

The interaction of disturbances and small mammal community dynamics in a lowland forest in Belize

R. KLINGER

Section of Evolution & Ecology, University of California, Davis, CA 95616, USA

Summary

1. Three floods (July 2000, August 2002, September 2003) and a hurricane (October 2001) that occurred in a lowland forest in the southern Maya Mountains of Belize presented an opportunity to evaluate the influence of these disturbances on the structure of a small mammal assemblage.
2. Four terrestrial and four primarily scansorial/arboreal species were trapped July 2000–March 2005 in six grids over 14 irregularly spaced trapping periods.
3. Community dynamics were characterized more by changes in species composition than changes in diversity. The dynamics were driven by species-specific variation in abundance, with changes in composition generally, but not exclusively, due to the occurrence or disappearance of species at low abundance. Despite the disturbances, species richness remained relatively constant. Evenness within the assemblage was consistently low, primarily as a result of dominance by one species, *Heteromys desmarestianus*.
4. Effects of flooding on community structure were direct but relatively brief (< 1 year), and varied with the duration and intensity of flooding. Effects from the hurricane were indirect but long-lasting and strongly related to severely reduced food resources.
5. This study suggests that long-term dynamics in the structure of many animal communities in the tropics often results from interactions between direct and indirect effects of disturbance. It also suggests that community resistance will depend on variation in disturbance type and regime, but resilience will be determined by the life-history characteristics of each species.

Key-words: community resilience, community resistance, community stability, diversity, resource limitation.

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Introduction

Considerable information now exists on the structure of small mammal communities in tropical forests (Voss & Emmons 1996), but knowledge of their temporal dynamics is largely lacking. This is a significant gap, because, beyond their importance as prey for carnivorous mammals, birds and reptiles, small mammals play important functional roles in tropical forests (Brewer & Rejmanek 1999). For example, changes in the structure of small mammal communities can alter plant–animal interactions, implying that long-term dynamics of small mammal communities may have strong effects on the structure and function of tropical forests (DeMattia, Curran & Rathke 2004).

Studies on the dynamics of small mammals in temperate regions have often focused on biotic interactions and climate (Meserve *et al.* 2003), but it is recognized that disturbance can be an important influence as well (Dunstan & Fox 1996). Most studies of disturbance in tropical forests have been focused on effects to ecosystem functioning and vegetation structure (Chazdon 2003). Far less attention has been directed at how these disturbances influence the structure and dynamics of animal communities (Waide 1991). Disturbances can have direct effects on animal communities as a result of differential mortality among species or age classes within populations. Recovery from direct effects are often rapid (Woolbright 1991), but indirect effects, such as changes in vegetation structure or resource levels (Karr, Schemske & Brokaw 1982; Levey 1988), may have longer-term consequences on animal community dynamics.

Understanding how direct and indirect effects from disturbances interact to influence small mammal

community structure is essential for a more general understanding of their dynamics, and also how these dynamics influence other interactions (Forget *et al.* 2002). Three floods and a hurricane that occurred over a 3-year period in the southern Maya Mountains of Belize provided an opportunity to analyse how these disturbances affected the dynamics of an assemblage of small mammals. A limited amount of information exists on direct and indirect effects of hurricanes on some animal communities, but virtually nothing is known of their effect on small mammals (Waide 1991). Studies in temperate regions have demonstrated that direct effects of flooding on small mammal communities can be pronounced, either as a result of mortality (Chamberlain & Leopold 2003), alteration of movement patterns (Andersen *et al.* 2000), or both. Presumably these patterns would be similar in tropical ecosystems, but flooding as a process structuring small mammal communities in tropical forests has largely been ignored. Therefore, the objectives of this study were to determine: (1) the degree to which the structure (e.g. species richness, evenness, and composition) of the small mammal assemblage was changed by the disturbances; (2) if the responses by the species to the disturbances tended to be unique for each species or if they were similar across the assemblage; (3) if changes in the structure of the assemblage were due to reduction in population size of dominant species and an increase in abundance of those species previously at low abundance, or if changes in abundance were independent of population size; and (4) what the relative importance of direct effects (e.g. mortality) and indirect effects (e.g. habitat alteration, changes in food production and availability) of the disturbances were on changes in the structure of the assemblage.

Materials and methods

STUDY AREA

The study was conducted from July 2000 to March 2005 in the Bladen Nature Reserve (BNR) in the south-eastern region of the Maya Mountains in southern Belize. There has not been any settlement in the BNR for more than 500 years, and population density in southern Belize is relatively low (5.01 individuals km⁻²). Several small villages (population < 300) are within 20 km of the reserve and the nearest paved road is 10 km away. The Bladen was established as a Nature Reserve in 1990, and no logging or hunting is permitted within the reserve boundaries.

The BNR is approximately 30 km inland from the Caribbean Sea and 80 km north of Belize's southern border with Guatemala. It is 350 km² in area and contains the headwaters and entire upper watershed of the Bladen Branch of the Monkey River. The river runs through the BNR in a south-west-to-north-east direction, with wide, alluvium covered flats in the floodplain of the eastern part of the watershed. The

annual rainfall is 2500–3000 mm, with 67–81% coming during the wet season (June–January; Belize Foundation for Research and Environmental Education unpubl. data). The mean annual minimum and maximum temperatures are 24 °C and 30 °C, respectively.

The main ridges are generally < 300 m in elevation, but the topography on the slopes is rugged and steep (mean angle = 38°). Soils are derived primarily from two geological formations; Coban limestone in the south-eastern section and Bladen volcanic formations in the north-western section (Bateson and Hall 1977). The vegetation in the BNR is primarily evergreen tropical forest (Beard 1944).

The fauna and flora in the BNR remain entirely intact. Based on range maps (Reid 1997), local checklists (McCarthy 1998), and habitat use the pool of small mammals (adult weight < 450 g) most likely to be trapped in the study included four species that occurred primarily on the forest floor, one arboreal species, and five scansorial species (Appendix 1).

DISTURBANCES

Four major disturbances occurred in the BNR between 2000 and 2003; a high intensity flood in July 2000 that covered 100% of the floodplain for 72 h, Hurricane Iris in October 2001, and two floods of low to moderate intensity in August 2002 (duration = 2 h, 25–50% of floodplain covered) and September 2003 (duration = 4 h, 50–75% of floodplain covered). Flooding in the BNR occurs in the wet season but it is not an annual event as in some other tropical ecosystems. No systematic records were kept on the flooding regime in the BNR prior to 1995, but local villagers state that floods occurred once or twice per decade. The last flood to occur in the BNR (defined as when the river rose above the main banks of the river) was in 1997 (J. Marlin, Belize Foundation for Research and Environmental Education pers. comm.). The floods that occurred 2000–03 were atypical in their frequency and extent (J. Marlin, pers. comm.). The 2000 flood was also unusual because of the rapid rate at which the water rose (> 1.5 m between 22.30 and 23.00 h) and long period of inundation (R. Klinger, pers. obs).

Hurricane Iris was a small but very severe hurricane (Category 4–maximum sustained winds 210–249 km h⁻¹; US National Oceanic and Atmospheric Administration National Hurricane Center <http://www.nhc.noaa.gov/2001iris.html>). It made landfall on October 9 with maximum sustained winds > 225 km h⁻¹. Although Iris moved through Belize within a few hours, a total of 310 000 ha were estimated to have been severely damaged, all in southern Belize (Meerman 2001). The eye of the hurricane passed directly over the BNR, and high winds in the reserve were sustained for approximately 6 h (J. Marlin, pers. comm.). The magnitude of damage to the forest was severe and extensive, with 75–100% of the trees in most areas defoliated, having their trunk snapped, or uprooted (Meerman 2001; R.

Klinger pers. obs). There are no records to confirm when the last hurricane to hit the BNR was, but there is no evidence indicating that the reserve has been seriously affected by one since the 1930s.

TRAPPING

Mark–recapture trapping was used to sample small mammal species in six permanent 0.5-ha plots from July 2000 to March 2005. The plots were established in June 2000 at randomly selected locations on the flats in the south-east region of the reserve. Distance between the plots was 125–375 m. The plots consisted of a grid of 100 trap stations divided equally among 10 lines and spaced 7 m apart. A single Sherman live trap (Model XLK; 8 cm × 10 cm × 38 cm) was placed at each station and baited with whole peanuts, whole raw corn kernels mixed with peanut butter, and a slice of banana or plantain. The traps were covered by a layer of leaves and/or soil and checked once a day (each morning).

Trapping was originally planned as a robust design protocol to be conducted in each of the grids in each of three equally spaced primary periods (Pollock 1982) each year from 2000 to 2003. However, the four disturbances created logistical and financial constraints, so trapping was conducted irregularly in each of 14 primary periods from July 2000 to March 2005. It was only possible to trap four grids in July 2000, and trapping could only be conducted in three primary periods from 2000 to 2001. No trapping occurred in 2003. Monthly trapping was conducted January–April 2004, and then at approximately 2-month intervals August 2004–March 2005.

Trapping was conducted for 5–6 days (secondary sessions) per grid in all primary periods except August 2000. Trapping in August 2000 was done to make an immediate assessment of the impact of the July 2000 flood on the small mammal assemblage. Trapping began 4–10 days after the flood. Fifty traps were placed at alternating stations in each of the four plots trapped in July and checked each morning for 3 days.

All captured individuals were identified to species and sex, ear-tagged with a unique identification number, weighed, evaluated for reproductive condition (females pregnant, lactating, or not active; males with testes descended or not), and assigned to an age class (adult, subadult or juvenile based on pelage, weight and reproductive status).

VEGETATION STRUCTURE AND FOOD AVAILABILITY

Estimates of vegetation structure were made in each grid during each of three time periods; August–September 2001, August–September 2002, and March–October 2004. Data were collected on 18 variables in a 2.5 m radius circle (20 m²) centred on each trap station (Appendix 2).

Food availability was monitored by conducting weekly searches of fruiting trees and vines in each plot.

The searches were done within 3–4 weeks of the beginning or end of trapping during each primary period. When a fruiting tree or vine was found, a count was made of the number of fruits or seeds on the ground in four 1-m² quadrats. One quadrat was located randomly along each of four 3-m transects orientated in the four cardinal directions from the main trunk of the tree or the main stem of the vine. The mean of the four counts was used as the estimate of fruit abundance for that species in that plot, and estimates were summed as the index for all fruiting tree and vine species in the plot. Counts of the number of infructescences per tree were done for *Astrocaryum mexicanum* within 2 weeks of the beginning or end of trapping during each primary period.

DATA ANALYSIS

Abundance and persistence

The minimum number known alive (MNKA) ha⁻¹ was used as an index of population density. Although MNKA is known to consistently underestimate population size (Otis *et al.* 1978), models used to estimate density require a relatively large amount of data to generate reasonably precise estimates (Parmenter *et al.* 2003). Most of the small mammal species we encountered in this study were uncommon (see Results), so attempts to derive estimates of density with such low sample sizes for most species would have been inappropriate.

Persistence in the assemblage was defined as the number of primary trapping periods a species occurred in. Least-squares linear regression was used to analyse the overall relationship between abundance (log₁₀ MNKA) and persistence. To determine if persistence was related to the disturbances, the relationship between abundance in the trapping period prior to the most recent disturbance (pre) and the relative change in MNKA following the disturbance (post) was analysed with least-squares linear regression. Relative change in MNKA was calculated as log_e(MNKA_{post}/MNKA_{pre}).

VEGETATION STRUCTURE

Canonical Variates Analysis (CVA, i.e. discriminant analysis) (Huberty 1994) was used to reduce the dimensionality of the 18 vegetation structure variables and describe differences in vegetation structure between the plots before and after the hurricane. Plots were the grouping variable, and the discriminant axes were calculated from the vegetation variables from each trap station within each plot. The CVA was conducted with CANOCO 4.5 (ter Braak & Smilauer 2002). The significance of the CVA in CANOCO 4.5 was determined by randomization tests consisting of 500 permutations constrained within each plot (variables were permuted between trap stations and years).

SPECIES COMPOSITION AND DIVERSITY

Rank-abundance plots were used to describe the relative abundance and diversity of the small mammal species assemblage (Tokeshi 1993). Differences in the number of species per grid between the primary trapping periods were tested with ANOVA, and a Chi-square test was used to analyse differences in the total number of species between primary trapping periods.

The overall pattern of changes in species composition across all 13 primary trapping periods was analysed with Principal Coordinates Analysis (PCoA). PCoA is a metric scaling method that represents a set of objects in a multidimensional space based on Cartesian coordinates (Gower 1966). It uses a matrix of dissimilarity between objects, and the extracted axes are ordered in importance based on their eigen values (λ). Because there was low evenness in the proportional abundance of the species (see Results) two different analyses were conducted; one that included all species and one without the dominant species (*Heteromys desmarestianus*). The MNKA of each species was pooled across the plots within each primary trapping period, which resulted in a data matrix of 13 periods \times 8 species. Euclidean distance was used to compute the dissimilarity matrices between the periods (Legendre & Legendre 1998). The PCoA was conducted with CANOCO 4.5 (ter Braak & Smilauer 2002).

SMALL MAMMAL SPECIES/VEGETATION STRUCTURE RELATIONSHIPS

Two methods were used to analyse the relationship between vegetation structure and distribution and abundance of small mammal species. Mantel tests (Legendre & Legendre 1998) were used to analyse the degree of spatial autocorrelation in vegetation structure and small mammal species distribution within plots, while Canonical Correspondence Analysis (ter Braak 1995) was used to evaluate associations of the small mammal species with specific vegetation structure variables.

Euclidean distance was used to calculate three dissimilarity matrices for the Mantel tests; intertrap distances, small mammal assemblage, and vegetation structure. Vegetation structure variables were standardized prior to calculation of the matrices, and the intertrap distance matrix consisted of the actual distances (in metres) between all traps. Analyses proceeded in three steps and were conducted for each plot in each year. First, a simple Mantel test was conducted on the intertrap distance and vegetation structure matrices, with a significant result indicating evidence of patchiness in vegetation structure. Partial Mantel tests were then conducted on (1) the correlation between the species and distance matrices with vegetation structure held constant, and (2) the correlation between the species and vegetation matrices with distance held constant. Significance of the tests was

calculated from 10 000 random permutations of the matrix elements. The Mantel tests were performed with the program ZT (Bonnet & Van de Peer 2002).

The CCA was conducted on matrices of the mammal species at each trap station (species matrix), vegetation structure at each trap station (environmental matrix), and coding that partitioned the data for each plot in each year (covariable matrix). Trap stations with no captures were included as a 'species' in the species matrix. Rare species in the species matrix were downweighted and all variables in the environmental matrix were log +1 transformed with the exception of the index of small vine (< 1 cm diameter) abundance. Permutation tests ($n = 499$ permutations per test) were used to determine the significance of variables in the ordination, the first ordination axis, and the overall ordination (ter Braak 1995). The CCA was based on the linear combination of plot scores, and permutation tests were conditioned on the covariable matrix and the spatial structure of the trap stations in the plots. CANOCO 4.5 was used to perform the CCA (ter Braak & Smilauer 2002).

Results

A total of eight small mammal species were captured in the 14 primary trapping periods, with a mean of 3.6 species per season (± 0.3 SE; Appendix 1). There was no significant difference in the mean number of species per plot ($F = 1.149$, d.f. = 12, 63, $P = 0.339$) or the total number of species between primary trapping periods ($\chi^2 = 1.50$, d.f. = 12, $P = 0.999$). The total number of species caught in the primary trapping periods ranged from 3 to 5 (Fig. 1), while the mean number of species per plot ranged from 1.7 to 2.8.

Fluctuations in MNKA were species-specific, and all species showed moderate to high variation in density (Fig. 2). Coefficients of variation in MNKA ranged from 39.4% to 136.1%, and only three species (*H. desmarestianus*, *Sigmodon hispidus*, *Ototylomys phyllotis*) occurred in > 50% of the trapping periods. *Oryzomys alfaroi*, *Tylomys nudicaudus*, *Marmosa robinsoni* and *Marmosa mexicana* occurred sporadically and at low abundance. Persistence of species in the assemblage was positively related to abundance ($r = 0.795$, $P = 0.018$; Fig. 3), but there was no significant relationship between $MNKA_{pre}$ and relative change in abundance ($P = 0.706$).

The assemblage was dominated by *H. desmarestianus*, regardless of season or the type and magnitude of disturbance (Fig. 1). Density of *H. desmarestianus* was an order of magnitude greater than any other species in every trapping period other than July 2000 (Fig. 2), with a mean relative abundance of 86.8% (± 1.8 SE). The population of *H. desmarestianus* went into a general decline in the year after the hurricane, but then increased almost threefold from January 2004 to March 2005.

Oryzomys rostratus was the second most abundant species in the first four trapping periods, but went into a sharp decline and disappeared from the assemblage

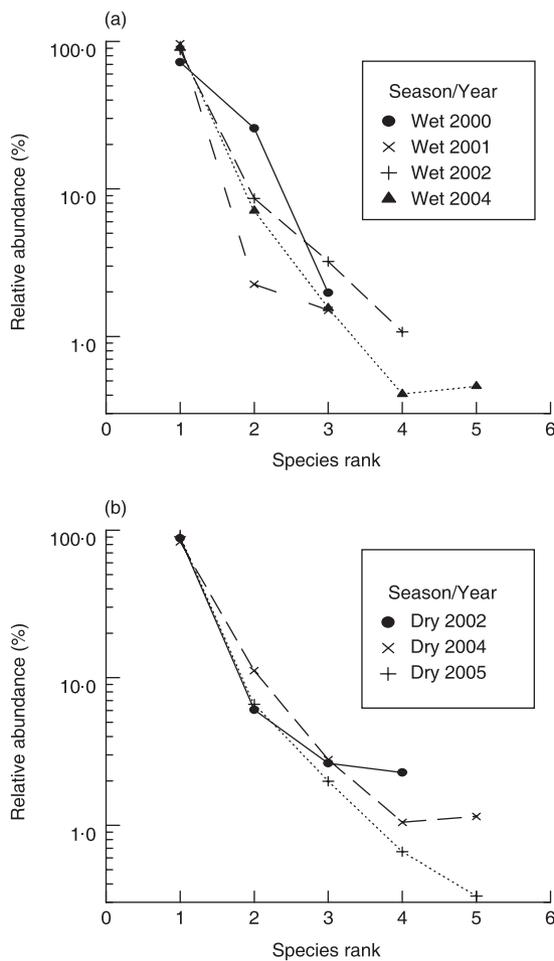


Fig. 1. Rank-abundance plots of a small mammal assemblage consisting of eight species in the Bladen Nature Reserve, Belize, July 2000–March 2005. The wet season (a) was June–December and the dry season (b) January–May.

from September 2002 to March 2005. In contrast, *S. hispidus* was not captured until after the hurricane, but it increased in density and persisted in the population through March 2005. *Ototylomys phyllotis* fluctuated throughout the study, and MNKA numbers were generally greater in the dry season than the wet season (Fig. 2).

The first axis of the PCoA for all species explained 97.5% ($\lambda = 0.975$) and the second axis 1.9% ($\lambda = 0.019$) of the variation in species composition between the 13 periods. For the PCoA without *H. desmarestianus* the

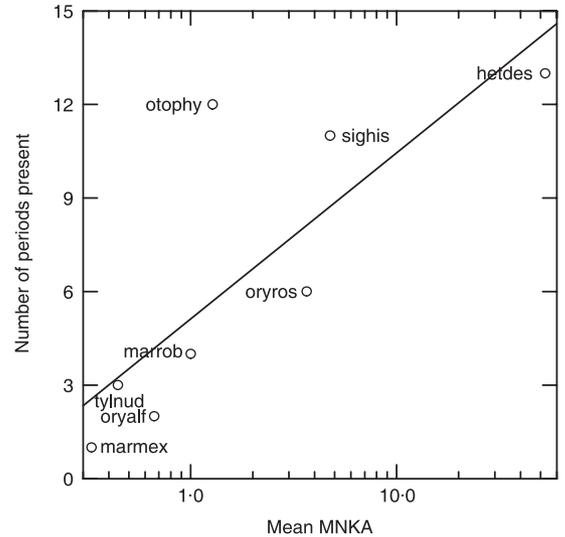


Fig. 3. The relationship between the \log_{10} mean population density (minimum number known alive; MNKA) and the number of primary periods ($n = 14$) small mammal species were captured in at the Bladen Nature Reserve, Belize, July 2000–March 2005.

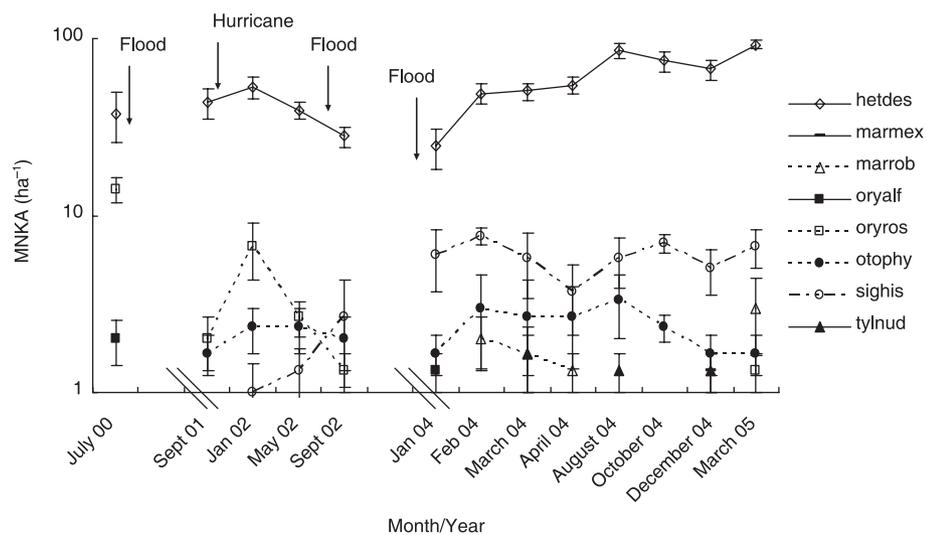


Fig. 2. Estimates of the minimum number of individuals known alive ha^{-1} ($\text{MNKA} \pm 1 \text{ SE}$) for eight small mammal species in the Bladen Nature Reserve, Belize. Double break lines on x-axis indicate periods > 1 year when trapping could not be conducted. No individuals of any species were captured in August 2000 (1 week after a major flood). Species names and their acronyms are: *Heteromys desmarestianus* (hetdes), *Ototylomys phyllotis* (otophy), *Sigmodon hispidus* (sighis), *Oryzomys rostratus* (oryros), *Oryzomys alfaroi* (oryalf), *Tylomys nudicaudus* (tylnud), *Marmosa mexicana* (marmex), and *Marmosa robinsoni* (marrob).

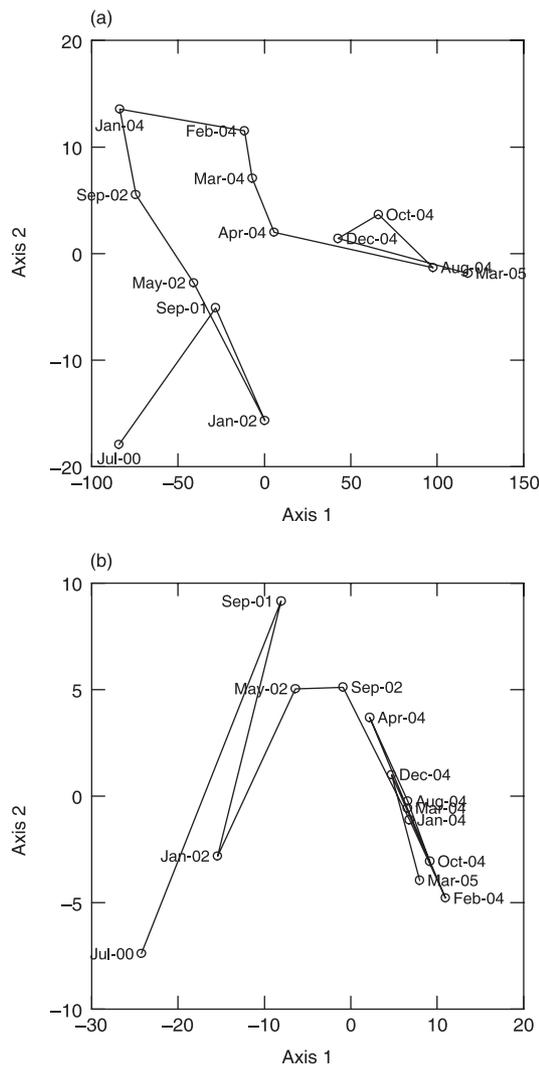


Fig. 4. Principal coordinates analysis plot of the changes in species composition for an assemblage of small mammal species in the Bladen Nature Reserve, Belize. (a) The entire eight-species assemblage, and (b) the assemblage with the dominant species *Heteromys desmarestianus* omitted.

first axis explained 80.4% ($\lambda = 0.804$) and the second axis 15.5% ($\lambda = 0.155$) of the variation between the periods. The PCoA axes are interpreted as two temporal gradients of change in the small mammal assemblage (Fig. 4). The patterns were similar for the PCoA for all species (Fig. 4a) and for the PCoA without *H. desmarestianus* (Fig. 4b). Axis 1 represented the long-term shift over the 5-year period from an assemblage characterized by *H. desmarestianus* and *Oryzomys rostratus* to an assemblage where the core species were *H. desmarestianus*, *Ototylomys phyllotis* and *S. hispidus*. Axis 2 represented more abrupt changes in the relative abundance of the species due to the disturbances, especially after the flood in July 2000 and the hurricane in October 2001.

No individuals of any species were captured in the primary trapping period immediately following the July 2000 flood, but there was no evidence that the other two floods had a similar magnitude of impact

on the assemblage. The greatest change in Euclidean distance in the ordination space was in the year after the July 2000 flood, regardless of whether *H. desmarestianus* was included in the PCoA or not. The change in Euclidean distance between the three flood events was proportionally greater for the PCoA without *H. desmarestianus* than the PCoA for all species, but the proportional change in Euclidean distance between the hurricane and the mean of the three flood events were comparable for the analyses with and without *H. desmarestianus*.

The CVA indicated that three complex gradients described changes in vegetation structure following the hurricane (Appendix 3). The first three axes explained 77.5% of the variation in vegetation structure and clearly depicted secondary succession from a pre-hurricane forest with a relatively open understory to a post-hurricane structure with a large proportion of understory growth, small vines and clusters of downed wood. The impact of the hurricane on the forest canopy and subsequent infusion of light is reflected by the percentage of tree and shrub cover < 2 m, percentage litter cover, percentage cover of ground vines, and number of small logs (< 5 cm diameter) weighing heavily on more than one of the standardized canonical axes (Fig. 5). The first CV axis was an understory/ground layer gradient separating the 2002 plots (1 year post-hurricane) from the other years. The second axis represented a canopy cover and understory gradient, with vegetation structure prior to the hurricane characterized by an intact canopy with relatively low amounts of small trees, shrubs, small vines and ground vines. The third axis characterized complexity in the understory layer, deepening of the litter layer, a profusion of small trees (< 5 cm d.b.h.), and development of an herbaceous layer. The separation of the 2002 and 2004 plots was primarily due to the increased amount of small hanging vines, small trees and downed branches (Fig. 5).

Mantel tests indicated that vegetation structure became increasingly patchy within the plots after the hurricane. The mean value of the normalized Mantel correlation coefficient (r) in 2001 was 0.0187, and only one plot showed any evidence of spatial autocorrelation in vegetation structure (Vegetation \times Distance correlation; Appendix 4). The mean value of r in 2002 was 0.0720 and four plots indicated increased patchiness in vegetation structure. By 2004 the mean value of r had increased to 0.1218 and all plots showed a significant level of patchiness. The pattern for spatial structuring of the small mammal species was less pronounced than that of vegetation structure, although there was a significant degree of aggregation in five of the six plots by 2004 (Species \times Distance correlation; Appendix 4). There was no evidence that the distribution of the small mammal species was related to patchiness in vegetation structure, either before or after the hurricane (Species \times Vegetation correlation; Appendix 4).

The CCA of the small mammal species was significant for both the first canonical axis ($F = 7.42$, $P = 0.002$)

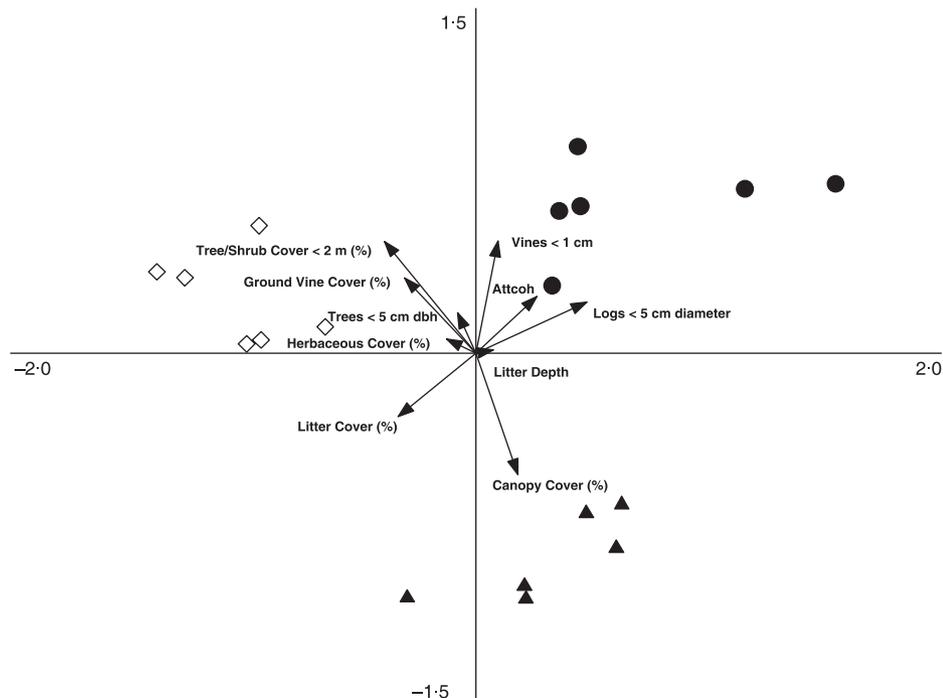


Fig. 5. Canonical variates analysis of changes in the vegetation structure of six small mammal trapping grids in the Bladen Nature Reserve, Belize. Solid triangles are symbols for the grids in 2001 (1 month pre-hurricane; sampling done September 2001), open diamonds are the grids in 2002 (one year post-hurricane; sampling done September 2002), and filled circles are the grids in 2004 (3 years post-hurricane; sampling done March–October).

and the overall ordination ($F = 3.30$, $P = 0.002$). However, the unconstrained canonical axes explained a very low proportion of the variation in species composition and the correlation of the linear combination of the vegetation structure variables with the canonical axes was low (Appendix 5). The first two axes of the constrained ordination explained 86.6% of the variation in species composition of the small mammal assemblage (Appendix 5). Five of the 18 vegetation structure variables had a significant relationship with small mammal distribution and abundance patterns. Canopy cover had a strong correlation and height of the herbaceous layer a moderately strong correlation with the first canonical axis. Herbaceous cover had a strong correlation with the second canonical axis, while trees > 25 cm d.b.h. and logs 5–25 cm diameter had moderately strong correlations with both canonical axes.

Heteromys desmarestianus and traps with no captures had no strong association with any of the vegetation structure variables (Fig. 6). *S. hispidus*, *Oryzomys rostratus* and *Ototylomys phyllotis* occurred most frequently in patches with canopy gaps. *S. hispidus* was trapped more frequently in patches with a well developed herbaceous layer, while *Oryzomys rostratus* and *Ototylomys phyllotis* occurred more frequently in patches with downed logs. There was an indication that *Oryzomys alfaroi* and *Marmosa mexicana* were trapped more frequently in patches with intact canopies, while *Tylomys nudicaudus* and *M. robinsoni* were trapped more frequently in gaps, but these patterns are tenuous because of the small number of captures for these species.

Fruit production was unaffected by the floods, but decreased dramatically after the hurricane (Fig. 7a). Only one species of tree (*Spondias mombin* L.; Anacardiaceae) was observed in the first 3 months after the hurricane with fruits, and these occurred mainly on broken branches that had fallen to the ground. Despite virtually no fruit production by other trees, the amount of *S. mombin* on the ground was very high, resulting in the index of fruit availability reaching a high in January 2002 (Fig. 7b). Fruit availability dropped precipitously after January 2002, and no trees or lianas were observed producing fruit during January–September 2002. Trees and lianas produced fruit again in January 2004, and the index of fruit availability increased greater than twofold from January 2004 to March 2005 (Fig. 7b). Least-squares regression analysis indicated that there was a significant positive correlation of mean fruit production with the MNKA for both *H. desmarestianus* ($r = 0.767$, $P = 0.002$) and the other small mammal species ($r = 0.632$, $P = 0.020$).

Similar to trees and lianas, flooding had no discernible effect on fruit production of *Astrocaryum mexicanum* (Fig. 7c). Production of infructescences by *A. mexicanum* decreased from September 2001 to January 2002 by 65%, but then increased rapidly through September 2002 from 1.1 to 2.4 infructescences per individual. Production by *A. mexicanum* had returned to pre-hurricane levels by January 2004 and remained relatively constant through October 2004, then dropped 38% through March 2005 (Fig. 7c).

Least-squares regression analysis indicated that there was no significant correlation between production of

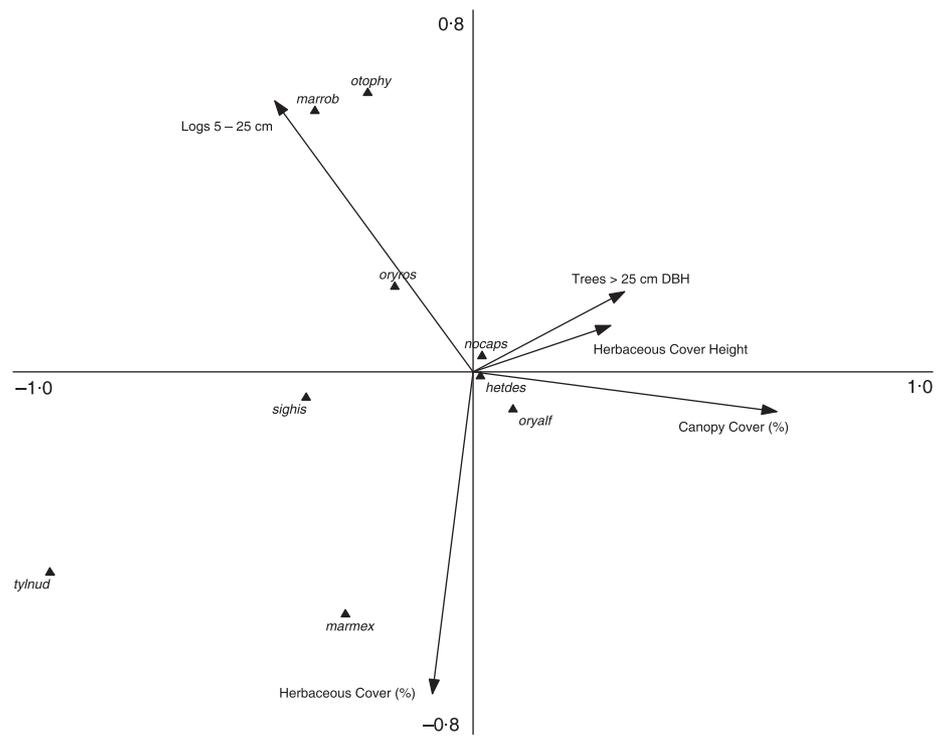


Fig. 6. Canonical Correspondence Analysis plot of the relationship between eight small mammal species and five vegetation structure variables that had a significant influence ($P = 0.05$) on small mammal occurrence in the Bladen Nature Reserve, Belize. Species names for the acronyms are in Appendix 1.

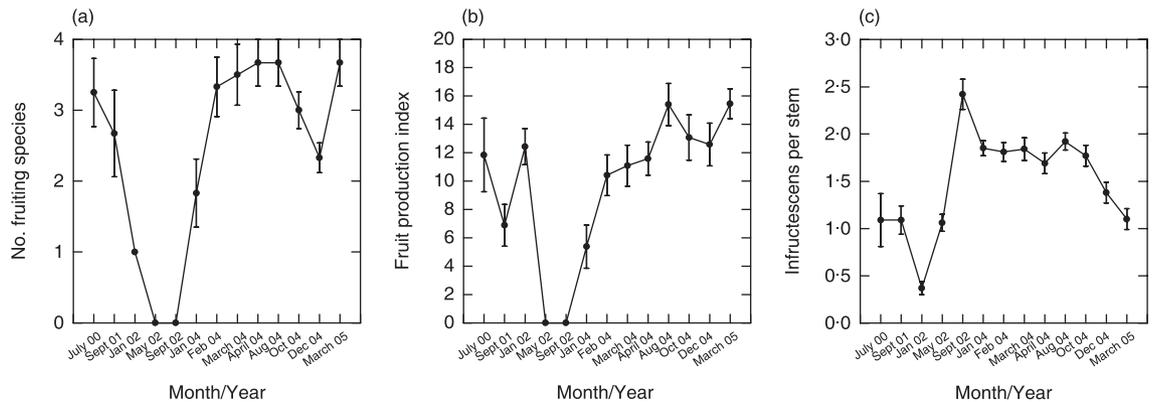


Fig. 7. Mean estimates (± 1 SE) of (a) the number of tree and vine species producing fruit, (b) an index of fruit abundance for trees and vines, and (c) the mean number of nuts per infructescens for the palm *Astrocaryum mexicanum* in the Bladen Nature Reserve, Belize. A hurricane occurred in October 2001, and floods in July 2000, August 2002, and September 2003.

nuts by *A. mexicanum* and MNKA for either *H. desmarestianus* ($P = 0.643$) or the other small mammal species ($P = 0.533$).

Discussion

The dynamics of the small mammal community in the BNR were characterized by a high degree of species-specific variability in population size. Persistence of species in the assemblage depended to a large degree on abundance, but there was no evidence that persistence was directly influenced by the disturbances. Changes in species composition were due primarily, but not entirely, to the unpredictable appearance and disappearance of

rare species. The influence of the disturbances on species composition depended upon both the type and the magnitude of the individual events, as well as the life-history traits of the species. Of perhaps greatest significance is that the floods and hurricane influenced the small mammal assemblage through different mechanisms, with long-term indirect effects of the hurricane having a far greater and much longer influence on the assemblage than the direct effects of the floods.

FLOODS

Floods can have severe, direct effects on small mammal populations, but effects typically vary with factors such

as intensity, seasonality and predictability (Sheppe 1972; Madsen & Shine 1999). Floods in the BNR are not uncommon, but they are not predictable events. Their effects on the small mammal assemblage in the BNR appear to be relatively brief (< 1 year), with severity not related strictly to the occurrence of flooding but to their duration and extent.

The July 2000 flood had a severe impact on the entire small mammal assemblage in the floodplain, for all intents and purposes eliminating it. The assemblage began to re-establish within a relatively brief period of time though, probably as a result of dispersal by individuals from the surrounding hillsides (R. Klinger unpubl. data). There was no change in the number of species that were captured prior to the 2000 flood and 1 year after, and the post-flood responses were species-specific. *Oryzomys alfaroi* virtually disappeared from the floodplain assemblage after the flood, but it also was not trapped in areas above the floodplain where it had once occurred (R. Klinger, unpublished data). *Oryzomys rostratus* continued to persist in the assemblage the year after the July 2000 flood, but its abundance was an order of magnitude lower than immediately prior to it. In contrast, within a year the abundance of *H. desmarestianus* had returned to pre-flood levels.

The floods in 2002 and 2003 were of much shorter duration and extent and appeared to have had only minor effects on the assemblage. Within 3 months of each of those floods there were no discernible changes in species composition or species richness. There was also no evidence the 2002 and 2003 floods had a consistent effect on abundance of the species. Density of two terrestrial species, *H. desmarestianus* and *Oryzomys rostratus*, were already in decline prior to the 2002 flood. It is possible the flood may have exacerbated their decline, but *S. hispidus*, another terrestrial species, showed a steady increase in density. Density of *Ototylomys phyllotis*, a scansorial species, appeared not to be influenced to any significant degree by the floods.

HURRICANE

In contrast with the floods, there was no evidence that the hurricane had direct, immediate impacts on the structure of the small mammal assemblage. Indirect effects were pronounced though and influenced the assemblage for a number of years, likely as a result of reduced food availability and, to a lesser degree, changes in vegetation structure.

Generally, small mammal abundance in the BNR was related to food. However, the degree to which food production influenced community dynamics was modified by the life-history characteristics and feeding behaviour of the individual species. The only species to show an increase in abundance between September 2001 and September 2002 was *S. hispidus*. Most of the small mammal species in the BNR are principally frugivorous and/or granivorous, but *S. hispidus* is

primarily herbivorous (Cameron & Spencer 1981). Fruit production virtually ceased for more than 2 years after the hurricane, most likely because trees that were still standing put most of their energy into leaf production (Barone 1998). However, herbaceous vegetation increased after the hurricane, presumably because the reduction in canopy cover resulted in greater levels of understory light (Fernandez & Fetcher 1991).

Density of *H. desmarestianus* was correlated with fruit production but not to production of *A. mexicanum* nuts. This is likely due to *A. mexicanum* being widespread, abundant and producing nuts throughout the year. *A. mexicanum* provides the main year-round food source for *H. desmarestianus*, but it is the production and availability of other fruits that influences changes in their density. The only food resource available in any abundance to terrestrial small mammals from January 2002 to January 2004 was *A. mexicanum* nuts. These nuts (17 g) are readily eaten and cached by *H. desmarestianus* (Brewer & Rejmanek 1999) but not by other small mammals (R. Klinger, unpublished data). Indeed, *A. mexicanum* nuts were likely the critical reason why the population of *H. desmarestianus* did not decline further in the year after the hurricane. Because they do not consume *A. mexicanum* nuts and production of other food resources was extremely low, *Ototylomys phyllotis* and *Oryzomys rostratus* declined in abundance in the year after the hurricane, with *Oryzomys rostratus* eventually disappearing for over 2 years.

The seasonal patterns observed from 2004 to 2005 supported the patterns from the first post-hurricane year. When fruit production began to increase in 2004 the abundance of *H. desmarestianus* and *Ototylomys phyllotis* also began to increase. The population of *S. hispidus* decreased in the dry season, a period when herbaceous vegetation in the BNR is largely desiccated. In contrast, the population of *Ototylomys phyllotis* decreased during the latter part of the wet season, when fruiting in the BNR was sparse.

Vegetation structure in the lower strata increased in both horizontal and vertical complexity after the hurricane, but this accounted for a relatively small proportion of the variation in small mammal distribution patterns. The relationship between vegetation structure and habitat selection has been shown to be important in other tropical small mammal assemblages (Williams, Marsh & Winter 2002), and it would be premature to conclude that it was not of importance in the BNR. The weak relationships could have been a statistical artefact related to small sample sizes for four of the species, species responding to factors other than vegetation structure (Adler 1995), or habitat-use patterns being scale-dependent (Williams *et al.* 2002).

DIVERSITY AND COMPOSITION PATTERNS

Despite the disturbances and temporal flux in population sizes and species composition, three consistent patterns emerged: (1) low alpha diversity resulting from both

low species richness and low evenness; (2) low abundance of most species; and (3) dominance of the assemblage by *H. desmarestianus*.

The low richness of small mammals in the BNR may be explained in part as simply reflecting large-scale geographical patterns (Voss & Emmons 1996). However, a comparison of mammal faunas at three sites within 30–60 km of each other in the Maya Mountains of southern Belize documented substantial intersite differences in species richness of small mammals, with the fewest being in the BNR (Caro *et al.* 2001). Climate, weather, biogeographical and physiographic patterns among the sites are similar, suggesting that local factors are influencing species richness as well.

The density of most of the species in the BNR was very low and highly variable. It is well understood that populations that are small and variable can be expected to have shorter persistence times than larger or less variable ones (Lande 1993). This explanation can only be extended so far though. While most species at low abundance in the BNR did have lower persistence times than abundant ones, *Oryzomys rostratus* was an exception. It was the second most abundant small mammal species at the beginning of the study, then crashed and virtually disappeared from the assemblage. This pattern is suggestive, because in a seasonal wet forest in Costa Rica DeMattia *et al.* (2004) observed a population crash for *Oryzomys talamancae*, which had been the most abundant small mammal species in that assemblage.

It does not appear to be uncommon for particular assemblages of Neotropical small mammals to be dominated by one or two species (Voss & Emmons 1996), but explanations for the existence of this pattern have largely been ignored. Intrinsic demographic rates and life-history characteristics may be the most important reasons why *H. desmarestianus* dominated the small mammal assemblage in the BNR. Although there is geographical variation in its density (DeMattia *et al.* 2004), *H. desmarestianus* has a relatively large range (Reid 1997) and is often considered to be the most abundant small mammal in many lowland forests of Central America (Sanchez-Cordero & Fleming 1993). *H. desmarestianus* is a generalist in both habitat use and diet, and it caches a high proportion of its food (Fleming 1983). This may allow it to exploit a wider range of food items than some of the other small mammal species in the BNR, as well as giving individuals a greater chance of surviving periods of food scarcity. Its demography, life-history and behaviour characteristics may simply allow it to reach greater density than other species and buffer potentially high fluctuations in population size.

Conclusions

In contrast with historical perspectives that animal populations were more constant and that large natural disturbances were less common in the tropics than in temperate regions (May 1973), it is now well under-

stood that disturbances are prevalent (Whitmore & Burslem 1998) and fluctuation in abundance of many vertebrate and invertebrate taxa in the tropics are common and often quite dramatic (Wolda 1978; Inoue *et al.* 1993; Wright *et al.* 1999). Biotic factors such as seasonal and interannual variation in food resources have often been found to have an important influence on animal community dynamics in the tropics (Karr *et al.* 1982; Levey 1988). However, the patterns observed for the small mammal assemblage in the BNR suggests that direct and indirect effects of disturbance may often modify biotic influences on these dynamics and leave a strong historical imprint on community structure.

Given the prevalence and variety of disturbances in the tropics, it is unlikely that many animal communities remain in even quasi-equilibrium for long periods of times. It can be expected that variation in the components that comprise different disturbance regimes (e.g. extent, intensity, duration, heterogeneity, frequency and timing) will determine the severity of disturbance on community stability, and that resistance may depend in large part on this variation. However, if the species-specific responses to disturbances observed in the BNR are representative of a broader pattern, then life-history characteristics will likely play an important part in resilience. Determining the generality of these patterns will have importance not just for gaining a better understanding of the dynamics of animal communities, but the degree to which these dynamics interact with and influence other processes as well.

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Supplementary material

The following supplementary material is available as part of the online article (full text) from <http://www.blackwell-synergy.com>

Appendix S1. Non-volant small mammal species known to occur and those potentially occurring in the Bladen Nature Reserve, Belize.

Appendix S2. Vegetation structure variables measured in a 2.5 m radius (20 m²) around each of 100 traps in each of six 0.5-ha small mammal trapping grids in the Bladen Nature Reserve, Belize.

Appendix S3. Canonical variates analysis statistics for vegetation structure in six small mammal trapping grids in the Bladen Nature Reserve, Belize.

Appendix S4. Mantel test statistics for an analysis of the correlation between captures of small mammals (Species), distance between trap stations (Distance), and vegetation structure (Vegetation) in six 0.5-ha plots in the Bladen Nature Reserve, Belize.

Appendix S5. Canonical Correspondence Analysis statistics for the relationship between eight small mammal species and vegetation structure in the Bladen Nature Reserve, Belize.