

Dietary diversity in fruit-eating birds: a biogeographic comparison between New Zealand and Canada

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Abstract: If deterministic processes consistently structure ecological communities, similar patterns in species interactions should be observed in different geographic areas that experience similar environmental conditions. I tested for convergent patterns in dietary diversity of fruit-eating birds inhabiting similar latitude forests in the Northern and Southern hemispheres. I observed birds foraging for fruits over two fruiting seasons in both Nelson Lakes National Park, South Island, New Zealand, and the Pacific Rim National Park, Vancouver Island, Canada. I then conducted rarefaction analyses to compare community-level and species-level dietary diversity between geographic locales. Relationships between the size of each bird species and the average size of fruits consumed were also assessed. Results showed that the New Zealand bird community had greater overall dietary diversity than the Canadian community. However, similar levels of dietary diversity were observed among species within communities in both hemispheres. Positive relationships between bird size and fruit size were observed in New Zealand, but not in Canada. Therefore, while results showed some support for dietary convergence between hemispheres, several substantial differences were also observed, leading to mixed support for convergent patterns in the diets of fruit-eating birds between hemispheres.

Keywords: convergence; frugivore; mutualism; seed dispersal

Introduction

Fleshy-fruits are an important component of the diet of many terrestrial bird species. However, few birds consume fleshy-fruits exclusively and their importance in bird diets varies in space and time. Frugivory is thought to be more common in the tropics, where a higher fraction of plant species produce fleshy-fruits (van der Pijl 1969). Frugivory is also thought to be more important during migratory periods, and less important when birds breed, because fruits typically contain low levels of protein needed for reproduction (see Levey & Martínez del Rio 2001). But beyond coarse generalisations, little is known about broad-scale patterns in the diets of fruit-eating birds.

Birds have been shown to select fruits based on a variety of characteristics, including fruit chemistry (Tewksbery & Nabhan 2001; Tang et al. 2005), colour (Burns & Dalen 2002; Schaefer et al. 2006), size (Korine et al. 2000; McConkey & Drake 2002), shape (Lord 2004; Forget et al. 2007) and energetic reward (Edwards 2006; Martínez et al. 2007). However, there is little evidence indicating that birds consistently prefer particular fruit traits (Herrera 2002). Avian fruit preferences often vary substantially among individuals, species and years (see Whelan & Wilson 1994; Fuentes 1995; Herrera 1998; Levey & Benkman 1999). Although abundances of birds

and fruits are typically correlated through space and time (Burns 2004; Sapir et al. 2004; Hanya 2005; Telleria et al. 2008; Guitián & Munilla 2008), spatial variation in bird–fruit interactions are under-studied, particularly at biogeographic scales (but see Bleher & Böhning-Gaese 2000; Márquez et al. 2004; Böhning-Gaese 2007; Kissling et al. 2008).

Geographically isolated locales that experience similar climatic conditions often contain analogous plant and animal communities. For example, the ‘Mediterranean’ climates of California, Central Chile, Western Australia, South Africa and Southern Europe support structurally similar scrublands comprised of distantly related species (Cody & Mooney 1978). This suggests that similar environments select for similar phenotypes in a process known as ‘convergence’ (see MacArthur & Levins 1967). Tests for convergence have traditionally focused on the effects of competition (e.g. Harmon et al. 2005). However, convergence can also result from other ecological processes, such as mutualistic interactions (Elias et al. 2008).

Here, I test for convergent patterns in dietary composition of fruit-eating birds inhabiting two temperate forests located in similar environments in the Northern and Southern hemispheres. I quantified bird–fruit interactions over two fruiting seasons both on Vancouver Island, Canada, and on the South Island, New Zealand. Data

were used to test for biogeographic similarity in: (1) community-level dietary diversity, or the total number of fruit species consumed per foraging bout by all bird species in each locale; (2) species-level dietary diversity, or the number of fruit species consumed per foraging bout by each bird species within locales; and (3) size-related constraints on the diets of fruit-eating birds.

Methods

Study sites and species

Observations in Canada were made in an old-growth forest within the Pacific Rim National Park, on Vancouver Island, British Columbia, Canada (48°50' N, 125°22' W; Fig. 1). The region receives nearly 3000 mm of precipitation annually and has an average temperature of c. 10°C. The prevailing vegetation type is conifer forest dominated by Sitka spruce (*Picea sitchensis*), western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*), all of which are wind-dispersed (nomenclature follows Hitchcock & Cronquist 1994). Fleshy-fruited trees and shrubs are common in the forest understorey. Eight fruit species were observed during the course of observations: *Cornus stolonifera*, *Gaultheria shallon*, *Lonicera involucrata*, *Rhamnus purshiana*, *Rubus parviflorus*, *R. spectabilis*, *Sambucus racemosa* and *Vaccinium parvifolium*. Although sometimes consumed by bears (*Ursus americanus*), fleshy-fruits are commonly consumed by birds. Seven fruit-eating bird species were observed during the course of observations: the American

robin (*Turdus migratorius*), cedar waxwing (*Bombycilla cedrorum*), European starling (*Sturnus vulgaris*), hermit thrush (*Catharus guttatus*), northwestern crow (*Corvus caurinus*), Steller's jay (*Cyanocitta stelleri*) and Swainson's thrush (*Catharus ustulatus*). All consume fruits to supplement diets comprised mostly of invertebrates, and all but one species (the European starling) are native to the area. Observations were made between July and August, during the annual peak in fruit production, in 2001 and 2007. Detailed descriptions of the site's natural history, climate and geology are in Klinka et al. (1989). Burns (2004, 2005a,b,c) provides a detailed description of the local seed dispersal mutualism.

Observations in New Zealand were made in Nelson Lakes National Park, which is located in the northern region of the South Island (41°48' S, 172°50' E; Fig. 1). The area experiences a mild climate with approximately 1000 mm annual precipitation and the same average temperature (c. 10°C) as the Canadian site. The prevailing vegetation type is *Nothofagus* forest (see Wardle 1984), which is dominated by three tree species, *Nothofagus fusca*, *N. menziesii* and *N. solandri*, all of which are wind-dispersed (nomenclature follows Allan (1961) and Connor & Edgar (1987)). Fleshy-fruited trees and shrubs are common beneath the forest canopy. Fourteen species were observed during the course of observations: *Carpodetus serratus*, *Coprosma foetidissima*, *C. linariifolia*, *C. propinqua*, *C. rigida*, *Coriaria arborea*, *Elaeocarpus hookerianus*, *Griselinia littoralis*, *Halocarpus biformis*, *Leucopogon fasciculatus*, *Myrsine divaricata*, *Neomyrtus pedunculatus*, *Pittosporum divaricatum*, *Pseudopanax*

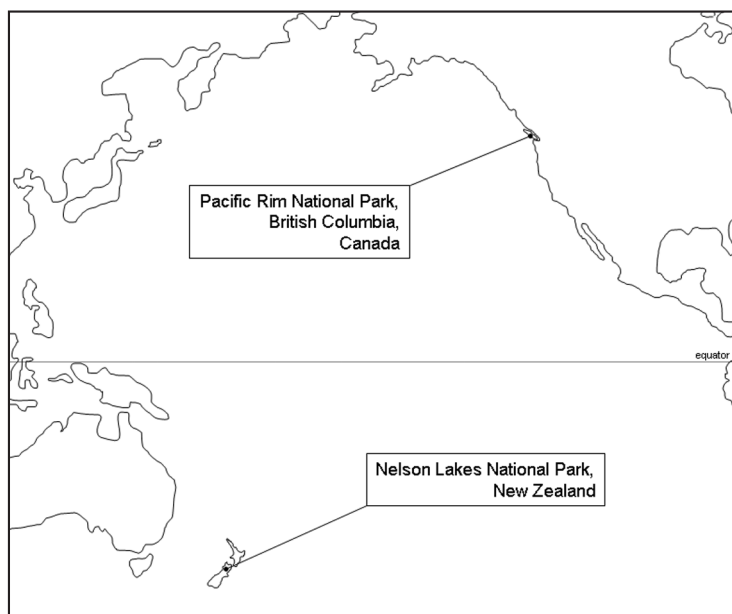


Figure 1. Map illustrating the location of study sites.

colensoi and *P. crassifolius*. New Zealand lacks native mammals (aside from two species of bat), so fleshy-fruits are dispersed mostly by birds (but see Duthie et al. 2006). Six fruit-eating bird species were observed. Three species are endemic to New Zealand, bellbird (*Anthornis melanura*), brown creeper (*Mohoua novaeseelandiae*) and tūī (*Prosthemadera novaeseelandiae*). One species, waxeye (*Zosterops lateralis*), naturally colonised New Zealand sometime in the last 200 years, and two were introduced from Europe, song thrush (*Turdus philomelos*) and blackbird (*T. merula*). Observations were made between March and April in 2007 and 2008, during the annual peak in fruit production. Detailed descriptions of the site's natural history, climate and geology are in Wardle (1984) and Dawson (1988).

The two study sites were chosen because of their ecological and climatic similarities. Arguably the strongest similarity between sites is the representation of dispersal mechanisms within each plant community. Both sites contain structurally simple forests dominated by a small number of canopy tree species that are all wind-dispersed. However, the understorey of both forests contains a much larger diversity of small tree and shrub species, nearly all of which produce fleshy-fruits. Therefore, vegetation structure, particularly as it pertains to seed dispersal mechanisms, is strongly similar between regions. Both sites are also situated on islands located at similar latitudes. They therefore experience similar climates, which are mild in comparison with other geographic locales at similar latitudes, due to their close proximity to the ocean.

Despite these similarities, the two sites differed in several notable respects. First, they have strongly divergent evolutionary histories. New Zealand separated from Gondwana c. 80 million years ago; therefore, much of the New Zealand flora and fauna has clear phylogenetic links to other Gondwanan landmasses, such as Australia and South America (Gibbs 2006). In contrast, Vancouver Island was attached to North America during the last glacial maximum, approximately 12 000 years ago and has a much shorter history of geologic isolation (Clague & James 2002); most of its flora and fauna are undifferentiated from the mainland. Other notable differences are the composition and migratory tendencies of their respective avifaunas. New Zealand has witnessed the extinction of nearly half its avifauna since the arrival of humans c. 750 years ago (Wilson 2004; Wilmshurst et al. 2008), and in the past century a variety of European birds have been introduced and are now commonplace. Conversely, there are relatively few introduced songbirds at the Canadian study site. Also many fruit-eating birds in Canada are strongly migratory and winter at lower latitudes. Conversely, all but two species of New Zealand songbirds are sedentary. The two sites also differ by approximately 7 degrees of latitude, with the Canadian site being located farther from the equator. However, the New Zealand site is located at a much higher elevation (approximately 650 m) than the Canadian site,

which is located at sea level. Therefore, while the climatic conditions are not identical, they are similar.

Sampling

Bird diets were quantified with the field observation protocol described by Burns (2005b). In both locales I made daily observations of birds foraging for fruits along a circular walking track, which took approximately 2 h to traverse. It was often difficult to accurately count individual fruits consumed by foraging birds, but observing foraging 'visits', wherein birds visited fruiting plants to consume fruits, whatever the exact number, was straightforward. Therefore, I scored a frugivore 'visit' when I observed a bird approach a plant and consume at least one fruit. Bird diets were then characterised by the number of times each bird species visited each plant species. To avoid multiple observations of the same bird during each census period, observations were halted after each sighting and resumed 10 m down the trail.

The size of all fruit species in each geographic locale was measured with vernier callipers. For each species, five fruits were randomly selected from five accessible plants growing along the observation route. Three measurements were made to the nearest millimetre. Fruit length was measured as the linear distance between the tip of the fruit and the point of petiole attachment. Fruit width was measured as the longest distance perpendicular to the length measurement. The shortest perpendicular width was also measured, because several fruit species had a pronounced flattened appearance in three dimensions. Both the longest and shortest widths were then averaged to obtain a single fruit-width measurement. Overall fruit size was then quantified as the product of fruit length and width measurements following Forget et al. (2007). Bird length measurements were taken from Heather & Robertson (2005) and Scott (1994) to characterise bird sizes.

Analyses

I conducted rarefaction analysis to test for community-level and species-level dietary diversity between locales. Rarefaction is commonly used to estimate species diversity on a per unit individual, rather than unit area basis (Simberloff 1972). The procedure uses a bootstrapping algorithm to randomly select subsets of individuals from the total pool sampled to obtain an expected species richness value for a given number of individuals (analytical solutions to this procedure are also available; see Gotelli & Colwell 2001). This bootstrapping procedure can then be repeated across a range of abundance values to obtain a rarefaction 'curve', relating species richness to the total number of individuals sampled. Rarefaction curves can also be bounded by confidence intervals to help compare curves representing different communities.

Although rarefaction is commonly used to characterise species diversity per unit sampling effort, it can also be used to solve other ecological problems. Here,

I used it to test for community-level differences in dietary diversity between geographic locales. More specifically, I used it to characterise the relationship between the total number of visits by fruit-eating birds at each locale to the total number of fruit species consumed. I used *rarefact 1.0* (http://people.hofstra.edu/j_b_bennington/research/paleoecology/rarefact.html) to conduct the bootstrapping procedure, which generated a rarefaction curve from the total number of visits made to each fruit species in each locale, along with its 95% confidence interval. The resulting curves for each geographic locale therefore represent the total number of fruit species consumed (i.e. 'dietary diversity') for a given sampling effort (i.e. 'visits'). Differences in dietary diversity between locales were established by visually comparing community-level rarefaction curves and their corresponding confidence intervals (Gotelli & Colwell 2001).

I also used rarefaction to evaluate species-level dietary diversity within locales. However, in this instance I used a slightly different application of the technique. I compared the observed number of fruit species consumed by each bird species in each locale to an expected value based on each species' total number of visits. Expected values of dietary diversity were obtained by calculating the number of fruit species consumed based on random samples of 'visits' from the total pool observed in that locale. Differences between observed and expected values of species-level dietary diversity were assessed using simple linear regression in SPSS (2007). Significant, positive relationships between observed and expected dietary diversity values indicate that dietary diversity was similar among species within each locale (i.e. birds show little tendency to specialise on particular fruit species). Maximum likelihoods were used to estimate slope and intercept parameters and their 95% confidence intervals. Slope parameters that do not differ from one, and intercept values that do not differ from zero, indicate similar patterns in species-level dietary diversity among species within each bird community.

Relationships between bird size and the size of fruits they consumed were assessed using the general linear model procedure in SPSS (2007) following Engqvist (2005). The average size (\log_{10} transformed to improve normality and homoscedasticity) of all fruits consumed by each species was used as the dependent variable. Bird length was included in the model as a covariate. Geographic locale was considered a fixed factor with two levels. The full model was assessed, including the fixed-factor, the covariate, and their interaction. Where the slope of the relationship between bird size and fruit size differed as indicated by a significant interaction between the fixed-factor and the covariate, separate linear regressions were conducted for each locale to identify functional differences in the relationships.

Results

Rarefaction curves relating the cumulative number of foraging observations (visits) to total dietary diversity (the total number of fruit species consumed) were asymptotic for both geographic locales (Fig. 2). Therefore, the total number of foraging observations made in each geographic locale provided an adequate estimate of total dietary diversity. Two aspects of the rarefaction curves differed between regions. First, the asymptote for New Zealand was higher than that for Canada, indicating that total dietary richness was higher in New Zealand. Second, dietary diversity per foraging observation was higher in New Zealand. For instance, at 100 foraging observations the mean and 95% confidence interval for total dietary diversity in New Zealand sat well above that for Canada (Fig. 2).

Similar relationships between observed and expected species-level dietary diversity were observed for each locale (Fig. 3). In Canada, the observed dietary diversity of each bird species was positively correlated with the expected dietary diversity values generated by rarefaction ($r^2 = 0.904$, $P < 0.001$). The slope of this relationship was statistically indistinguishable ($\pm 95\%$ CI) from 1 (0.984 ± 0.256) and the intercept was indistinguishable from zero (-0.532 ± 1.420). In New Zealand, the observed number of fruit species was again correlated with the expected number of fruit species ($r^2 = 0.898$, $P = 0.006$). The slope of this relationship was statistically indistinguishable ($\pm 95\%$ CI) from 1 (0.808 ± 0.266) and the intercept was indistinguishable from zero (0.628 ± 2.042).

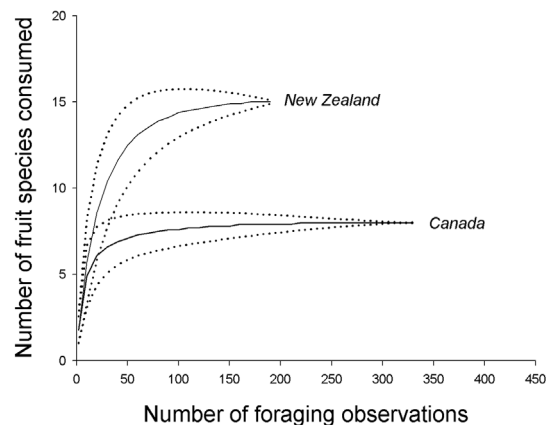


Figure 2. Rarefaction curves relating the total number of fruit species consumed by bird communities in Canada and New Zealand to the total number of foraging observations collected at each site. Solid lines show averages for each locale and hatched lines the upper and lower 95% confidence intervals.

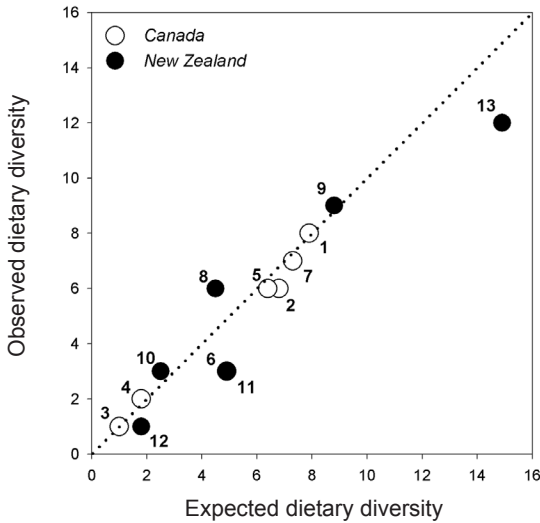


Figure 3. Relationship between the observed number of fruit species consumed by each bird species and the expected number generated by rarefaction analyses. Canadian bird species are shown as open symbols and New Zealand bird species as closed symbols. Numbers beside symbols refer to bird species (Canada: 1. American robin, 2. cedar waxwing, 3. European starling, 4. hermit thrush, 5. northwestern crow, 6. Steller’s jay, 7. Swainson’s thrush; New Zealand: 8. bellbird, 9. blackbird, 10. brown creeper, 11. song thrush, 12. tūi, 13. waxeye).

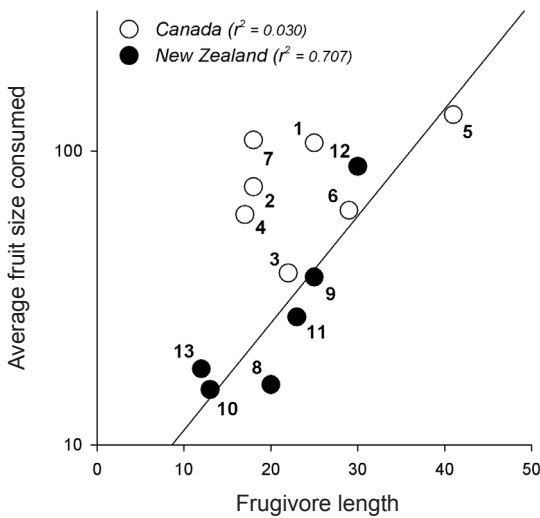


Figure 4. Relationship between the size of each frugivore species (bird length, cm) and the average size of the fruits they consumed (fruit length × fruit width, mm). Bird size was correlated with fruit size in New Zealand (closed symbols, regression line), but not in Canada (open symbols, no regression line). Numbers refer to bird species as in Fig. 3.

Size-related coupling of bird–fruit interactions was observed in New Zealand but not Canada (Fig. 4). The size of each fruit-eating bird species was positively correlated with the average size of fruits they consumed ($F_{1,10} = 10.925, P = 0.008$). However, an interaction was observed, indicating that the slopes of relationships between average fruit size and bird size differed between geographic locales ($F_{1,10} = 5.467, P = 0.041$). Average fruit size increased with bird size in New Zealand ($r^2 = 0.707, P = 0.023$), but not in Canada ($r^2 = 0.030, P = 0.407$).

Discussion

Several marked differences were observed between the diets of fruit-eating birds in Canada and New Zealand. New Zealand birds consumed greater total numbers of fruit species, as well as greater numbers of fruit species per foraging visit. New Zealand birds also consumed fruits according to their size, with bigger bird species consuming larger fruits than smaller bird species. However, size-related coupling of birds and fruits was not observed in Canada. Although species-level dietary specialisation was similar between locales, overall results did not show strong support for dietary convergence between geographic locales.

Differences in community-level dietary diversity between study sites likely resulted from a higher regional diversity of fleshy-fruited plant species, which is typically higher per unit area in southern hemisphere than northern forests (Burns 2007). Given the insularity of New Zealand, several lineages of fleshy-fruited plants have also radiated extensively, resulting in large numbers of closely related fruit species. The genus *Coprosma* is particularly diverse and >10 species co-occur in the Nelson Lakes area. New Zealand bird species may therefore have included more fruit species in their diets simply because there were more fleshy-fruited plant species available for consumption. However, regional abundances of fleshy-fruited plant species were not measured, so this explanation for greater dietary diversity in New Zealand remains speculative.

Patterns of species-level dietary diversity suggest that bird species in the two communities did not specialise on particular fruit species. Dietary diversity of species in both geographic locales was closely associated with predicted values of dietary diversity based on random subsamples of all foraging observations collected in each locale. In other words, the number of fruit species consumed increased with sampling effort at the same rate among bird species in both locales. Therefore, species-level dietary diversity did not differ between locales, even though community-level dietary diversity differed geographically.

This result supports a ‘non-equilibrial’ or ‘neutral’ view of dietary diversity (see Herrera 1998, 2002; Levey & Benkman 1999), whereby fruit-eating birds show undifferentiated or random preferences for particular

fruit species (cf. Hubbell 2001; Whitfield 2002; Chave 2004). According to this view, plant and bird species are functionally redundant and play similar ecological roles in the mutualism (Zamora 2000). Approximately 35% of all species interactions at the New Zealand site involved bird species introduced from Europe, all of which lack an evolutionary history with the New Zealand flora. Results from this site therefore may not be surprising. However, an almost identical relationship was observed at the Canadian site, where the contribution of introduced species to the avifauna was much reduced. Burns (2006) showed that Canadian birds foraged randomly for fruits, and that differences in dietary composition between species resulted from correspondence between the migratory schedules of bird species and the fruit phenology of plant species. These circumstances led to random but predictable fruit choice patterns.

Although the number of fruit species in the diets of New Zealand birds showed few interspecific differences, the types of fruit species included in the diets of each bird species varied non-randomly. More specifically, bigger birds tended to eat bigger fruits and smaller birds tended to eat smaller fruits. This result supports a large number of studies documenting size-related coupling of bird–fruit interactions in other locales (see Diamond 1973; Noma & Yumoto 1997; Herrera 2002) and likely results from physical constraints imposed by differences in the size of birds and fruits. For example, the largest fruit species at the New Zealand study site, *Elaeocarpus hookerianus*, is simply too large to be consumed by the smallest bird species, *Zosterops lateralis*. It might also be more energetically efficient for bigger bird species to specialise on big fruits, because handling costs are likely to be higher for smaller fruits (Stephens & Krebs 1986).

Interestingly, no evidence for size-related coupling was observed in the diets of Canadian birds. The biggest fruit species in Canada, *Rubus spectabilis*, is too large to be consumed whole by the smallest bird species, *Catharus ustulatus*. However, fruits produced by *R. spectabilis* are composite drupes, and because of their composite nature, they are typically torn apart prior to consumption and eaten piecemeal (author's observations). Other large-sized fruit species have similar, composite fruit morphology. Therefore, the large size of Canadian fruits does not impose a physical constraint against their consumption by smaller sized birds. No fruit species in New Zealand can be dismembered in this way and all must be consumed whole. Therefore, geographic differences in size-related coupling of bird diets result from differences in fruit morphology and the capacity of birds to eat them piecemeal.

Overall, the results of my study failed to find strong evidence for convergence in the dietary diversity of fruit-eating birds between sites in the northern and southern hemispheres. While one notable similarity was observed, several strong dietary differences were also found. Incongruence is a common feature in the literature

on avian frugivory (Levey & Martinez del Rio 2001; Herrera 2002). Many previous studies have documented deterministic patterns in fruit choice, whereas others have documented stochastic patterns in fruit diets. However, previous work is dominated by studies documenting population-level processes on fine spatial and temporal scales (see Stanton 2003). Relatively few studies have focused on biogeographic processes across larger scales (e.g. Böhning-Gaese 2007). Results of the present study suggest that focusing on larger scales may provide a fresh perspective to help reconcile the often conflicting results of population-level studies.

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