

# Low functional diversity and no redundancy in British avian assemblages

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## Summary

1. Spatial and temporal patterns in functional diversity can reveal the patterns and processes behind community assembly and whether ecological redundancy exists. Here, we analyse functional diversity in British avian assemblages over a period of about 20 years.
2. Functional diversity is generally lower than expected by chance, indicating that assemblages contain species with relatively similar functional traits. One potential explanation is filtering for traits suitable to particular habitats, though other explanations exist.
3. There was no evidence of ecological redundancy over the 20 years. In fact, changes in functional diversity were almost exactly proportional to changes in species richness.
4. The absence of functional redundancy results from little redundancy intrinsic to the species' functional relationships and also because compositional change was non-random. Observed extinction and colonization events caused greater changes in functional diversity than if these events were random.
5. Our findings suggest that community assembly is influenced by the traits of species and that observed changes in functional diversity provide no reason to believe that the functioning of natural systems is buffered against change by ecological redundancy.

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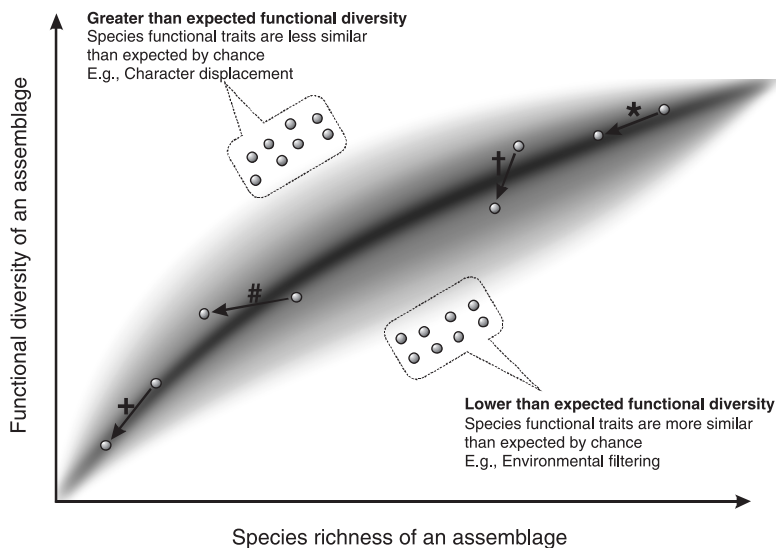
## Introduction

Variation in the structure of ecological assemblages through space and time is a fundamental property of the natural world (Brown 1995; Rosenzweig 1995; Gaston 1996; Gaston & Spicer 2003). The patterns in this variation have mostly been documented using taxonomic measures of diversity, such as species richness. However, some species are more similar than others, for example in their evolutionary history (May 1990), enabling studies of the phylogenetic diversity of assemblages (Faith 1992; Losos 1996; Purvis *et al.* 2000; Webb 2000; Rodrigues & Gaston 2002). Species are also more or less similar in their functional characteristics (Root 1967; Simberloff & Dayan 1991; Díaz & Cabido 2001; Chalcraft & Reseritis 2003; Chown, Gaston & Robinson 2004), enabling studies of the functional diversity (FD) of assemblages (Anderson 1997; Díaz & Cabido 1997; Stevens *et al.* 2003; Fukami

*et al.* 2005; Heino 2005; Micheli & Halpern 2005; Petchey & Gaston 2006).

Understanding spatial and temporal patterns of FD and their determinants is important because different functional trait distributions may imply the operation of different assembly processes (Weiher, Clarke & Keddy 1998; Stubbs & Wilson 2004; Mayfield *et al.* 2005; Cornwell, Schilck & Ackerly 2006; McGill *et al.* 2006). If local assemblages are composed of random sets of species, their FD will tend to be randomly distributed. Nonrandom distributions of species' traits could indicate that processes such as limiting similarity or environmental filtering structure local assemblages (Holdaway & Sparrow 2006) (Fig. 1). By comparing observed patterns in FD to different null expectations we can test among different classes of hypotheses about community assembly. We can also test explicitly whether environmental filtering influences community assembly, as this should lead to relatively high values of FD in more heterogeneous habitats.

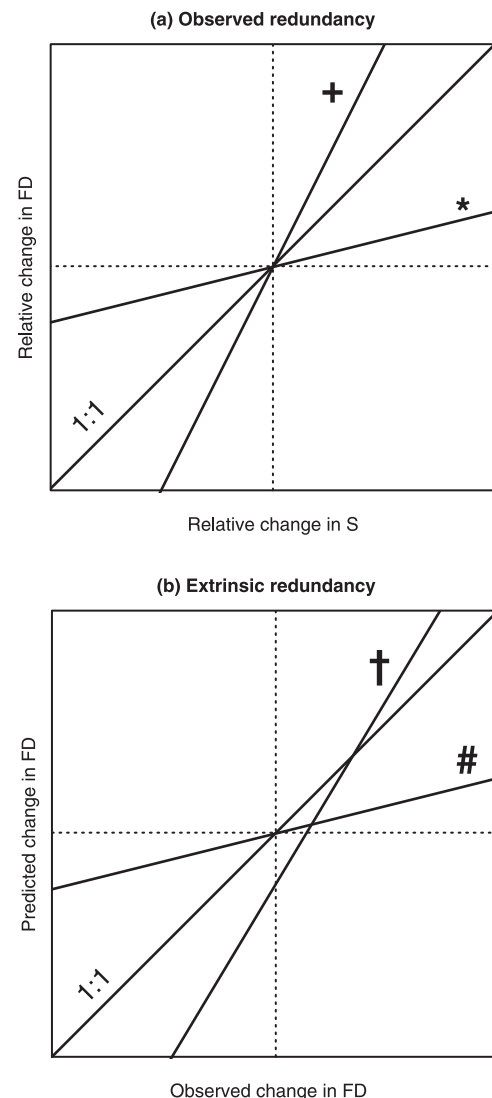
The composition of assemblages changes through time as some species colonize and others go extinct. This can result in net increases or decreases in species richness, altered community structure, FD, and ecosystem



**Fig. 1.** Hypothetical relationships between functional diversity and species richness. The grey-shaded region is the expected distribution of functional diversity, with the likeliest values of functional diversity in darker grey. Its shape is largely arbitrary but resembles some real distributions. Small spheres represent hypothetical assemblages. Assemblages with high functional diversity for their given level of species richness (the spheres above the grey region, surrounded by a dashed line) contain species that are more dispersed in functional trait values than expected by chance. Assemblages with low functional diversity for their given level of species richness (the spheres below the grey region, surrounded by a dashed line) contain species that have more similar functional trait values than expected by chance. Spheres connected by an arrow indicate temporal changes in functional diversity caused by changes in species richness and composition and the symbols correspond with those in Fig. 2. The temporal changes refer to (\*) high intrinsic redundancy (+) low intrinsic redundancy (†) low extrinsic redundancy, and (#) high extrinsic redundancy.

processes (Naeem & Wright 2003; Hooper *et al.* 2005). Redundancy occurs when changes in species richness and composition have relatively little effect on FD (\* in Figs 1 and 2a) (Walker 1992). If changes in FD are proportionally greater than changes in species richness there is functional sensitivity (+ in Figs 1 and 2a). The middle ground, a lack of redundancy and sensitivity, occurs when changes in FD are proportional to changes in species richness (Fig. 2a). A recent study of temporal changes in the FD of coastal marine assemblages used this logic to conclude that there was low redundancy, i.e. slopes of change in richness against change in FD approached 1 (Micheli & Halpern 2005).

Observed redundancy can be partitioned into two causes, which we term intrinsic and extrinsic redundancy. Intrinsic redundancy results from the patterns of functional similarity among species. If, for example, an assemblage contains many similar species, it will have high intrinsic redundancy (the change illustrated by \* in Figs 1 and 2b). Here, random changes in species composition will have little effect on FD. In contrast, an assemblage in which all species are rather unique will have low intrinsic redundancy, and random compositional change will cause changes in FD. One of the prime determinants of the extent of intrinsic redundancy is the effective dimensionality of functional trait



**Fig. 2.** Temporal change in functional diversity that results from compositional change between two samples can be understood by comparison of the observed change in functional diversity to the observed change in species richness (a) and the change in FD predicted by random compositional change (b). The 1 : 1 lines indicate expected values are equal to predicted. Deviations from 1 : 1 indicate (\*) high intrinsic redundancy (+) low intrinsic redundancy (†) low extrinsic redundancy, and (#) high extrinsic redundancy, as in Fig. 1.

space (Petchey & Gaston 2002a). Another is the number of species in the assemblage (Fig. 1).

Extrinsic redundancy (or lack thereof) can result from nonrandom compositional change that is non-random with respect to functional traits. For example, loss of relatively unique species will cause a relatively large decrease in FD (the change illustrated by the † in Figs 1 and 2b). Lack of extrinsic redundancy can occur when extinctions are trait dependent (Petchey & Gaston 2002a).

Previous studies of spatial and temporal variation in FD have used the number of functional groups, a discontinuous measure of that diversity (e.g. Stevens *et al.* 2003; Heino 2005; Micheli & Halpern 2005).

**Table 1.** Traits used to measure avian functional diversity. Egg volume was calculated as  $\text{volume} = 0.5 \times \text{length} \times \text{width}^2$  (van Noordwijk *et al.* 1981)

Trait type	Trait	Scale and categories
Resource quantity	1. Body mass	Continuous
Resource quantity	2. Annual reproductive output (no. of clutches $\times$ clutch size $\times$ egg volume)	Continuous
Main components of diet(s)	3. Vertebrates	Binary
	4. Invertebrates	Binary
	5. Plants	Binary
Main foraging method(s)	6. Pursuit	Binary
	7. Gleaning	Binary
	8. Pouncing	Binary
	9. Grazing	Binary
	10. Digging	Binary
	11. Scavenging	Binary
	12. Probing	Binary
Main foraging substrate(s)	13. Water	Binary
	14. Mud	Binary
	15. Ground	Binary
	16. Vegetation	Binary
	17. Air	Binary
Main foraging period	18. Nocturnal	Binary

While this approach has proven valuable, theoretical advantages (Petchey & Gaston 2002b) and empirical evidence (Petchey, Hector & Gaston 2004) suggest that continuous measures provide more accurate and less arbitrary estimates of FD.

In this paper we use a continuous measure of FD to: (1) document spatial and temporal variation in that diversity; (2) examine in what sense any patterns are nonrandom, and if possible identify their potential causes; and (3) estimate the extent of functional redundancy. We use the British breeding avifauna as a case study.

## Materials and methods

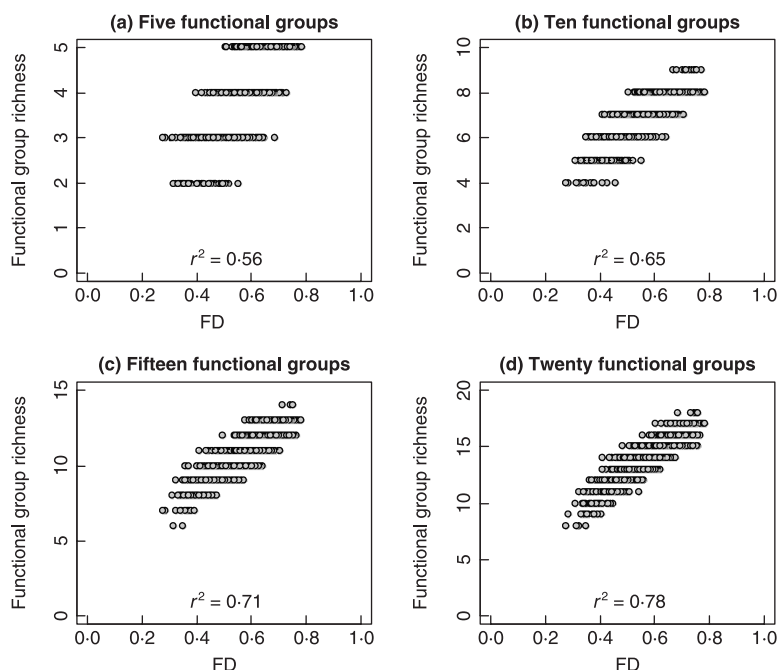
### AVIAN DISTRIBUTION

We used the summer (breeding) distribution of the British avifauna recorded from two distinct surveys coordinated by the British Trust for Ornithology, during late April to July in 1968–72 (Sharrock 1976) (hereafter referred to as *Atlas 1*) and 1988–91 (Gibbons, Reid & Chapman 1993) (hereafter referred to as *Atlas 2*). These data record species' presence/absence at a resolution of 10 km  $\times$  10 km quadrats on a continuous grid. Quadrats containing less than 50% land were excluded, giving a total of 2298. We excluded marine species and vagrants, but retained introduced species with self-sustaining populations and more regular sporadic breeders, giving a total of 192 species. Recording effort for the vast majority of species was intensive and relatively consistent between survey periods (Gibbons *et al.* 1993). However, the range of change in richness between the two Atlases was from –65 to +40 species, which seem unlikely magnitudes of change. In case these result from unequal sampling effort, we

excluded the quadrats with upper and lower *c.* 2.5% of values of change in richness. In addition, eight species were relatively under-recorded in *Atlas 2* due to their nocturnal habit (*Porzana porzana*, *Rallus aquaticus*, *Scolopax rusticola*, *Tyto alba*, *Strix aluco*, *Asio otus*, *Asio flammeus* and *Caprimulgus europaeus*) (Gibbons *et al.* 1993). The results of analyses conducted with and without these species were qualitatively very similar and we only present the former. We treated the Scottish crossbill *Loxia scotica* and common crossbill *Loxia curvirostra* as a single taxon, as well as the carrion crow *Corvus corone* and hooded crow *Corvus cornix* because *Atlas* data did not consistently distinguish these recently split sister species. These data have been used to study temporal changes in the British breeding avifauna (e.g. Donald & Greenwood 2001; Gaston & Blackburn 2002; Evans, Greenwood & Gaston 2005).

### MEASURING FUNCTIONAL DIVERSITY

Our aim was to assess avian FD with regard to resource use. We therefore used traits that measured: (1) the quantity of resources consumed; (2) feeding behaviour; and (3) activity period (Table 1). These traits represent many aspects of resource use, i.e. the quantity and type of resources used by each species and the methods used to acquire them. They also encompass the type of trait data previously used in other investigations of the FD of avian resource use, although many of these studies concerned functional groups or guilds rather than FD *per se* (e.g. Holmes, Bonney & Pacala 1979; Bailey *et al.* 2004). Trait data were extracted from Cramp (1977–94) using information for British populations or subspecies that occurred in Britain whenever possible. Categorical traits (e.g. foraging method: pouncing, gleaning, grazing, digging) were split into binary traits (Table 1) because



**Fig. 3.** Relationships between functional group richness and FD (Petchey & Gaston 2002b) for the assemblages in Atlas 1. Functional group richness is calculated by dividing the species among (a) five, (b) 10, (c) 15 or (d) 20 functional groups by cutting the functional dendrogram (Fig. 4) at the appropriate level of difference (Diaz & Cabido 1997). Even though based on a mixture of categorical and continuous trait information, functional group richness is a discontinuous measure. FD is continuous, even if based on the same categorical and continuous traits.

these characteristics are not mutually exclusive. Hence, a species might pounce and dig, but not glean or graze.

The 18 traits of the 192 bird species were used to calculate the FD of the bird assemblage in each of the 2298 quadrats in each of the two periods, following the methods of Petchey & Gaston (2002b). The measure of FD, is an estimate of how dispersed an assemblage of species is in trait space that automatically accounts for covariance between traits (Petchey & Gaston 2002a). To calculate FD, the species by trait matrix was converted into a distance matrix and this was clustered to produce a dendrogram that depicts the functional relationships among the avian assemblage (Petchey & Gaston 2002b). Euclidean distance and UPGMA clustering (Pielou 1984) were used throughout because these produced a dendrogram with the highest cophenetic correlation (0.85) (Sneath & Sokal 1973). The FD of a notional assemblage of all 192 species is the total branch length of this dendrogram and all measures of FD are standardized by this value, so that variation in FD ranges from 0 to 1, where a value of zero occurs for single species communities (Petchey & Gaston 2006). The FD of the bird assemblage is the total length of the branches required to connect all of the species in the assemblage (Petchey & Gaston 2006). Standardization of FD and species richness between 0 and 1 has no quantitative effect on our results.

Although we use categorical functional traits to calculate FD (Petchey & Gaston 2002b), FD remains a

continuous measure of FD. This occurs because there are many categorical traits (16) and also because there are two continuous traits. Hence, even when some traits are categorical, variation in FD can be continuous. This is quite different from if one measures FD as the number of functional groups represented by the species in an assemblage, termed functional group richness. Here, regardless of how many categorical or continuous traits are used in calculations, variation in functional group richness remains discrete (Fig. 3).

#### TESTING FOR RANDOMNESS

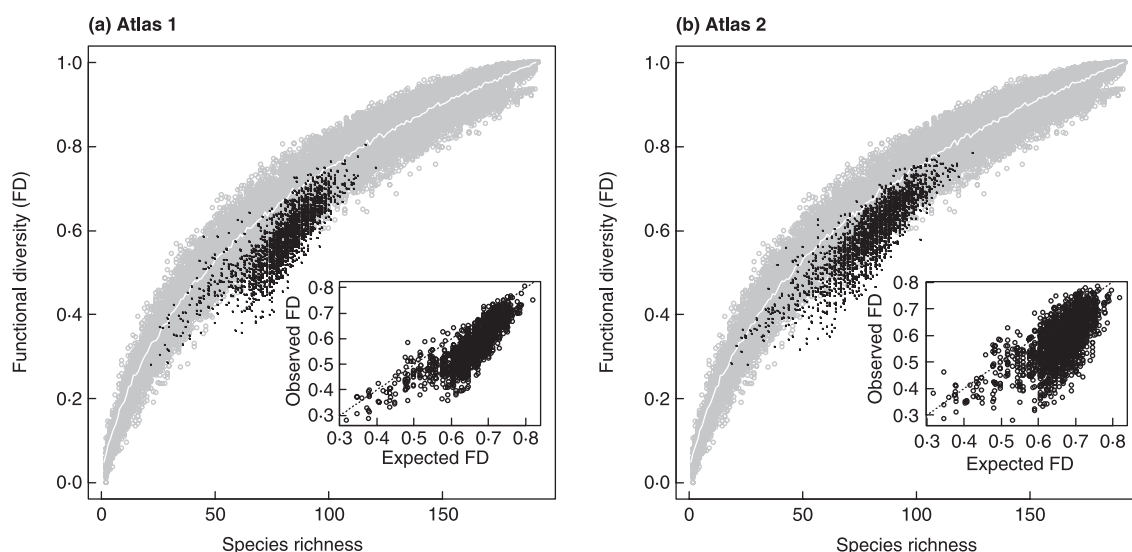
Observed patterns in the FD of the real assemblages were compared with the FD of random assemblages. These were random combinations of the 192 species, controlled for number of species. Because there are many possible random assemblages with a particular species richness, we repeated the exercise 100 times. The mean of these 100 values was the expected level of FD for a given species richness. We confirmed that parameter estimates had stabilized after 100 iterations. To test whether observed FD differs significantly from expected we used generalized linear models with covariance structure that accounted for spatial autocorrelation. Observed FD was the response variable and expected FD was the explanatory variable. Spatial correlation within the data set, for example if closely spaced assemblages are more compositionally similar than more distant assemblages, made it necessary to include the spatial structure of the data in our statistical models. We trialled exponential, spherical, Gaussian, and ratio covariance structures, and found very little difference between their likelihood (Akaike Information Criterion) or the parameter estimates returned, and present only the results of the exponential model. More details about this type of analysis can be found in Evans *et al.* (2005) and references therein.

The observed change in FD through time was compared with the change in species richness that occurred over the same period and also to the change in FD expected if change in species composition were random. For the latter, the observed number of colonization and extinction events were applied randomly to each assemblage quadrat in Atlas 1, to produce a new assemblage. This was repeated 50 times (not 100, due to resource limitations) and the mean of these taken. Observed change in FD was compared with observed change in species richness (e.g. Fig. 2a) and to expected change in FD (Fig. 2b) using generalized linear models, with spatial covariance structures, as described above.

To further investigate whether colonizations and extinctions were random with respect to species' traits, we calculated the mean functional originality (Pavoine, Ollier & Dufour 2005) of the species within an assemblage, and compared this with the mean functional originality of species that colonized the assemblage and those that went extinct from the assemblage. Functional originality is a measure of how distinct or unique







**Fig. 5.** Relationships between functional diversity and species richness of bird assemblages across Britain during (a) 1968–72 and (b) 1988–91. In both cases black symbols are the real assemblages, grey ones are random assemblages, and the white line is the mean of the random assemblages. Inset shows observed vs. expected FD with the 1 : 1 relationship indicated by the dashed line. Here, species richness and functional diversity are standardized to the interval [0, 1].

**Table 2.** Summary of the four main statistical tests and results. Each method was a generalized linear model with an exponential spatial covariance structure, to account for spatial autocorrelation in the data set. Errors are 1 standard error. For the third analysis, intercept and slopes are given when all 18 traits are included in the analysis, and averages when 16, 12, 8 or 4 are selected at random 20 times each

Response variable	Explanatory variable	Intercept	Slope	Interpretation
Observed functional diversity	Expected functional diversity	(18) $-0.18 \pm 0.04$	(18) $1.19 \pm 0.02$	Observed functional diversity is significantly lower than expected functional diversity (Atlas 1)
Observed functional diversity	Expected functional diversity	(18) $0.02 \pm 0.02$	(18) $0.86 \pm 0.03$	Observed functional diversity is significantly lower than expected functional diversity (Atlas 2)
Observed change in functional diversity	Observed change in species richness	(18) $0.01 \pm 0.00$ (16) $0.01$ (12) $0.00$ (8) $0.01$ (4) $0.01$	(18) $0.99 \pm 0.02$ (16) $0.96^*$ (12) $0.94^\dagger$ (8) $0.88^\dagger$ (4) $0.67^\dagger$	No redundancy in change in functional diversity
Observed change in functional diversity	Expected change in functional diversity	(18) $-0.02 \pm 0.00$	(18) $1.10 \pm 0.02$	Absence of extrinsic redundancy

\*Denotes that the empirical 95% confidence interval of the average slope does not overlap 1;  $^\dagger$  denotes that the confidence interval does overlap 1.

1 and from 0.28 to 0.78 (mean  $\pm$  1 SD =  $0.59 \pm 0.09$ ) in Atlas 2 (note that FD is standardized to [0, 1]).

The FD observed in the real bird assemblages is on average lower than expected by chance in both atlases (Fig. 5). This is reflected in the relationship between observed and expected FD. For Atlas 1 data the intercept of this relationship is negative and for Atlas 2 the slope is less than 1, both implying that the model predicts observed FD is lower than expected over the range of observed values (Table 2 and Fig. 5 inset panels).

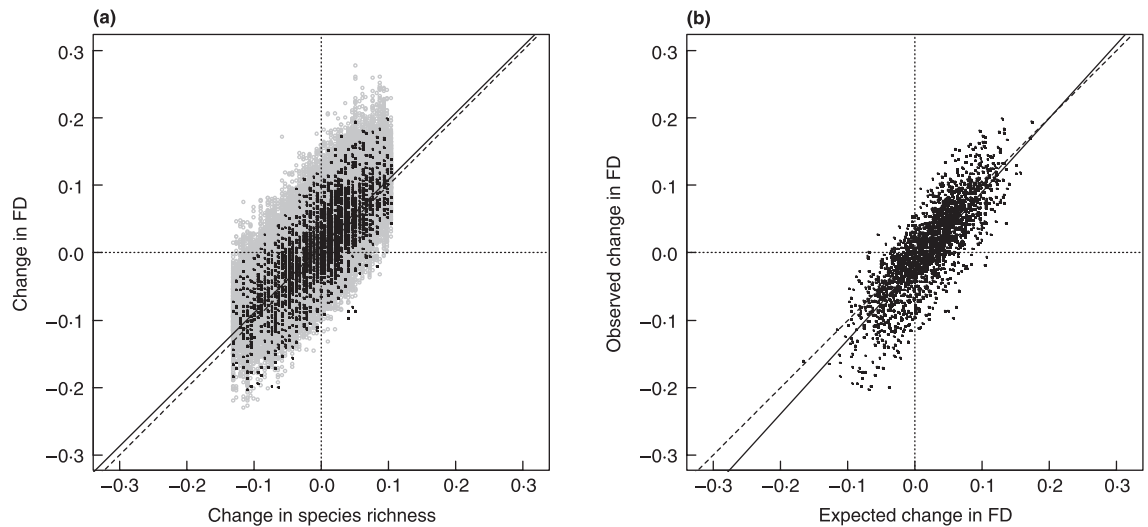
Relationships between the deviation between observed and expected FD and habitat richness are weak but significant ( $R^2$  values for Atlas 1 and 2 are 8% and 2%, respectively). The relationships are positive such that deviation increases from negative values in

areas with low habitat richness to close to zero at higher habitat richness.

#### FUNCTIONAL REDUNDANCY PATTERNS

During the *c.* 20 years between Atlas 1 and Atlas 2, species richness increased in 1051 quadrats, decreased in 1047, and remained constant in 76. Change in the species richness ranged from  $-25$  to  $+20$  (mean =  $-0.6$ ). FD increased in 1244 quadrats and decreased in 930. Change in FD ranged from  $-0.20$  to  $+0.20$  (mean =  $0.01$ ).

Across all quadrats, the change in FD was, on average, proportional to the change in species richness. The slope of the relationship between change in FD



**Fig. 6.** Temporal change in species richness and functional diversity between the periods 1968–72 and 1988–91. (a) Observed changes in species richness and functional diversity are shown by black circles; expected change in functional diversity given the observed change in number of species is shown by grey circles. The distributions in panel (a) are truncated because we excluded the lowest and highest 2.5% of the values of change in species richness (see methods). (b) The expected change in functional diversity, given the observed change in species richness, and the observed change in functional diversity. Dashed lines are the 1 : 1 relationship, solid lines the model predicted relationship. Horizontal and vertical dotted lines indicate the origin.

and change in species richness was  $0.99 \pm 0.02$  (1 SE), which is not significantly different from 1 (Table 2; Fig. 6a). Reducing the number of traits gradually increased the perception of redundancy (Table 2). However, the empirical 95% CI of the slope overlapped 1 at all numbers of traits, apart from 16 where the slope was 0.96, indicating that our general conclusion is robust to considerable variation in the number of traits.

Change in FD was greater than would be expected if extinction and colonization events were random with respect to species' functional originality. The slope of the relationship between observed and expected change in FD was slightly greater than 1 ( $1.10 \pm 0.02$ ) (Table 2; Fig. 6b). This slope was not greatly or systematically affected by the number of traits included in the measurement of FD. The mean functional originality of the species that colonized was on average greater than the mean functional originality of the species that went extinct (*T*-test on log originalities,  $t = 8.8$ , d.f. = 2272,  $P < 0.0001$ ).

## Discussion

Avian FD across Great Britain is lower than expected by chance; co-occurring species are more similar in their functional traits than a random set of species of identical number. Though we cannot identify specific mechanisms from these patterns, one explanation is that environmental filtering occurs, so that the species occurring in an area are particularly suited to that environment and habitat. This interpretation is supported by the positive though weak effect of habitat diversity on levels of FD. The observed levels of FD are inconsistent with strong limiting similarity and or competition,

which would result in greater dissimilarity in species' functional traits, and higher than expected FD. While it is possible that effects of limiting similarity occur, these must be weak relative to processes, such as environmental filtering, which lower FD.

In a similar analysis of the FD of New World bat communities over a wide latitudinal range (approximately 30°S to 40°N) there was also deviation from levels of FD expected if assemblages were random sets of species (Stevens *et al.* 2003). In particular there was lower than expected FD at the northern latitudes closest to those of Britain. However, this result disappeared when analyses were constrained to account for regional differences in the composition of bat communities (e.g. so that in the randomizations, tropical bat species could not occur in temperate regions). Our results indicate that lower than expected FD occurs *within* regional scales. Explanations of this difference between ours and these findings are myriad, from real differences between the ecology and evolution of the species, to differences caused by using different measures of FD. Specifically, Stevens *et al.* (2003) use functional groups to construct a measure of FD, and this will discount any ecologically significant variation that occurs within groups (because species within groups are considered functionally identical).

We found no evidence for redundancy in the temporal dynamics of FD in British bird assemblages. Indeed, changes in FD were, on average, almost exactly proportional to changes in species richness. This occurs despite the saturating relationship between FD and species richness that occurs in random assemblages (Fig. 5, grey circles), and which indicates some intrinsic redundancy in the entire collection of 192 species. Two

factors appear to contribute to the lack of any observed redundancy. First, observed assemblages contain many fewer than 192 species, and at the observed levels of species richness there is little intrinsic redundancy. That is, the real assemblages have too few species to have any intrinsic redundancy. Second, there is no evidence of extrinsic redundancy. Indeed, there is evidence of sensitivity, such that changes in FD are greater than would be expected if extinction and colonization were random. Comparing the mean functional originality (Pavoine *et al.* 2005) of the species that colonized an assemblage and those that went extinct indicates that colonizers were, on average, more unique than species suffering extinction. Thus, if an assemblage lost and gained the same number of species, its FD would tend to increase. An assemblage that gains more species than it loses would increase in FD more than if colonizations and extinctions were random with respect to functional redundancy. This nonrandomness of extinctions and colonizations, with respect to functional traits, is the driving force behind any extrinsic redundancy, or the lack of it that we find here. It may reflect that extinctions are clumped in functional trait space in a similar manner to which they are phylogenetically clumped (Purvis *et al.* 2000). Indeed, ecological traits can predict the magnitude of population decline among British farmland birds (Shultz *et al.* 2005).

In contrast, Micheli & Halpern (2005) report the presence of functional redundancy in marine communities. Slopes of the relationship between change in species richness and change in FD in their study ranged from 0.16 to 1.1, depending on the measure of FD used. A slope of 0.16 indicates very strong redundancy, with large changes in species richness causing very little change in FD. Differences between our and their findings could again result from the different measures of FD used in the two studies. In particular, Micheli & Halpern (2005) use functional group richness. While they report that their results are robust, in the sense of ubiquitous positive and significant relationships, to changes in the criteria used to assign species to functional groups, the slope of the relationship differs as expected. In addition, Micheli & Halpern (2005) used log-ratios to measure change in biodiversity, we did not. There are too many differences between our study and that of Micheli & Halpern (2005) to attribute a cause for differences in results.

We have previously shown that the number of functional traits used in the measure of FD can, but does not have to, affect the level of observed redundancy (Petchey & Gaston 2002a). A greater number of uncorrelated traits will decrease perceived redundancy, but correlation between traits tends to cancel this effect. For this and other reasons (see Petchey *et al.* 2004) great care needs to be taken in identifying functionally important traits (Petchey *et al.* 2004; Petchey & Gaston 2006). Here, we used traits that are widely recognized as being associated with resource use differences among bird species and that are of the type used in previous

studies of avian assemblages (e.g. Holmes *et al.* 1979; Bailey *et al.* 2004). While it is possible that other traits are important, a well informed pragmatic a priori decision must be made in order to make progress. We were asked to investigate the effects of using fewer traits to calculate FD. As expected, there was a systematic increase in perceived redundancy as fewer traits were used to calculate FD. A further advised step, that we cannot use here, is to validate the significance of the functional traits through experimentation (Petchey *et al.* 2004).

Research on functional traits represents the use of natural history to understand biodiversity and test ecological theories. For example, our results show that assemblages are different from those one would expect if functional traits were unimportant, or if assemblages were simply random sets of species. Consequently, functional trait research can provide evidence for or against neutral theories of biodiversity (Hubbell 2001). Other evidence that links functional traits with species' abundances can also challenge neutral theory, such as correlations between species abundances and trait uniqueness (Sugihara *et al.* 2003), and convergence or divergence in the traits of co-occurring species (Stubbs & Wilson 2004; Fukami *et al.* 2005; Mayfield *et al.* 2005; Cornwell *et al.* 2006). These studies and ours present results that are inconsistent with neutral theories. Finding similar and different ways to use functional traits to understand ecology will likely be an interesting and profitable pursuit (McGill *et al.* 2006).

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