12

Frugivorous Birds in Fragmented Neotropical Montane Forests: Landscape Pattern and Body Mass Distribution

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TRANSFORMATION of tropical landscapes by humans has influenced plant and animal assemblages in many ways. Most studies have examined how species abundance and richness change with increasing forest fragmentation (Quintela 1985; Bierregaard and Lovejoy 1989; Klein 1989; Newmark 1991; Estrada et al. 1993; Kattan, Alvarez-López, and Giraldo 1994; Laurance 1994; Malcolm 1994; Didham, chap. 5; Warburton, chap. 13; Lynam, chap. 15), or with the transformation of native forests into second-growth or managed ecosystems (Holloway, Kirk-Spriggs, and Chey 1992; Johns 1992b; Lambert 1992; Thiollay 1992; Andrade and Rubio 1994; Escobar 1994). The results of these studies, however, have varied considerably, probably reflecting the complex relationships between habitat modification and biodiversity loss, the inherent differences among study sites, and possibly a mismatch between the scale of the problems being addressed and the methods used. As a consequence, it has often been difficult to establish patterns reflecting the effects of habitat modification on biodiversity and, moreover, how these factors interact to influence ecosystem processes (Vitousek 1990; Kruess and Tschnarntke 1994; Pimm and Sugden 1994; Tilman and Downing 1994; Turner, Gardner, and O'Neill 1995).

Holling et al. (in press) presented a novel conceptual framework that may help to integrate the above issues. First, long-term research has shown that ecosystems are structured by a few processes that generate discontinuities at various spatial and temporal scales (e.g., Clark, Jones, and Holling 1979; Harris 1980; Gunderson 1992). Second, the discontinuous nature of ecosystems influences the behavior and morphology of organisms. In particular, Holling (1992) found that the body masses of boreal birds and mammals are discontinuously distributed, such that species of similar mass tend to aggregate or lump together, in a manner suggesting that they exploit a common suite of resources (but see Manly 1996). Third, differences in the lump structure of animal body masses reflect differences in ecosystem structure. Holling (1992) showed that the distribution of body mass lumps of boreal forest and boreal prairie birds and mammals has a characteristic signature, reflecting the structure of those ecosystems. Hence, a focus on body mass lump structure offers a new way to investigate the complex relationships between landscape pattern, the structure of animal assemblages, and ecosystem processes at broad scales.

In this chapter we ask how changes in landscape pattern affect assemblages of frugivorous birds in Neotropical mountains. We concentrate on frugivores because seed dispersal by birds is especially important in Neotropical mountains as compared with the lowlands (Terborgh 1977; Gentry 1983; Stiles 1985; Renjifo et al., in press), offering an opportunity to relate the process of seed dispersal to landscape pattern. We focus on mountains because natural and human disturbances have generated complex landscapes over small areas (Haslett 1994), offering an ideal opportunity to assess how changes in landscape pattern influence animal assemblages.

We present four comparisons representing two different scales of inquiry to assess how lump structure in body masses of frugivorous birds changes from areas covered mostly by forest to areas covered by open vegetation. The first scale is defined by elevational zones within the mountains of Colombia, and the second by sites within these elevational zones that have been differently affected by human activities. We use body mass as an attribute that reflects information on life history traits, such as fecundity and dispersal ability, that can influence both a species' response to habitat fragmentation (Laurance 1991a; Lawton et al. 1994; Brown 1995; Gaston and Blackburn 1995; Sieving and Karr, chap. 11) and aspects of its foraging behavior, such as the size of seeds it can ingest and disperse (Moermond and Denslow 1985).

METHODS
Study Area

Our study focused on the Andes of Colombia, South America. The Andes consist of three mountain ranges of different geological origin, each running in a north-south direction (Irving 1975). We defined montane habitats as those above the 800 m topographic contour line (fig. 12.1). In the absence of human disturbance this region would be covered by forest, except for the páramo (above 3,400 m) and small areas affected by rain shadows (Cuatrecasas 1958). Forest composition, structure, and physiognomy change with elevation, from the complex lowland tropical forest to the simpler páramos (Cuatrecasas 1958; Espinal et al. 1977).

The area encompassed by this study represents less than 35% of the total area of Colombia (1,380,000 km^2), yet harbors one of the richest biotas in all of the Neotropics (Duellman 1979; Henderson, Churchill, and Luteyn 1991; Gentry 1992a,b; Renjifo et al., in press). It has been postulated that the high levels of diversity and endemism in this area are the result of an intense disturbance regime (Gentry 1992a; J. Luteyn, pers. comm.). A complex topography and geology, combined with high precipitation, generates landslides, mudflows, avalanches, and volcanic eruptions, which continuously transform these mountains (Mejía et al. 1994; Velásquez et al. 1994).

Superimposed on this natural disturbance regime are the effects of human activities. At least 50% of the total population of Colombia (37 million people) has settled in montane areas (Banguero 1993). Presently, less than 30% of this area is covered by forest, most of which is found either at elevations above 2,500 m or on the wetter slopes of the cordilleras (Cavelier and Etter 1995). The remaining area has been transformed into pastures, cultivated fields, coffee and tree plantations, and urban areas. A recent surge in
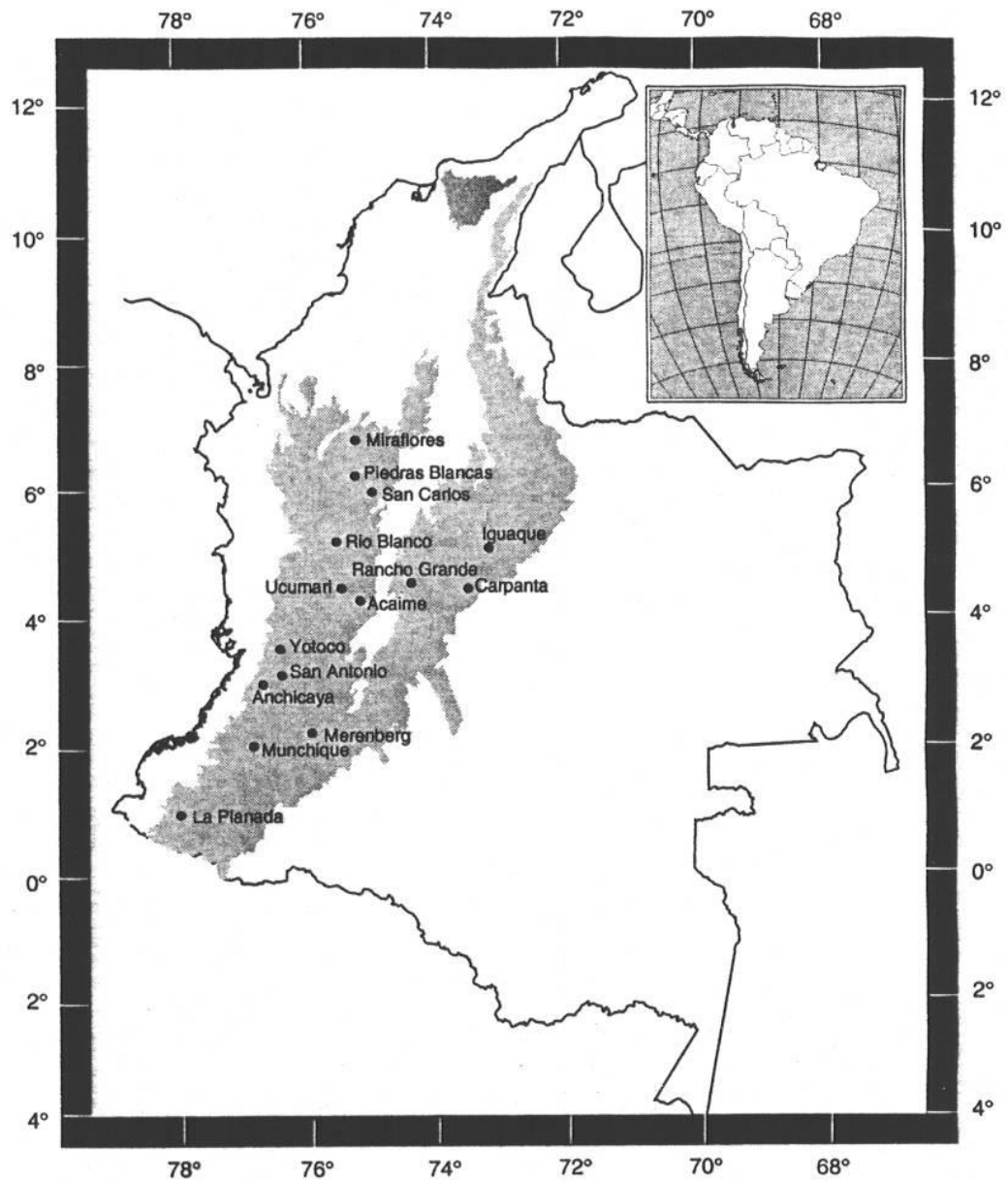
Figure 12.1. Montane habitats of Colombia (shaded areas indicate land above 800 m), showing the locations of sites included in this study.

Table 12.1 Sites included in this study.

Site	Coordinates	Elevation (m)	Life zone[a] (*sensu* Holdrige)	Land use[b]	References[c]
Upper lowland (600/800 to 1,400/1,500 m)					
Anchicaya-Alto Yunda, PNN, Farallones de Cali (AN)	3°32′ N 76°48′ W	1,050	TP-rf	F/F, SG	7, 28
Reserva Forestal Yotoco (YO)	3°52′ N 76°33′ W	1,500	TP-df/mf	F/P, CT	14, 30
Represa San Carlos (SC)	6°13′ N 74°51′ W	750	TP-mf/wf	SG[d]/F, P	22
Finca La Esmeralda (LE)		1,250	TP-wf	CT/CT, P	4
Finca El Ocaso (EO)		1,000	TP-wf	P/F[e]	4
Lower montane (1,400–1,600 to 2,300/2,600 m)					
Reserva Natural La Planada (LP)	1°10′ N 78°00′ W	1,800	TP-rf	F/SG	6, 15, 18, 26
Parque Regional Ucumari, Ucumari Bajo (UB)	4°47′ N 75°32′ W	1,850	TLM-wf	F/SG, TPE[f,h]	6, 13, 16, 25, 27
Bosque Protector, San Antonio (SA)	3°29′ N 76°38′ W	2,000	TLM-wf	F/SG, U	6, 9, 10, 25, 26, 29
Empresas Publicas de Manizales, Río Blanco (RB)	5°28′ N 75°32′ W	2,400		SG, TPN[g], P	21, 24, 27
Finca Merenberg (ME)	2°14′ N 76°08′ W	2,300	TLM-wf	P/F	6, 19, 31
Represa Miraflores (MI)	6°45′ N 75°20′ W	2,130	TLM-wf	SG/P	5
Finca Rancho Grande (RG)	4°36′ N 74°20′ W	1,700		P/CT, SG, U	12
Finca Mirador, Munchique (MU)	2°30′ N 76°59′ W	2,300	TLM-wf	TPE[h]/SG, P	11
Piedras Blancas (PB)	6°18′ N 75°30′ W	2,350	TLM-wf	TPE[h]	8
Upper montane (2,300/2,600 to 3,100/3,400 m)					
Reserva Natural Carpanta-Estacion Sietecuerales (CA)	4°34′ N 73°41′ W	2,700		F/SG	2
Reserva Natural Alto Quindio, Acaime (AC)	4°37′ N 75°20′ W	2,800	TM-wf	SG/TPN[g], F, P	3, 17
Parque Regional Ucumari, Ucumari Alto (UA)	4°47′ N 75°32′ W	2,500		SG/TPN[g], F, P	6, 13, 16, 20, 25, 27
Santuario de Flora y Fauna Iguaque-Cañon, Mamarramos (IG)	5°40′ N 73°30′ W	2,600	TLM/TM-mf	SG/P, F[d]	1, 20, 23, 24
Páramo (3,100/3,400 to 4,800 m)[i]					

a. Life zones: TP-df = tropical premontane dry forest; TP-mf = tropical premontane moist forest; TP-wf = tropical premontane wet forest; TP-rf = tropical premontane rain forest; TLM-wf = tropical lower montane wet forest; TLM-mf = tropical lower montane moist forest; TM-wf = tropical montane wet forest.

b. Land uses; F = native forest; SG = second growth; P = pasture; CT = shaded coffee plantation; TPE = tree plantations with exotic species; TPN = tree plantations with native species; U = weekend cottages.

c. References: (1) Acevedo 1987; (2) Andrade 1993; (3) Arango 1994; (4) Corredor 1989; (5) Cuadros 1988; (6) Gentry 1992a; (7) Hilty 1980; (8) Johnels and Cuadros 1986; (9) Kattan, Restrepo, and Giraldo 1984; (10) Kattan, Alvarez-Lopez, and Giraldo 1994; (11) Mondragón 1989; (12) Munves 1975; (13) Naranjo 1994; (14) Orejuela, Raitt, and Alvarez 1979; (15) Orejuela and Cantillo 1990; (16) Rangel 1994; (17) Renjifo 1988; (18) Restrepo 1990; (19) Ridgely and Gaulin 1980; (20) Rosas 1986; (21) Uribe 1986; (22) Velásquez 1992; (23) Velez 1987; (24) N. Arango, pers. comm.; (25) G. Kattan, pers. comm.; (26) C. Restrepo, pers. obs.; (27) L. M. Renjifo, pers. obs.; (28) S. Hilty, unpublished list; (29) G. Kattan, H. Alvarez, and M. Giraldo, unpublished list; (30) H. Alvarez, unpublished list; (31) G. Kattan, H. Alvarez, and E. Buttkus, unpublished list.

d. Selectively logged native forest.   e. Native forest dominated by the giant bamboo *Bambusa guadua*.

f. Plantations with *Fraxinus sinensis*.   g. Plantations with *Alnus acuminata*.   h. Plantations with *Pinus patula* and *Cupressus lusitanicus*.

i. Because no site-specific bird species inventories were available for páramo, we did not compare sites within this elevational zone.

demand for opium derivatives has prompted forest clear-cutting at higher altitudes to grow poppies (*Papaver somniferum*: Cavelier and Etter 1995).

Frugivorous Birds

We included in our analysis all bird species (both residents and migrants) that were reported to consume fruits or seeds to any degree (Fitzpatrick 1980; Hilty and Brown 1986; Isler and Isler 1987; Renjifo 1988; Ridgely and Tudor 1989; Stiles and Skutch 1989; Fjeldså and Krabbe 1990; Velásquez 1992; Arango 1993, 1994; Ridgely and Tudor 1994; L. M. Renjifo and C. Restrepo, pers. obs.) and were found in the Andes at or above an elevation of 800 m. Thus, our data set (476 species) combines both seed dispersers and seed consumers.

Body mass data were obtained from published records (Goodwin 1976; Isler and Isler 1987; Stiles and Skutch 1989; Hoyo, Elliott, and Sargatal, 1992; Dunning 1993; Arango 1993), museum specimens (Colección de Ornitología, Universidad del Valle, Cali, Colombia), and our own field observations. For bird species for which we could not obtain mass measurements, we averaged the recorded masses of congeners of the same length. We could not estimate body mass for a small fraction (2%) of the species, and these were not included in the analyses.

To explore the relationship between body mass and landscape pattern along the elevational gradient, we classified birds into four groups (table 12.1) based on their elevational ranges: upper lowland (ca. 800–1,500 m), lower montane (ca. 1,500–2,400 m), upper montane (ca. 2,400–3,400 m), and páramo (ca. 3,400–4,800 m). Some species fell into more than one zone and were entered into the analyses two or more times. Elevational zones follow Chapman (1917); elevational ranges were taken from Hilty and Brown (1986).

To explore the relationship between body mass and landscape pattern along a gradient of land use, we compared subsets of the birds found in each elevational zone (eighteen subsets or sites: table 12.1). Inventories at each site were conducted by experienced ornithologists over periods of at least one year and included visual, auditory, and mist-netting observations. The authors of these lists reported that few species were being added to their lists in the latter periods of their studies, suggesting that the lists are fairly complete inventories. The eighteen sites were grouped according to elevational zone and type of land use. Within each elevational zone we arranged sites from those covered mostly by forest to those covered by open vegetation (table 12.1).

Our approach relies on two assumptions; first, that there is a common pool of species for elevational zones and sites, but historical, geographic, and climatic events, and more recently human activities, have determined the set of species found today at any one site; and second, that within elevational zones, the less disturbed sites represent the conditions that existed at the other sites prior to human intervention.

Data Analysis

We used the "lump analysis-gap rarity index" (LA_{GRI}) technique to identify aggregates or lumps in the distribution of body masses of frugivorous birds (Holling et al., in press).

The LA_{GRI} index, which is being developed by one of the authors (P. M.) in collaboration with C. S. Holling, relies on the generation of a null distribution from input data ($\log_{10}$[body mass] in this case) and the calculation of the gap rarity index statistic (GRI). This statistic tests whether any observed discontinuity or gap in the distribution of rank-ordered data (fig. 12.2A) occurs by chance alone in data sets sampled from a continuous, unimodal null distribution fit to the observed data. Significant gaps between individual data points separate lumps.

The null distribution is obtained by constructing a normal kernel density estimate that uses the smallest window width (h) that smooths an observed frequency distribution into a continuous, unimodal distribution (Silverman 1986). GRI values are generated by sampling the null distribution 10,000 times and calculating for each data point the absolute discontinuity value (d_i) as $d_i = S_{i+1} - S_i$, where S_i is the $\log_{10}$ of body mass of the ith species in a rank-size ordered data set. The GRI represents the proportion of simulated absolute discontinuities that are smaller than those observed.

The significance of GRI values is established by comparing them against a critical value (fig. 12.2B) for various alpha values. These critical values are associated with probabilities under the null hypothesis that gaps in an observed frequency distribution are artifacts of random sampling.

Sample size and the trade-off between Type I and Type II errors influence lump structure. In data sets with a large number of data points, small values of α will reveal only the most pronounced gaps (large GRI values), whereas large values of α will reveal many more gaps (fig. 12.2B). The detection of many more gaps, however, might increase the probability of detecting gaps that are sampling artifacts (increase of Type I error). In data sets with a small number of data points, small values of α will reveal no gaps, whereas large values of α will reveal gaps. In this situation, increasing α reduces the probability of not detecting gaps that do exist (reduction of Type II error).

This interplay between sample size and the two types of statistical error should be taken into account when comparing multiple data sets. (See Lipsey 1990 for an excellent discussion of the importance of using different values of α when detection of pattern is important). For simplicity, we kept the α level constant within each comparison. We set α to 0.05 when the average number of species within the comparisons was 81 or more (range 30–395), and set α to 0.1 when the average number of species was less than 81 (range 30–141).

LA_{GRI} generates two types of outputs. The first is the distribution of GRI values against body mass (fig. 12.2B). The second, derived from the first, is the distribution of lumps and the proportion of species falling within each lump for a given data set (e.g., fig. 12.3). The lump structure for a given data set can be described by the number and size of the lumps and the proportion of species falling within each lump. The "size" of a lump represents the range of body masses between two significant gaps and varies with the chosen α level (fig. 12.2B). The proportion of species falling within a lump largely varies independently of lump size; in some data sets, large lumps contain relatively few species, whereas in other data sets large lumps contain
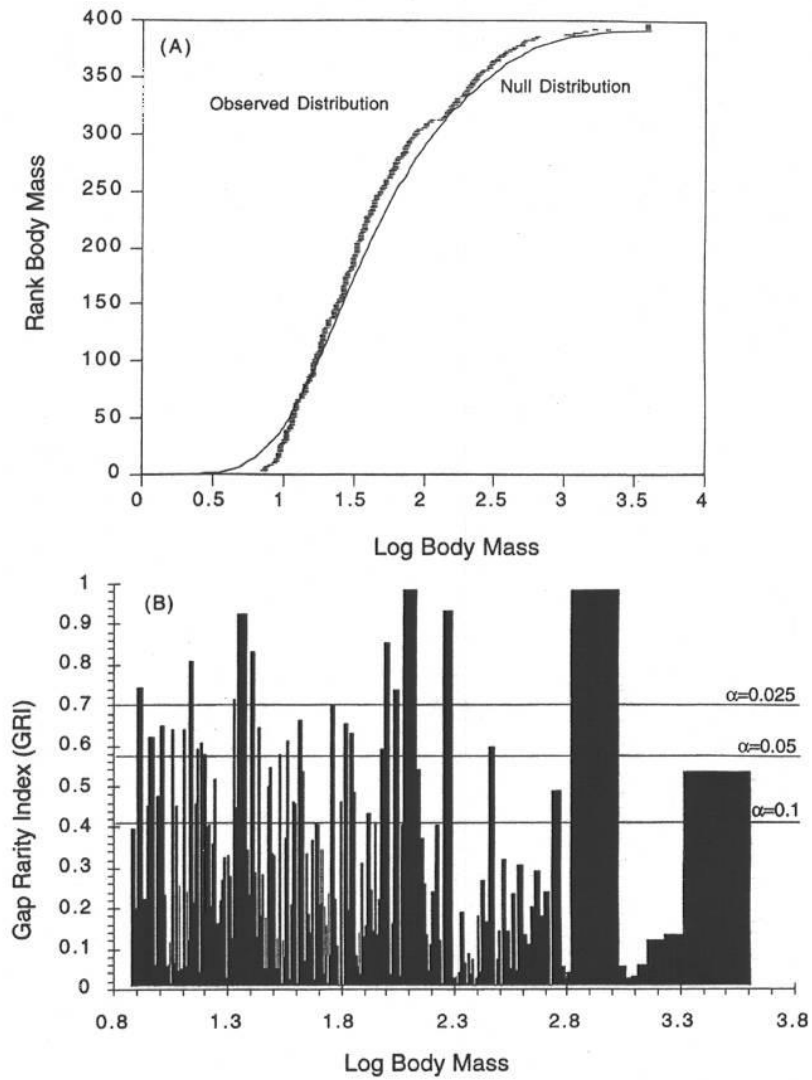
Figure 12.2. *(A)* Observed and smoothed rank-ordered body mass distributions and *(B)* rank-ordered body mass versus gap rarity index (GRI) values for frugivorous birds in upper lowland forest in Colombia. In *(B)*, potential gaps between lumps (shaded bars) are represented by GRI values that exceed the criterion lines (α values). The lump structure generated from this distribution for $\alpha = 0.05$ is the upper lowland species group shown in figure 12.3.
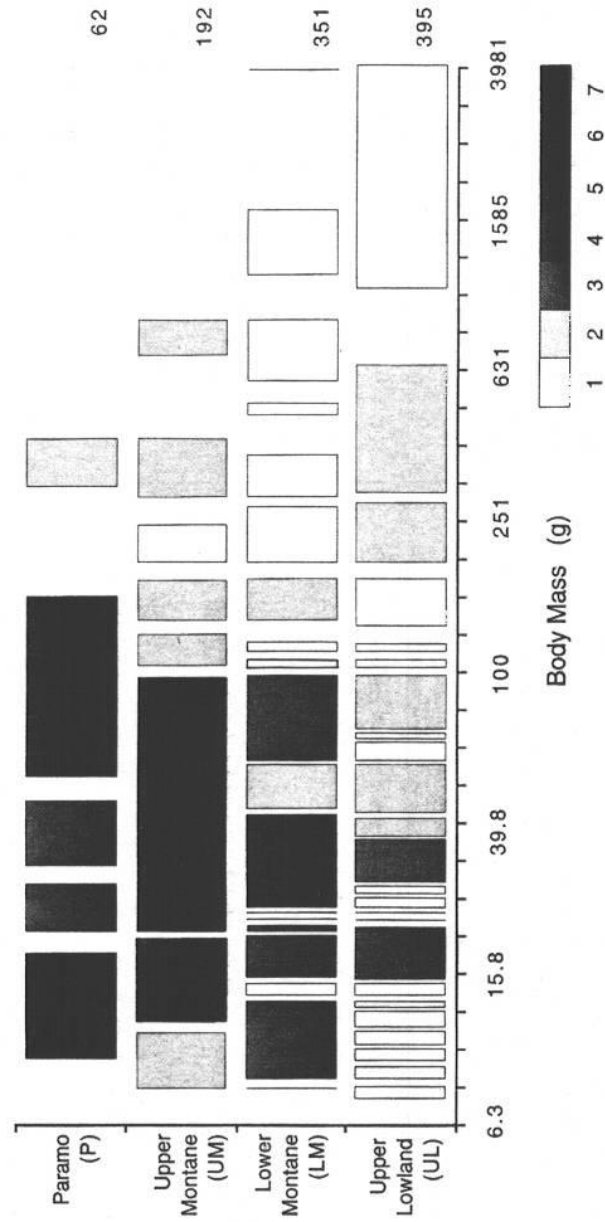
Figure 12.3. Lump structures of Colombian montane frugivorous birds according to elevational zone from forest (bottom) to páramo (top). UL = upper lowland; LM = lower montane; UM = upper montane; P = páramo. Each box represents a lump, and the spaces between boxes represent gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps: (1) 0–5%, (2) 5–10%, (3) 10–20%, (4) 20–30%, (5) 30–45%, (6) 45–60%, and (7) 60–100%. Vertical lines represent less than 5% of species. Numbers on the right indicate the number of species for the corresponding data set.

many species. Graphically, lumps are depicted as boxes along the axis of body mass, with the proportion of species within each lump depicted by different shades of gray (e.g., fig. 12.3).

While the identification of lumps and gaps in individual data sets marks the extent of our statistical analysis, a much more revealing analysis can be accomplished by comparing lump structure among multiple data sets in an attempt to find a consistent pattern. The statistical comparison of lump structure among multiple data sets, however, is still in development, so in this chapter we compare lump structure by eye. In so doing we look at the distributions of lumps over the entire body mass range, the locations of gaps within the data sets, and the proportions of species falling within lumps.

For our comparisons we derived four continuous unimodal distributions. The four elevational zones (upper lowland, lower montane, upper montane, and páramo) were compared using a null distribution generated from the database on all frugivorous montane birds, while sites within three of the elevational zones were compared using a null distribution generated from the database on frugivorous birds for the corresponding zone.

RESULTS
Elevational Zones and Body Mass Distributions

We examined the lump structure of the birds of the four elevational zones ($\alpha = 0.05$) and found that the number of lumps decreased sharply from the upper lowland (twenty-four lumps) to the páramo zone (five lumps: fig. 12.3). Across this gradient, many lumps were lost from the upper range (> 316 g) and few from the lower range (< 10 g) of body mass. The lumps at both extremes of the body mass range contained the smallest proportions of species for the upper lowland, lower montane, and upper montane zones, but not for the páramo.

The positions of gaps and lumps in the body mass range from 12 to 575 g showed some similarities in the upper lowland and lower montane zones. However, the proportions of species in these lumps differed between the two zones. The lump structure of the upper montane zone resembled that of the upper lowland and lower montane zones in the body mass range of 83–316 g, but not above or below that range. The páramo zone shared only one lump (> 301 g) with the other three zones.

Sites and Body Mass Distribution
Upper Lowland Zone

The number of lumps ($\alpha = 0.05$) decreased from the site covered extensively by forest, Anchicaya (AN: eight lumps), to the site dominated by pastures, El Ocaso (EO: three lumps; fig. 12.4). Lumps were lost only at the upper end of the body mass range (> 316 g).

The positions of gaps and lumps were most similar between two pairs of sites—Anchicaya (AN) and Yotoco (YO), and San Carlos (SC) and La Esmeralda (LE)—even though AN and SC have twice as many species as YO and LE, respectively (fig. 12.4). The similarities spanned almost the entire range of body masses. In contrast, the lump
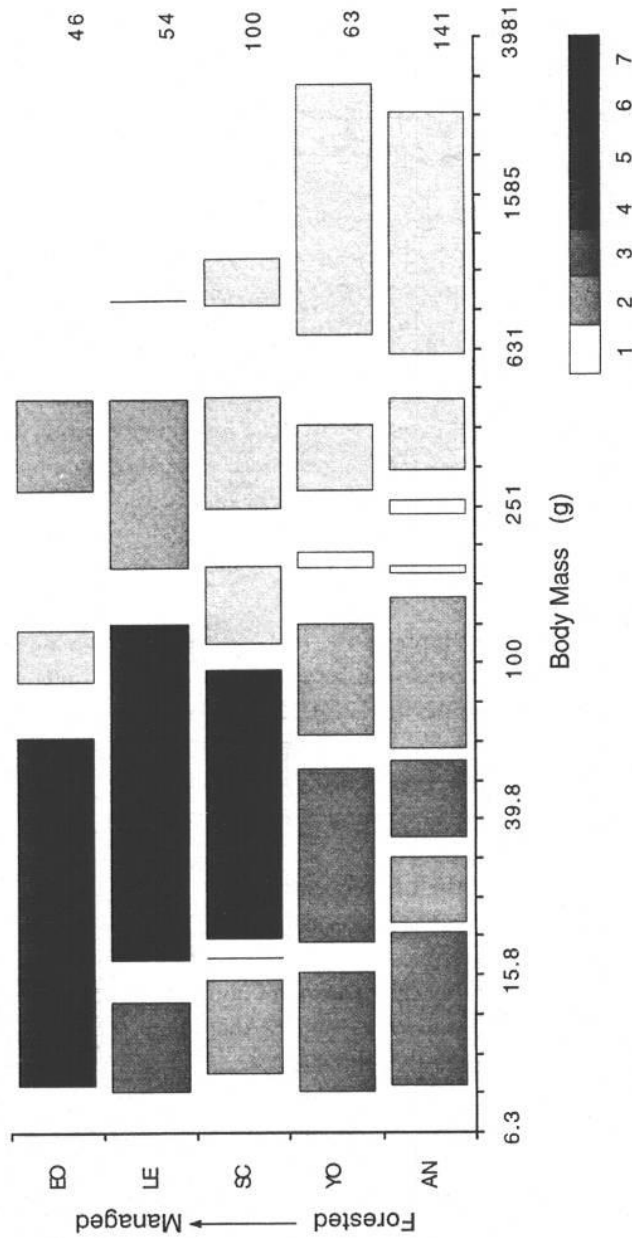
Figure 12.4. Lump structures of Colombian frugivorous birds within the upper lowland zone. Sites are arranged from those covered mostly by forest (bottom) to those highly transformed by human activities (top). AN = Anchicaya; YO = Yotoco; SC = San Carlos; LE = La Esmeralda; EO = El Ocaso. Each box represents a lump, and the spaces between boxes indicate gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps: (1) 0–5%, (2) 5–10%, (3) 10–20%, (4) 20–30%, (5) 30–45%, (6) 45–60%, and (7) 60–100%. Vertical lines represent less than 5% of species. Numbers on the right indicate the number of species for the corresponding data set.

structures of LE and EO showed important differences, even though these two sites have a similar number of species and are separated by only 7 kilometers.

Lower Montane Zone

The number of lumps ($\alpha = 0.1$) decreased from sites covered extensively by forest (La Planada, LP, Ucumarí Bajo, UB, and San Antonio, SA), with an average of eight lumps, to sites in which the original forest has been replaced by orchards (Rancho Grande, RG) or forestry plantations of exotic species (Munchique, MU, and Piedras Blancas, PB), with an average of only four lumps (fig. 12.5).

We grouped the lower montane sites according to major land use types. Three of the sites are covered extensively by forests in which second growth (LP), second growth and forestry plantations (UB), or second growth, pastures, and weekend cottages (SA) cover less than 50% of the land (see table 12.1). The lump structure of LP and UB was similar over almost the entire range of body masses, despite the fact that these sites had different numbers of species. The lump structure of SA was similar to that of UB in the 63–313 g range, but differed below 63 g, despite the fact that these sites had a similar number of species.

Three sites are covered half by native forests and half by pastures (Merenberg, ME), second growth and selectively logged forests (Miraflores, MI), or tree plantations established for watershed restoration (Río Blanco, RB). The lump structures of RB and ME showed similarities below 39 g and above 301 g, and they differed greatly from MI over most of the 15–251 g range of body masses.

In the last three sites, native forest has been replaced almost entirely by coffee plantations and orchards (Rancho Grande, RG), or by tree plantations of exotic species for wood production (Munchique, MU, and Piedras Blancas, PB). RG and MU showed different lump structures, even though they had the same number of species. The lump structures of MU and PB were very similar, but the lump representing birds over 398 g was much smaller in PB than in MU.

Upper Montane Zone

We did not find marked variation in the number of lumps among the four upper montane sites ($\alpha = 0.1$). Iguaque (IG), the most disturbed site, had four lumps, and the remaining three sites had five each (fig. 12.6). Lumps at the upper end of the body mass range for two sites (Carpanta, CA, and Ucumarí Alto, UA) showed a high proportion of species, but the opposite was true of the other two sites (Acaime, AC, and Iguaque, IG). More interesting, however, was the finding that lumps at the lower end of the body mass range (< 12 g) tended to decrease in size.

Carpanta (CA), the least disturbed site, is covered by native forest and second growth, and its lump structure differed from those of AC and UA, particularly for species above 25 g. It is noteworthy that the highest proportion of species in CA was in the lump representing species over 63 g; for little-disturbed sites in the other elevational zones, lumps representing the largest birds always contained the smallest proportion of species. The lump structures of AC and UA were similar; both of these sites have been planted
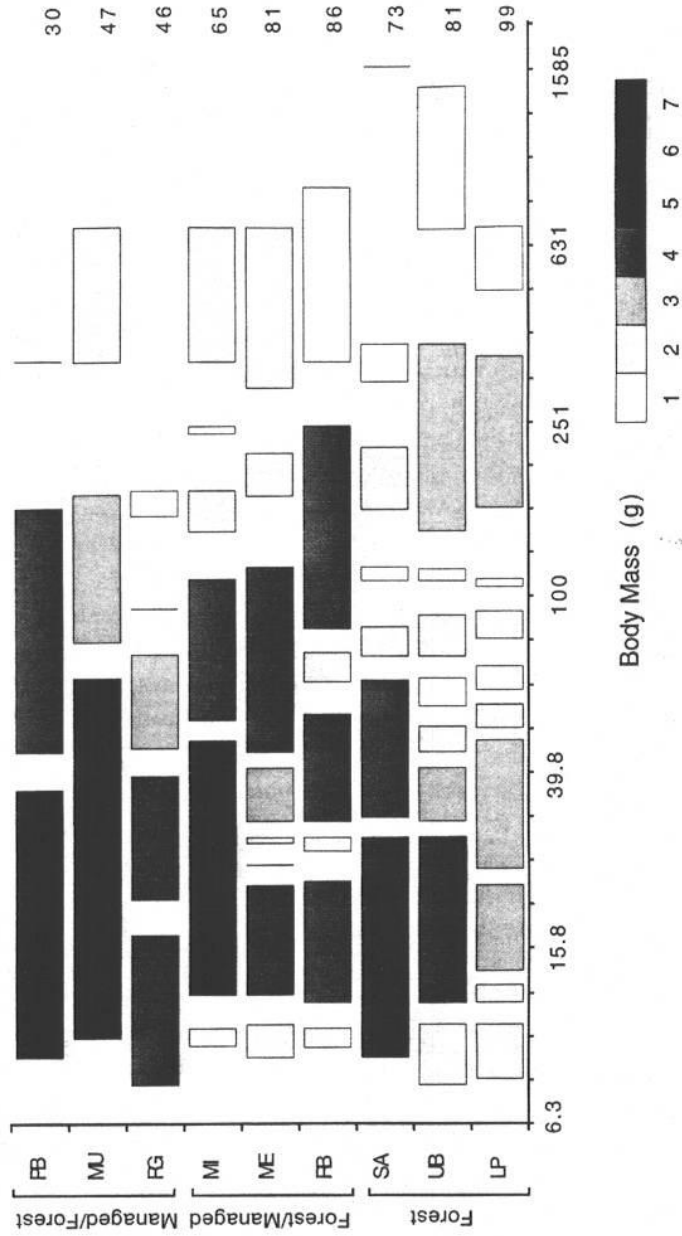
Figure 12.5. Lump structures of Colombian frugivorous birds within the lower montane zone. Sites are arranged from those covered mostly by forest (bottom) to those highly transformed by human activities (top). LP = La Planada; UB = Ucumarí Bajo; SA = San Antonio; MI = Miraflores; ME = Merenberg; RB = Río Blanco; RG = Rancho Grande; MU = Munchique; PB = Piedras Blancas. Each box represents a lump, and the spaces between boxes indicate gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps: (1) 0–5%, (2) 5–10%, (3) 10–20%, (4) 20–30%, (5) 30–45%, (6) 45–60%, and (7) 60–100%. Vertical lines represent less than 5% of species. Numbers on the right indicate the number of species for the corresponding data set.
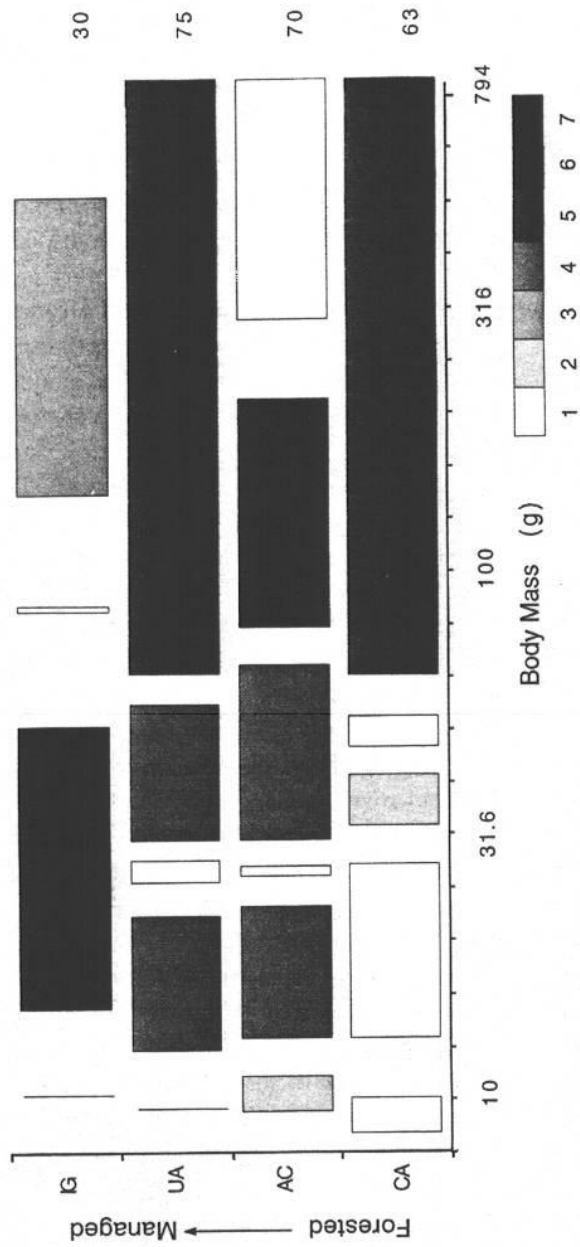
Figure 12.6. Lump structures of Colombian montane frugivorous birds within the upper montane zone. Sites are arranged from those covered mostly by forest (bottom) to those highly transformed by human activities (top). CA = Carpanta; AC = Acaime; UA = Ucumarí Alto; IG = Iguaque. Each box represents a lump, and the spaces between boxes indicate gaps in the distribution of body mass. The different shades indicate the proportion of species falling within lumps: (1) 0–5%, (2) 5–10%, (3) 10–20%, (4) 20–30%, (5) 30–45%, (6) 45–60%, and (7) 60–100%. Vertical lines represent less than 5% of species. Numbers on the right indicate the number of species for the corresponding data set.

with native trees in an effort to restore land previously used for cattle ranching (see table 12.1). Finally, the lump structure of IG was very different from those of the other three sites.

DISCUSSION

Because of the exploratory nature of this work, and because techniques for testing ecosystem "lumpiness" are still in the formative stages, our interpretations are intended as working hypotheses rather than conclusions. Our analyses are exploratory in the sense that we made use of available information and thus could not control for many factors that might confound the results, including size of area surveyed, effects of hunting, and differences in vegetation types. However, the repetition of some patterns among our four analyses suggests that lump structure of body mass in Andean frugivores changes as landscapes are modified by human activities.

Patterns in Lump Structure

In general, the number of lumps (aggregates of species with a similar body mass) decreased from areas covered by continuous native forest to those where forest has been replaced by simpler vegetation types. It might be argued that this trend simply reflects a decrease in the number of species, which in turn results from reduced habitat complexity (e.g., Karr and Roth 1971; Terborgh 1977); that is, with fewer species, we might expect to find fewer lumps. Several of our data sets, however, suggest other relationships. For example, three pairs of sites with differing frugivore richness exhibited similar lump structures (Anchicaya vs. Yotoco, San Carlos vs. La Esmeralda: fig. 12.4; Carpanta vs. Ucumarí Alto: fig. 12.6). In contrast, two pairs of sites with similar frugivore richness exhibited different lump structures (Merenberg vs. Ucumarí Bajo, Rancho Grande vs. Munchique: fig. 12.5). A close examination of the information available for the sites shows slight differences between members of a pair for the former, whereas the contrary is true for the latter (see table 12.1). This suggests that lump structure of body mass in frugivorous birds reflects to some degree the structure of landscapes and provides information not contained in simple counts of species richness.

Major changes in lump structure were observed at the upper and lower ends of the body mass range, in the lumps that contained the smallest proportion of species. For example, lumps representing the largest bird species were lost when moving from areas covered mostly by native forest to those where the forest was replaced by páramo (across elevational zones) or pasture (within the upper lowland zone). Lumps representing the smallest bird species were lost across the land use gradient in the upper montane zone. The lower montane zone exhibited an intermediate pattern (see figs. 12.3–12.6). These results suggest that human activities in Neotropical montane landscapes affect the smallest and largest frugivorous species, often to the point of eliminating entire aggregates of species.

Other changes in lump structure were represented by lumps that fused or broke down among sites representing different landscapes. This pattern indicates that gaps in the

distribution of body mass are being closed and opened, probably as a result of the replacement of species across different elevational zones (Terborgh 1971; Hooghiemstra 1984; Gentry 1992a), as well as local extinctions and invasions by species that were formerly rare or absent at a site (Pacheco et al. 1994; Lynam, chap. 15).

Similarities in lump structure across elevational zones and across sites within elevational zones resulted from the persistence of some lumps. The structure of these lumps remained relatively unchanged, probably due to the presence of the same species across the elevational or land use gradient and/or the replacement of species by congeners of similar size. For example, the twenty-first upper lowland (UL), thirteenth lower montane (LM), and fifth upper montane (UM) lumps contain a total of seventeen, thirteen, and ten species respectively (see fig. 12.3). Five species are shared by UL, LM, and UM, three by UL and LM, five by LM and UM, and nine are exclusive to UL, suggesting that some species—those shared by UL, LM, and UM—maintain the structure of these lumps, while other species—those exclusive to one or two zones—are not crucial to the maintenance of lump structure. In other words, these two groups of species may represent the drivers (keystone species) and passengers (redundant species), respectively, mentioned by Walker (1992) when discussing the role of biodiversity in ecosystem processes.

The presence of lumps in distributions of animal body masses, however, is a matter of debate, mainly because of the lack of well-known statistical techniques to identify them. For example, Manly (1996) reanalyzed Holling's (1992) data and found lumps in the body mass distributions of boreal forest and prairie birds, but not as many as Holling reported. Manly advocated the use of Silverman's (1981) "bump-hunting" technique, but recognized that it is difficult to identify lumps even if they are in fact present in a distribution of body mass. We believe that the "bump-hunting" technique is extremely prone to Type II errors; the development of LA_{GRI} is an attempt to overcome this limitation while avoiding some of the problems associated with Holling's (1992) and Manly's (1996) approaches.

Causes of Lump Structure

The comparisons that we set up among different elevational zones, and among different sites within the same elevational zone, represent two different scales of inquiry, yet produced similar results. That is, at both scales we found lumps in the body mass distributions of frugivores and a decrease in the number of lumps from complex to simple ecosystems. Elevational zones, and sites within elevational zones, were arranged from those covered mostly by native forest to those in which the native forest has been replaced by open vegetation (páramo) or by managed ecosystems (pastures or tree plantations) in which scattered forest fragments remain. Thus, changes in lump structure seem to reflect a common causality best explained by landscape complexity, which is probably a function of the vertical and horizontal structure of vegetation. Our proposition is supported by work in other regions (August 1983; Thiollay 1992; Lescourret and Genard 1994).

The vertical structure of vegetation refers to the height of vegetation and the diversity of growth forms, and it becomes simpler as one moves from the lowlands to the páramo,

or from forest to pasture. Along the elevational gradient, fog, air temperature, and radiation climate are proximate factors that explain changes in the vertical structure of the vegetation (Leigh 1975; Grubb 1977a). Along the gradient of land use, soil and rainfall distribution account for changes in patterns of land exploitation and hence the structure of the vegetation (e.g., Holdridge et al. 1971). In addition, within forest fragments, wind shear forces, atmospheric humidity, and soil moisture can affect the vertical structure of forest vegetation (Esseen 1994; Laurance 1991b, chap. 6; Kapos et al., chap. 3).

The horizontal structure of vegetation refers to the spatial distribution of vegetation types resulting from changes in abiotic conditions or disturbance (Wiens, Crawford, and Gosz 1985). In Colombia, horizontal structure becomes simpler as one moves from the lowlands to the páramo, or from more natural to highly modified landscapes. At lower and middle elevations, landslides result locally in the development of stands of second growth (Gardwood, Janos, and Brokaw 1979; Mejía et al. 1994; Velásquez et al. 1994), while at higher altitudes, climate and soil determine the presence of elfin forest and páramo (Cuatrecasas 1958; Espinal et al. 1977). Along the gradient of land use, abiotic and socioeconomic factors determine not only rates of deforestation but also the type of matrix in which forest fragments are embedded.

Two sites in the lower montane zone, Rancho Grande (RG) and Munchique (MU), show how vertical and horizontal vegetation structure may relate to lump structure. Rancho Grande and Munchique represent highly modified landscapes where fragments of degraded native forest are interspersed with orchards and pastures (RG) or even-aged pine plantations (MU: Munves 1975; Mondragón 1989). The spatial distribution of vegetation types at the two sites is similar, but the vertical structure of the vegetation types differs. The presence of pastures and orchards with shade trees suggests that RG has a more complex vertical structure than MU, where high densities of pine trees inhibit the development of other plant species. The two sites have similar numbers of species, but RG has more lumps, and species are more evenly distributed among lumps, than at MU (see fig. 12.5).

Even though there are reasons to believe that lump structure results from the interplay of the vertical and horizontal structure of the vegetation, we cannot discard other possibilities. Lumps in body mass distributions of frugivores may result from the response of frugivores to other features of landscapes (Trophic-Through Hypothesis: Holling 1992) or from phylogenetic constraints (Urtier-Historical Hypothesis: Holling 1992). Features that are correlated with landscape structure and that can generate lumps in body mass distributions include seed and fruit patch size. For example, seed size influences the behavior of frugivores (Moermond and Denslow 1985), but is also correlated with both the dispersal and regeneration modes of plants (Salisbury 1974; Martin 1985; Hughes et al. 1994; Osunkoya et al. 1994). Phylogeny may constrain the range of body masses within a family and may explain why closely related species are distributed more often among lumps within a given range of body mass. However, it does not explain the presence of discontinuities in a frequency distribution of body mass, since gaps do not separate lumps composed exclusively of species belonging to the same family.
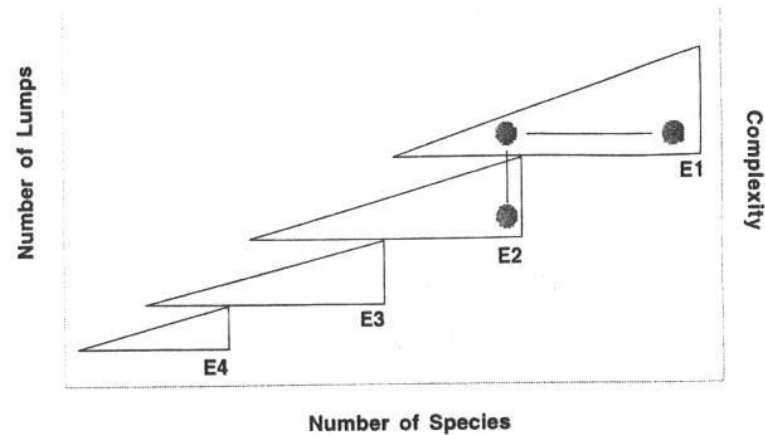
Figure 12.7. Relationship between species richness and lump structure in landscapes of varying complexity. The triangles represent ecosystems from the most complex (E1) to the simplest (E4). Circles within a triangle indicate changes in species richness while lump number remains relatively constant; circles in two different triangles indicate important changes in lump number while species richness remains relatively constant.

A Model Linking Lumps and Species Diversity in Landscapes

Our results reveal relationships between lump structure and number of species along a gradient of landscape structural complexity. In addition, they hint at a relationship between lump structure and ecosystem resilience. Resilience, as defined by Holling (1973), is a measure of the amount of disturbance or change that an ecosystem can absorb before turning into a different one.

We summarize our findings in a graphical model (fig. 12.7) that links numbers of species and lumps. In the model, the triangles represent different ecosystems (E1–E4), arranged from the most complex (top) to the simplest (bottom). The arrangement of these triangles along a diagonal reflects a general trend in which the number of lumps tends to decline as species richness declines. Ecosystems are depicted as triangles to reflect the same positive association between species richness and lump number, with historical, climatic, and edaphic factors and human activities contributing to the variability in species richness and lump number within each ecosystem.

In a given ecosystem, lump structure (the vertical dimension of each triangle, simplified here to just the number of lumps) can remain relatively unchanged despite marked differences in the number of species between sites (the horizontal dimension of each triangle). In our data sets, changes in species richness, but not lump number, were associated with changes in species numbers within a given type of land use. However, as one approaches the apex of each triangle, the probability that important shifts in lump structure will occur increases, even though species richness can remain nearly constant. In our data sets, such shifts were associated with changes in land use. Each jump into a succes-

sively simpler ecosystem (from top to bottom) is accompanied by a reduction in the number of lumps.

The model generates a set of testable hypotheses and predictions that could contribute to our understanding of how landscape pattern, biodiversity, and ecosystem processes interact at broad spatial scales. The predictions are as follows:

1. Among different sites, there is a threshold in species number below which lump structure changes dramatically, as indicated by a decrease in the number of lumps.
2. The number and size of lumps is maintained by the persistence of certain species. Their disappearance may alter lump structure in important ways.
3. The lump structure of bird assemblages reflects the resilience of a given ecosystem. Removal of species may have less impact on lump structure in highly diverse ecosystems (top triangles, fig. 12.7) than in less diverse ecosystems (bottom triangles, fig. 12.7).

Natural and anthropogenic disturbances, either alone or in concert, can affect landscapes over spatial and temporal scales ranging from hundreds of meters to hundreds of kilometers and years to decades, respectively. The inherent complexity of landscapes on this spatiotemporal scale justifies a search for new approaches and methods for understanding the relationships among biodiversity, landscape patterns, and ecosystem processes. Rather than focusing on individual parts, these new approaches should concentrate on aggregates of parts and the key processes that structure ecosystems (Hay 1994; Turner, Gardner, and O'Neill 1995; Holling et al., in press). The "lump" approach discussed here represents one of these new lines of inquiry.

GENERAL IMPLICATIONS

1. The lump structure (distribution of body mass aggregates, or lumps) of animal assemblages provides a measure of diversity that captures information not contained in simple counts of species richness.
2. In assemblages of frugivorous birds in Colombia, there were distinct relationships between lump structure and landscape complexity, and these were quite consistent at two different scales of inquiry (between elevational zones, and at sites within elevational zones). This finding suggests that similar processes are responsible for generating lump structure in different regions and at different spatial scales, and that management should focus on these processes.
3. There is some indication that assemblages of Neotropical montane frugivorous birds are robust to human disturbance, provided that landscapes are not severely modified.
4. In Neotropical montane ecosystems, the disappearance of particular lumps (species of common body mass) of frugivorous birds may reflect important changes in seed dispersal, and thus regeneration trajectories of vegetation after disturbance.
5. The fragmentation and transformation of Neotropical montane ecosystems does not seem to generate the same patterns in assemblages of frugivorous birds at low, middle, and high altitudes. These differences may have important consequences for the conservation and management of ecosystems along the elevational gradient.

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