the lack of any omnipresent species, many trees occur in multiple plots across the climatic gradient.

Gradient analysis

A clear pattern of floristic compositions was identified through indirect gradient analysis. The strongest gradient appears to run between Fort Sherman and Cocoli, paralleling the regional trends in precipitation and dry season severity. The first axis of a 45 plot, centered NMDS solution was best fit by median annual precipitation (p-value < 0.001, R^2 = 0.62, n = 45) (Fig. 4). Substituting the alternative dry-season precipitation index (cumulative May precipitation) resulted in a slightly worse fit to the NMDS scores (p-value < 0.001, R^2 = 0.53, n = 45). This relationship was also significant in a Mantel test. A randomized Monte Carlo method rejected the null hypothesis (no effect by precipitation) at a level of alpha = 0.95 (Standardized Mantel statistic, r = 0.879, p = 0.001). Consequently, the test supports a strong, positive association between differences in precipitation and floristic distance as measured by the

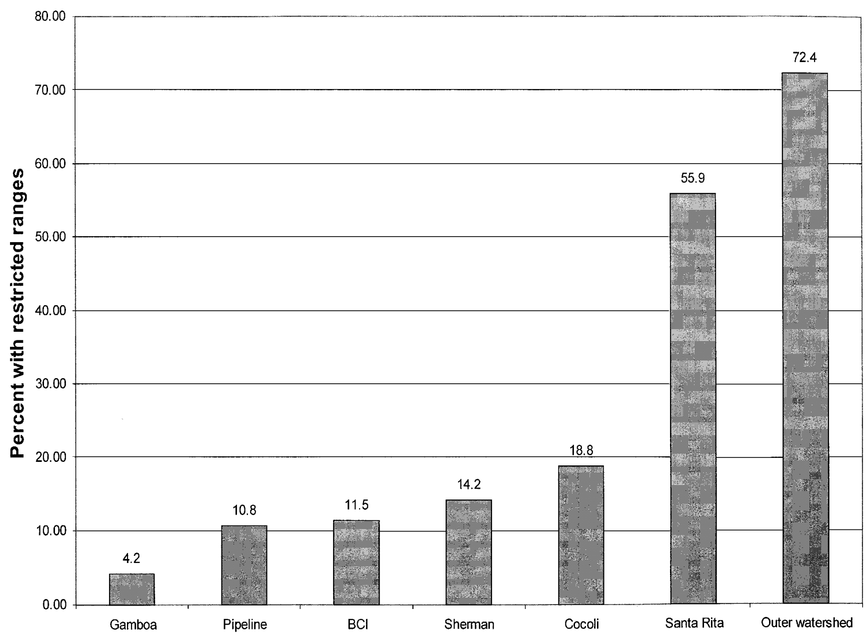

Fig. 3. Percentage of species restricted to a given floristic area within the Canal watershed. In this case, species with restricted ranges occur only in the indicated area and nowhere else in the study watershed. The local distribution of these species may not be indicative of their regional or global distribution. Locations are identified in Fig. 1.

Table 4. Comparison of the most abundant species within three well-sampled areas, BCI, Cocoli and Fort Sherman, in the tropical moist forest life zone. Second row: number of 1-ha plots. Third row: Nr. of stems.

	BCI	Cocoli	Fort Sherman
	6	4	6
	2558	1085	3239
Rank			
1	*Acacia 2* (*Fabaceae*)	*Mammea immansueta* (*Sapotaceae*)	*Pouteria 34* (*Clusiaceae*)
2	*Acacia melanoceras* (*Fabaceae*)	*Mangifera indica* (*Anacardiaceae*)	*Pouteria 35* (*Sapotaceae*)
3	*Acacia riparia* (*Fabaceae*)	*Manilkara bidentata* (*Sapotaceae*)	*Pouteria 36* (*Sapotaceae*)
4	*Acalypha diversifolia* (*Euphorbiaceae*)	*M. zapota* (*Sapotaceae*)	*Pouteria 37* (*Sapotaceae*)
5	*Acalypha macrostachya* (*Euphorbiaceae*)	*Maquira costaricana* (*Moraceae*)	*Pouteria 4* (*Sapotaceae*)
6	*Adelia triloba* (*Euphorbiaceae*)	*Marila 1* (*Clusiaceae*)	*Pouteria 7* (*Sapotaceae*)
7	*Aegiphila anomala* (*Verbenaceae*)	*Marila 2* (*Clusiaceae*)	*Pouteria 8* (*Sapotaceae*)
8	*Aegiphila panamensis* (*Verbenaceae*)	*Marila 3* (*Clusiaceae*)	*Pouteria 9* (*Sapotaceae*)
9	*Aiouea 1* (*Lauraceae*)	*M. domingensis* (*Clusiaceae*)	*P. buenaventurensis* (*Sapotaceae*)
10	*Albizia adinocephala* (*Fabaceae*)	*M. lactogena* (*Clusiaceae*)	*P. campechiana* (*Sapotaceae*)

Sørensen similarity measure. As geographic distance and precipitation are closely linked in this landscape, the Mantel test cannot decouple their effects (see Spatial Structure below). A Mantel test comparing geographic distance and annual precipitation distance indicated a very strong positive association (Standardized Mantel statistic, r = 0.878, p = 0.001).

First axis DCA scores indicated the same strong indirect gradient identified by NMDS (Fig. 5). DCA provided additional information about the strength of the derived axes. DCA was used to estimate the strength of the floristic gradient across levels of taxonomic organization. At the species level, DCA returned a first axis eigenvalue of 0.70 (Fig. 6). Aggregating species to genera produced a weaker indirect gradient (Axis 1, eigenvalue 0.59; Fig. 6). Families provided the weakest response, and the DCA generated only a diffuse cloud of points with limited gradient structure (Axis 1, eigenvalue: 0.34; Fig. 7). Mantel tests were again applied to examine the correlation between geographic distance and similarity, this time across levels of floristic organization. Mantel's asymptotic approximation methods indicated significant correlations at the alpha = 0.05 level for only the species scores. The genera and family-level aggregations did not have significant spatial structure (Table 5). This interesting pattern cannot be fully decoupled from species-level gradient responses. Most genera (165 out of a total of 231 genera) and some families (23 families out of a total of 69 families) were represented by only a single species. Taxonomic aggregation has no impact on these taxa, and species-level responses continue to contribute to the higher-level ordinations. The vestigial gradient structure apparent in the genera and, especially family-level, ordinations may be produced primarily by these monotypic taxa.

Spatial structure

The Mantel tests indicate that in aggregate, the lowland forest is strongly spatially structured. We can apply a different set of tools to investigate these patterns in more detail. Scatter plots comparing floristic similarity and geographic distance indicate that forest composition changes very quickly as one moves away from any given plot (Fig. 8).

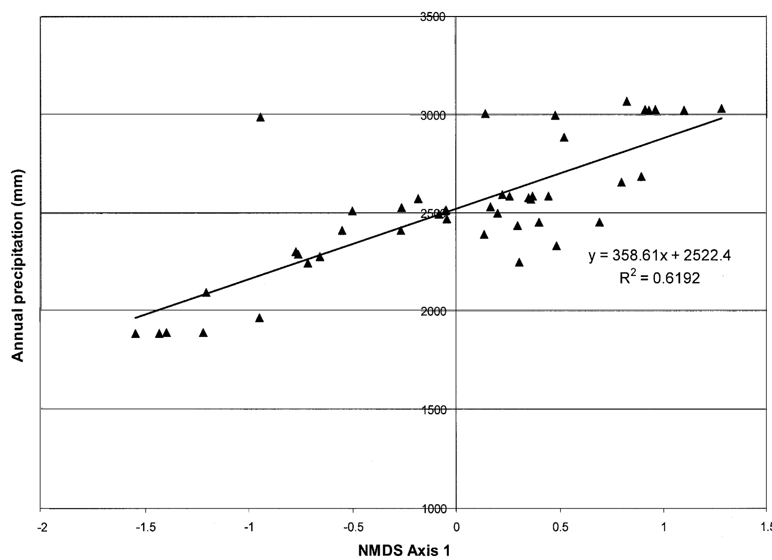

Fig. 4. Scatter plot illustrating the correlation between interpolated total annual precipitation (Equation 1, y_{total}) and axis-1 NMDS scores. Note, the NMDS scores used for this analysis were derived from a separate analysis for only the 45 Canal Area plots.

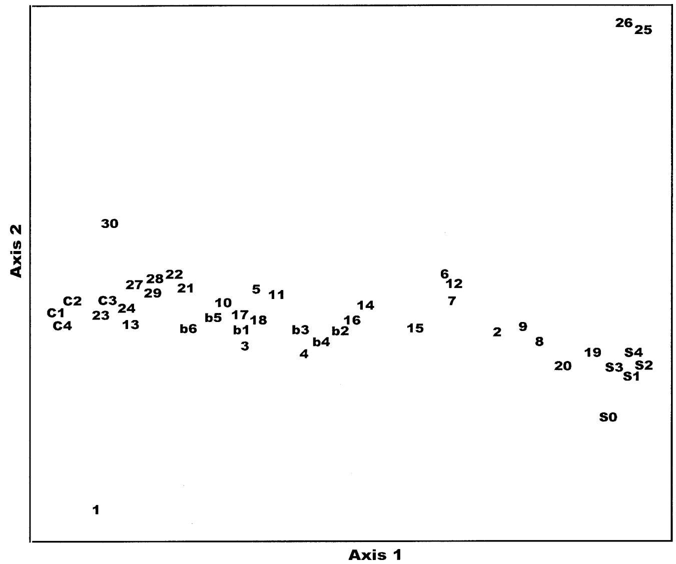

Fig. 5. Detrended Correspondence Analysis for 45 lowland plots and 417 species. Eigenvalue for Axis 1 = 0.7027.

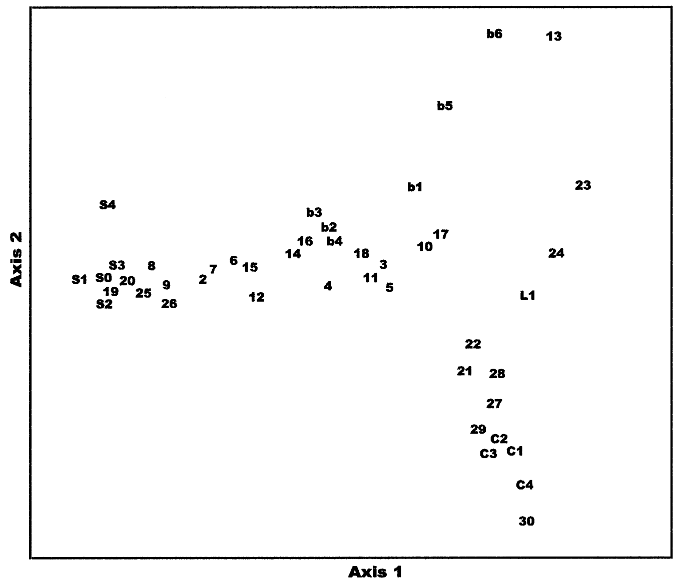

Fig. 6. Detrended Correspondence Analysis of 45 plots based on 231 genera. Eigenvalue for Axis 1 = 0.5925.

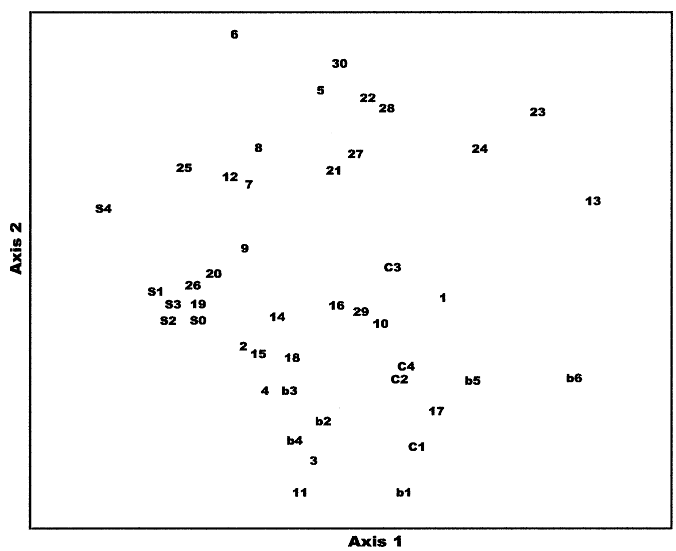

Fig. 7. Detrended Correspondence Analysis of 45 plots based on 68 families. Eigenvalue for Axis 1 = 0.3404.

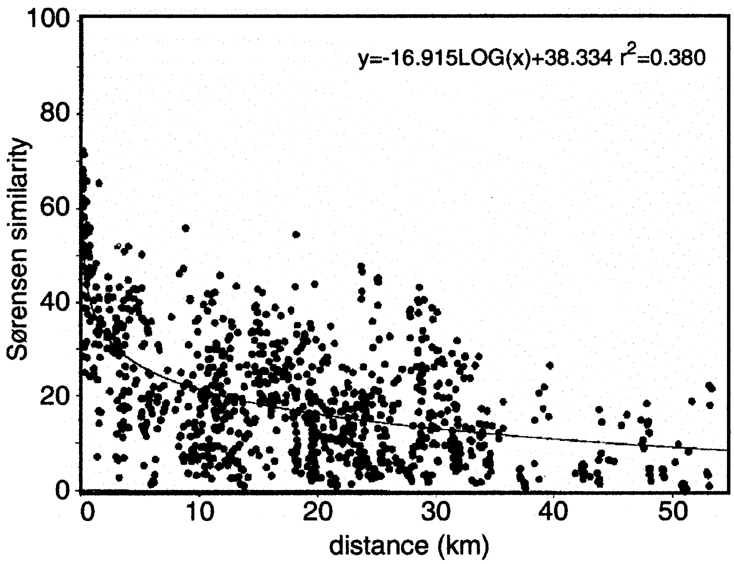

Fig. 8. Scatter plot analysis indicating the decay of floristic similarity with distance.

However, these simple figures are partially confounded by the fact that climatic conditions and geographic distance are highly correlated across the lowland landscape (e.g. plots far apart tend to have dissimilar climate). Fig. 9a illustrates a semi-variogram for first-axis NMDS ordination scores. The data climb in a linear fashion and no sill is visible. This pattern suggests that the data are dominated by a global trend across the samples. This obviously supports the results of the gradient analysis showing the overriding influence of the precipitation gradient and its correlates. We can remove this global trend by using the regression model (Eq. 1) fitted to the first-axis NMDS scores. After subtracting the predicted model values, we then evaluated the spatial structure of the model residuals. The residual semi-variogram in Fig. 9b presents a different picture of the landscape: a sill appears in the variogram at ca. 5-km distance. This indicates local spatial autocorrelation in species composition extending out 5 km around sampled locations. This autocorrelation manifests itself as local-scale variations in species composition superimposed on landscape-scale patterns dominated by climatic and geologic factors.

Table 5. Mantel scores and statistics for three levels of taxonomic aggregation along the trans-isthmian gradient. The test compares a similarity matrix with a matrix of geographic distances. In this case, the null hypothesis is that distance does not predict similarity. This is rejected for species, but not genera or families.

Level of aggregation	Mantel's asymptotic approximation	Equivalent *t*-statistic	*P*-value
Species	0.098	2.268	0.024
Genera	0.084	1.825	0.068
Family	0.862	0.862	0.389

Discussion

Regional forest classification

In the tropics, difficult plant taxonomy and logistical considerations have frequently led to the use of physiognomic and climatic parameters for the classification of tropical vegetation (Holdridge et al. 1971; Weishampel et al. 1990; Mackey 1993, 1994). These systems often do not explicitly consider the species composition of various forest types, and their applicability to botanical investigations is an area of research. Conservation practice, including international conventions for the protection of biodiversity, typically emphasize the protection of individual species. Consequently, research must assist in linking regional physiognomic assessments (e.g., based on remote sensing or climatic parameters) to species-level biology. This study indicates that established bioclimatic Life Zones (Holdridge & Budowski 1959) adequately describe major subdivisions in the flora of lowland Panama. However, the Holdridge Life Zones have minimal provisions for accommodating continuous change within units. As such, they mask intra-unit variability, and consequently, forest composition along the Panama Canal. This investigation indicates the positive aspects of Life Zone classification at regional scales, while simultaneously highlighting its inadequacy for finer scales of analysis and resource management.

Controls on lowland forest composition

The data presented here strongly suggest the dominance of environmental controls as drivers of species assemblage. While this study indicated the importance

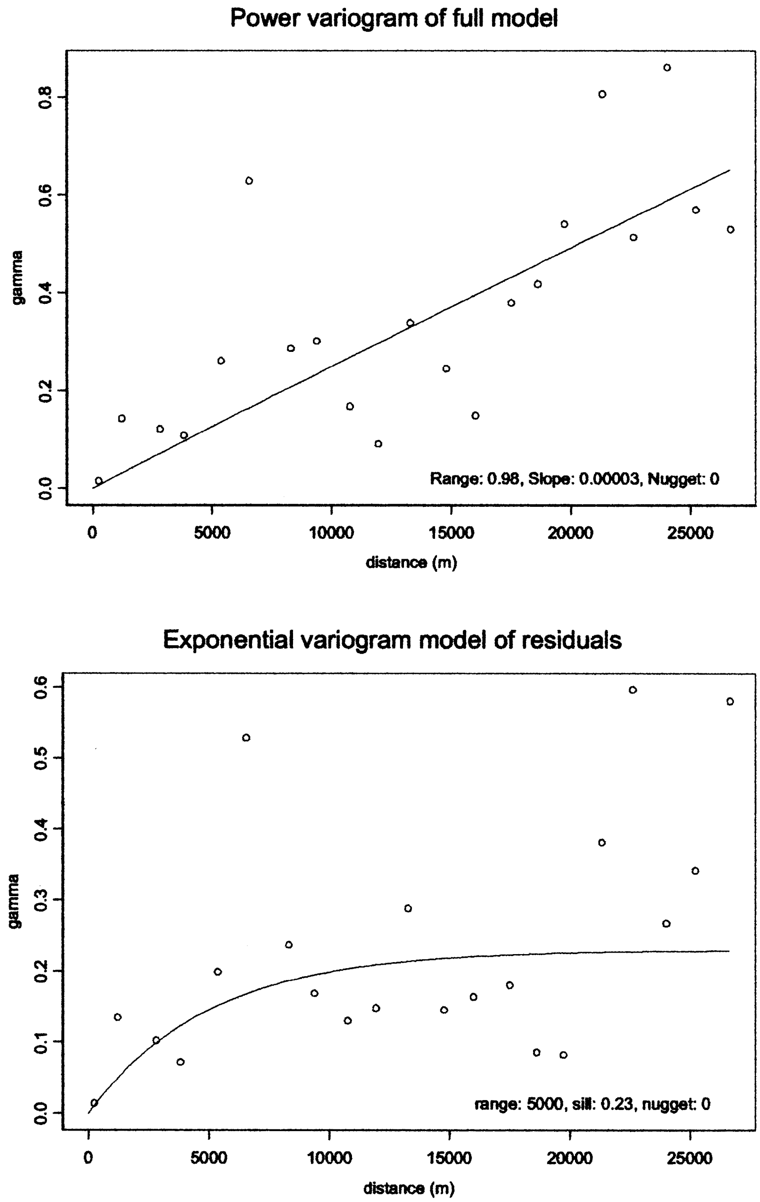

Fig. 9. Semi-variogram analysis of NMDS axis 1 scores across the 45 Canal Area 1-ha plots. **a.** Semi-variogram for NMDS scores, the lack of a sill indicates the presence of a spatial trend in the data. **b.** Semi-variogram for NMDS axis 1 residuals after the precipitation trend was removed – NMDS axis 1 = – 4.3553 + 0.0017 * medppt, ($r^2 = 0.6192$, *F*-statistic *p*-value = $1.47*10^{6}$).

of distance affects over relatively short distances (< 5 km), only precipitation and geology were useful for predicting species-level floristic variation at broader scales. Two specific observations reinforce these conclusions about the organizing role of regional watershed environmental gradients. Plot L1 is located on the Caribbean side of the isthmus on shallow, presumably droughty, limestone soils. The flora sampled at L1 is most similar to plots 50 km away on the drier, Pacific side of the isthmus, while the surrounding Fort Sherman forest is more closely allied with the wettest sites on the Santa Rita ridge. The L1 example provides an instance of a relatively dry forest type occurring in an area dominated by wet forest assemblages. Plots m25 and m26 reverse this example by illustrating the presence of floristically wet forest in an area nominally associated with a relatively dry species assemblage. Despite being surrounded by typical mid-isthmus forest at Pipeline Road, and Barro Colorado Island, these plots support tree assemblages most similar to Fort Sherman on the wet Caribbean coast. Plots m25 and m26 straddle ridge and summit hillslope positions, and nothing in the local terrain indicate that they receive significantly more moisture than the nearby Pipeline Road forest. Plots m25 and m26 do share one important attribute with floristically similar plots on Fort Sherman: acidic soils. The soils underlying plot m25 and m26 have pH values much closer to the Fort Sherman plots (~ pH 4.6) than the nearby BCI and Pipeline Road plots (~ pH 5.7). These unreplicated observations suggest that the forest composition may be sensitive to soil factors correlated with soil acidity rather than simply precipitation. Both sets of observations suggest that dispersal limitation is a secondary driver of floristic organization at the landscape scale.

These examples could be considered in light of a pair of biogeographic hypotheses. The dry forest at L1 or the wet forest at plots 25 and 26 may be refugial distributions. For example, at some point in the past the entire region may have been suitable for the drier forest assemblage. Subsequent changes in climate may have forced remnants of the biota into suitable, but restricted, microsites. If L1 is actually a dry forest refugia, one could hypothesize that the modern Pacific coast forest once covered the entire isthmus during drier climatic conditions. The argument would follow that changes in climate lead to increased precipitation and the expansion of a wet forest type that has replaced the drier forest. The Pacific coast forest-type survives in the L1 micro-site conditions that are inhospitable to the now dominant Caribbean forest-type. Differences between L1 and the modern Pacific coast forest sampled at Cocoli could be explained with evolutionary phenomena such as founder effects, genetic drift, local selective pressures, or simply sampling effects between diverse plots with limited replication. If the refugial hypothesis holds, we must then imagine that the climate has oscillated from wet to dry in the past, allowing first the Pacific forest elements to spread north, then the Atlantic forest elements to spread south. Alternatively, it is possible that the L1 forest was established under relatively constant climatic conditions by long distance dispersal from a source forest on the Pacific side. Differences between the Cocoli plots and L1 forest might then be explained as artifacts from sampling among trees with different dispersal vectors and colonization abilities. Similar arguments could be applied to the patch of wet forest at plots 25 and 26.

Initially, the dispersal hypothesis appears unlikely given contemporary characterizations of the dispersal abilities of lowland tree species (Harms 1997; Hubbell et al. 1999). However, the situation is complicated by a diverse landscape mosaic that provides many possible locations for dry forest refugia (e.g., outcrops of limestone or other well-drained substrates), and consequently, might facilitate dispersal through a series of ‘jumps’. The climate-shift hypothesis may be supported by palaeoclimatic evidence (Bush & Colinvaux 1990; Haberle & Maslin 1999). Three periods of recent large-scale floristic reorganization have been identified in the Panamanian lowland: 14 300-13 500 yr BP, 11 000-10 300 yr BP, and < 10 000 yr BP – human disturbance during the Holocene (Bush & Colinvaux 1990). The authors also note a conspicuous ‘dry phase’ between ca. 8200-5500 yr BP. These records were taken from lowland sites of equivalent elevation, and the authors indicate that their records show at least regional synchronization between Panama and Costa Rica.

Recent ecological studies (Condit et al. 1992, 1995b, 1996a, b) indicate that the Panamanian flora, as represented by the forest dynamics plot on BCI, is tightly coupled to decadal-scale climatic forcing. Condit et al. (1995) have examined population trends for 205 species of trees and shrubs within the 50-ha BCI plot and found that they respond dramatically to even short-term climatic disturbances (e.g. the 1982-1983 El Niño drought). They note that a 25-yr drying trend on BCI is having clear implications for forest composition, and Condit et al. (1992) concluded that BCI is remarkably sensitive to subtle climatic shifts.

The limestone outcrops in this landscape provide an exceptional opportunity for future research. In fact, they may provide a naturally replicated set of dry micro-sites across this precipitation gradient. These patches are typically more deciduous than the surrounding forest, and they can often be identified through aerial photography taken during the dry season. A future experimental design might examine stand structure and recruitment in these isolated forests and attempt to evaluate the relative controls of dispersal and climate in determining their composition.

Maintenance of biodiversity across spatial scales

A significant challenge confronting ecologists is the integration of mechanisms acting at multiple scales. Studies at BCI suggest that at scales of < 1 km, random forces play a large role in determining species composition, through dispersal limitation (Harms 1997; Hubbell et al. 1999). Our spatial analysis extends this somewhat by indicating that dispersal limitation plays an important role in structuring species composition over distances less than 5 km. However, data from this study demonstrate that the Panamanian forest is not randomly assembled at the larger scales, and to the contrary, it has clear patterns of spatial organization. The strong correlation between precipitation, geology, and floristic composition suggest that dispersal limitation and random processes are overlain on a landscape pattern primarily created by environmental gradients. However, these environmental correlations are not perfect, and chance events can break down these patterns and leave some species with peculiar and inexplicable distributions. In conclusion, it appears that the high levels of beta-diversity observed in lowland Panama are generated by a combination of fluctuating climate and randomly expressed local processes interacting across a complex physical landscape.

Acknowledgements. The authors would like to acknowledge the support of the U.S. Agency for International Development, through the Panama Canal Watershed Monitoring Project, especially R. Ibañez, M. Somoza, and I. Tejada, and the Smithsonian Tropical Research Institute. C.R. Pyke was supported through the National Science Foundation-funded Research Training Group in Spatial Ecology administered by the Departments of Ecology, Evolution, and Marine Biology and Geography at the University of California, Santa Barbara. We thank F. Davis, O. Chadwick, and D. Stoms for their comments and constructive criticism.

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Received 29 June 2000;
Revision received 22 February 2001;
Final revision received 13 April 2001;
Accepted 11 May 2001.
Coordinating Editor: J. Denslow.