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Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function

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RESEARCH ARTICLE

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Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function

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Abstract

1. Functional diversity metrics based on species traits are widely used to investigate ecosystem functioning. In theory, such metrics have different implications depending on whether they are calculated from traits mediating responses to environmental change (response traits) or those regulating function (effect traits), yet trait choice in diversity metrics is rarely scrutinized.
2. Here, we compile effect and response traits for British bird species supplying two key ecological services—seed dispersal and insect predation—to assess the relationship between functional diversity and both mean and stability of community abundance over time.
3. As predicted, functional diversity correlates with stability in community abundance of seed dispersers when calculated using response traits. However, we found a negative relationship between functional diversity and mean community abundance of seed dispersers when calculated using effect traits. Subsequently, when combining all traits together, we found inconsistent results with functional diversity correlating with reduced stability in insectivores, but greater stability in seed dispersers.
4. Our findings suggest that trait choice should be considered more carefully when applying such metrics in ecosystem management.

KEYWORDS

community dynamics, ecological function, functional diversity, functional traits, insurance hypothesis

1 | INTRODUCTION

Ecosystem services, and the functions underpinning them, are crucial for human survival (Millennium Ecosystem Assessment, 2005). There is now unequivocal evidence that biodiversity enhances the provision of ecosystem functions (Delgado-Baquerizo et al., 2020; Hooper et al., 2005; Loreau et al., 2001; Tilman et al., 2014), and due to human activity, we are losing biodiversity, thus threatening the delivery of ecosystem functions across the globe (Cardinale et al., 2012; IPBES, 2019). Initial research into the relationship between biodiversity and ecosystem function used basic measures such as species richness, which provide relatively crude information

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about the differences between species and their ecological functions (Díaz & Cabido, 2001). To provide further insight, ecologists now more commonly estimate the extent of functional differences in a community (i.e. functional diversity) using functional traits that reflect differences in species' resource use as well as their responses to environmental change (Cadotte et al., 2011; Hooper et al., 2005; Violle et al., 2007). Previous analyses have shown that such measures of functional trait diversity perform better than species richness in predicting key aspects of ecosystem function (Gagic et al., 2015). However, the trait-based approach is sensitive to a number of methodological details, including the number and type of traits available for each species.

The choice of traits is a key factor in particular because it can influence the ability of functional diversity estimates to predict ecosystem processes (Lefcheck et al., 2015; Maire et al., 2015; Petchey & Gaston, 2006; Petchey et al., 2009). Different combinations of traits affect the strength of association between functional diversity indices and basic ecosystem properties such as species richness (Zhu et al., 2017). Furthermore, different categories of traits may provide insight into contrasting aspects of biodiversity related to ecosystem function (Tobias et al., 2020). For example, ecologists investigating the impacts of environmental change increasingly use traits that reflect species' responses to environmental conditions (i.e. 'response traits'), for example, traits relating to species' reproductive effect (Luck et al., 2012). To understand the relationship between functional diversity and ecosystem functioning, ecologists use traits that determine the effect a species has on ecosystem functioning (i.e. 'effect traits'), for example, bill morphology (Luck et al., 2012). However, some features act simultaneously as an effect and response trait (e.g. body size, Díaz et al., 2013; Luck et al., 2012). Since multivariate functional diversity metrics routinely combine response and effect traits to produce a single index (Gagic et al., 2015), it is not clear whether additional information could be obtained from calculating response and effect trait diversity separately.

From ecological theory, we would expect communities with a high diversity of response traits to have more stable ecological function, based on the insurance hypothesis where greater response diversity buffers ecosystems against the loss of function caused by environmental change (Yachi & Loreau, 1999). Communities with high response diversity will have a more diverse set of environmental requirements and tolerances, resulting in asynchronous community dynamics leading to increased community stability (Loreau & de Mazancourt, 2013; Yachi & Loreau, 1999). This association has been observed in many real-world systems (Catano et al., 2020; Elmqvist et al., 2003), including wild bee populations wherein increased response diversity—measured by changes in species' abundance after perturbations—contributes to the stability of pollinator abundance (Winfree & Kremen, 2009). Communities with high diversity of effect traits are expected to have higher mean levels of ecosystem function delivery, thereby enhancing ecosystem service provision; for example, providing greater levels of pollen transfer in a given year, reducing the likelihood of pollination deficit and reduced crop yield. Such communities may deliver ecosystem services more efficiently because higher niche partitioning and reduced competitive exclusion allow species to coexist and have larger populations (Cardinale, 2011; Macarthur & Levins, 1967). In practice, the mean and stability of ecosystem functions provided over time are related (Oliver et al., 2015; Redhead et al., 2020). For example, Garibaldi et al. (2011) found pollinator communities with low abundance provided less stable and lower rates of pollination services, which could be driven by low response diversity. However, it has not yet been investigated whether functional diversity metrics calculated using different combinations of response and effect traits provide different insights into the functioning of ecological communities, despite the growing use of functional diversity metrics in guiding ecosystem restoration (Cadotte et al., 2011; Manning et al., 2019).

Here, we compiled data on the ecological and morphological traits of functionally important bird species to examine how long-term community dynamics are related to the diversity of response and effect traits. We focus on 105 British bird species that provide two key ecosystem functions: seed dispersal and insect predation. In the absence of direct measures of these functions, and their variation over time, we analyse the total abundance of the relevant community. We do not presume that total abundance equates to ecosystem functioning, simply that the two are related (Kleijn et al., 2015; Winfree et al., 2015). Total community abundance refers to the total number of individuals contributing a particular function within a community, often related to biomass and is a good predictor of ecosystem functioning in a variety of ecosystems (Dangles & Malmqvist, 2004; Grime, 1998; Smith & Knapp, 2003). The link between total community abundance and any particular ecosystem function can arise due to the 'mass ratio hypothesis' whereby the level of function delivered is driven by the most common species in a community (Grime, 1998). This is supported by empirical evidence in pollination systems where dominant species provide greater ecosystem services than rarer species (Kleijn et al., 2015; Winfree et al., 2015). Therefore, total community abundance is assessed here as an important metric that is relevant to ecosystem functioning. However, we recognize that levels of functional redundancy versus complementarity between species, as well as the existence of saturating relationships between abundance and ecosystem function, can potentially make relationships nonlinear.

We test whether functional diversity is associated with either the mean or stability of total community abundance over time, and how this relationship varies according to whether metrics are calculated using response traits, effect traits or a mix of both. To measure total community abundance for each functional group (seed dispersers and insectivores), we use Breeding Bird Survey (hereafter BBS) data over 15 breeding seasons (2004–2018) at 200 sites. We then relate these community dynamics to functional diversity measured using functional dispersion (F_{DIS}; Laliberté & Legendre, 2010) using three different combinations of traits: (a) effect only, (b) response only and (c) effect only, response only and both (i.e. traits classed as both effect and response) traits pooled together (hereafter 'all traits'). Based on the ecological theory outlined above, we test a priori hypotheses where we hypothesize that higher functional

diversity measured using response traits will provide a more stable community abundance, whereas higher functional diversity measured using effect traits will have a higher mean community abundance measured as the total community abundance, averaged over time. Our goal is to establish how trait choice in functional diversity metrics is related to our ability to observe patterns in community structure and dynamics, and thus to enable more appropriate use of such metrics in ecosystem management.

2 | MATERIALS AND METHODS

2.1 | Bird abundance data

We obtained abundance data from the Breeding Bird Survey (BBS), which has been running since 1994 with over 4,000 sites currently monitored. The BBS uses a stratified random sampling design with skilled volunteers surveying two parallel 1-km transects twice a year (April to early May to capture the early breeding season and late May to June for the late breeding season) between 6 a.m. and 7 a.m., avoiding poor weather conditions. Birds seen and heard are recorded along the two 1-km line transects in four distance categories (0–25 m from the line, 25–100 m, >100 m and flying over). Each transect is split into 200-m sections, in each of which habitat is recorded using a hierarchical coding system with nine broad categories (woodland, scrubland, semi-natural grassland/marsh, farmland, waterbodies, human sites, coastal, inland rock and miscellaneous; Crick, 1992). The total number of adult birds of each species detected in each 1-km square, that is, summed over all distance categories, and transect sections, is calculated for each year. We obtained complete time series of annual abundances for a 15-year period (2004–2018) for 108 species, which represents the time period where the greatest number of BBS sites was surveyed. Abundance data were adjusted for detectability, using calculations outlined below by supplementing our data with additional BBS transect data.

2.2 | Site selection

Sites were only included if they were surveyed during each of the 15 years (2004–2018) of the study. Population dynamics can be mediated by both landscape heterogeneity and position in geographic range (Mills et al., 2017; Oliver et al., 2010). These factors also influence species richness (Jonsen & Fahrig, 1997; Weibull et al., 2000) and functional diversity. Sites with higher species richness have been shown to have higher community-level stability by promoting diversity in their response to environmental fluctuations (Ives et al., 2000). Our sampling controlled for these issues by being restricted to one bioclimatic zone—that is, the Atlantic Central (Metzger et al., 2013)—with survey sites distributed evenly along a gradient of species richness. Finally, sites were split into 10 categories of increasing species richness and 20 random sites from each category of species richness were chosen, resulting in 200 selected sites (Figure S1).

2.3 | Accounting for detectability

As heterogeneity in detectability may result in biased abundance estimates, we calculated detectability estimates for each species–site–visit combination using a distance sampling approach using data for all BBS squares south of 54°N within England and Wales (Buckland et al., 2001; Massimino et al., 2015). To estimate site-, visit- and species-specific detection probabilities, analysis was conducted at the 200 m transect level (assuming that birds on the transect line were detected), using the number of individual birds of each species detected in each distance band. We then estimated the half-normal detection function for each species, with 'habitat type' and 'visit' as co-variates. Detectability estimates were produced for each species, BBS square and visit (early or late). The detectability estimated from this model was used to adjust the abundance value at each site (adjusted abundance = observed abundance/detectability probability). Finally, the maximum adjusted abundance value of the two visits (early and late) was used as the annual measure of abundance at each site (Harris et al., 2019). Detectability data were missing for 70 sites and 12 species (*Anas querquedula*, *Anthus petrosus*, *Bucephala clangula*, *Caprimulgus europaeus*, *Coccothraustes coccothraustes*, *Coturnix coturnix*, *Grus grus*, *Melanitta nigra*, *Pernis apivorus*, *Pyrrhocorax pyrrhocorax*, *Scolopax rusticola* and *Turdus iliacus*) either due to lack of BBS data to fit a detection function or sites were missing habitat data for at least one year. To deal with this, we took two approaches. First, we removed the missing data, resulting in the removal of 12 species and 70 sites from our analysis, resulting in a complete detectability dataset (n = 96 species and 130 sites). Second, we filled in data gaps in detectability using available data from Johnston et al. (2014) for 9 of the 12 species (removing *Grus grus*, *Melanitta nigra* and *Pernis apivorus* from the analysis). To fill in gaps for the site−−species combinations with no detectability data (i.e. the 70 sites with missing habitat data), we took the average of non-missing values for the site–species combinations, resulting in an interpolated dataset (n = 105 species and 200 sites, with 7.2% of the total dataset interpolated). We ran the analysis separately on the complete dataset and the one with interpolated detectability. The two datasets produced very similar results, so we present those from the interpolated detectability dataset here with the alternative results presented in Supporting Information.

2.4 | Functional groups

We used dietary data for the world's birds (Tobias & Pigot, 2019) to identify species performing functions as seed dispersers and insectivores, which include a combination of both breeding and non-breeding diets depending on where data were available. Seed dispersers included both frugivores and granivores; insectivores

included terrestrial invertivores (i.e. non-aquatic invertivores) which use a variety of foraging techniques (e.g. invertivore glean, invertivore aerial, invertivore ground; Pigot et al., 2020). Specifically, we classified species as important seed dispersers if their diets comprised at least 30% of seeds and fruit combined, and as insectivores if their diet comprised at least 30% of terrestrial invertebrates (see Table S1 for species list and functional group classification). To focus on species most closely associated with control of insect populations, we excluded aquatic invertivores consuming non-insect prey—including molluscs, crustaceans, annelids worms—following more recent published dietary classifications (Pigot et al., 2020).

2.5 | Functional traits

We grouped traits into two types—those that reflect species' response to environmental conditions (i.e. 'response traits'; Lavorel & Garnier, 2002) and those that determine the effect species has on ecosystem functioning (i.e. 'effect traits'; Lavorel & Garnier, 2002), with some traits occurring in both categories (i.e. 'both traits'; rationale outlined in Table 1; Luck et al., 2012). Our trait selection resulted in four effect traits, seven response traits and five both traits (Table 1). Where species had missing trait data, we selected congeneric species to fill in these gaps, because deleting taxa with missing data can reduce statistical power and lead to biased results (Nakagawa & Freckleton, 2008). The only gaps in data that needed filling in this way were life span for *Sylvia undata* (surrogate species: *Sylvia melanocephala*) and *Regulus ignicapillus* (surrogate species: *Regulus regulus*), and gape width for *Actitis hypoleucos* (surrogate species: *Actitis macularius*). The resulting dataset had 48 seed-dispersing bird species and 87 insect-eating bird species, with some species performing both functions, making a combined total of 105 species (Table S1).

2.6 | Total community abundance of functional groups

To estimate key aspects of community dynamics, we calculated the mean total community abundance and stability of total community abundance over time for both our focal functional groups. To calculate mean abundance at each site, we used the total community abundance of species in either functional group averaged across all 15 years. To measure stability over time, we took the reciprocal of the coefficient of variation in annual abundance, 1/CV (e.g. Hautier et al., 2015), also known as invariability (Schlapfer & Schmid, 1999). This resulted in an estimate of mean total abundance and stability of each functional group for each site.

2.7 | Functional diversity metrics

To visualize trait variation among species, we projected species-level data into a multivariate trait space (termed 'morpho-space'), commonly used to assess the volume of variation in functional traits, that is, functional diversity. To quantify functional diversity at each survey site, we used functional dispersion (F_{DIS}; Laliberté & Legendre, 2010) which measures the mean distance of all species, weighted by abundance, relative to the community mean trait value. While a number of different functional diversity metrics exist, each with different advantages and drawbacks, F_{DIS} is less sensitive to species richness per se and more sensitive to the overall spread of traits in morpho-space than most alternative metrics (Laliberté & Legendre, 2010) and is widely used in studies of functional diversity in ecological communities (Bregman et al., 2016; Cadotte, 2017). All functional traits were standardized with a mean of 0 and standard deviation of 1. As functional traits in birds are often strongly correlated, we used a principal component analysis (PCA) to obtain independent trait axes and reduce dimensionality (Villéger et al., 2008). PCAs were undertaken separately on three groups of traits: effect, response and all traits together (see Tables S2–S7 for trait loadings). Previous studies have shown that the description of species niche space requires at least a three-dimensional trait morphospace (Maire et al., 2015; Pigot et al., 2020). Hence, we selected a minimum of three PCA axes while also maintaining a minimum of 85% explained variation which resulted in three axes for effect traits, four axes for response traits and five axes for all traits. See Figures 1 and 2 for the variation in effect and response traits for each ecological function. F_{DIS} was calculated for each site using a species x species distance matrix and a matrix containing the average abundance of species at each site using the *dbFD* function (FD package, Laliberté et al., 2014). This analysis was undertaken for each functional group separately.

2.8 | Statistical analysis

All statistical analysis was undertaken using R version 3.5.3 (R Core Team, 2019). We fitted linear regression models with either the mean total abundance of species or stability of total community abundance over time as the response variable and functional dispersion using different combinations of traits as the explanatory variable. Mean and stability measures were log-transformed to meet assumptions of normal distribution. As sites that are closer together could have more similar abundances, we tested for spatial autocorrelation in the residuals from each model. We used the *correlog* function (NCF package, Bjornstad, 2020) to estimate the spatial dependence and plot Mantel correlograms, which showed no evidence of spatial autocorrelation. Furthermore, we examined the Pearson's correlation between F_{DIS} effect and F_{DIS} response values for both functional groups. The resulting correlation between effect and response trait diversity could be due to the co-occurrence of traits within individuals, that is, effect and response traits are positively or negatively correlated within individuals—indicated by our simulated communities showing this correlation, or due to differences in the composition of the specific communities we observed—indicated by this correlation being present in real communities but absent in simulated communities. To test for this, we compared the correlations between F_{DIS}

TABLE 1 Functional traits chosen for the analysis, description of each trait, the category chosen (effect, response or both), the rationale for including the trait as either effect, response or both and source of trait data

Trait	Description	Category	Rationale	Source
Beak length	Length from the anterior edge of the nostril to the tip of the beak	Effect	Bill shape and size predict the size and type of food (i.e. seeds and insects) to be handled and consumed (Luck et al., 2012; Wheelwright, 1985)	Pigot et al. (2020)
Beak width	Width of the beak measured from the anterior edge of the nostril			
Beak depth	Vertical height measured from the anterior edge of the nostril			
Gape width	The external distance between commissural points			
Species specialization index	Coefficient of variation (*SD*/mean) of the species density in six habitat categories—high values indicate more specialized species and low values indicate more generalized species	Response	More specialized species have traits associated with slow reproduction (Mckinney & Lockwood, 1999) and are less able to respond to environmental variation and novel environments (Sol et al., 2002)	Johnston et al. (2014)
Species temperature index	Long-term average temperature experienced by individuals over its breeding range		Species temperature index indicates a species climate envelope, with warm species better able to adapt to increasing temperatures (Devictor et al., 2012)	Devictor et al. (2012)
Thermal maximum	Mean temperature of the 5% hottest cells of the breeding range		Species with a lower thermal maximum are less tolerant to changing climatic conditions and show negative population trends (Jiguet et al., 2007)	Jiguet et al. (2007)
Mean latitude	The mean latitude of an individual species calculated from its geographic range		Changes in temperature are strongest at northern latitudes; hence, these species are likely to respond more strongly to these changes (Parmesan, 2007)	http://datazone.birdlife.org/
Lifespan	Maximum recorded longevity for a species		Long lifespan can be correlated with small clutch size and infrequent breeding (Zammuto, 1986); therefore, species are less able to recover from environmental perturbations (Luck et al., 2012)	Myhrvold et al. (2015)
Clutch size	Number of eggs per clutch		These traits measure the reproductive potential of species, and species with high clutch size/multiple broods will recover more quickly after an environmental disturbance (Newbold et al., 2013)	Myhrvold et al. (2015)
Number of broods	Number of clutches produced per year			Myhrvold et al. (2015) and Johnston et al. (2014)
Body mass	Geometric mean of average values provided for both sexes	Both	Body size is strongly related to resource use and foraging behaviour, hence indicates species' capacity to consume seeds and invertebrates (Luck et al., 2012) Body mass is also strongly related to reproductive output, longevity and dispersal abilities (Luck et al., 2012), and hence species' response to environmental conditions	Pigot et al. (2020) and Sheard et al. (2020)
Hand-wing index	Aspect ratio of the wing		Wing and leg morphological traits align with movement or dispersal ability, which in turn influences resource use and frugivore (Luck et al., 2012; Miles et al., 1987; Sheard et al., 2020) These traits also indicate locomotory behaviour (Miles et al., 1987) and provide species with the ability to withstand environmental changes, for example, disrupted landscape connectivity (Luck et al., 2012)	
Kipp's distance	The distance between the tip of the longest primary and the first secondary feather measured on the folded wing			
Wing length	The distance between the bend of the wing and the tip of the longest primary feather			
Tarsus length	Length from the middle of the rear ankle joint to the end of the last scale of acrotarsium			

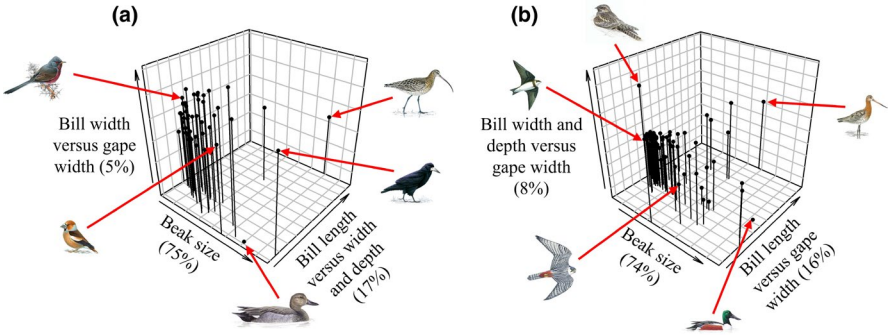


FIGURE 1 Variation in effect traits (beak length, width, depth and gape width) for (a) seed dispersers and (b) insectivores. Each point represents a single bird species and each axis is derived from a principal component analysis showing percentage of variance in functional traits explained. See Tables S2 and S5 for trait loadings. Images reproduced with permission from Mike Langman (www.rspb-images.com)

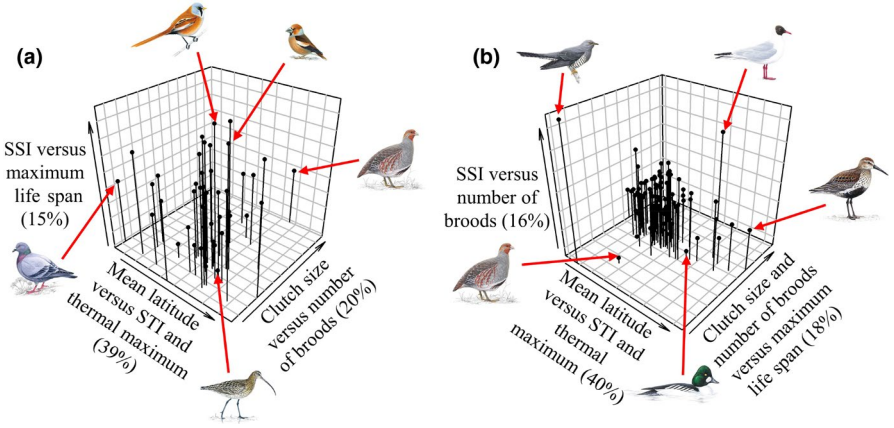


FIGURE 2 Variation in response traits for (a) seed dispersers and (b) insectivores. Each point represents a single bird species and each axis is derived from a principal component analysis showing percentage of variance in functional traits explained. Abbreviations as follows: SSI, species specialization index; STI, species temperature index; mean latitude, average latitude calculated from all grid cells in the global geographical range; thermal max, mean temperature of the 5% hottest cells of the breeding range. See Tables S3 and S6 for trait loadings. Images reproduced with permission from Mike Langman (www.rspb-images.com)

effect diversity and F_{DIS} response diversity for the observed communities with correlations of simulated communities. We used the same species richness at each site over time to select 100 random communities (by randomly drawing species) and calculated F_{DIS} using effect traits and response traits separately for each simulated community. The Pearson's correlation coefficients between F_{DIS} effect diversity and F_{DIS} response diversity for simulated communities was then compared with that of the true observed communities.

3 | RESULTS

3.1 | Summary statistics

Species richness at each site ranged from 12 to 35 species for seed-dispersing communities, and 18 to 56 species for insectivore communities. Total community abundance averaged over time for each site ranged from 70.9 to 1,432.5 for seed-dispersing communities and 107.0 to 1,005.4 for insectivore communities. Stability of total community abundance for each site, as measured by 1/CV, ranged from 1.89 to 11.94 for seed-dispersing communities and 1.42 to 18.72 for insectivore communities.

3.2 | Seed dispersers

We found a positive relationship between response trait diversity and mean total community abundance for seed dispersers (Figure 3c; Table S8). A similar result was found for 'all trait' diversity (i.e. both response and effect trait diversity; Figure 3b). However, we found a negative relationship for effect trait diversity (Figure 3a), although this result was non-significant in the complete case data, that is, where we removed species and sites where detectability could not be estimated (Table S10). For community stability, we found a positive relationship with response trait diversity (Figure 3f; Table S8), as predicted, and a similar result for all trait diversity (Figure 3e). However, we found no significant relationship with effect trait diversity (Figure 3d). These results were the same when we used the complete case data (Table S10). Our significant positive results here could have been driven by outlying points with high functional diversity driving positive trends (Figure 3b,c,e,f). Therefore, we removed outlying points as identified using Cook's distance with a threshold of $D < 4/n$. Our results remained the same after these points were removed (Figure S2).

Functional dispersion of effect and response traits was negatively correlated (Pearson's $r = -0.29$, $p < 0.001$; Figure 5a). To

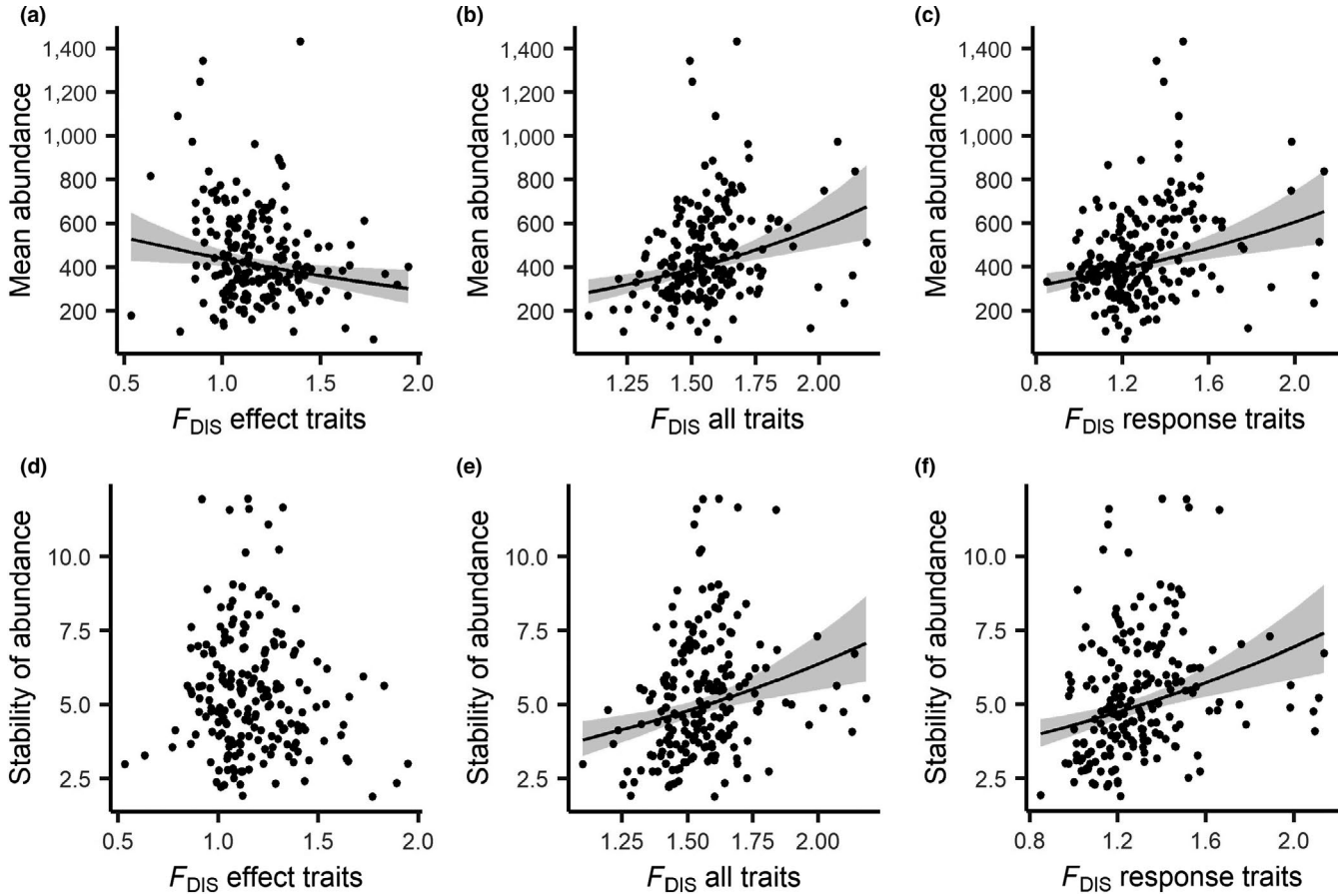


FIGURE 3 Relationships between the mean total community abundance of seed dispersers and functional dispersion (F_{DIS}) of effect traits (a), all traits (b) and F_{DIS} response traits (c). Lower panel shows relationships between the temporal stability of total seed disperser abundance and functional dispersion of effect traits (d), all traits (e) and response traits (f). In both cases, results are for 48 birds at 200 sites. Shaded areas around the line show 95% confidence intervals around significant slope coefficients (see Table S8)

understand whether this relationship was due to the relationship between the traits themselves or due to differences in the composition of the specific communities we observed, we compared this to 100 randomly selected communities of the same species richness which showed similar negative relationships (Figure 5a). The average correlation coefficient of the 100 iterations was −0.19. We found a weak positive relationship between mean and stability of total community abundance of observed communities (Pearson's $r = 0.39$, $p < 0.001$).

3.3 | Insectivores

For insectivores, we found no significant relationships between functional diversity and mean total community abundance (Figure 4a–c; Table S9). For community stability, we found a negative relationship with effect trait diversity (Figure 4d; Table S9) and all trait diversity (Figure 4e). However, we found no significant relationship with response trait diversity (Figure 4f). These results were consistent when the complete case data were used (Table S11).

Functional dispersion of effect and response traits was not significantly correlated (Pearson's $r = -0.12$, $p = 0.08$). When compared to 100 randomly selected communities of the same species richness, we found relationships in the same negative direction between functional dispersion of effect and response traits compared to the observed communities (Figure 5b). The average correlation coefficient of the 100 iterations was −0.08. We found a weak positive relationship between mean and stability of total community abundance of observed communities (Pearson's $r = 0.26$, $p < 0.001$).

4 | DISCUSSION

Our results show that communities of seed dispersers with high response trait diversity have more stable total community abundance over time, in line with predictions of the insurance hypothesis (Yachi & Loreau, 1999). Most existing support for this hypothesis has been found in synthetic plant communities, often at small spatial scales (Allan et al., 2011; Pillar et al., 2013; Craven et al., 2018; van Klink et al., 2019, but see Wilcox et al., 2017). Our finding that response trait diversity in assemblages of wild birds can predict stability in a property linked closely to ecosystem function suggests that the insurance hypothesis applies more generally and at larger spatial scales, with implications for how functional diversity metrics are

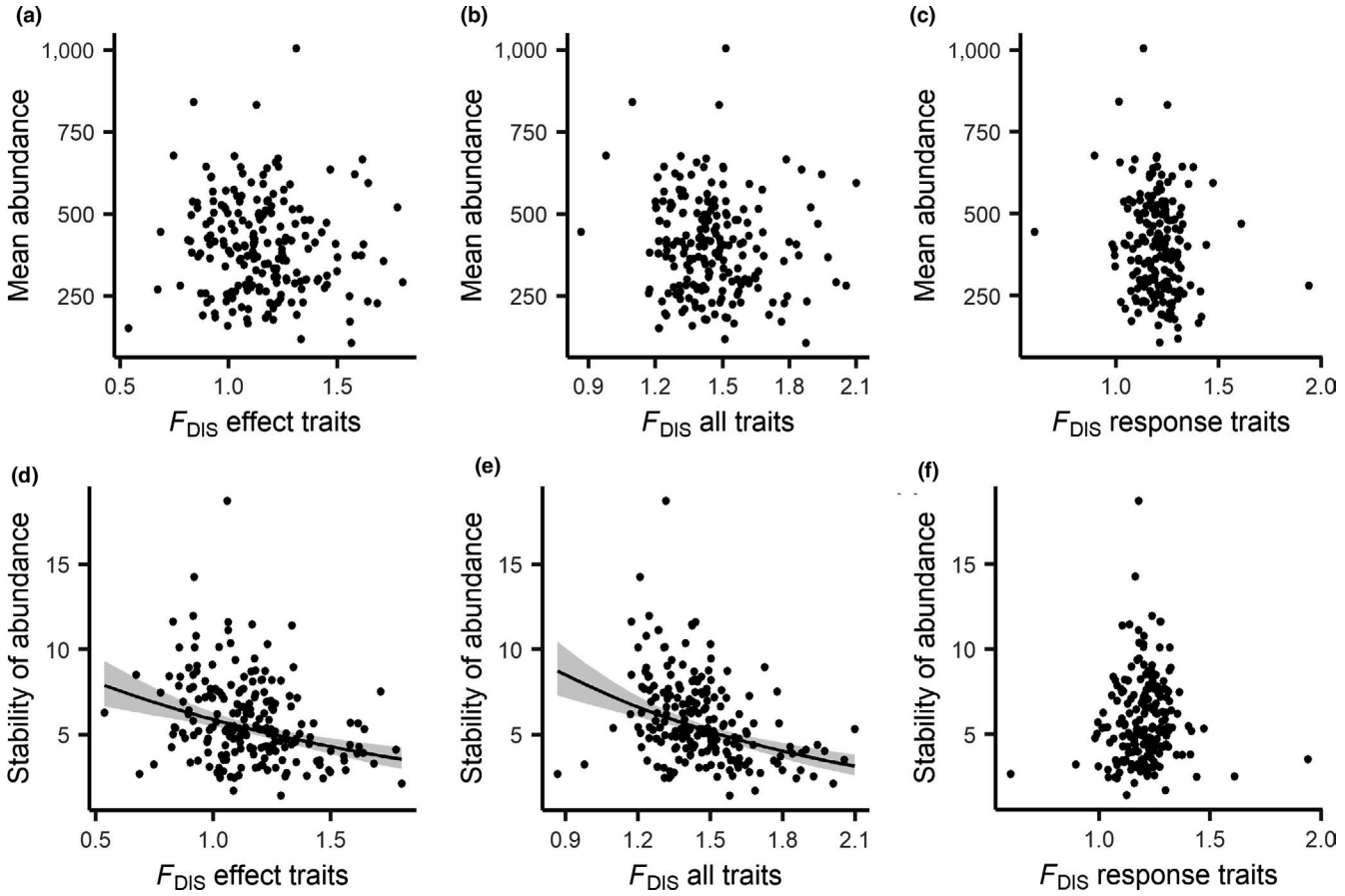
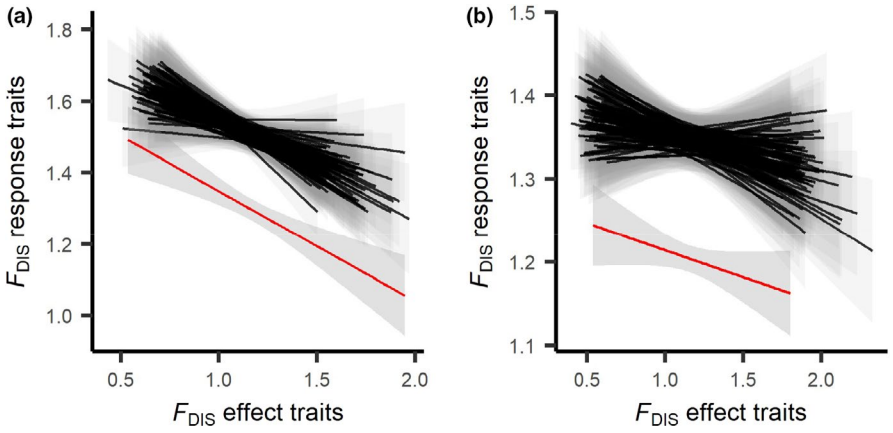


FIGURE 4 Relationships between the mean total abundance of insectivores and functional dispersion (F_{DIS}) of effect traits (a), all traits (b) and F_{DIS} response traits (c). Lower panel shows relationships between the temporal stability of total insectivore abundance and functional dispersion of effect traits (d), all traits (e) and response traits (f) for 87 birds at 200 sites. Shaded areas around the line show 95% confidence intervals around significant slope coefficients (see Table S9)

FIGURE 5 Correlation between F_{DIS} response traits and F_{DIS} effect traits for (a) seed dispersers and (b) insectivores. Red line shows results from observed communities; black lines show results from 100 randomly selected communities of the same species richness. Grey areas around the lines represent 95% confidence intervals



used in ecosystem management (Manning et al., 2019). In particular, the relationship we establish between response (but not effect) trait diversity and the stability of total community abundance over time suggests that the type of traits used to calculate functional diversity metrics influences which aspect of ecosystem function these metrics are likely to reflect.

Focusing on a different type of trait, we tested the hypothesis that communities with high effect trait diversity should have higher mean total community abundance. In other words, an assemblage composed of species with divergent niche requirements should have more available resources due to reduced interspecific competition, and therefore, populations of each species may be larger, generating higher total community abundance (Abrams, 1983; Macarthur & Levins, 1967). However, our results run counter to these predictions in that communities of seed dispersers with high effect trait diversity had lower mean total community abundance (Figure 3a), while effect traits had no significant relationship with total abundance of insectivores (Figure 4a). Our findings, therefore, add to a growing

number of empirical studies finding little support for a positive association between effect trait diversity and total community abundance (e.g. see Thompson et al., 2010). This is perhaps unsurprising since the core regions of trait morphospace can be densely packed in bird assemblages (Pigot et al., 2016) with trait overdispersion in co-occurring species being relatively slight (Ulrich et al., 2017), and mostly at smaller spatial scales (Trisos et al., 2014). In addition, vertebrate species at the periphery of morphospace tend to be rarer than those at the core (Ripple et al., 2017), suggesting that assemblages with a higher proportion of morphologically unusual species may have fewer individuals, perhaps explaining the negative relationship we detected between effect diversity and community abundance in avian seed dispersers.

A surprising result from our study was that insectivore bird communities with higher effect trait diversity tended to have less stable total abundance over time (Figure 4d). A possible explanation is the negative correlation we found between effect and response diversity for both functional groups. To assess whether this relationship was a result of species composition in real communities (i.e. a product of environmental filtering and/or competitive interactions), we also tested for correlations in simulated communities. There was no relationship between effect and response diversity of randomly selected insectivore communities, whereas real communities showed a weak negative relationship, although this was non-significant (Figure 5b). Randomly selected seed-dispersing communities showed much weaker negative relationships between effect and response diversity because response diversity was consistently high compared to real communities (Figure 5a). Therefore, as these simulated communities did not show the same relationship as our real communities, the negative correlation between effect and response diversity is likely due to environmental filtering and/or competitive interactions.

In real communities, environmental filtering, which selects for species that are well suited to the average environmental conditions (Kraft et al., 2015), can lead to a subset of species with more similar response traits (i.e. lower response diversity) than the full range possible. Competitive exclusion is also common among species with more similar traits, which leads to overdispersion in traits of coexisting species. However, competitive exclusion can result in trait clustering (Cadotte & Tucker, 2017) if particular traits are associated with higher average fitness (Kraft et al., 2015). Disentangling environmental filtering and competitive exclusion is difficult because the two processes can leave similar signatures in the phylogenetic or trait structures of assemblages and may operate simultaneously (Kraft et al., 2015; Mayfield & Levine, 2010). However, our results suggest that the latter process is important here because we found that seed-dispersing communities are less likely to be formed of species with low diversity of both effect and response traits (Figure 5). In contrast, when response diversity is high, then species with low effect trait diversity can coexist. A possible explanation is that temporal variation in the environment promotes coexistence in species which would otherwise compete (Hutchinson, 1961; Kirk, 2002), that is, responding differently to weather conditions leads to reduced competition between species with similar effect traits allowing them to coexist in the same communities (Hutchinson, 1961; Li & Chesson, 2016; Roth & Schreiber, 2014).

Having shown the influence of response trait diversity on community abundance differs from that of effect trait diversity, we tested whether the standard approach of mixing both types of trait together results in a best-of-both-worlds scenario for functional diversity metrics. This was true for seed disperser communities, where we found that combined functional trait diversity was positively related to mean community abundance (Figure 3b) and to the stability of total abundance (Figure 3e), equivalent to the results found for response diversity. However, for insectivore communities, we found a negative relationship of all trait diversity with stability of total abundance (Figure 4e), comparable to the relationship found with effect diversity. These inconsistent results highlight an important trade-off between evidence for mean and stability of abundance in UK bird communities. Studies using indices of functional diversity often use traits regarded as effect traits (e.g. foraging type) and both traits (e.g. body size; Prescott et al., 2016). Our results highlight that communities with high diversity of such traits can potentially indicate low stability. Ecologists have suggested maximizing functional diversity when restoring communities (Cadotte et al., 2011), but depending on how this is calculated it could lead to communities with unstable abundance, risking years of low ecosystem functioning (as well as high).

Our results also emphasize that different functional groups of birds respond differently to the same group of traits used in our measure of functional diversity. Response trait diversity acts similar to all trait diversity for seed dispersers, whereas effect trait diversity acts similar to all trait diversity in insectivores. Therefore, it may be advisable to maximize functional diversity within functional groups, as opposed to the entire bird community, with the specific traits used in metrics of functional diversity guided by research such as that shown here. It is unclear to what extent our results hold for bird guilds in different bioregions (e.g. desert, tropics), emphasizing the need for further work on this topic.

Our approach has some limitations worth outlining. The proportion of variance in community dynamics explained by functional diversity was low, varying from 3.1% to 15.0% (Tables S8–S11). Our predictive ability was not improved by removing outlying points in our seed disperser dataset (Figure S1) where some sites had extreme functional diversity values. The low proportion of variance could partly be due observer bias including identification mistakes or sampling error related to habitat type (Johnston et al., 2014); however, we accounted for heterogeneity in detectability, by adjusting the raw abundance data by a detectability probability coefficient (Johnston et al., 2014; Massimino et al., 2015). Furthermore, our measurements of functional diversity could also be imprecise due to missing data in functional trait datasets leading to low r-squared values. 'Hard' functional traits with more proximate effects on ecosystem functioning are often more difficult or expensive to measure (Hodgson et al., 1999; Violle et al., 2007). Due to this, some 'soft' traits were used in this analysis (e.g. reproductive traits such as clutch size), although these often correlate with hard traits (Violle et al., 2007). A further source of error in functional diversity estimates could be due

to the use of mean trait values per species. Including intraspecific variation in traits has been shown to improve the ability to detect niche differentiation processes (Jung et al., 2010). Disregarding this variation underestimates the degree of niche and trait overlap between species (Violle et al., 2012); however, Pigot et al. (2020) found most variation in global bird trait values existed across rather than within species. Finally, there was higher variance in total mean abundance between sites versus variance in functional diversity, which might also reduce the degree of fit in their relationship.

Although we find many significant relationships between functional diversity and mean and stability of abundance, our low predictive ability highlights the difficulty in linking functional traits to community abundance, and the additional step of linking to ecosystem functioning. However, we demonstrate that effect and response traits provide different information on community abundance which can be used to inform management actions to maintain ecosystem functioning.

Our findings extend previous research emphasizing the importance of trait choice methodology in producing accurate functional diversity measures and deriving accurate ecological conclusions (Maire et al., 2015; Zhu et al., 2017) while demonstrating a novel link between trait choice and community dynamics. This can help infer whether increased functional diversity will lead to higher mean or stability of community dynamics, and therefore ecosystem functioning. In particular, to measure the stability of total community abundance, it appears crucial to include in functional diversity metrics traits reflecting the response of species to environmental conditions. Selecting functional traits appropriately will enable conservation practitioners to use functional diversity metrics in informative ways to ensure the long-term stability of ecosystem functioning.

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AUTHORS' CONTRIBUTIONS

L.A.H., O.L.P., J.A.T. and T.H.O. designed the study; L.A.H. conducted statistical analysis. All authors contributed to the writing of the manuscript.

DATA AVAILABILITY STATEMENT

Data are deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.jwstqjq8v (Hordley et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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