Darwin's finches and their diet niches: the sympatric coexistence of imperfect generalists

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Abstract

Adaptive radiation can be strongly influenced by interspecific competition for resources, which can lead to diverse outcomes ranging from competitive exclusion to character displacement. In each case, sympatric species are expected to evolve into distinct ecological niches, such as different food types, yet this expectation is not always met when such species are examined in nature. The most common hypotheses to account for the coexistence of species with substantial diet overlap rest on temporal variation in niches (often diets). Yet spatial variation in niche overlap might also be important, pointing to the need for spatiotemporal analyses of diet and diet overlap between closely related species persisting in sympatry. We here perform such an analysis by characterizing the diets of, and diet overlap among, four sympatric Darwin's ground finch species at three sites and over 5 years on a single Galápagos island (Santa Cruz). We find that the different species have broadly similar and overlapping diets – they are to some extent generalists and opportunists – yet we also find that each species retains some 'private' resources for which their morphologies are best suited. Importantly, use of these private resources increased considerably, and diet overlap decreased accordingly, when the availability of preferred shared foods, such as arthropods, was reduced during drought conditions. Spatial variation in food resources was also important. These results together suggest that the ground finches are 'imperfect generalists' that use overlapping resources under benign conditions (in space or time), but then retreat to resources for which they are best adapted during periods of food limitation. These conditions likely promote local and regional coexistence.

Introduction

The coexistence of closely related species within adaptive radiations is thought to be strongly influenced by interspecific competition. When competition is initially high, species might either exclude a close competitor from a given location (Gause, 1932; Hardin, 1960; MacArthur & Levins, 1967), or else undergo ecological

character displacement that reduces competition (Brown & Wilson, 1956; Bulmer, 1974; Abrams, 1986; Grant & Grant, 2006). When competition is initially low, species might coexist even without character displacement (e.g. Frakes & Johnson, 1982; Martin & Genner, 2009). Classical theory thus predicts that closely related sympatric species in adaptive radiations should show low niche overlap. Motivated by this expectation, many studies have measured niche (often diet) overlap between closely related species, sometimes finding strong niche divergence (e.g. Herrera, 1978; Hogstad, 1978; Alatalo et al., 1986) but at other times finding broad niche overlap (e.g. Lister, 1981; Wiens, 1989; Hickey et al., 1996; Martin & Genner, 2009). A perennial question is how

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closely related species with seemingly broad niche overlap continue to coexist in sympatry?

The usual approach for addressing this question is to consider temporal variation in niches and their overlap: sympatric species might share a common resource set when resources are abundant but might specialize on distinct resource sets when resources become limited (Grant *et al.*, 1976; Smith *et al.*, 1978; Schoener, 1982; Smith, 1991; Robinson & Wilson, 1998). The specific periods of diet divergence are thus expected to be the main cause of adaptive divergence in morphology and performance. If so, investigations of closely related sympatric species might reveal diet divergence and clear diet-performance-morphology links only during periods of scarcity (Robinson & Wilson, 1998).

Although less often considered, spatial variation in niche overlap could have a similar effect – even in the absence of temporal variation. In particular, nearly all species will exist across a range of habitats that vary in the level of available resources (e.g. Addicott *et al.*, 1987; Dunning *et al.*, 1992). Where resources are sparse, we might expect species to benefit by being able to access 'private' resources; this could, when combined with dispersal, maintain system-wide coexistence, including in habitats with high niche overlap. In short, dispersal from areas of strong among-species divergence in resource use could promote species coexistence in areas of weak divergence in resource use. Under this perspective, 'periods' of food scarcity in the normal temporal perspective might be equated with 'areas' of food scarcity in a spatial perspective (Miyazaki *et al.*, 2006). This argument is reminiscent of hot and cold spots in a geographical mosaic of co-evolution and coexistence (Thompson, 1997).

Integrating these two perspectives, we can consider spatiotemporal variation. One important question here is which aspect of this variation (time or space) is most important – a question that few studies have yet addressed. Also important will be the extent to which temporal variation is asynchronous across space, which might enhance or degrade species coexistence. For an enhancing effect, asynchrony could mean that food resources are scare (and private resources therefore important) in at least one part of a species range at any given time. For a degrading effect, asynchrony could mean that food resources are less likely to be scarce across the species range at any one time. Similar questions echo through the work on local and regional coexistence in metacommunity theory (Levins, 1969; Mouquet & Loreau, 2002). At present, however, the degrading vs. enhancing effects of spatiotemporal variation have not been an important focus of studies attempting to understand how adaptive radiation can support closely related sympatric species.

The expectation arising from the recognition of temporal, spatial and spatiotemporal variation in resources might be of an adaptive radiation of 'imperfect generalists' (*sensu* Barrett *et al.*, 2005) that share many resources but, during critical periods/locations, specialize on resources for which they are differentially adapted (Robinson & Wilson, 1998). These variable differences in resource use might be crucial for coexistence – and might well have caused divergence in the first place by selecting for optimal morphologies that reduce competition for resources. We here explore the possibility that coexistence might be enhanced through spatiotemporal variation in resource use by examining a group of closely related Darwin's finches on Santa Cruz Island, Galápagos, Ecuador.

Our study

The adaptive radiation of Darwin's finches is thought to have resulted from specialization on alternative food types, partly owing to interspecific competition (Lack, 1947; Bowman, 1961; Grant, 1999; Grant & Grant, 2008). At deeper levels in the Darwin's finch phylogeny, niche differences are often large and relatively consistent through space and time: the ground finches (*Geospiza* spp.) typically feed on seeds, the tree finches (*Camarhynchus* spp.) typically feed on fruits and arthropod in trees, the vegetarian finch (*Platyspiza crassirostris*) typically feeds on leaves and fruit and the warbler finches (*Certhidia* spp.) typically feed on arthropods (Lack, 1947; Bowman, 1961; Grant, 1999; Grant & Grant, 2008). These large differences in diet are coupled to large and adaptive differences in beak morphology (Lack, 1947; Bowman, 1961; Grant, 1999; Herrel *et al.*, 2005; Kleindorfer *et al.*, 2006; Foster *et al.*, 2008; Grant & Grant, 2008; Sulloway & Kleindorfer, 2013). Overall, it seems certain that competition is currently weak among these species sets. At shallower levels in the Darwin's finch phylogeny, corresponding to recent and ongoing divergence, diet overlap and competition are much more likely; for instance, all of the *Geospiza* ground finches (Fig. 1) feed on seeds as well as arthropods when available. And yet the potential for diet divergence is present even at this level because some aspects of diet seem to diverge in ways that match beak morphology (Fig. 1; Abbott *et al.*, 1977; Smith *et al.*, 1978; Schluter, 1982; Boag & Grant, 1984; Grant & Grant, 2006).

We investigate diets of the four ground finch species on Santa Cruz Island with the aim of quantifying how they overlap through space (three locations) and time (5 years) in relation to the abundance of local food types and changing environmental conditions (wet or dry). If spatiotemporal variation in resource availability facilitates the coexistence of closely related species, we expect that niche overlap will be highest in times/places with abundant resources but lowest in times/places with scarce resources. We therefore focus our efforts on distributions of food resources and their use by finches, rather than on the much-more-difficult-to-quantify

Fig. 1 The four focal species of Darwin's ground finches and some of the foods they often feed on. Shown beside *Geospiza scandens* are the flowers and fruit of *Opuntia echios.* Shown beside *G. fuliginosa* are a *Portulaca oleracea* fruit and seeds, *Cryptocarpus pyriformes* fruits and seeds, a *Tournefortia psilostachya* fruit and seeds and *Commicarpus tuberosus* fruits. Shown beside *G. fortis* are a *Scutia spicata* fruit and seeds, a *Tournefortia pubescens* fruit and seed and a *Bastardia viscosa* seed case and seeds. Shown beside *G. magnirostris* are a *Cordia lutea* fruit and seed, a *Vallesia glabra* fruit and seed and a *Castela galapageia* fruit and seed (Photograph credit: L. F. De León).
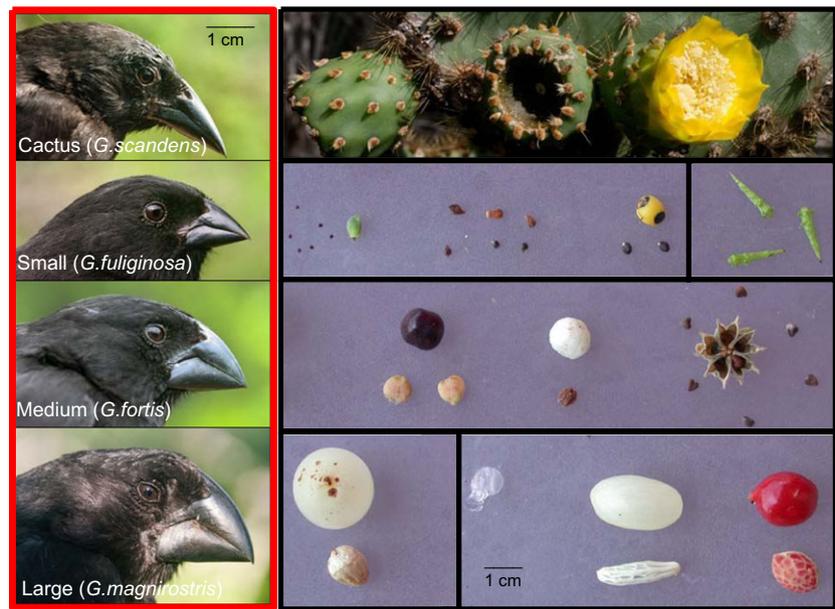
level of competition *per se* (or finch density). Previous work has shown that competition among Darwin's finches is high during periods of low resource availability (Boag & Grant, 1984; Grant, 1999; Grant & Grant, 2002), and so we took that effect as a given.

Although a number of previous studies have examined the diets of Darwin's finches, our study adds four important novel elements. First, we focus on how diets vary across multiple expected 'wet' seasons (January to May), as opposed to how they differ between the classic wet and dry seasons (e.g. Abbott *et al.*, 1977; Smith *et al.*, 1978). This alternative temporal perspective is important because wet seasons should be the 'easy' periods when finch diets are expected to overlap, and a wet season normally provides enough resources to see finches through to the subsequent dry season (Grant & Grant, 1980a,b, 1993). In some years, however, wet seasons are not very wet (little rainfall), and plant and arthropod availability is correspondingly sparse. In these years, finches can severely deplete the seed bank (Grant & Grant, 1980a,b; Boag & Grant, 1981, 1984; Grant, 1999) and might thus rely on private resources more heavily and for much longer. Second, we analyse how diets vary across a single large and heterogeneous island, whereas most previous work focused on small and relatively homogenous islands (Grant & Grant, 1980a,b; Boag & Grant, 1981, 1984) or used a single resource distribution to represent even large and heterogeneous islands (cf. Grant *et al.*, 1976; Schluter & Grant, 1984). Our within-island spatial perspective on finch diets provides an important backdrop for recently work on within-island spatial variation in finch morphology (Kleindorfer *et al.*, 2006; De León *et al.* 2010; Sulloway & Kleindorfer, 2013). Third, we here – for the

first time in Darwin's finches – merge temporal and spatial perspectives so as to consider their relative influences on finch diets and diet overlap. Finally, most previous work on Darwin's finch diets was completed more than 25 years ago. Given dramatic recent changes in Galápagos – especially in relation to the human introduction and expansion of non-native foods – it is important to consider if historical diet and morphology associations persist in the present (Hendry *et al.*, 2006; De León *et al.*, 2011).

Materials and methods

Study sites

We studied the four ground finch species (*Geospiza fuliginosa*, *G. fortis*, *G. magnirostris* and *G. scandens*; Fig. 1) with breeding populations on Santa Cruz Island, Galápagos, Ecuador. Santa Cruz is one of the largest, highest and most ecologically diverse islands of the Archipelago, with considerable variation in plant species distributions and abundance (Wiggins & Porter, 1971; Grant *et al.*, 1976; Abbott *et al.*, 1977; Smith *et al.*, 1978; De León *et al.*, 2011). Santa Cruz is characterized by a strongly seasonal climate, with plants producing seeds mainly during the wet season (Wiggins & Porter, 1971; Grant, 1999), and dramatic differences among years in precipitation and therefore plant reproduction (Grant, 1999; Grant & Grant, 2006). This variation could promote wide variation in finch competition and niche overlap over both space and time.

We worked at three sites: Academy Bay, El Garrapatero and Borrero Bay (for a map, see Fig. S1). Academy Bay is located on the southern edge of the island and is

characterized by a dense belt of coastal vegetation dominated by *Cryptocarpus pyriformes* and *Scutia spicata*. El Garrapatero is located on the eastern edge of the island about 11 km from Academy Bay and is dominated by *Bursera graveolens* and *Cordia lutea* trees, as well as by the cactus *Opuntia echios*. Beneath these trees, the vegetation is relatively open and is dominated, during wet conditions, by herbaceous plants and grasses. Borreo Bay is located on the northern edge of the island and is characterized by only a narrow and patchy band of coastal vegetation (dominated by *Bursera graveolens* trees and shrubs of *Scalesia* and *Hibiscus*). This site is drier than Academy Bay and El Garrapatero because it lies in the rain shadow of the Santa Cruz highlands (Grant, 1999).

Following Abbott *et al.* (1977), we surveyed available foods within 50 randomly placed (by GPS) 1-m^2 plots at each site. Within each plot, we quantified seeds, flowers and fruits on the standing vegetation for each plant species. We also quantified seeds on the ground, both on the surface of a 10-cm^2 subplot in the field, and in a superficial soil sample of approximately 45 g sorted under a stereoscope in the laboratory. We sampled the same plots (with new subplots) in three consecutive years (2005, 2006 and 2007) at Academy Bay and El Garrapatero, and in 2 years (2005 and 2007) at Borrero Bay. The Shannon–Weiner diversity index and Hurlbert's (1971) evenness index were used to quantify the diversity of food types in various combinations of site and year.

For the most common seed types consumed by finches, we measured the length, width, depth (in millimetres) and hardness (in newtons) of 10 intact seeds collected haphazardly from the ground. Hardness was estimated by cracking individual seeds with a Kistler force transducer attached to a handheld Kistler charge amplifier (Kistler Inc., Winterthur, Switzerland). Abbott *et al.* (1977) made similar measurements but not for all of the plant species we studied. We then generated an index of seed size/hardness (*Hi*) for each species as a combined measure of mean seed depth (D) and hardness (H): $Hi = \sqrt{HD}$. This index is thought to provide a good integrated measure of the difficulty of cracking a seed and it is closely correlated with beak size (Abbott *et al.*, 1977; Grant, 1999). We also estimated seed volume for round seeds using the formula: $V = 4/3\pi r^3$.

Feeding observations

We used binoculars to identify birds to species and to determine the plants they were eating, including when applicable the specific plant part (seeds, fruits, leaves or flowers). This procedure is straightforward because Darwin's finches are tame and can be observed at short distances (2–5 m) without disturbance. In some cases, we used more general food categories, including 'arthropod' (feeding on or searching for arthropods is

an obvious behaviour in the field), 'ground' (small unidentified seeds on the ground) and 'grass' (common Gramineae species). After one observation for a given bird, we moved on to the next bird so as to maintain independence of our feeding observations. Our feeding data represent counts of discrete feeding observations by particular species on particular food types (for more details see De León *et al.*, 2011, 2012). The value of this 'point observation' procedure – over the earlier method of following individual birds and recording their diets for extended time (Abbott *et al.*, 1977; Smith *et al.*, 1978; Boag & Grant, 1981, 1984) – is increased independence of the observations for a given bird. Regardless, data from the two methods are comparable as both represent proportions of time birds feed on a given food type. To assess whether our sample size was sufficient to represent the diet breath of each finch species, we built accumulation curves depicting total diet richness as function of the number of feeding observations across the entire data set (all sites and years combined). A tendency for these curves to approach saturation would indicate that we had enough observations. Some site/year combinations were excluded from this analysis because of low sample sizes (<10).

Feeding observations were conducted from 2003 through 2007 during the Galápagos 'wet' season, January to April. Importantly, however, very little rain fell during the 'wet' seasons of 2003–2004, effectively making them extended dry seasons (Grant & Grant, 2006; Hendry *et al.*, 2009; Trueman & d'Ozouville, 2010). Given that variation in precipitation directly shapes the availability of food resources for finches (Grant & Grant, 1993, 2002; Grant, 1999), our data thus encompass the full range of environmental conditions from very wet to very dry despite all being collected during ostensibly 'wet' seasons (Fig. 2).

Partitioning the variance in diet

Our next goal was to quantify how ground finch diets vary in relation to available food types, and as a function of year and site. First, we log-transformed data as needed to improve normality. Second, we used CANOCO 4.53 (Microcomputer Power, Ithaca, NY, USA) to perform an unconstrained ordination principal components analysis (PCA) on all the feeding observations. This allowed us to infer degrees of diet differences among species/site/year combinations. Third, we used CANOCO to perform redundancy analysis (RDA), which partitioned the variance in species-specific diets according to year, site and shared (year-by-site) effects (Borcard *et al.*, 1992). Statistical significance for site and year contributions was assessed with the unbiased variance partitioning estimator developed by Peres-Neto *et al.* (2006). Fourth, we performed a nonparametric multivariate analysis of variance, which allowed us to infer diet differences among finch species, sites and years. Finally, to formally test for the extent of

Fig. 2 Patterns of precipitation on Santa Cruz Island (indexed at Academy Bay) during each month and year of our study. Although the entire study was carried out during the ostensibly 'wet' seasons, little rain fell during the first 2 years (2003 and 2004). More typical wet seasons were observed during the rest of the study period (2005–2007). The month of December in each graph refers to December of the previous year. Error bars represent standard error of the mean. (Data source: Charles Darwin Research Station).
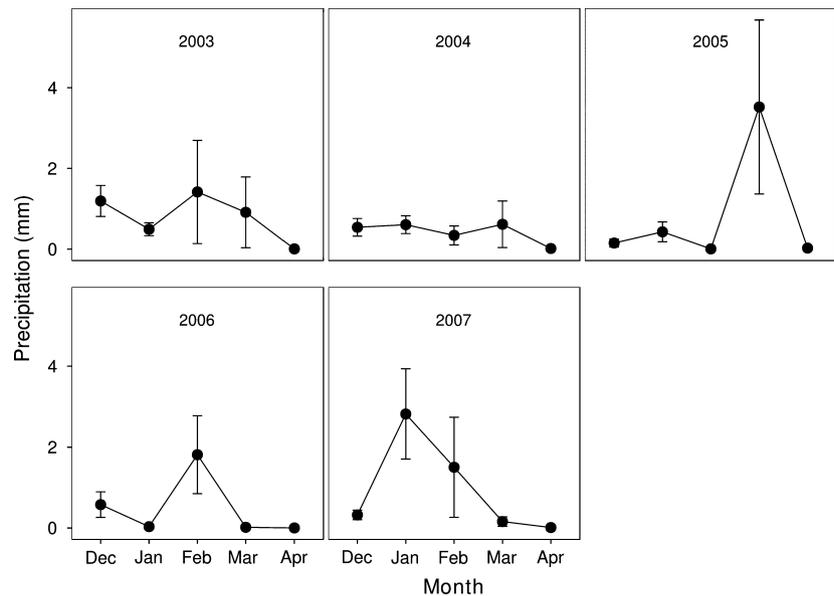
diet similarity among species, site and years, we performed an analysis of similarity (ANOSIM). This analysis generates an *R* value between −1 and +1 that indicates the degree of similarity among groups. A value < 0 is obtained when variability within groups is greater than among groups, a value of 0 is obtained when there is complete similarity among groups, and a value > 0 is obtained when variability among groups is greater than within groups. These analyses were based on Bray–Curtis distance matrices of proportionally scaled diets using the Adonis function (Anderson, 2001) implemented in the R package vegan. In both cases, statistical significance was assessed by 1000 permutations of the raw data.

Niche overlap and diet similarity

We calculated niche overlap among finch species pairs at four levels: (i) pooling across all sites and years, (ii) at particular sites (pooled across years), (iii) in particular years (pooled across sites) and (iv) for each combination of site and year. In all cases, we calculated Pianka's (1973) and Czechanowski's (Feinsinger *et al.*, 1981) niche overlap indices as implemented in ECOSIM V.7.72 (Gotelli & Entsminger, 2009). These indices range from zero (no food types in common) to unity (perfect overlap in food types), and they were calculated directly ('uncorrected') and after correcting (Hurlbert, 1978) for available food types by dividing the frequency of each food type in the diet by its availability in the field. These latter analyses excluded food types not recorded in the available food surveys (e.g. arthropods, ground and grass) and were calculated only for sites and years where both diet and available food data were available.

EcoSim was also used to generate null models of expected niche overlap (Gotelli & Entsminger, 2009). These models allowed us to infer whether niche overlap differed significantly from random expectations under a given randomization algorithm. We used 1000 permutations of the RA3 algorithm (Lawlor, 1980) – similar results were obtained using different algorithms (results not shown). In order to provide a general comparative context for our niche overlap results, we reviewed the literature on bird communities to compile published estimates of Pianka's (1973) niche overlap.

Results

Available foods

We identified 56 plant species (Table S1) representing a wide distribution of seed size/hardness (e.g. Fig. 1). Most available seeds were soft and small, and the hardest seeds were especially rare at Borrero Bay (Fig. S2). The distribution of specific plant species (Table S1) and the proportion of the most common plant foods by frequency and volume (Table S2) differed widely among the three sites. The three sites also differed strongly in the diversity and evenness of food resources, with both metrics being highest at El Garrapatero and (often) lowest at Borrero Bay. For instance, Shannon–Weiner indices of plant diversity by frequency and volume were (respectively) 2.02 and 1.93 for Academy Bay, 1.03 and 1.56 for Borrero Bay, and 2.43 and 2.14 for El Garrapatero. Hurlbert's index of evenness by frequency and volume was (respectively) 0.56 and 0.74 for Academy Bay, 0.73 and 0.62 for Borrero Bay, and 0.91 and 0.76 for El Garrapatero.

Diet variation

We obtained a total of 7373 feeding observations of ground finches (Table S3), with all four species being observed at all three sites. Uneven sample sizes among species, sites and years reflected variation in both species abundances (*G. magnirostris* were least common) and sampling effort (fewer days were devoted to feeding observations in 2007 and at Borrero Bay). Thirty-four plant species, plus other food categories, were consumed by ground finches (Tables S4–S7) and their contribution to finch diets varied markedly among the three sites (e.g. Table S8). Despite variation in sampling effort, accumulation curves based on diet richness indicate an approach to saturation even at relatively low numbers of feeding observations, implying that our effort was sufficient to represent the breadth of species' diets (Fig. S3).

Overall, the different finch species overlapped broadly in the major food types in their diets (Tables S4–S7). For example, all of the species fed to at least some extent on *Scutia spicata*. However, the frequencies of consumption of different food types differed among species, as indicated by our PCA based on diet frequency (Fig. 3) and our multivariate analyses based on distance matrices (Table 1). For instance, the most common food type for *G. fuliginosa* was *Cryptocarpus pyriformis*, for *G. fortis* was *S. spicata*, for *G. magnirostris* was *Cordia lutea* and for *G. scandens* was *Opuntia echios*. We note, however, that these diet differences are not particularly robust, as indicated by the degree of similarity among species, which overall produced *R* values lower than 0.5 (Fig. 4).

Beyond the above observations, an extensive amount of diet variation was present in space and time for each species (Fig. 3; Table 1). *Geospiza fortis* had the most
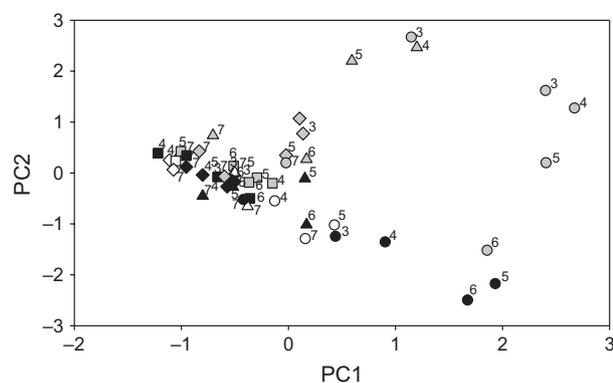
Table 1 Permutational multivariate analyses of variance using diet distance matrices. The data are frequencies of feeding on different food types with (top panel) and without (bottom panel) correcting for available resources. The model analyses variation in relation to the four species, the three sites, the different years and interactions.

	d.f.	SS	MS	F	R²	P
(A) Without correcting for available food types						
Species pair	3	3.054	1.018	10.123	0.258	<0.001
Site	2	1.491	0.745	7.412	0.126	<0.001
Year	1	1.794	1.794	17.845	0.151	<0.001
Species*site	6	1.275	0.212	2.114	0.108	0.002
Species*year	3	0.486	0.162	1.612	0.041	0.056
Site*year	2	0.698	0.348	3.470	0.059	<0.001
Species*site*year	5	0.536	0.107	1.065	0.045	0.396
Residuals	25	2.514	0.1		0.21	
(B) After correcting for available food types						
Species pair	3	1.422	0.474	1.659	0.114	0.018
Site	2	1.553	0.776	2.718	0.124	0.002
Year	1	1.435	1.435	5.024	0.115	<0.001
Species*site	6	2.347	0.391	1.369	0.188	0.063
Species*year	3	0.976	0.325	1.139	0.0783	0.292
Site*year	2	1.041	0.520	1.821	0.083	0.011
Species*site*year	5	1.411	0.282	0.988	0.113	0.536
Residuals	8	2.286	0.286		0.18	

P-values are obtained from 1000 permutations.

variable diets and correspondingly showed the strongest differences among sites and years. *Geospiza magnirostris* and *G. scandens* had the least variable diets, and *G. fuliginosa* was intermediate. Formal variance partitioning using RDA revealed that 23% of the variation in species diets could be attributed to differences among sites ($P = 0.04$), 15% to differences among years ($P = 0.01$) and 11% to the combined effects of site and year. Strong site effects were most evident for *G. fortis* and *G. fuliginosa*, whose diets sometimes clustered more closely by site than by their species identity (Fig. 3).

The most common food types in the diets of ground finches were partly determined by the most abundant available foods at a given site/year (Table S1 vs. Tables S4–S7). This association is seen in the strong correlation between the frequency of available food types and frequency of feeding on those food types (Fig. 5). Ground finches are thus somewhat opportunistic in their diets, feeding most on foods of the highest availability. As evident in the large spread around the relationship, however (Fig. 5), species differences do arise in the frequency of use of those different food types – and these differences vary in time and space.

Fig. 3 Principal component analysis (PCA) on the diet of the species Darwin's ground finches on Santa Cruz Island, Galápagos. Symbol shade indicates different sites: Academy Bay (grey), Borrero Bay (white) and El Garrapatero (black). Shape indicates different species: (*Geospiza fortis* (circles), *G. magnirostris* (squares), *G. scandens* (rhomboids) and *G. fuliginosa* (triangles), and numbers indicate different sampling years from 2003 to 2007.

Niche overlap

Pianka's niche overlap (Czechanowski's gave similar results – not shown) across all sites and years, before correcting for available foods, indicated higher diet overlap than expected by chance (Fig. S4). However,
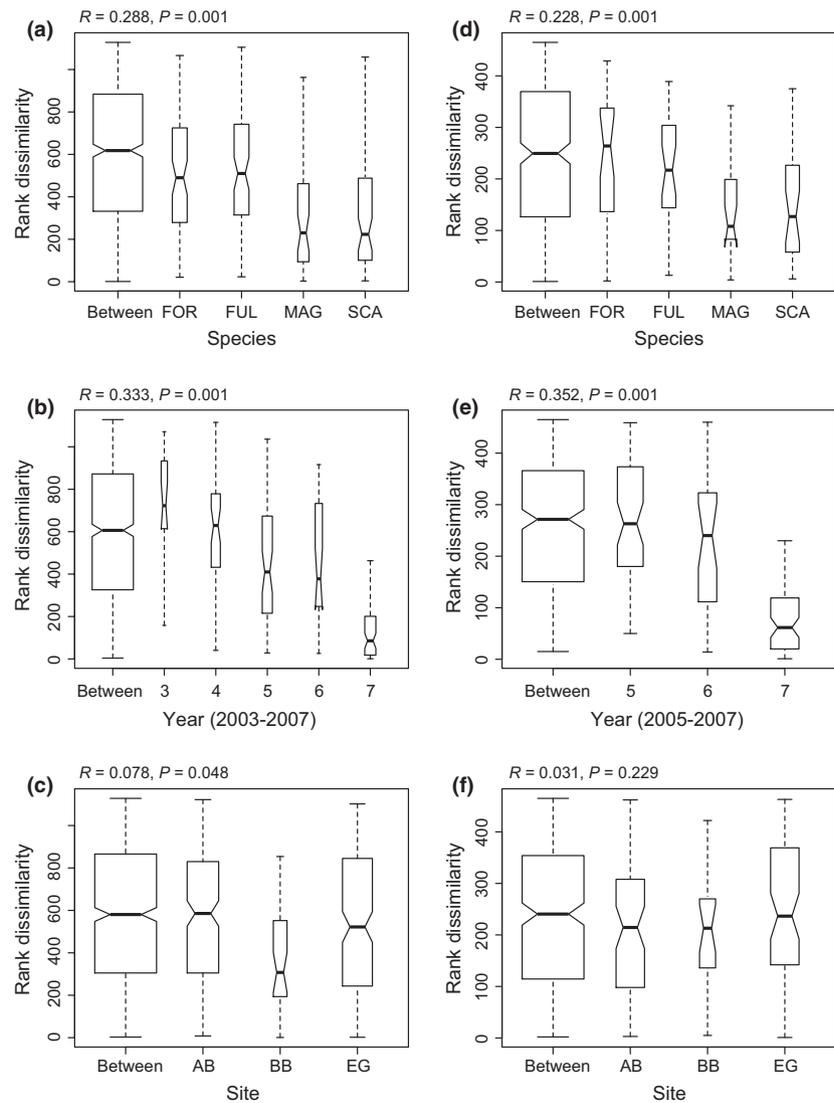
Fig. 4 Analysis of diet similarity for species (a, d), years (b, e) and sites (c, f) before (left) and after (right) correcting for available foods. The analyses are based on distance matrices as implemented in ANOSIM (see Materials and methods). Box plots show the median (solid bar), interquartile range (box) and full range (whiskers) of the data.

the extent of diet overlap varied widely among the species: from 0.08 between *G. fuliginosa* and *G. magnirostris* to 0.96 between *G. fortis* and *G. magnirostris* (Fig. 6). After correcting for available foods, diet overlap was much lower, ranging from 0.0001 between *G. fuliginosa* and *G. magnirostris* to 0.77 between *G. fortis* and *G. magnirostris*. Many of these corrected values were significantly lower than expected at random, except for *G. fortis* vs. *G. fuliginosa* and *G. fortis* vs. *G. magnirostris* (Fig. 6). Ground finches thus overlap considerably in diet but the extent of this overlap is much lower for species with more divergent beaks (Fig. S5).

Diet overlap also varied considerably in space and time. Considered across sites, average diet overlap was highest at Borrero Bay (0.69), followed by Academy Bay (0.53) and El Garrapatero (0.50). Considered through time, diet overlap generally increased from dry years (0.42 in 2003 and 0.39 in 2004), when available foods were low overall, to wet years (0.57 in 2005, 0.66 in 2006 and 0.74 in 2007), when available foods were high overall (Figs S4 and S6).

To help interpret this variation, we applied a general linear model (species pair, site, year and interactions) to the diet overlap values for Academy Bay and El Garrapatero in 2004–2007 (these particular sites and years present a balanced structure with high sample sizes). We performed this analysis as a variance partitioning tool (variance in diet overlap explained by space, time and their interaction – see Introduction), rather than for hypothesis testing (the *P*-values will not be reliable because the data points are not independent). When not correcting for available foods, most variation in diet overlap was explained by year (64%), species pair (48%), the species pair by site interaction (40%) and the species pair by year interaction (36%) (Table 2).
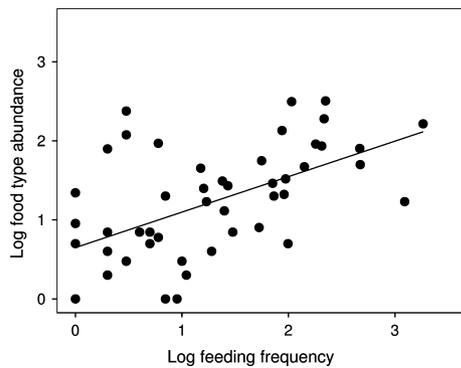
Fig. 5 The diet of ground finches is strongly influenced by the abundance of available resources. The data are the frequency of different available food types in the diet of ground finch species at each site and in each year. The data points might not be independent and so statistical significance could be questionable but, for the record: $r = 0.56$, $P < 0.001$.

When correcting for available foods, most of the variation in diet overlap was explained by species pair (57%), the species pair by year interaction (36%), site (12%) and the species pair by site interaction (9%) (Table 2).

We interpret these findings as follows. First, ground finches at Academy Bay and El Garrapatero show similar average diet overlap, whereas those at Borrero Bay show higher overlap (Fig. 6). Second, *G. fortis* shows relatively high diet overlap with the three other species, whereas *G. fuliginosa* and *G. magnirostris* show conspicuously low overlap with each other – especially at Academy Bay. Third, niche overlap varies through time (Fig. 6 and Fig. S6), being lower early in the time series (dry conditions; Fig. 2) and higher late in the time series (wet conditions; Fig. 2).

Discussion

Ground finches are imperfect generalists

As expected, Darwin's ground finches show some feeding differences related to beak morphology and feeding performance (Table 1; Fig. 3). *Geospiza magnirostris*, which has the largest beak and the highest bite force, was the only species to feed on the very large/hard seeds of *Cordia lutea* and it fed on these seeds regularly. *Geospiza scandens*, which has the longest beak, was often seen probing the flowers of *Optuntia* cactus, whereas this behaviour was rare for the other species. *Geospiza fuliginosa*, which has the smallest beak and the lowest bite force, often fed on the very small seeds of *Cryptocarpus piryformis*, whereas this behaviour was uncommon for the other species. *Geospiza fortis*, which is intermediate in beak size and bite force, fed more often on the intermediate seed-sized *Scutia spicata* than did
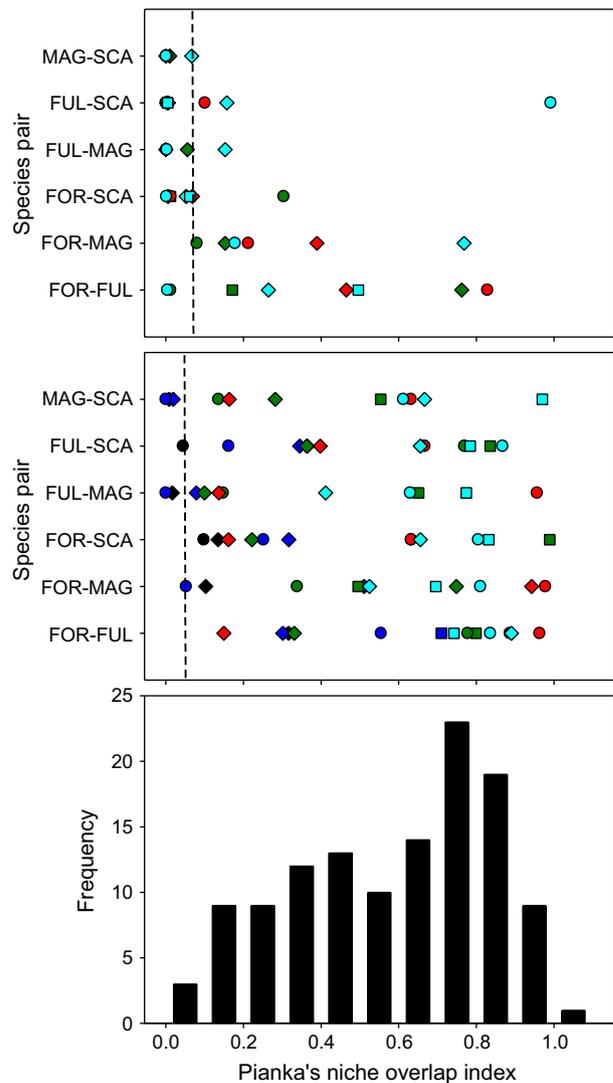

Fig. 6 Temporal and spatial variation in niche (diet) overlap between pairs of species of Darwin's ground finches from Santa Cruz Island. The upper panel shows niche overlap correcting for available foods. The middle panel shows values of niche overlap when not correcting for available foods. The data are 7373 feeding observations at three different sites: Academy Bay (diamonds), Borrero Bay (squares) and El Garrapatero (circles); and in five different years: 2003 (black), 2004 (dark blue), 2005 (green), 2006 (red) and 2007 (light blue). The vertical line in each panel is the null expectation (dashed line) after 1000 simulations. The lower panel shows the frequency distribution of niche overlap in sympatric birds derived from 123 estimates of Pianka's (1973) niche overlap index found in the literature (Appendix S1), and is not corrected for available resources.

the other species. Diet differences of this sort, and their association with beak size and shape, have been previously reported for Darwin's finches (Lack, 1947;

Table 2 General linear models describing variation in diet overlap among ground finches on Santa Cruz Island, with (B) and without (A) correcting for available foods. The data are Pianka's niche overlap index between each pair of species at two sites (Academy Bay and El Garrapatero) and in 4 years (2004–2007). Note that this is an exercise in variance partitioning rather than hypothesis testing – because the data points are not independent. Effect sizes are given by the correlation ratio R^2 ($\eta^2 = SS_{factor}/SS_{total}$) and the partial R^2 (Partial $\eta^2 = SS_{factor}/SS_{factor} + SS_{error}$).

	d.f.	SS	MS	F	R^2	Partial R^2	P
(A) Without correcting for available food types							
Species pair	5	3.782	0.756	4.372	0.186	0.476	0.006
Year	1	7.525	7.525	43.496	0.371	0.644	<0.001
Site	1	0.056	0.056	0.322	0.003	0.0132	0.576
Species*year	5	2.365	0.473	2.734	0.117	0.363	0.043
Species*site	5	2.803	0.561	3.240	0.138	0.403	0.022
Year*site	1	2.019	2.019	11.668	0.100	0.327	0.002
Species*year*site	5	1.741	0.348	2.013	0.086	0.295	0.113
Residuals	24	4.152	0.173				
(B) After correcting for available food types							
Species pair	5	98.210	19.642	3.199	0.520	0.57	0.046
Year	1	6.936	6.936	1.130	0.037	0.086	0.309
Site	1	9.683	9.683	1.577	0.051	0.116	0.233
Species*year	5	42.699	8.540	1.391	0.224	0.367	0.295
Species*site	5	7.656	1.531	0.249	0.040	0.094	0.932
Year*site	1	1.709	1.709	0.278	0.009	0.023	0.607
Species*year*site	5	21.946	4.389	0.715	0.113	0.229	0.624
Residuals	12	73.681	6.140				

Bowman, 1961; Abbott *et al.*, 1977; Smith *et al.*, 1978; Schluter & Grant, 1984; Kleindorfer *et al.*, 2006; Sulloway & Kleindorfer, 2013). Our data thus broadly conform to the established idea that the adaptive radiation in the ground finches involved divergence along an axis of seed size/hardness, bite force and beak size (Schluter & Grant, 1984; Grant & Grant, 1996, 2008; Herrel *et al.*, 2005; Foster *et al.*, 2008; De León *et al.*, 2011, 2012).

Despite the above differences, however, our results also illustrate that the ground finches overlap more in diet than would be expected by chance (Fig. 6). This suggests that the finches are actually opportunistic as feeders, in spite of prior emphases on resources they typically favour. When correcting for food availability, diet overlap decreased to the point that it was often lower than expected by chance, except for the species closest to each other in beak morphology. In particular, *G. fortis* continued to show high overlap with the two species (*G. fuliginosa* and *G. magnirostris*) to which it is similar in beak shape and intermediate in beak size (Lack, 1947; Bowman, 1961; Grant *et al.*, 1985; Foster *et al.*, 2008). This diet overlap is not surprising given that all of the ground finches feed on a diversity of seeds. Moreover, our finding that Darwin's finches are somewhat opportunistic in their diets suggests that a number of food types can be consumed by all of the species and that these food types are frequently used when they are available in abundance. These patterns are also generally consistent with previous work showing that ground finches often overlap in diet and thereby compete for shared resources (Abbott *et al.*, 1977; Smith *et al.*, 1978; Schluter, 1982; Grant & Grant, 2006).

Based on these properties, we suggest that the ground finches represent an adaptive radiation of 'imperfect generalists', where different species evolve to use a variety of overlapping resources, but with this overlap being incomplete. Interestingly, experimental evolution studies in the laboratory have shown that imperfect generalists are precisely what arise when adaptive radiation proceeds in complex environments (Barrett *et al.*, 2005). In such radiations, sympatric coexistence is facilitated by frequency-dependent processes where genotypes that have at least some private resources cannot be eliminated by other genotypes (Barrett *et al.*, 2005). A key to this idea is that the use of private resources is sometimes necessary for coexistence (Robinson & Wilson, 1998), and we will in the next section suggest that these situations are episodically provided by spatial and temporal variation in the environment.

Spatiotemporal variation and species coexistence

Spatiotemporal variation in diet and diet overlap was substantial, spanning almost the entire range of values observed in studies of other sympatric bird species, which themselves span the entire range from zero to unity (Fig. 6). The most striking pattern in our data was that diet overlap increased from 2003 to 2007 (Fig. 6 and Figs S4, S6), a pattern that we interpret as a result of changes in precipitation from the earlier dry years to the later wet years (Fig. 2). This between-year association with climate provides a new dimension to previously described seasonal (wet vs. dry season) effects (Smith *et al.*, 1978). Both levels of temporal variation – between seasons and among years – are partly driven by changes in the abundance of arthropods. During wet periods, many finch species converge on this easily accessible and nutritious food. When conditions are less wet, different finch species continue to share other widely available and broadly preferred foods, such as the fruits and seeds of *Scutia spicata*.

During very dry periods, however, these preferred resources become scarce and finch species diverge onto resources for which their morphologies are best suited (Abbott *et al.*, 1977; Smith *et al.*, 1978; Schluter, 1982; Boag & Grant, 1984; Grant & Grant, 2006). In the present study, the larger species increasingly used large/hard seeds and the smaller species increasingly used small/soft seeds. These results also fit nicely with comparative (Schoener, 1982; Smith, 1991) and experimental (Svanbäck & Bolnick, 2007) studies in other taxa showing that greater resource limitation leads to greater specialization on foods for which a species' or individual's morphology is best suited. Darwin's finches thus illustrate the hypothesis that the sympatric coexistence of imperfect generalists is facilitated by episodic periods of resource limitation, where diets diverge onto foods for which species are differentially adapted.

Variation in diet and diet overlap was also substantial across space, with ground finch diets sometimes clustering as strongly by site as by species or year (Fig. 3). Although site as a factor explained very little of the total variation in diet overlap before correcting for available foods, it was more important than year as a factor after this correction (Table 2). Spatial variation in diets and diet overlap arose because ground finches are opportunists, and because different sites have different available foods (Tables S1 and S2; Abbott *et al.*, 1977; Smith *et al.*, 1978). It therefore seems possible that spatial variation in diet and diet overlap could provide an important complement to the usually emphasized temporal variation when considering mechanisms of species coexistence.

Of additional interest, diet and diet overlap were influenced by the interaction between time and space (Table 2A). Specifically, Darwin's finches at each site converged at high-resource times on the locally most abundant and highest quality foods, such as arthropods in certain years at El Garrapatero and *Scutia spicata* at Academy Bay. When these preferred foods become limited, finches were seen to retreat towards the local private resources for which they are best adapted, and those resources differ among sites. When this happens, we would expect the relative success of different species to differ among sites. When resources become flush again, and population sizes increase, dispersal among sites should help to maintain system-wide coexistence. In short, we suggest that dispersal among sites with different resources can help to maintain the local and regional coexistence of imperfect generalists in a metacommunity dynamic (*sensu* Levins, 1969; Mouquet & Loreau, 2002; Galligan *et al.*, 2012).

Conclusions

Darwin's ground finches in Galápagos are best thought of as imperfect generalists that use a diversity of partially overlapping resources but retain a set of 'private' resources on which they are superior competitors. For the coexistence of such species, temporal variation might be very important. When conditions are favourable (e.g. high rainfall), all species converge on the best resources – often arthropods. When conditions deteriorate, multiple species might still prefer any abundant resources that remain, such as the fruits of *Scutia spicata*. When conditions are very bad (e.g. drought) and food resources become rare overall, species increasingly use those resources for which their morphologies are best adapted: small seeds for *G. fuliginosa*, medium seeds for *G. fortis*, large seeds for *G. magnirostris* and cacti for *G. scandens*. Our data suggest that spatial variation could also be very important – because available foods and finch diets differ among sites on an island. This variation likely means that no single species can be a superior competitor for the island as a whole – and ongoing dispersal will thus maintain metacommunities of species with partially overlapping niches. We encourage further efforts to evaluate the relative roles of spatial, temporal and spatiotemporal variation in niches and niche overlap, to help explain the coexistence of closely related species within adaptive radiations.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Literature review: references for the estimates of Pianka's niche overlap in birds.

Figure S1 Study sites on Santa Cruz Island, Galápagos, Ecuador.

Figure S2 Histograms of the traits of seeds available to finches at three sites on Santa Cruz Island.

Figure S3 Accumulation curves based on diet richness across sites and years for *Geospiza fortis* (A, $n = 5044$), *Geospiza fuliginosa* (B, $n = 1342$), *Geospiza magnirostris* (C, $n = 285$), and *Geospiza scandens* (D, $n = 482$).

Figure S4 Mean niche overlap between different pairs of species of ground finches from Santa Cruz Island.

Figure S5 Pairwise beak-size difference as a function of niche overlap in Ground finches.

Figure S6 Yearly variation in Pianka's niche overlap index between pairs of species of ground finches in Santa Cruz Island.

Table S1 Available foods for Darwin's finches on Santa Cruz Island, Galápagos, Ecuador.

Table S2 Proportion of the most common plant foods by frequency and volume at three sites on Santa Cruz Island, Galápagos, Ecuador.

Table S3 Feeding observations from Darwin's finches recorded at different sites and in different years on Santa Cruz Island, Galápagos, Ecuador.

Table S4 Diet of the medium ground finch (*Geospiza fortis*) at three different sites on Santa Cruz Island: Academy Bay (AB), Borrero Bay (BB) and El Garrapatero (EG).

Table S5 Diet of the small ground finch (*Geospiza fuliginosa*) at three different sites on Santa Cruz Island: Academy Bay (AB), Borrero Bay (BB) and El Garrapatero (EG).

Table S6 Diet of the large ground finch (*Geospiza magnirostris*) at three different sites on Santa Cruz Island: Academy Bay (AB), Borrero Bay (BB) and El Garrapatero (EG).

Table S7 Diet of the cactus finch (*Geospiza scandens*) at three different sites on Santa Cruz Island: Academy Bay (AB), Borrero Bay (BB) and El Garrapatero (EG).

Table S8 Proportion of the most common food items consume by Ground finches at three sites on Santa Cruz Island, Galápagos, Ecuador.