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Ecological Redundancy in Seed Dispersal Systems: A Comparison Between Manakins (Aves: Pipridae) in Two Tropical Forests

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Introduction

Redundancy in ecological function may enhance ecosystem resilience in the face of disturbance, and thus serve to conserve biological diversity (Naeem *et al.*, 1994; Walker, 1995). For example, high-diversity grassland ecosystems are more resistant to disturbance and recover more fully than lower-diversity grasslands (Tilman and Downing, 1994). When more species within an ecosystem offer equivalent ecological services, such as dispersal of plant seeds, then decline or local extinction of one species is offset by other species because of their ecological equivalency. Such redundancy in ecological services, in essence, buffers ecosystems from disturbance. Given present-day concerns about how diversity and stability of ecosystems are affected by disturbance, understanding the degree to which species are redundant in ecological function has received considerable attention in recent years (Ehrlich and Walker, 1998; Naeem, 1998; Chong *et al.*, 2000; Wellnitz and Poff, 2001; Slater and du Toit, 2002).

Seed dispersal is an important ecological process that provides a number of ecosystem services and economic benefits, such as removal of seeds from parent plants where seed and seedling mortality is high, escape from seed predators, enhanced germination, increased gene flow, and regeneration in and restoration of natural and disturbed habitats (Şekercioğlu *et al.*, 2004). Unless compensated, loss of seed dispersers can be expected to result in a reduction in numbers of seeds removed, clumping of seeds below the parent plant, increased predation of seeds and seedlings, reduction in recruitment and gene flow, and declines in (or extinction of) dependent species of plant (see, e.g. Cardoso da Silva and Tabarelli, 2000; Cordeiro and Howe, 2003). From a plant perspective, ecologically redundant dispersers are those that, at

the least, remove a proportionally equivalent number of seeds from the plant and offer similar treatment to seeds. Given the importance of establishment limitation in recruitment, it can also be argued that ecologically equivalent species also deposit seeds in similar environments. Here, we address the question of whether seed dispersers in species-rich forests overlap more in ecological function than do seed dispersers in less diverse forests. If so, then increased biological diversity, at least in terms of seed dispersal processes, may increase ecosystem resilience.

Interactions between fruiting plants and their seed dispersers are now largely recognized as diffuse mutualisms with seeds dispersed by an array of fruit consumers, whose behaviour and composition may vary both geographically and temporally (Wheelwright and Orians, 1982; Herrera, 1985, 1986; Gautier-Hion *et al.*, 1993; Chapman and Chapman, 2002; Dennis and Westcott, Chapter 9, this volume). Tight co-evolutionary relationships between plants and seed dispersers are considered rare and limited to cases where seed size constrains a potential disperser assemblage, or to areas where the disperser community is impoverished (Rick and Bowman, 1961; Chapman *et al.*, 1992; Chapman and Chapman, 2002). If interactions between fruiting plants and seed dispersers are diffuse, and if they vary over space and time, then the relative importance of individual dispersers as selective agents on plant traits and their influence on plant community structure and composition are expected to be weak. Diffuse relationships, however, do not preclude dispersers from potentially having selective impacts on plant fitness. If dispersers largely overlap in ecological function, then these species as a group directly influence quantity of seeds removed and early patterns of seed and seedling establishment and, thus, act as selective forces on plant traits.

In neotropical wet forests, a vast majority of woody plant species rely on animals to disperse their seeds (Gentry, 1982) and a rich assemblage of fruit-eating vertebrates can be found (e.g. Karr *et al.*, 1990; Terborgh *et al.*, 1990; Robinson *et al.*, 2000; Blake and Loiselle, 2000, 2001). The high diversity of fleshy-fruited plants and vertebrate frugivores has resulted in complex webs of interactions among plants and their consumers (e.g. McDiarmid *et al.*, 1977; Lambert 1989; Silva *et al.*, 2002; see Silva *et al.*, Chapter 26, this volume). Yet, from a plant's perspective, the ecological roles of dispersers are not necessarily equivalent and, in some cases, an individual species may be irreplaceable (e.g. Stocker and Irvine, 1983; Wenny and Levey, 1998; see Dennis and Westcott, Chapter 9, this volume). In understory plants of lowland wet forest in Costa Rica, we found that plant–disperser interactions can be largely asymmetric, with a relatively small suite of species dominating the interactions (Loiselle and Blake, 1999, 2002; see also Silva *et al.*, 2002). Dominance by a few dispersers may have ecological consequences for plants and, potentially, evolutionary consequences if gene flow is limited and interaction strengths remain relatively constant over time. Moreover, if the interactions are dominated by species that are at risk of extinction, whose roles are largely irreplaceable, then plants may be subject to dissemination limitation and population reductions following the decline or loss of strong

interactors (e.g. Rainey *et al.*, 1995; Hamann and Curio, 1999; Tabarelli *et al.*, 1999; McConkey and Drake, 2002; Cordeiro and Howe, 2001, 2003; see Silva *et al.*, Chapter 26, this volume).

Here we are interested in whether plant populations in species-rich areas (i.e. areas with many dispersal agents) are potentially buffered from disturbance of disperser communities as a result of increased overlap in ecological function (i.e. redundancy) of seed dispersers. We measure ecological redundancy in seed dispersers based on overlap in species consumed (cf. Jaksic *et al.*, 1996; Slater and du Toit, 2002) and overlap in environments that dispersers occupy and, presumably, disseminate seeds into. We compare our results from species-rich forests in eastern Ecuador to those from Costa Rica, which although biologically diverse, are less so than Amazonian forests. We focus on manakins (Pipridae), which are the predominant arboreal frugivores in the understorey of these two forests (Levey, 1988; Loiselle and Blake, 1991; English, 1998; J.G. Blake and B.A. Loiselle, 2006, unpublished results). We restrict our analyses to manakins, which are the numerically dominant frugivores captured in mist-nets at these sites, to control, in part, for potential effects of phylogeny on fruit selection. We later discuss how manakins fit within the entire frugivore community.

Manakins, which feed primarily on fruit, exhibit lek-mating systems where the males spend much of their day at display arenas (H^oQglund and Alatalo, 1995). Females visit the leks to select males for mating and are solely responsible for nest-building and all parental duties. These large sexual differences in the behavioural ecology of manakins may influence their respective roles as seed dispersers, such that differences between sexes may rival, or even excel, differences among species. At La Selva Biological Station in Costa Rica, two species of manakin are regularly found in the understorey of old-growth forest, *Pipra mentalis* and *Corapipo altera*, although the latter species breeds at higher elevations and is only a seasonal visitor (4–6 months) at this site (Levey, 1988; Loiselle and Blake, 1991; Rosselli, 1994). In eastern Ecuador, six species of manakin are regularly observed and breed in the forest understorey.

To examine ecological redundancy in seed disperser roles of manakins in these two forests, which differ in biological diversity, we specifically ask

1. whether species significantly overlap in fruit diet
2. whether species overlap in use of forest environments
3. whether the diet and environmental overlap among manakins is greater in the more species-rich forests of eastern Ecuador when compared with Costa Rica.

In addition, we examine whether seed-dispersal roles of manakins in Ecuador differ between sexes, which would imply that studies focusing on ecological function should treat male and female manakins as separate experimental units. Our prediction is that higher species diversity in eastern Ecuador forests will lead to greater redundancy in the ecological functions of species, when compared to Costa Rican forests where local

extinction of even one species would theoretically have significant impacts on the spatial dissemination of seeds (Loiselle and Blake, 2002).

Methods

Data on diets of manakins from Ecuador were collected during a 3-year period (2001–2004) at Tiputini Biodiversity Station (TBS), Orellana Province, Ecuador ($\sim 0^{\circ}38' \text{ S}$, $76^{\circ}08' \text{ W}$). TBS was established in 1994 by the Universidad San Francisco de Quito (USFQ) on a tract of undisturbed lowland rain forest within the 1.5-million-ha Yasuní Biosphere Reserve, a region noted for its biological diversity. There are approximately 300+ species of trees ($>10 \text{ cm}$ diameter at breast height) per hectare (Kreft *et al.*, 2004), over 525 species of birds, including 12 within the family Pipridae, and more than 150 species of mammals. The station and nearby areas contain a variety of habitats that include *terra firme* and *várzea* forest, palm swamps and other wetlands, as well as numerous areas of natural regrowth (i.e. blow-down areas in various stages of succession). Within TBS, two 100 ha plots ($\sim 1 \text{ km} \times 1 \text{ km}$ each) were established in *terra firme* forest during 2001 (see Ryder *et al.*, 2006; Loiselle *et al.*, 2007, for a description of Harpia and Puma plots).

Between 2001 and 2004 (February–March 2001; May–August 2002; December 2001–March 2002; May–August 2003; December 2002–March 2003; December 2003–March 2004), the distribution and abundance of manakins was studied on the two plots, using mist-nets, spot-mapping and intensive observations. When possible, faecal samples were collected from manakins captured in mist-nets ($12 \text{ m} \times 2.8 \text{ m}$; 36 mm mesh); mist-nets were distributed throughout the study plots. Here, we report on the diets of four species of manakin based on a total of 428 faecal samples that contained plant seeds (Table 8.1). We recognize, however, that faecal samples are biased towards small-seeded plants, as larger seeds are often regurgitated. Therefore our study describes the component of manakin diets that achieves dispersal through the gut. We also examine overlap in habitat use by comparing the spatial distribution of captures at 96 net-sites on each plot. We restrict our comparisons to these 96 net-sites because

Table 8.1. Number of faecal samples containing plant seeds and number of plant species found in faecal samples for four manakin (Pipridae) species in eastern Ecuador based on data collected in 2001–2004.

Species	Number of faecal samples	Number of plant species
<i>Lepidothrix coronata</i>	206	49
<i>Pipra erythrocephala</i>	43	27
<i>Pipra filicauda</i>	56	33
<i>Pipra pipra</i>	123	44
Total	428	85

these sites were systematically sampled during January and March of all four years. We assume that capture sites of birds are likely to represent environments where plant seeds are deposited (cf. Levey, 1988; Loiselle and Blake, 1993, 2002; Blake and Loiselle, 2001).

Diets of manakins from Costa Rica were studied in tropical lowland wet forest at La Selva Biological Station between 1985 and 1993; except for 1985, diets were sampled in conjunction with systematic mist-net studies between December and April (for a complete description of study methods from Costa Rica see Loiselle and Blake, 1990, 1991, 1993, 2002). These months correspond to the time when both *Pipra mentalis* and *Corapipo altera* co-occur in old-growth forest at this site. Comparisons of overlap in diet and habitat-use follow methods used for manakins in Ecuador. In Costa Rica, nets were placed at similar distance intervals, but covered a smaller area.

We evaluated the degree to which diets of manakins were sampled by plotting species accumulation curves and examined differences in the diversity of plant species in manakin diets using rarefaction. Rarefaction uses probability theory to derive an expected number of species and its variance for a sample of a given size (Hurlbert, 1971). We used EcoSim version 6.18 (Gotelli and Entsminger, 2001) to randomly draw a set of diet samples of a specified abundance. We repeated the random draws for each abundance level 1000 times to generate a mean and variance of plant species found in the diet. We repeated this process for each species of manakin separately, as well as for all species combined, at each study site.

To determine whether or not species of manakin overlapped significantly in fruit diet, we constructed a bird-species \times plant-species matrix, where the frequency of faecal samples that contained seeds of a given plant filled the cells. We then compared interspecific niche overlap against a random model using EcoSim version 6.18 (Gotelli and Entsminger, 2001). We used Pianka's (1973) pairwise index to calculate niche overlap where

$$O_{12} = O_{21} = \frac{\sum_{i=1}^n p_{2i} p_{1i}}{\sqrt{\sum_{i=1}^n (p_{2i}^2)(p_{1i}^2)}}$$

O_{12} , which equals O_{21} , is the overlap of species 1 with species 2, p_{2i} and p_{1i} is the proportion of plant species i in the diet of species 2 and species 1, respectively. We then examined whether species overlapped more or less than expected by chance using the mean of observed overlaps between pairs of species compared to that produced by an algorithm that retains the niche breadth of each species of manakin, but randomizes which particular species of plant is included in the diet (Winemiller and Pianka, 1990; Gotelli and Entsminger, 2001). This randomization algorithm simply reshuffles cells within each row of the matrix, thus retaining the same niche breadth of the species while assuming that each species of manakin can potentially feed on any given species of plant (i.e. it assumes that birds

are physiologically and morphologically capable of feeding on all food items in the matrix). Given the similarities in morphology, body size and foraging manoeuvres among these four species of manakin, we felt the latter assumption was justified. We used 1000 simulations to derive the expected values of niche overlap for species pairs.

To determine whether the spatial distributions of manakin captures were similar on the two study plots, we used GEODISTN.BAS, a QuickBasic 4.5 program that tests for differences between two spatial distributions (Syrjala, 1996). This non-parametric test examines the null hypothesis that two populations have the same spatial distribution. We used the Cramér-von Mises test statistic because it is relatively insensitive to a small number of extreme observations (Syrjala, 1996). We ran 1000 permutations to determine the test statistic. For each species pair on each plot, we provided the x - y location of the net-site and the number of captures for each species of manakin. A significant test statistic indicates that the spatial distribution of captures for species 1 is different from the spatial distribution of captures for species 2. In Costa Rica, we compared the spatial distribution of manakin captures over a total of 60 net-sites. In Ecuador, manakin captures were compared over 96 net-sites in each of the two study plots.

To compare the forest environments where the manakins were captured and assumed to disseminate seeds (cf. Levey, 1988; Loiselle and Blake, 1993, 2002) in Costa Rica, we assigned net-sites to one of five habitats (ridge, upper-slope, mid-slope, lower-slope, and valley bottoms and other low-lying habitats) (see Loiselle and Blake, 1993, 2002). We then compared the distribution of captures of manakin species among habitats using a χ^2 heterogeneity test. In Ecuador, where plots were georeferenced and GIS databases existed for topography and streams, we established a sample area of 12.5 m radius around the centre of each mist-net location where a manakin was captured. This area was divided into 1×1 m cells, within which we measured elevation (m), slope (degrees), aspect, and distance from stream (m). We then used zonal statistics in GIS (Spatial Analyst; ESRI), with each net-site defining a zone, to calculate means and standard deviations for each environmental variable within each zone. To visualize the variation in environmental characteristics of sample areas around net-sites within each plot, we used principal components analysis where zone/net-sites are the rows and environmental variables (means and standard deviations) are the columns. Net-sites were ordinated in environmental space using a correlation matrix and Euclidean distance measure, using factor analysis in SPSS version 10 (SPSS, 1999). To determine whether species of manakin in Ecuador were captured in different forest environments and, thus, expected to disseminate seeds to qualitatively different sites, we used the net-site \times environment data matrix for analysis of similarity (ANOSIM, described by Clarke and Warwick, 2001). ANOSIM is a nonparametric permutation procedure that is combined with a Monte Carlo test to determine the level of similarity of captures among net-sites across species. The significance of the ANOSIM test statistics was determined by comparison with the values obtained by the randomization procedure.

Results

Diet overlap

We found 81 species of plants in the diets of *Pipra mentalis* and *Corapipo altera* in old-growth forests of Costa Rica (see also Loiselle and Blake, 1990, 1999, 2002). *P. mentalis* contained 70 species in 441 faecal samples, while *C. altera* had 39 species in 152 faecal samples; the seeds of 35 species were recorded only once in the diets. Genera of plants commonly encountered in the diets of Costa Rican manakins included *Henriettea*, *Clidemia*, *Ossaea*, *Miconia* and *Leandra* (Melastomataceae), *Psychotria* (Rubiaceae), *Hampea* (Malvaceae) and *Pinzona* (Dilleniaceae). Using all species of plant in the diets, we found that niche overlap between these two manakins was 0.874; using only the 46 species that were recorded at least twice, niche overlap was 0.876. In either case, manakin diets overlapped significantly more than expected by chance ($P < 0.001$). Species accumulation curves for plants revealed that species were still being added to manakin diets and, thus, diet breadth was underestimated for both species in old-growth forests at La Selva (Fig. 8.1). Using rarefaction analysis (Gotelli and Entsminger, 2001), we found that the two species did not differ significantly in diet diversity when samples were corrected for effort. Costa Rican manakins, therefore, generally feed on a similar suite of plants in similar proportions and diversity.

We found 85 species of plants in the diets of the four species of manakins in Ecuador (Table 8.1). Genera of plants commonly encountered in Ecuadorian manakin diets included *Anthurium* and *Philodendron* (Araceae), *Coussapoa* and *Cecropia* (Cecropiaceae), *Miconia* and *Henriettea* (Melastomataceae), *Besleria* (Gesneriaceae) and *Ficus* (Moraceae). Nearly half of all species ($n = 42$ species) were recorded only once in the diets. Thirty species of plants were represented in at least four faecal samples, and thus could potentially be found in the diets of all four species of manakin. Thirteen of these were included in the diets of all four manakins, and an additional eight were found in the diets of at least three species of manakin. Using only those 30 species of plant that were recorded four or more times in the diets of all manakins combined, we found significantly greater niche overlap (mean pairwise niche overlap = 0.874; $P < 0.001$) than expected by chance (Table 8.2). When all 85 plant species were used to calculate

Table 8.2. Pairwise niche overlap values based on plant species found in at least four faecal samples ($n = 30$ plant species) for species of manakin found in Ecuador. When all 85 plant species are included, pairwise values differed by less than 0.02 in all cases.

Species	<i>L. coronata</i>	<i>P. erythrocephala</i>	<i>P. filicauda</i>	<i>P. pipra</i>
<i>L. coronata</i>	–	0.962	0.834	0.936
<i>P. erythrocephala</i>	–	–	0.854	0.919
<i>P. filicauda</i>	–	–	–	0.741

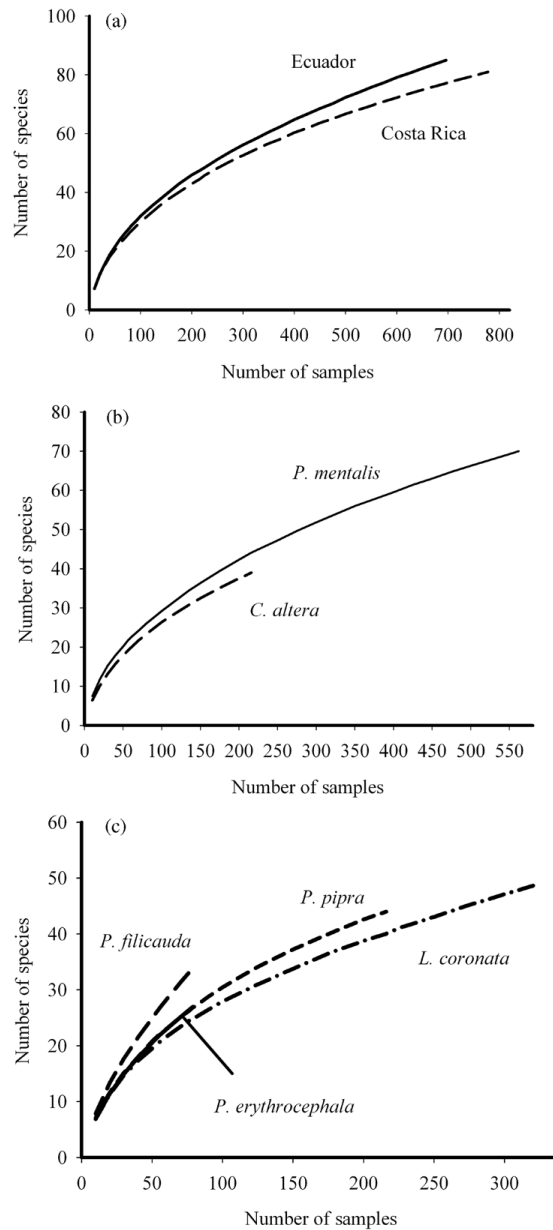


Fig. 8.1. Species accumulation curves for number of species of plants in the diet of manakins in lowland wet forests of Costa Rica and Ecuador: (a) all species combined in Costa Rica (2 species; dashed line) and Ecuador (4 species; solid line), which includes a total of 81 species of plant in 778 samples in Costa Rica and 85 species of plant in 696 samples in Ecuador (number of samples exceeds number of faecal samples reported in the text as >1 species of plant can be found in a single faecal sample); (b) the two Costa Rican manakins separately (*P. mentalis*, solid line; *C. altera*, dashed line); (c) the four Ecuadorian manakins (*P. filicauda*, *P. pipra*, *P. erythrocephala* and *I. coronata*) separately.

pairwise niche overlap values, we found that values were nearly identical (<0.02 difference in all cases) to this reduced set of 30 species; overall the mean value for pairwise niche overlap was 0.862). Species accumulation curves for plants revealed that more effort is needed to characterize the diets of these four species of manakin in Ecuador; species are still being added even after all samples are combined (Fig. 8.1). Using rarefaction analysis (Gotelli and Entsminger, 2001), we found that the diet of *P. filicauda*, with 33 species, was significantly more diverse ($P < 0.05$) when sample effort was standardized at 76 samples (the cumulative number of samples for *P. filicauda*) than the other three species of manakins; the latter three species did not differ significantly in number of plant species consumed. These results suggest that these four species of manakins are, for the most part, ecologically equivalent in the quantitative and diversity components of seed-disperser effectiveness because they feed on a similar suite of plant species in similar proportions. However, *P. filicauda* was the most different in diet, with relatively lower pairwise values for niche overlap (0.741–0.854) and more plant species consumed after correcting for sampling effort. When *P. filicauda* is excluded, mean pairwise overlap among the remaining three species increased to 0.939 (with the 30 most common species; or 0.934 with all 85 plant species).

Habitat overlap

In old-growth forest of La Selva, 181 *Corapipo altera* and 470 *Pipra mentalis* were captured between 1985 and 1993. The spatial distribution of captures between these two species differed significantly among the 60 mist-net sites (Cramér–von Mises test, $P = 0.043$). Differences in the spatial dissemination of seeds do not necessarily mean that seeds are deposited into different forest environments. When we compared the distribution of captures as a function of forest environments, we found that *P. mentalis* was captured more frequently in ridge habitats, while *C. altera* was captured more frequently in valley bottoms and other low-lying habitats within the sample area ($\chi^2 = 20.3$, $df = 4$, $P < 0.005$) (see also Loiselle and Blake, 1999, 2002). Consequently, these two manakins apparently differ in the local spatial dissemination of seeds, as well as the proportional deposition of seeds into different forest environments. Consequently, differential habitat use by Costa Rican manakins results in a divergence of ecological roles (i.e. lower ecological redundancy) for this component of the seed dispersal process.

In Ecuador, the relative abundance of manakins captured on the two 100 ha study plots differed, with *P. filicauda* captured more frequently on Puma plot, and *P. pipra* more frequently on Harpia plot; *Lepidothrix coronata* was the most frequently captured manakin on both plots (Table 8.3). The relative ranking of each species on each plot based on captures is supported by census data (J.G. Blake, eastern Ecuador, 2006, unpublished results). Differences in these large-scale patterns of

Table 8.3. Number of manakin captures on the two 100 ha study plots in lowland wet forest of eastern Ecuador. Sampling effort is equivalent on the two plots (see Methods).

Species	Harpia	Puma
<i>L. coronata</i>	182	183
<i>P. erythrocephala</i>	29	18
<i>P. filicauda</i>	28	143
<i>P. pipra</i>	85	30

captures were also reflected locally within plots. We found that the spatial distribution of captures between species of manakin differed significantly in nine of 12 pairwise comparisons (Table 8.4). However, patterns were not necessarily consistent between the two study plots. These results suggest that manakins deposit seeds in different locations, except for *P. filicauda* and *L. coronata* on Puma plot, and *L. coronata* and *P. erythrocephala*, or *P. erythrocephala* and *P. pipra* on Harpia plot (Table 8.4).

When we examined the forest environment at net-sites where manakins were captured, as defined largely by topographic features and their heterogeneity (elevation, slope, aspect, and distance to stream), we found few significant differences between sites (Harpia ANOSIM: Global $R = 0.026$, $P = 0.062$; Puma ANOSIM: Global $R = 0.024$, $P = 0.143$). Only on Harpia plot did we find that *P. filicauda* generally frequented different forest environments than *P. erythrocephala* ($P = 0.001$) or *P. pipra* ($P = 0.008$) did (Fig. 8.2). Consequently, these results suggest that although manakins may differ in the spatial dissemination of seeds (results of Cramér–von Mises test above), seeds are expected to arrive into similar forest environments, except as noted above. Thus, there appears to be considerable ecological redundancy among species of Ecuadorian manakin in the forest environments where seeds are disseminated; a qualitative component of disperser effectiveness. However, as we observed in diet overlap, *P. filicauda* was the most distinct of the four species in terms of forest environments frequented.

Table 8.4. Results of the Cramér–Von Mises test examining differences in the spatial distribution of captures between species of manakin in Ecuador. P values for Harpia plot are shown above the diagonal, while values for Puma plot are shown below the diagonal.

Species	<i>L. coronata</i>	<i>P. erythrocephala</i>	<i>P. filicauda</i>	<i>P. pipra</i>
<i>L. coronata</i>	–	0.538	0.001	0.003
<i>P. erythrocephala</i>	0.029	–	0.004	0.340
<i>P. filicauda</i>	0.288	0.028	–	0.001
<i>P. pipra</i>	0.001	0.020	0.001	–

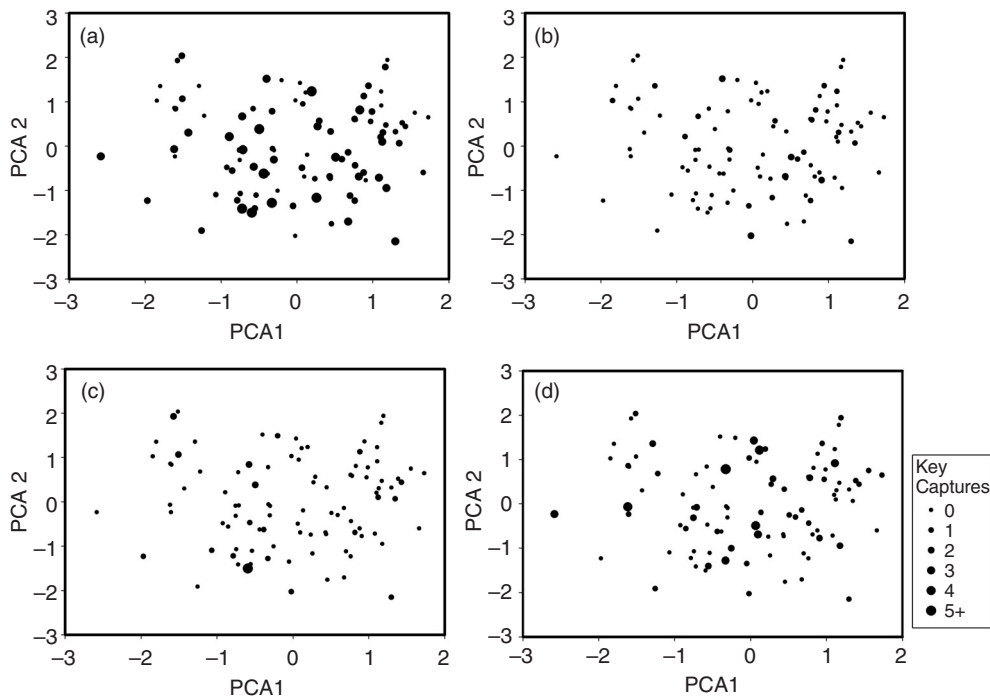


Fig. 8.2. Overlay of manakin captures on net-sites plotted in environmental space based on results from a principal components analysis (PCA) using data from Harpia study plot in Ecuador. The first two principal components accounted for 55.6% of the total variance. Species are displayed as follows: (a) *Lepidothrix coronata*, (b) *Pipra erythrocephala*, (c) *Pipra filicauda* and (d) *Pipra pipra*.

Discussion

Local extinction of strong interactors can result in significant changes in ecosystem structure and function (e.g. Paine, 1969; Flecker, 1996). Consequently, the existence of ecologically redundant species in ecosystems has been hypothesized to buffer ecosystems from disturbance or loss of component species (Naeem *et al.*, 1995; Loreau, 2000). Evidence that redundancy in ecological function exists has been shown experimentally in studies that examined aquatic microbial decomposition (Naeem and Li, 1997; Scarff and Bradley, 2002) and plant productivity (Walker *et al.*, 1999). Moreover, some studies have demonstrated that increased biological diversity buffers ecological function (Naeem *et al.*, 1994, Tilman and Downing, 1994). Increased biological diversity theoretically leads to increased ecological overlap among species. Consequently, the presence of more species performing similar ecological roles offers greater resilience in the face of disturbance, as ecologically equivalent species can compensate for the loss of one or more other species within the same functional group

(Walker, 1995). However, even in biologically diverse communities, the ecological function of some species may be unique. For example, the experimental exclusion of *Prochilodus mariae*, an Andean detritivorous fish, led to large changes in sediment deposition and algal and invertebrate communities (Flecker, 1996). Similarly, the ecological roles of some seed dispersers in species-rich forests appear to be irreplaceable (Stocker and Irvine, 1983; Wenny and Levey, 1998). For example, bellbirds in Costa Rica uniquely disseminate seeds of Lauraceae to favourable sites for germination (Wenny and Levey, 1998). The local extinction of this species would hypothetically cause declines of these trees over time due to recruitment limitation. In a number of cases, local extinction or declines of dominant seed dispersers have resulted in declines in dependent plant species (e.g. Tabarelli *et al.*, 1999; Cordeiro and Howe, 2001, 2003).

Our prediction that manakins in species-rich forests of Ecuador are more ecologically redundant in their roles as seed dispersers than manakins in relatively less diverse forests of Costa Rica was largely upheld. In both forests, pairwise niche overlap values were nearly identical (0.874 vs 0.862 using all plant species in Costa Rica and Ecuador, respectively) suggesting that different species fed on a similar suite of plant species in similar proportions. Yet when *Pipra filicauda* is excluded, pairwise niche overlap for the three remaining species in Ecuador increased to 0.934 (range 0.912–0.957 using all plant species; see also Table 8.2). In addition, manakins in Ecuador were much more likely to disseminate seeds into similar forest environments when compared with Costa Rican manakins, which differed significantly in their use of forest habitats. We also expect that species of manakin overlap considerably in other qualitative components of disperser effectiveness. Given the similar body size and digestive morphologies, we expect that seeds receive similar treatment as they pass through the digestive tract of these manakins (see Traveset *et al.*, Chapter 4, this volume). Fruit-eating birds directly affect plant recruitment through patterns of fruit removal, seed treatment, gut-mixing of seeds, and habitat selection (Schupp, 1993; Jordano and Herrera, 1995). In species-rich forests in Ecuador, the seed-dispersal roles of manakins appear to be quite redundant. Consequently, plants in Ecuador are expected to be less vulnerable to declines or variation in population abundance of one or more of their seed dispersers when compared with Costa Rica or other relatively species-poor forests, where fewer species dominate disperser–plant interactions (Loiselle and Blake, 2002; McConkey and Drake, 2002; Silva *et al.*, Chapter 26, this volume). In addition, ecological equivalency may also mean that different species of disperser probably exert similar selective pressures on plant recruitment and, thus, may influence the evolution of plant traits.

Our conclusions that manakins from species-rich forests overlap more in ecological function than do manakins in less diverse forests, and therefore that these forests may be more resilient to disturbance, should be treated with caution for several reasons. First, species accumulation curves revealed that we have yet to adequately sample the diets of these manakins. In all

cases, species accumulation curves have not levelled out, even when samples are combined across species (Fig. 8.1). Second, many species of plant are only recorded rarely in the diet and, thus, for many species the ecological overlap in seed dispersal roles remains unknown. Furthermore, rare events may be particularly significant in seed dispersal (e.g. rare long-distance dispersal events), and if such rare dispersal events are restricted to one species of disperser, then loss or decline of this species could significantly impact plant populations.

Our comparisons among manakins may also mask important differences in disperser effectiveness between sexes within a species. As lek-breeding birds, male manakins spend considerable time at aggregated display sites during an extended breeding season (Snow, 1962; Sick, 1967; Lill, 1976; Schwartz and Snow, 1978; Tello, 2001). Consequently, movement patterns and habitat use of males may differ from those of females, and such differences are likely to affect qualitative components of disperser effectiveness. Nonetheless, when we separately examined the forest environments where males and females were captured, our results paralleled those reported for the species as a whole, such that few or no differences were found between species in forest environments where manakins were captured. However, we have found that the environmental conditions at lek sites where males aggregate does differ significantly among species of manakin (Loiselle *et al.*, 2007). Thus, even though males overlap substantially in diet, they are more likely to differ in the forest environments into which they disseminate seeds, given the substantial amount of their time spent at lek sites (see also Théry, 1992). If male manakins bring plant seeds to different forest environments, then we might expect that seed survival and seedling establishment in certain lek environments of some plant species may be limited, whereas in others the environmental conditions might favour establishment. Thus, if the original template of seeds dispersed at leks by manakins is similar (as indicated by large diet overlap) and plant recruitment probabilities do not change markedly over time at a site (but see Schupp, Chapter 20, this volume), then we would expect seed and seedling communities to diverge due to post-dispersal processes acting on plant recruitment. The consequences would be that species composition of manakin food plants around leks should differ among species. Indeed, Ryder *et al.* (2006) found significant differences in the species composition of fruiting plants in the vicinity of leks at our site in a study involving three of the four species of manakin. Other studies involving lek-mating birds have also demonstrated that plants found within leks differ from those found in surrounding environments, and that they are dominated by fruiting species consumed by lek inhabitants (e.g. Théry and Larpin, 1993; Krijger *et al.*, 1997). Moreover, Krijger and Opdam (1995) found that seed germination of Melastomataceae was lower in manakin leks when compared with treefall gaps, which probably results in lower effectiveness of seed dispersal by male manakins for Melastomataceae. These results suggest that the mating system of manakins has probably resulted in intersexual differences in some

components of seed-disperser effectiveness and, thus, in the case of male manakins, our estimates of ecological redundancy may be overestimated.

Our analysis of ecological redundancy in seed-dispersal function in these two forests which differ in biological diversity was restricted to manakins. Although manakins are the predominant understory frugivores in these two forests, many other species also feed on fruits at these sites (see, e.g. Karr *et al.*, 1990; English, 1998; B.A. Loiselle, P.G. Blendinger and J.G. Blake, 2006, unpublished results). In Costa Rica, we found that a few species tended to dominate plant–disperser interactions in the forest understory (Loiselle and Blake, 1999, 2002). Although we have yet to quantify the diets of other frugivores in the forest understory in Ecuador, including two other species of manakin regularly found in the understory (*Chiroxiphia pareola*, *Machaeropterus regulus*), our preliminary results point to considerable diet overlap between these other frugivorous species and manakins, as well as some differences (B.A. Loiselle *et al.*, 2006, unpublished results). For example, plants from Araceae (*Anthurium*, *Philodendron*) were important components of manakin diets in Ecuador and Costa Rica. Araceae have also been recorded regularly in diets of at least six other understory frugivores in Ecuador (e.g. *Chiroxiphia pareola*, *Chloropipo holochlora*, Pipridae; *Turdus albicollis*, *Catharus minimus*, Turdidae; *Euphonia xanthogaster*, *E. rufiventris*, Emberizidae), but not others (e.g. *Pteroglossus azarae*, Ramphastidae; *Momotus momota*, *Baryphengus martii*, Momotidae). In Costa Rica we only recorded Araceae (i.e. *Anthurium* spp.) in the diets of two other frugivores, *Euphonia gouldi* and *Mionectes oleaginous* (Tyrannidae). Thus, we expect that the trend of increased ecological redundancy in Ecuadorian forests will hold when more seed dispersers are included.

Despite this apparent increased redundancy in ecological roles, the presence of ecologically equivalent species does not guarantee that ecosystem function and structure will be conserved under scenarios of disturbance. Seed dispersers have been shown to be more extinction-prone than species from other functional groups (e.g. Terborgh and Winter, 1980; Renjifo, 1999; Şekercioglu *et al.*, 2004), and even in species-rich forests, plants whose seeds are dispersed by a suite of apparently ecologically equivalent species have experienced significant declines in recruitment following forest fragmentation (Cordeiro and Howe, 2001, 2003). Consequently, conservation efforts should be targeted to conserve key ecological processes such as seed dispersal. To do so requires an understanding of the complex interactions between plants and their dispersers, which include identifying suites of functionally equivalent species. Although ecological redundancy may offer greater ecosystem resilience under conditions of disturbance, natural resource managers should recognize that it is no guarantee.

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