



Effects of large-scale disturbance on metacommunity structure of terrestrial gastropods: temporal trends in nestedness

Christopher P. Bloch, Christopher L. Higgins and Michael R. Willig

C. P. Bloch (cbloch@bridgew.edu), C. L. Higgins and M. R. Willig, Dept of Biological Sciences and The Museum, Texas Tech Univ., Lubbock, TX 79409-3131, USA. Present address for CPB: Dept of Biological Sciences, Bridgewater State College, Bridgewater, MA 02325, USA. Present address for CLH: Dept of Biological Sciences, Tarleton State Univ., Stephenville, TX 76402-0100, USA. Present address for MRW: Center for Environmental Sciences and Engineering and Dept of Ecology and Evolutionary Biology, Univ. of Connecticut, Storrs, CT 06269-5210, USA.

Distributions of species often exhibit nested structure, such that assemblages at species-poor sites are proper subsets of taxa at more species-rich sites. Traditionally, this has been viewed as a large-scale biogeographic pattern and treated implicitly as static from a temporal perspective. Nonetheless, recent work suggests that nestedness may arise at multiple spatio-temporal scales. A 13-year data set encompassing the effects of two large-scale natural disturbances (hurricanes Hugo and Georges) on terrestrial gastropod assemblages was used to test the hypothesis that changes in species composition resulting from disturbance alter the degree of nestedness exhibited over time at two spatial scales. Gastropod assemblages were least nested immediately following disturbance, and nestedness increased thereafter. Although land-use history influenced the degree of nestedness, trajectories of nestedness following disturbance were similar irrespective of disturbance history or hurricane identity. The effects of hurricanes with respect to nestedness of terrestrial gastropods may be general and predictable, even though species respond to hurricanes in disparate fashions. By damaging some localities within the forest more severely than others, a hurricane dismantles extant patterns of species composition and severs connections among sites, as inhospitable microclimatic conditions limit dispersal of gastropods. As time passes and the forest canopy regenerates, conditions ameliorate, and movement among sites becomes more frequent. Thus, a conclusion based on a single time period may not characterize the study system in general. Consequently, explanations for nested structure that incorporate variability in ecological as well as evolutionary time will improve the applicability and comparability of nested subsets analysis across study systems.

Much of ecology has been devoted to describing patterns of species distribution and community composition, or to elucidating causative mechanisms that underlie these patterns (Allen and Hoekstra 1992, Pickett et al. 1994). A spatial perspective is particularly important as it affects our perception of the environment (Levin 1992). Several patterns of spatial organization have been identified, including checkerboards (Diamond 1975), Clementsian gradients (Clements 1916), Gleasonian gradients (Gleason 1926), nestedness (Patterson and Atmar 1986), and random distributions (Simberloff 1983). Of these, nestedness, the extent to which taxa found in species-poor areas are proper subsets of those in species-rich areas (Patterson

and Atmar 1986), is among the most frequently cited patterns. Although nestedness most often is used to characterize the structure of metacommunities, such as islands within an archipelago, habitat patches within a landscape, and isolated peaks along a mountain range (Patterson 1990, Cook 1995, Wright et al. 1998), it also is useful as a descriptor of spatial distribution of species in less discrete habitats (Patterson and Brown 1991, Hausdorf and Hennig 2003, Sfenthourakis et al. 2004). Despite the ubiquity of nestedness, mechanisms that produce it at various spatial and temporal scales are multifarious and remain subject to debate.

Traditionally, nestedness has been viewed as a large-scale, static pattern derived from biogeographic

processes such as differential extinction (Cutler 1991, Wright et al. 1998) or colonization (Patterson 1990, Cook and Quinn 1995). However, communities are dynamic, changing in richness and composition over ecological as well as evolutionary time (Magurran 2004). These ecological dynamics may be reflected in varying degrees of nestedness (Kaufman et al. 2000, Norton et al. 2004). In addition, nestedness may be a pattern evident at multiple spatial scales, with different mechanisms driving the pattern at each scale (Summerville et al. 2002, Sfenthourakis et al. 2004).

Temporal changes in nestedness likely are profound in communities that periodically experience large-scale disturbances (*sensu* White and Pickett 1985). Perhaps the most obvious effect of disturbance is to alter population densities, either directly through disturbance-induced mortality or indirectly through changes in habitat structure, resource availability, or density of predators or competitors. Disturbance-mediated changes in population densities, if species-specific, could produce species–abundance distributions that are strongly dominated by one or two species. If an individual, regardless of species, is equally likely to be present at each site, such that differences in abundance primarily determine differences in composition among patches or islands (i.e. passive sampling; Coleman 1981, Coleman et al. 1982), then nestedness may appear more prevalent simply because differences in abundances of species are large (Andrén 1994, Cutler 1994, Fischer and Lindenmayer 2002, Higgins et al. 2006). Intense disturbances may drive local populations to extinction, directly altering patterns of nestedness at small spatial scales. Conversely, periodic disturbance can facilitate the coexistence of species that otherwise might exclude one another (Connell 1978, Sousa 1979, Denslow 1985, Petraitis et al. 1989). Competitive exclusion decreases nestedness by promoting species turnover or checkerboard patterns (Leibold and Mikkelson 2002); therefore, mechanisms that prevent competitive exclusion, such as disturbance-mediated coexistence, could maintain or even increase nestedness.

Although disturbance may contribute strongly to the development of nested patterns of species composition (Worthen et al. 1998, Fleishman and Murphy 1999, Fernández-Juricic 2002), it is unknown how nestedness may change as a consequence of post-disturbance secondary succession. In fact, only a few studies have focused on temporal changes in nestedness at either evolutionary (Patterson 1990, Hadly and Maurer 2001) or ecological time scales (Loo et al. 2002, Vidal-Martínez and Poulin 2003, Norton et al. 2004). Nevertheless, anthropogenic modification of the biosphere is proceeding at a rapid pace, and the long-term effects of human-induced disturbance are not well understood (Vitousek et al. 1997, McKinney 2002, Turner et al. 2002). Nested subsets analysis is particu-

larly relevant to conservation efforts, as it may help to predict relative vulnerabilities of species to extinction or to identify conservation priorities (Patterson 1987, Ganzhorn and Eisenbeiß 2001, Maron et al. 2004). However, the utility of such approaches may be, in part, a function of the magnitude and frequency of temporal changes in nestedness, particularly as influenced by disturbance. If community structure changes greatly over time, then the predictive ability of nestedness models may be compromised unless a long-term approach is taken to understand the tempo and mode of such changes. Regardless, analysis of temporal changes in the degree of nestedness has the potential to provide insight into the resilience of communities with respect to disturbance events.

We use long-term data to evaluate temporal changes in nestedness of terrestrial gastropod assemblages at 40 sites in a hurricane-prone tropical wet forest in Puerto Rico. We hypothesize that behavioral and distributional constraints on terrestrial gastropods in disturbed environments reduce opportunities for dispersal among sites. If nestedness largely derives from stochastic processes, such as the dispersal of individuals across a landscape (Higgins et al. 2006), then a large-scale disturbance, such as a hurricane, that decreases the potential for such dispersal should reduce nestedness. Subsequently, the canopy closes and microclimate returns to a state similar to undisturbed conditions. At the same time, population densities of gastropods recover and the spread of abundant, generalist species should contribute to an increase in nestedness. Thus, evaluations of large-scale assemblage structure based on a single sampling period probably are incomplete and may lead to inaccurate conclusions about community dynamics.

Material and methods

Study organisms

Terrestrial gastropods are useful for studying the effects of disturbance on community structure. In addition to being taxonomically diverse and numerically abundant in many ecosystems, gastropods are ectotherms, are constrained in distribution and behavior by desiccation stress (Russell-Hunter 1983, Cook 2001), and are not particularly vagile. Thus, they strongly respond to disturbance and its often substantial modification of microclimate (Willig and Camilo 1991, Alvarez and Willig 1993, Willig et al. 1998, Hylander et al. 2004, Bloch and Willig 2006). Moreover, the relatively sedentary nature of terrestrial snails and their high site fidelity (Heatwole and Heatwole 1978, Cary 1992) increase the likelihood of isolation and insularity at even relatively small spatial scales.

Field methods

Long-term censuses of terrestrial gastropods occurred on the Luquillo Forest Dynamics Plot (LFDP), a 16-ha grid near El Verde Field Station, in the northwestern region of the Luquillo Experimental Forest (LEF; 18°10'N, 65°30'W). The LFDP resides in well-studied tabonuco (*Dacryodes excelsa*) forest (Odum and Pigeon 1970, Reagan and Waide 1996), which occurs below 600 m in elevation. Rainfall in tabonuco forest is substantial, averaging 346 cm per year (McDowell and Estrada-Pinto 1988), with a modestly drier period from January to April. Humidity is consistently high, and relatively little seasonal or diurnal variation occurs in temperature (Odum and Pigeon 1970). In the last 20 years, two major hurricanes (Hugo in 1989 and Georges in 1998) have passed over eastern Puerto Rico. Although both produced widespread damage in the tabonuco forest, the two hurricanes differed in intensity and severity. Hurricane Hugo, a category 4 storm with sustained winds of 166 km h⁻¹ (Scatena and Larsen 1991), produced larger canopy openings and deposited more debris than did hurricane Georges, a category 3 storm (Lugo and Frangi 2003, Ostertag et al. 2003). In addition to experiencing natural disturbances, such as hurricanes, the LFDP was disturbed by various anthropogenic activities (e.g. logging and agriculture) in the past (Thompson et al. 2002). The land was purchased by the US Forest Service in 1934 and allowed to revert to closed-canopy forest, although limited selective logging persisted until the 1950s. Despite this dramatic reduction in land use, differences in tree species composition among areas of the LFDP continue to reflect the history of human activity (Willig et al. 1996, Thompson et al. 2002). As such, the history of anthropogenic disturbance is relevant to extant patterns of species composition and abundance in gastropod assemblages. Using aerial photographs and US Forest Service records, locations on the LFDP can be allocated into four categories (hereafter, cover classes; Thompson et al. 2002). For this study, cover classes 1 and 2 were combined to increase sample size, resulting in three regions of historic land use (Fig. 1a). Cover classes 1 and 2 (0–49% canopy cover in 1936) experienced the most intensive logging and agriculture prior to 1934. Cover class 3 (50–80% canopy cover in 1936) was used for small-scale mixed agriculture (especially cultivation of shade coffee) before 1934. Cover class 4 (80–100% canopy cover in 1936) was lightly selectively logged up to the 1950s.

Circular plots (3 m radius) were established on the LFDP at 40 points and spaced evenly such that 60 m intervene between adjacent points along a row or column within a rectilinear grid (Fig. 1a). Of these plots, 13 were located in cover class 1 (intensive logging), 14 in cover class two (coffee plantations)

and 13 in cover class 3 (selective logging). From 1991 to 2003, gastropod surveys were conducted twice annually to account for seasonal variation in rainfall. The first survey of each year was conducted in March (dry season) and the second during the summer (wet season). The lone exception was the dry season of 1999, when dry-season sampling was conducted in January rather than March to assess the effects of Hurricane Georges as soon as possible after the storm.

Sampling intensity differed over time. Each plot was sampled once in the dry season of 1991, twice in each season from the wet season of 1991 to the wet season of 1993, three times per season from the dry season of 1994 to the dry season of 1995, and four times per season thereafter, except for the dry season of 2003 (two surveys). Although these differences in sampling intensity affected abundance estimates, they did not qualitatively alter species co-occurrence patterns (i.e. the outcome of analyses were qualitatively identical for analyses conducted using a single sample from each time period compared to those conducted using data from all samples). Consequently, we used data from all samples, regardless of differences in sampling effort, because they provide the best available estimates of assemblage composition in each time period. A minimum of two days was maintained between samples to allow gastropods to recover from displacement during previous surveys. All surveys were conducted at night (19:30 to 03:00 h) to coincide with peak snail activity (Cary 1992, Willig et al. 1998).

Each time a plot was sampled, at least two people surveyed it for a minimum of 15 min, during which they searched for snails and slugs on all available surfaces (e.g. soil, litter, rocks, vegetation). To minimize alteration of long-term study sites, substrate was not manipulated to search for specimens. All gastropods were identified to species in the field and returned as closely as possible to the point of capture, and always within the same plot.

Estimation of nestedness

Nestedness was estimated using species presence-absence data at two spatial extents: within each of the cover classes and on the LFDP as a whole. At each spatial extent, nestedness was estimated separately for each survey from the dry season of 1991 to the wet season of 2003. Although a number of measures exist that reflect nestedness, we chose to use PN_C (Wright et al. 1998), a standardized version of the N_C measure that removes the correlation between the size of the data matrix and the magnitude of the measure (Wright and Reeves 1992, Wright et al. 1998). The calculation of N_C is rooted in basic probability theory and is calculated as the sum of all conditional probabilities

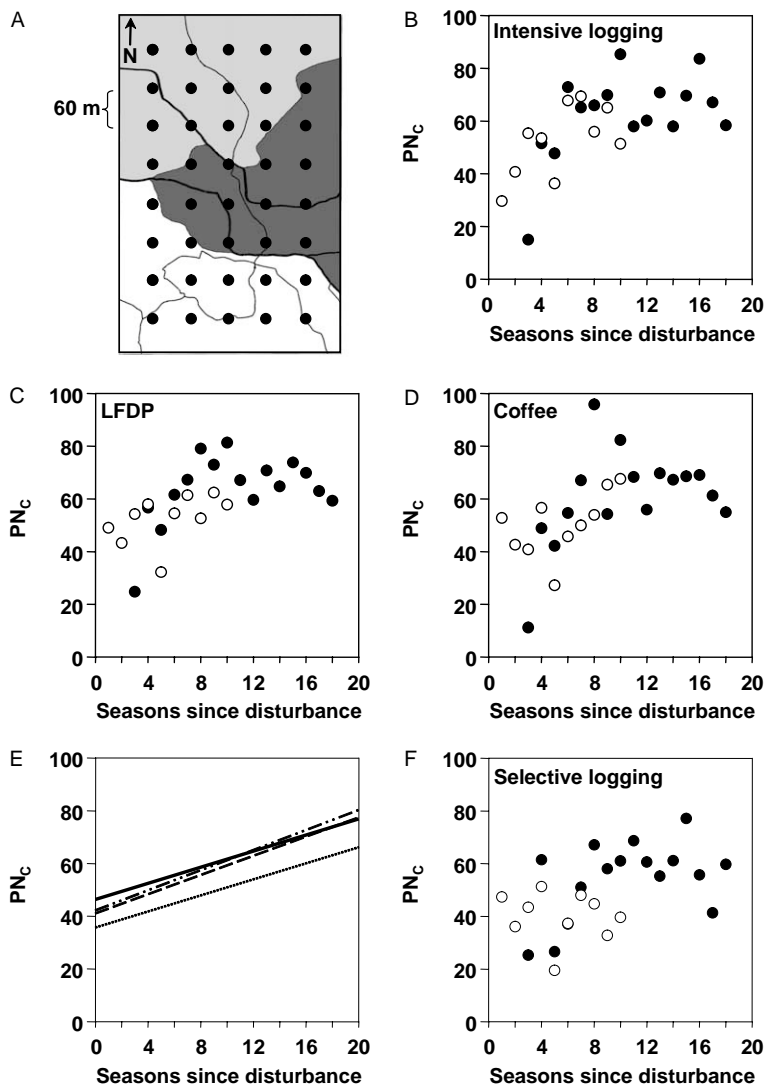


Fig. 1. Temporal variation in nestedness (PN_C) of terrestrial gastropod metacommunities within cover classes and across the LFDP. (a) Diagrammatic representation of the LFDP (redrawn from Willig et al. 1996), with cover classes indicated by shading (dark gray, cover classes 1 and 2 combined; light gray, cover class 3; unshaded, cover class 4). Circles represent sampling plots (spaced 60 m apart), thick black lines represent streams, and thin black lines indicate trails. Trajectories of PN_C following disturbance in each region of the LFDP: (b) cover classes 1 and 2 combined, (d) cover class 3, (f) cover class 4, and for the entire LFDP (c). Filled circles represent nestedness following hurricane Hugo, and open circles represent nestedness following hurricane Georges. (e) Trajectories of nestedness over time within each cover class (cover classes 1 and 2 combined, short and long dashes; cover class 3, long dashes; cover class 4, short dashes) as well as for the entire LFDP (solid line), as indicated by least-squares estimates for ANCOVAs.

that species will be present at a site, given their presence at more depauperate sites. Hence, it can be viewed as the number of times a species presence at one locality correctly predicts its presence at equally rich or richer localities, summed across species and sites (Wright and Reeves 1992). The N_C measure also can be viewed as the total number of species shared in all unique pairwise combinations of sites, which places it in context of

many similarity measures that are widely used in ecology (Wright and Reeves 1992).

To assess the contribution of each circular plot to the overall pattern of nestedness, we estimated an index of effect (I_E). The index for plot i was calculated as $I_{Ei} = PN_C$ (including all plots) $- PN_{Ci}$ (without plot i). That is, for each season we estimated PN_C incorporating all 40 sites and all 17 species. Next, we systematically

removed each site, one at a time, from the analysis and recalculated PN_{C_i} for each i . The difference between the two estimates of PN_C provided a quantitative index of each site's contribution to overall nestedness for each season. Positive values indicate the system was less nested without that plot (i.e. the plot enhanced overall nestedness). Negative values indicate the system was more nested without the plot (i.e. the plot diminished overall nestedness).

Statistical design and analysis

Statistical significance for PN_C was tested by performing a z-transformation (i.e. standardizing it as a standard normal deviate by subtracting the mean and dividing by the standard deviation; Sokal and Rohlf 1995) and comparing the z-score to zero (Patterson and Atmar 1986, Wright and Reeves 1992). The z-transformations were calculated using the means and standard deviations of randomized distributions of PN_C based on 1000 iterations of the RANDOM0 null model (Patterson and Atmar 1986, Wright et al. 1998). RANDOM0 is but one of several null models available for analysis of nestedness (Jonsson 2001), although one of the most venerable and extensively tested metrics. It remains one of only a few such null models that are not strongly susceptible to type I and type II errors (Gotelli 2000).

Proper choice of a null model is critical in this study because the null model serves two purposes. First, it serves as a tool to create a null distribution with which we assess statistical significance. Second, the null distribution is used to generate "expected" values of nestedness. The standardized measure of N_C (PN_C) is based on the observed value of N_C , the expected value of N_C , and the maximum value of N_C :

$$PN_C = \frac{N_C - \text{expected } \{N_C\}}{\max\{N_C\} - \text{expected } \{N_C\}}.$$

The mean value of N_C , based on 1000 randomized matrices produced from the null model, is used as the expected value. Clearly, then, the wrong null model could lead to biased results. To guard against this possibility, consistency of results was evaluated among a suite of 9 null models that differ in the degree to which they constrain row and column totals in randomizing species occurrence matrices (Gotelli 2000). Three of the null models (SIM3, SIM5, and SIM9) constrain the column totals to equal those of the observed matrix. Because N_C , the basis of PN_C before standardization, is dependent on incidence totals, each randomized value in these null models is identical to the observed matrix. This forces the value of PN_C to be 0 and its significance to be 1, and makes these null models unsuitable for use with PN_C . All six remaining null models suggested by

Gotelli (2000) confirmed the results of analyses using randomizations based on the RANDOM0 procedure. As such, all results presented herein were derived using RANDOM0. All simulations were performed with algorithms written in MATLAB v.6.0 (MATLAB 2001).

To determine whether nonsignificant patterns of nestedness resulted from an alternative nonrandom structure (species turnover) or from random distributions of species, the methodology of Leibold and Mikkelsen (2002) was used. That is, for each season the original data matrix was ordinated through reciprocal averaging, coherence was assessed based on the number of embedded absences, and species turnover was quantified using the number of replacements as a test statistic (Leibold and Mikkelsen 2002). No analyses of temporal dynamics were conducted using this measure, however, because number of species and number of occupied sites differ among seasons, thereby changing the size of the species presence-absence matrix. As the test statistic of Leibold and Mikkelsen (2002) is not standardized by matrix size, it would be inappropriate for use in comparisons among time periods. Instead, analyses of change in assemblage structure over time were based on PN_C .

Analysis of covariance (ANCOVA) evaluated temporal trends in nestedness. Two factors were of interest: cover class and hurricane. The first factor, cover class, characterized the plot based on anthropogenic disturbance history, whereas the second, hurricane, indicated whether an observation came from the time period following hurricane Hugo and before hurricane Georges (1991–1998) or that following hurricane Georges (1999–2003). The covariate, time since disturbance, was measured as the number of sampling periods (two per year) elapsed since the more recent hurricane. As a consequence, it was possible to distinguish whether nestedness changed linearly over time following each hurricane, whether such responses were consistent among cover classes, and whether mean nestedness differed among cover classes or between time sequences (i.e. following hurricane Hugo versus Georges) while accounting for the effect of time since disturbance. Significant F-tests for individual terms of an ANCOVA were interpreted only if the overall model was significant at $\alpha = 0.05$. A significant interaction between hurricane and time since disturbance indicates that response to disturbance is hurricane-specific; that is, the trajectory of change in nestedness (i.e. slope) differs between hurricanes. Similarly, a significant interaction between cover class and time since disturbance indicates that trajectories of nestedness differ among cover classes. If an interaction was nonsignificant, that term was removed from the model, the overall slope for the relationship between nestedness and time since disturbance was estimated using pooled

data (Sokal and Rohlf 1995), and significant main effects were interpreted. A significant effect of time since disturbance indicates a consistent linear response of nestedness to time elapsed following a hurricane, regardless of its identity. A significant effect of hurricane implied that mean nestedness differs between hurricanes, after accounting for the effect of time since disturbance. A similar ANCOVA evaluated temporal trends in I_E but did not include hurricane identity as a factor of interest. All ANCOVAs were conducted using SPSS version 9.0 (SPSS 1998).

Patterns of spatial distribution of species, such as nestedness, may be scale-dependent. For example, if distributions of some gastropod species are restricted to one cover class, either via differences in composition or diversity of vegetation, structural heterogeneity, or other relevant environmental characteristics, then the anthropogenic disturbance history of the LFDP could cause the overall distribution of species to be non-nested (i.e. the three cover classes have exclusive or somewhat exclusive species distributions) even if nestedness characterized assemblages within each cover class. Consequently, PN_C was quantified and its dynamics assessed for the entire LFDP using the same set of simulations and analyses as were used for nestedness within cover classes, except that cover class was excluded from the design of ANCOVA models.

Results

From 1991 to 2003, 18 species of terrestrial gastropods representing 14 genera were captured on the LFDP

(Bloch and Willig 2006, Table 1). Two species (*Oleacina interrupta* and *O. playa*) were relatively uncommon, morphologically similar, and sometimes difficult to distinguish in the field. Because it is impossible to verify identities of individuals subsequent to their release, the two species are treated as a single entity in all analyses. The number of species captured in a sampling period ranged from eight (dry season 1991) to 16 (multiple sampling periods), with a mean of 13.5 species. In each sampling period, most sites were occupied by at least one species. The number of occupied sites ranged from 34 (dry season 1991) to all 40 (multiple sampling periods), with a mean of 39.4 sites. Distributions and abundances differed considerably among species (Table 1). Three species were consistently abundant and widespread (*Caracolus caracolla*, *Nenia tridens* and *Gaeotis nigrolineata*). Four species were intermediate in occurrence (*Alcacia striata*, *Cepolis squamosa*, *Platysuccinea portoricensis* and *Polydontes acutangula*), and the remaining species were uncommon or rare.

Temporal variability in nestedness was non-random (Table 2). Within each cover class, spatial structure was least nested immediately following a hurricane and became more nested through time (Fig. 1). However, neither the hurricane effect nor any interaction term was significant. Hurricanes Hugo and Georges caused spatial structure to change, but nestedness, on average, did not differ between hurricanes, and both hurricanes influenced nestedness in the same manner. Moreover, nestedness differed among cover classes, indicating that the legacy of anthropogenic disturbance from 70 years ago influenced patterns of species distribution (Fig. 1e).

Table 1. Terrestrial gastropod species captured on the LFDP from 1991–2003, their mean abundances over that time (± 1 SD), and their mean occurrences (number of plots occupied) in a sampling period (± 1 SD).

Species	Abundance (individuals ha ⁻¹)		Number of occurrences	
	Mean	SD	Mean	SD
<i>Alcacia alta</i>	14.8	17.4	2.8	2.5
<i>Alcacia striata</i>	68.3	50.4	12.3	5.9
<i>Austroselenites alticola</i>	8.8	11	2.4	2.9
<i>Caracolus caracolla</i>	955.8	364.5	35.0	4.1
<i>Caracolus marginella</i>	8.1	13.2	1.8	2.3
<i>Cepolis squamosa</i>	43.9	35.1	7.1	4.6
<i>Gaeotis nigrolineata</i>	584.6	499.8	29.2	8.4
<i>Lamellaxis gracilis</i>	3.6	6.5	1.0	2.0
<i>Megalomastoma croceum</i>	8.4	11.4	1.7	1.6
<i>Nenia tridens</i>	997.6	718	30.5	8.0
<i>Obeliscus terebraster</i>	1.4	2.6	0.4	0.9
<i>Oleacina glabra</i>	10.4	10.2	3.2	3.3
<i>Oleacina playa</i> ^a	12.4	8.1	3.8	2.3
<i>Platysuccinea portoricensis</i>	55.9	41.9	9.3	6.4
<i>Polydontes acutangula</i>	61.6	37	10.3	5.0
<i>Subulina octona</i>	23.5	39.4	2.5	2.8
<i>Vaginulus occidentalis</i>	7.3	10.8	2.1	2.3

^aincludes *O. interrupta*

Table 2. Results of ANCOVAs of PN_C at two spatial scales (within cover classes and for the entire LFDP). Cover class and hurricane identity were categorical factors, and time since disturbance was the covariate. Because interaction terms were nonsignificant in all cases, parameter estimates and levels of significance were calculated while excluding interactions.

Spatial scale	Cover class			Time since disturbance				Hurricane			Overall ANCOVA		
	DF	F	p	DF	Slope	F	p	DF	F	p	F	p	
Cover classes	2,73	4.00	0.022	1,73	1.55	17.05	<0.001	1,73	1.09	0.301	9.70	<0.001	
LFDP	–	–	–	1,23	1.27	5.639	0.026	1,23	0.89	0.355	6.03	0.008	

After accounting for the effect of time since disturbance, nestedness was lowest in cover class 4. Magnitude of nestedness was similar between the other two cover classes. When cover classes were ignored and the domain of interest comprised the entire LFDP, nestedness increased over time following disturbance (Fig. 1c). Moreover, the trajectory of increase was the same regardless of hurricane identity (i.e. no significant hurricane by time interaction; Table 2). Number of replacements (Leibold and Mikkelsen 2002) consistently was less than expected, even when the snail assemblage was least nested (dry season 1991). Instead of displaying anti-nested structure (i.e. significant species turnover), assemblage structure in this season was most consistent with a random pattern of species distribution.

Plots belonging to cover classes 1–3 generally contributed positively to overall nestedness on the LFDP (i.e. $I_E > 0$). That is, if a plot from cover classes 1–3 were removed from consideration, the overall nestedness of the LFDP would decrease. In contrast, plots belonging to cover class 4 were more prone to contribute negatively to overall nestedness (i.e. $I_E < 0$). The difference in mean plot effect (I_E) between cover class 4 and the other cover classes was significant and consistent (i.e. the interaction was nonsignificant) regardless of time since disturbance (effect of cover class: $F = 13.41$, $p < 0.001$; effect of time since disturbance: $F = 1.00$; $p = 0.319$).

Discussion

The degree of nestedness of gastropod distributions among sites in the tabonuco forest was dynamic with respect to time. Specifically, spatial structure of gastropod assemblages was least nested (i.e. most random) immediately following hurricane disturbance and became more nested thereafter. Although this pattern was observed in all anthropogenic land use categories, historical factors influenced the effects of disturbance. That is, anthropogenic land use from the early 1900s influenced how hurricanes Hugo and Georges altered distributions of species. Sites that historically experienced the least severe anthropogenic disturbance (selective logging) consistently were less nested in terms of gastropod assemblage structure than were those that were more severely disturbed, regardless of time since a hurricane. Nevertheless, gastropod assemblages within the three cover classes displayed comparable resilience to hurricane disturbance, as there was no difference in trajectory of response.

Hurricanes produce large, widespread openings in the canopy, which are characterized by increased soil and air temperature, increased evaporation rates, and decreased relative humidity compared to undisturbed

forest (Denslow 1980, Fernández and Fetcher 1991). Moreover, the degree of difference in environmental conditions between a gap and undisturbed forest increases with the size of the canopy opening (Lee 1978). Because desiccation is a primary cause of mortality for terrestrial gastropods (Solem 1984), especially for eggs and early growth stages (Heatwole and Heatwole 1978, Riddle 1983, Baur and Baur 1993), species-specific tolerances to desiccation likely influence the composition of local assemblages in post-hurricane environments. Such interspecific differences in tolerance to desiccation have been demonstrated for gastropods in several systems (Cameron 1970, Arad et al. 1989), including the LEF (Heatwole and Heatwole 1978); hence, desiccation resistance represents a plausible mechanism leading to changes in gastropod composition following disturbance. Indeed, at least one species in the LEF (*N. tridens*) exploits resource pulses in relatively small-scale disturbances (i.e. treefall gaps), whereas another (*C. caracolla*) remains more restricted to undisturbed forest (Alvarez and Willig 1993).

Spatial variation in environmental conditions is a common consequence of hurricane disturbance, as topographic features protect some areas from the most severe effects of wind and rain. Such variation, coupled with a hierarchy in breadth of species-specific tolerances to environmental conditions, could result in a strongly nested system (Worthen et al. 1998, Fernández-Juricic 2002, Hausdorf and Hennig 2003, Baber et al. 2004, Cook et al. 2004), as the most tolerant species (i.e. those that survive the broadest range of conditions) will be most widespread, and the least tolerant will be restricted in distribution. Indeed, nested habitat quality explained the nestedness of terrestrial gastropod assemblages in boreal forests in Sweden (Hylander et al. 2005). Among gastropods in the LEF, a hierarchy of disturbance tolerance may exist, at least with respect to small-scale disturbances (i.e. some species may tolerate conditions in treefall gaps better than others; Alvarez and Willig 1993). The effect of a hurricane, however, covers a greater area than does an individual treefall and produces many large gaps comprising multiple treefalls. Therefore, hurricanes probably create more extreme environmental conditions (including conditions outside the fundamental niches of at least some gastropod species in the LEF) than do individual treefalls. A threshold of desiccation stress likely exists, beyond which even the most disturbance-tolerant species cannot survive for a prolonged time. In such a case, the nested structure generally associated with a hierarchy of environmental tolerances may be disrupted, as a site with conditions at or near this threshold may contain only a random assemblage of transients rather than a subset of species characteristic of that part of an environmental gradient.

A disturbance can cause a change from nested to non-nested structure if rare species are eliminated (Báldi 2003) or if local extinctions are density-independent (i.e. rare species do not have a greater likelihood of extinction than do common species). The former is unlikely in our study, as neither total species richness of the LFDP nor mean richness of plots changed significantly over time, although species richness did increase over time within cover classes (Bloch 2004). In contrast, density-independent extinction is consistent with observations. Hurricane Hugo severely reduced densities and frequencies of even the most abundant and widespread species (Willig and Camilo 1991), including *N. tridens*, a species that is more abundant in treefall gaps than in undisturbed forest (Alvarez and Willig 1993). Hurricane Georges, similarly, had the most obvious effects on abundances of common species (Bloch 2004). In terms of presences and absences, common species occupied fewer sites following hurricane Georges, and the sites that they occupied were distributed more randomly, leading to decreased nestedness. Preferential removal of rare species by a disturbance would decrease beta diversity among plots; however, this result did not characterize gastropods on the LFDP. Instead, beta diversity was high in the immediate aftermath of hurricane disturbance and declined over time (Bloch 2004).

As well as influencing survivorship, unfavorable microclimatic conditions reduce gastropod activity (reviewed by Cook 2001). Dispersal rates are restricted by distance between or low availability of suitable habitat patches (Baur 1988, Baur and Baur 1993, 1995, Schilthuizen and Lombaerts 1994, Kasigwa 1999), both of which would characterize a recently disturbed forest. Long-distance dispersal would be a risky and costly proposition soon after a hurricane, when large canopy gaps occur throughout the forest. As the canopy regenerates and microclimatic conditions become more similar to those of undisturbed forest, conditions which restrict movement of gastropods should ameliorate, allowing species with good dispersal ability to become widespread, thereby increasing nestedness. This is consistent with previous studies that have demonstrated that differential dispersal and colonization contribute to the development of nestedness over multiple spatial and temporal scales (Loo et al. 2002, Hausdorf and Hennig 2003, Ficetola and De Bernardi 2004).

The effect of natural disturbance on community structure may be complicated by historical factors, including the legacies of previous disturbance. Both species composition of trees and stand age influence the degree of damage a forest experiences during a hurricane. Tree species differ in susceptibility to wind-throw (Zimmerman et al. 1994, Brokaw 1998, Uriarte et al. 2004). In addition, younger, shorter trees

generally suffer less damage from a windstorm than do older, taller ones (Brokaw 1985, Runkle 1985). Because microclimatic conditions in canopy gaps often are unfavorable to terrestrial snails, the effect of disturbance on snails should be less severe when the hurricane strikes a relatively young forest than an older forest.

Several types of anthropogenic disturbance (i.e. selective logging, clear-cutting, agriculture) historically occurred on the LFDP. Subsequent succession and a number of natural disturbances have not masked the effect of land use on tree species composition (Thompson et al. 2002). Such differences in composition and mean stand age among cover classes influence the amount of canopy damage produced by hurricanes (Thompson et al. 2002, Uriarte et al. 2004). Thus, differences among cover classes in the degree of nestedness of gastropod assemblages were not unexpected, although it was surprising that the degree of nestedness, regardless of time since disturbance, was lowest in the cover class 4, the selectively logged region, where historic disturbance and subsequent hurricane damage were lowest. Plots from this region generally had a negative effect on the overall nestedness of the system, in stark contrast to the other regions. However, the relative contributions of plots from the different cover classes did not change appreciably over time.

The negative contribution of plots from cover class 4 to overall nestedness is consistent with its persistent differences in species composition of gastropods compared to the other regions. Cover class 4 contained several sites from which the two most abundant and widespread species, *C. caracolla* and *N. tridens*, were often absent, possibly because the complexity of vertical structure and the amount of decaying plant matter were low relative to the other regions of the LFDP (Willig et al., unpubl.). In addition, some infrequent species, such as *A. striata* and especially *P. portoricensis*, were more common at such sites, often occupying those devoid of the more widespread species. This pattern of species distribution resulted in a greater number of holes and outliers (and, therefore, lower nestedness) associated with cover class 4 than elsewhere. Remarkably, however, the effect of hurricanes on nestedness, as evidenced by temporal trajectories, was consistent regardless of these differences among regions, regardless of the spatial scale examined, and regardless of differences in the intensities of the two storms.

Conclusion

The analysis of nested patterns of species distributions has received considerable interest in recent years, in part because of its potential role in conservation efforts (Boecklen 1997, Maron et al. 2004). In this context, it has been used to estimate minimum viable population

size, to estimate minimum size of habitat fragments that can be used by specialist species, to evaluate connectivity among fragments, and to predict vulnerability of species to extinction (Ganzhorn and Eisenbeiß 2001). Although such approaches can be used to make predictions in the absence of long-term data (Ganzhorn and Eisenbeiß 2001), they may best be treated with caution. Considerable variation can characterize community structure over time at multiple spatial scales, and such variability may be reflected in the degree to which nestedness is evident (Kaufman et al. 2000, Vidal-Martínez and Poulin 2003, Norton et al. 2004). Thus, a conclusion based on a single time period may not characterize the study system in general. For example, a single assessment in the dry season of 1991 would lead to the conclusion that spatial structure of terrestrial gastropod assemblages in the LEF was non-nested; a similar study in 1994 would suggest that the same system was nested. Consequently, explanations for nested structure that incorporate variability in ecological as well as evolutionary time will improve the applicability and comparability of nested subsets analysis across study systems.

Acknowledgements – This research was supported by grants BSR-8811902, DEB 9411973, DEB 0080538, and DEB 0218039 from NSF to the Inst. for Tropical Ecosystem Studies, Univ. of Puerto Rico, and to the Int. Inst. of Tropical Forestry, USDA Forest Service, as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest. The USDA Forest Service, US Dept of Energy, the Univ. of Puerto Rico, the Howard Hughes Medical Institute, and Texas Tech Univ. provided additional support. Nick Brokaw, Steven Presley and Jill Thompson provided insightful comments that improved earlier drafts of this manuscript. Finally, we thank the staff of El Verde Field Station, as well as the students and colleagues, too many to name individually, who assisted with field work over the years.

References

- Allen, T. F. H. and Hoekstra, T. W. 1992. *Toward a unified ecology*. – Columbia Univ. Press.
- Alvarez, J. and Willig, M. R. 1993. Effects of treefall gaps on the density of land snails in the Luquillo Experimental Forest. – *Biotropica* 25: 100–110.
- Andrén, H. 1994. Can one use nested subset pattern to reject the random sample hypothesis? Examples from boreal bird communities. – *Oikos* 70: 489–491.
- Arad, Z. et al. 1989. Resistance to desiccation and distribution patterns in the land snail *Sphincterochila*. – *J. Zool.* 218: 353–364.
- Baber, M. J. et al. 2004. The relationship between wetland hydroperiod and nestedness patterns in assemblages of larval amphibians and predatory macroinvertebrates. – *Oikos* 107: 16–27.

- Báldi, A. 2003. Extinction disorders the species composition of metacommunities. – *Acta Zool. Acad. Sci. Hung.* 49: 159–165.
- Baur, B. 1988. Microgeographical variation in shell size of the land snail *Chondrina clienta*. – *Biol. J. Linn. Soc.* 35: 247–259.
- Baur, B. and Baur, A. 1993. Climatic warming due to thermal-radiation from an urban area as possible cause for the local extinction of a land snail. – *J. Appl. Ecol.* 30: 333–340.
- Baur, B. and Baur, A. 1995. Habitat-related dispersal in the rock-dwelling land snail *Chondrina clienta*. – *Ecography* 18: 123–130.
- Bloch, C. P. 2004. Long-term responses of snail populations and communities to disturbance in the Luquillo Experimental Forest, Puerto Rico. PhD thesis, Texas Tech Univ., Lubbock, Texas.
- Bloch, C. P. and Willig, M. R. 2006. Context-dependence of long-term responses of terrestrial gastropod populations to large-scale disturbance. – *J. Trop. Ecol.* 22: 111–122.
- Boecklen, W. J. 1997. Nestedness, biogeographic theory, and the design of nature reserves. – *Oecologia* 112: 123–142.
- Brokaw, N. V. L. 1985. Treefalls, regrowth, and community structure in tropical forests. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, pp. 53–69.
- Brokaw, N. V. L. 1998. *Cecropia schreberiana* in the Luquillo Mountains of Puerto Rico. – *Bot. Rev.* 64: 91–120.
- Cameron, R. A. D. 1970. The survival, weight-loss and behaviour of three species of land snail in conditions of low humidity. – *J. Zool.* 160: 143–157.
- Cary, J. F. 1992. Habitat selection, home range, and population dynamics of *Caracolus caracolla* in the Luquillo Experimental Forest of Puerto Rico. MSci thesis, Texas Tech Univ., Lubbock, Texas.
- Clements, F. E. 1916. Plant succession: an analysis of the development of vegetation. – *Carnegie Inst. of Washington*.
- Coleman, B. D. 1981. On random placement and species-area relations. – *Math. Biosci.* 54: 191–215.
- Coleman, B. D. et al. 1982. Randomness, area, and species richness. – *Ecology* 63: 1121–1133.
- Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. – *Science* 199: 1302–1310.
- Cook, A. 2001. Behavioural ecology: on doing the right thing, in the right place at the right time. – In: Barker, G. M. (ed.), *The biology of terrestrial molluscs*. CAB International, pp. 447–487.
- Cook, R. R. 1995. The relationship between nested subsets, habitat subdivision, and species diversity. – *Oecologia* 101: 204–210.
- Cook, R. R. and Quinn, J. F. 1995. The influence of colonization in nested species subsets. – *Oecologia* 102: 413–424.
- Cook, R. R. et al. 2004. Geographic variation in patterns of nestedness among local stream fish assemblages in Virginia. – *Oecologia* 140: 639–649.
- Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. – *Conserv. Biol.* 5: 496–505.
- Cutler, A. 1994. Nested biotas and biological conservation: metrics, mechanisms, and meaning of nestedness. – *Landscape Urban Planning* 28: 73–82.
- Denslow, J. S. 1980. Patterns of plant species diversity during succession under different disturbance regimes. – *Oecologia* 46: 18–21.
- Denslow, J. S. 1985. Disturbance-mediated coexistence of species. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, pp. 307–323.
- Diamond, J. M. 1975. Assembly of species communities. – In: Diamond, J. M. (ed.), *Ecology and evolution of communities*. Harvard Univ. Press, pp. 342–444.
- Fernández, D. S. and Fetcher, N. 1991. Changes in light availability following hurricane Hugo in a subtropical montane forest in Puerto Rico. – *Biotropica* 23: 393–399.
- Fernández-Juricic, E. 2002. Can human disturbance promote nestedness? A case study with breeding birds in urban habitat fragments. – *Oecologia* 131: 269–278.
- Ficetola, G. F. and De Bernardi, F. 2004. Amphibians in a human-dominated landscape: the community structure is related to habitat features and isolation. – *Biol. Conserv.* 119: 219–230.
- Fischer, J. and Lindenmayer, D. B. 2002. Treating the nestedness temperature calculator as a “black box” can lead to false conclusions. – *Oikos* 99: 193–199.
- Fleishman, E. and Murphy, D. D. 1999. Patterns and processes of nestedness in a Great Basin butterfly community. – *Oecologia* 119: 133–139.
- Ganzhorn, J. U. and Eisenbeiß, B. 2001. The concept of nested species assemblages and its utility for understanding effects of habitat fragmentation. – *Basic Appl. Ecol.* 2: 87–95.
- Gleason, H. A. 1926. The individualistic concept of the plant association. – *Bull. Torrey Bot. Club* 53: 7–26.
- Gotelli, N. J. 2000. Null model analysis of species co-occurrence patterns. – *Ecology* 81: 2606–2621.
- Hadly, E. A. and Maurer, B. A. 2001. Spatial and temporal patterns of species diversity in montane mammal communities of western North America. – *Evol. Ecol. Res.* 3: 477–486.
- Hausdorf, B. and Hennig, C. 2003. Nestedness of north-west European land snail ranges as a consequence of differential immigration from Pleistocene glacial refuges. – *Oecologia* 135: 102–109.
- Heatwole, H. and Heatwole, A. 1978. Ecology of the Puerto Rican camaenid tree-snails. – *Malacologia* 17: 241–315.
- Higgins, C. L. et al. 2006. The role of stochastic processes in producing nested patterns of species distributions. – *Oikos* 114: 159–167.
- Hylander, K. et al. 2004. Effects of buffer-strip retention and clearcutting on land snails in boreal riparian forests. – *Conserv. Biol.* 18: 1052–1062.
- Hylander, K. et al. 2005. Differences in habitat quality explain nestedness in a land snail meta-community. – *Oikos* 108: 351–361.
- Jonsson, B. G. 2001. A null model for randomization of nestedness in species assemblages. – *Oecologia* 127: 309–313.

- Kasigwa, P. F. 1999. Dispersion factors in the arboreal snail *Sitala jenynsi* (Gastropoda: Ariophantidae). – *S. Afr. J. Zool.* 34: 145–153.
- Kaufman, D. M. et al. 2000. Faunal structure of small mammals in tallgrass prairie: an evaluation of richness and spatiotemporal nestedness. – *Fort Hays Studies Spec. Iss.* 1: 47–70.
- Lee, R. 1978. *Forest microclimatology*. – Columbia Univ. Press.
- Leibold, M. A. and Mikkelsen, G. M. 2002. Coherence, species turnover, and boundary clumping: elements of meta-community structure. – *Oikos* 97: 237–250.
- Levin, S. A. 1992. The problem of pattern and scale in ecology. – *Ecology* 73: 1943–1967.
- Loo, S. E. et al. 2002. An experimental examination of colonization as a generator of biotic nestedness. – *Oecologia* 132: 118–124.
- Lugo, A.E. and Frangi, J. L. 2003. Changes in necromass and nutrients on the forest floor of a palm floodplain forest in the Luquillo Mountains of Puerto Rico. – *Caribbean J. Sci.* 39: 265–272.
- Magurran, A. E. 2004. *Measuring biological diversity*. – Blackwell Science.
- Maron, M. et al. 2004. Can the biotic nestedness matrix be used predictively? – *Oikos* 106: 433–444.
- MATLAB. 2001. – The Mathworks, Inc.
- McDowell, W. H. and Estrada-Pinto, A. 1988. Rainfall at the El Verde Field Station, 1964–1986. Rep. No. CEER-T-228. – Center for Energy and Environment Research.
- McKinney, M. L. 2002. Urbanization, biodiversity, and conservation. – *Bioscience* 52: 883–890.
- Norton, J. et al. 2004. Temporal and spatial patterns of nestedness in eel macroparasite communities. – *Parasitology* 129: 203–211.
- Odum, H. T. and Pigeon, R. F. (eds) 1970. *A tropical rain forest: a study of irradiation and ecology at El Verde, Puerto Rico*. – US Atomic Energy Commission.
- Ostertag, R. et al. 2003. Forest floor decomposition following hurricane litter inputs in several Puerto Rican forests. – *Ecosystems* 6: 261–273.
- Patterson, B. D. 1987. The principle of nested subsets and its implications for biological conservation. – *Conserv. Biol.* 1: 323–334.
- Patterson, B. D. 1990. On the temporal development of nested subset patterns of species composition. – *Oikos* 59: 330–342.
- Patterson, B. D. and Atmar, W. 1986. Nested subsets and the structure of insular mammalian faunas and archipelagos. – *Biol. J. Linn. Soc.* 28: 65–82.
- Patterson, B. D. and Brown, J. H. 1991. Regionally nested patterns of species composition in granivorous rodent assemblages. – *J. Biogeogr.* 18: 395–402.
- Petraitis, P. S. et al. 1989. The maintenance of species diversity by disturbance. – *Q. Rev. Biol.* 64: 393–418.
- Pickett, S. T. A. et al. 1994. *Ecological understanding: the nature of theory and the theory of nature*. – Academic Press.
- Reagan, D. P. and Waide, R. B. (eds) 1996. *The food web of a tropical rain forest*. – Univ. of Chicago Press.
- Riddle, W. A. 1983. Physiological ecology of land snails and slugs. – In: Russell-Hunter, W. D. (ed.), *The Mollusca*. Vol. 6, *Ecology*. Academic Press, pp. 431–461.
- Runkle, J. R. 1985. Disturbance regimes in temperate forests. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, pp. 17–33.
- Russell-Hunter, W. D. 1983. Overview: planetary distribution of and ecological constraints upon the Mollusca. – In: Russell-Hunter, W. D. (ed.), *The Mollusca*. Vol. 6, *Ecology*. Academic Press, pp. 1–27.
- Scatena, F. N. and Larsen, M. C. 1991. Physical aspects of hurricane Hugo in Puerto Rico. – *Biotropica* 23: 317–323.
- Schilthuizen, M. and Lombaerts, M. 1994. Population structure and levels of gene flow in the Mediterranean land snail *Albinaria corrugata* (Pulmonata: Clausiliidae). – *Evolution* 48: 577–586.
- Sfenthourakis, S. et al. 2004. From sampling stations to archipelagos: investigating aspects of the assemblage of insular biota. – *Global Ecol. Biogeogr.* 13: 23–35.
- Simberloff, D. 1983. Competition theory, hypothesis testing, and other community ecological buzzwords. – *Am. Nat.* 122: 626–635.
- Sokal, R. R. and Rohlf, F. J. 1995. *Biometry: the principles and practice of statistics in biological research*. – W. H. Freeman and Company.
- Solem, A. 1984. A world model of land snail diversity and abundance. – In: Solem, A. and van Bruggen, A. C. (eds), *World-wide snails: biogeographical studies on non-marine Mollusca*. E.J. Brill, pp. 6–22.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. – *Ecology* 60: 1225–1239.
- SPSS 1998. *Base system user's guide*. – SPSS, Inc.
- Summerville, K. S. et al. 2002. Does variation in patch use among butterfly species contribute to nestedness at fine spatial scales? – *Oikos* 97: 195–204.
- Thompson, J. et al. 2002. Land use history, environment, and tree composition in a tropical forest. – *Ecol. Appl.* 12: 1344–1363.
- Turner, W. R. et al. 2002. Global urbanization and the separation of humans from nature. – *Bioscience* 54: 585–590.
- Uriarte, M. et al. 2004. A neighborhood analysis of tree growth and survival in a hurricane-driven tropical forest. – *Ecol. Monogr.* 74: 591–614.
- Vidal-Martínez, V. M. and Poulin, R. 2003. Spatial and temporal repeatability in parasite community structure of tropical fish hosts. – *Parasitology* 127: 387–398.
- Vitousek, P. M. et al. 1997. Human domination of Earth's ecosystems. – *Science* 277: 494–499.
- White, P. S. and Pickett, S. T. A. 1985. Natural disturbance and patch dynamics: an introduction. – In: Pickett, S. T. A. and White, P. S. (eds), *The ecology of natural disturbance and patch dynamics*. Academic Press, pp. 3–13.
- Willig, M. R. and Camilo, G. R. 1991. The effect of hurricane Hugo on six invertebrate species in the Luquillo

- Experimental Forest of Puerto Rico. – *Biotropica* 23: 455–461.
- Willig, M. R. et al. 1996. Functional diversity of soil bacterial communities in the tabonuco forest: interaction of anthropogenic and natural disturbance. – *Biotropica* 28: 471–483.
- Willig, M. R. et al. 1998. Long-term monitoring of snails in the Luquillo Experimental Forest of Puerto Rico: heterogeneity, scale, disturbance, and recovery. – In: Dallmeier, F. and Comisky, J. (eds), *Forest biodiversity in North, Central, and South America and the Caribbean: research and monitoring*. UNESCO and The Parthenon Press, pp. 293–322.
- Worthen, W. B. et al. 1998. Community structure and environmental stress: desiccation promotes nestedness in mycophagous fly communities. – *Oikos* 81: 45–54.
- Wright, D. H. et al. 1998. A comparative analysis of nested subset patterns of species composition. – *Oecologia* 113: 1–20.
- Wright, D. H. and Reeves, J. H. 1992. On the meaning and measurement of nestedness of species assemblages. – *Oecologia* 92: 416–428.
- Zimmerman, J. K. et al. 1994. Responses of tree species to hurricane winds in subtropical wet forest in Puerto Rico: implications for tropical tree life histories. – *J. Ecol.* 82: 911–922.