

RESEARCH ARTICLE

Variable relationships between trait diversity and avian ecological functions in agroecosystems

Rocío Peña¹  | Matthias Schleuning²  | Marcos Miñarro³  | Daniel García¹ 

¹Departamento Biología de Organismos y Sistemas (Universidad de Oviedo) and Instituto Mixto de Investigación en Biodiversidad (IMIB CSIC-Universidad de Oviedo-Principado de Asturias), Oviedo, Spain

²Senckenberg Biodiversity and Climate Research Centre (SBIK-F), Frankfurt (Main), Germany

³Servicio Regional de Investigación y Desarrollo Agroalimentario (SERIDA), Villaviciosa, Spain

Correspondence

Daniel García
Email: Danielgarcia@uniovi.es

Rocío Peña
Email: rocpengar@gmail.com

Funding information

Fundación BBVA, Grant/Award Number: 044-2019; MinECo/FEDER, Grant/Award Number: BES-2016-078260 and GL2015-68963-C2-2-R

Handling Editor: Enrico Rezende

Abstract

1. The diversity of traits within animal assemblages has been shown to affect the magnitude of animal-provided ecological functions. However, little is known about how consistent trait diversity effects are across ecological functions and ecosystems. More importantly, the importance of trait diversity in driving ecosystem functioning, relative to other components of biodiversity, has rarely been assessed. It also remains unclear how environmental gradients filter trait diversity and, ultimately, modulate ecological functions.
2. Here, we test how different biodiversity components (i.e., trait diversity, phylogenetic diversity and abundance) affect the magnitude of avian seed dispersal and insect predation along large environmental gradients. We sampled frugivorous and insectivorous birds and their ecological functions across gradients of forest cover and fruit and insect abundances in woodland pastures and apple orchards in Northern Spain. We measured 6 morphological traits and compiled phylogenetic information on 43 bird species. We used Structural Equation Models to disentangle the effects of environmental gradients and biodiversity components on ecological functions.
3. We found that different avian functions in the same agroecosystem were controlled by different biodiversity components. While seed dispersal was positively driven by bird abundance in woodland pastures, insect predation responded positively to trait and phylogenetic diversity. The positive effects of trait diversity on insect predation were, on the other hand, consistent across woodland pastures and apple orchards.
4. Our results also pinpointed forest cover and resource availability as filters of the different components of avian diversity, suggesting that environmental gradients condition the effects of biodiversity on avian ecological functions.
5. Our findings reveal variable effects of trait diversity on two different avian ecological functions, but consistent effects on the same function across agroecosystems. Consolidating the generalities of trait diversity effects will require further multi-function studies, as well as a unifying framework for animal-driven functions that integrates the causal links between environmental gradients, the different biodiversity components, and ecological functions.

Read the free [Plain Language Summary](#) for this article on the Journal blog.

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](#) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2022 The Authors. *Functional Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

KEYWORDS

bird abundance, environmental filtering, functional diversity, insect predation, phylogenetic diversity, seed dispersal

1 | INTRODUCTION

Species traits have become a cornerstone to understanding and predicting the consequences of biodiversity loss for ecosystem functioning (Cadotte et al., 2011; Cardinale et al., 2012). Previous work has shown that traits can properly represent the functional roles of many species in ecosystems (Díaz & Cabido, 2001) and that trait variability across species, as a measure of functional diversity, is often better suited than species richness for describing the relationship between biodiversity and ecological functions (Biodiversity and Ecosystem Functioning [BEF] framework; Cadotte et al., 2011; Hillebrand & Matthiessen, 2009). While these ideas were initially developed for plant species and functions such as primary production (de Bello et al., 2010), since then they have been generalized to animal assemblages and to ecological functions derived from trophic interactions (e.g., pollination, nutrient cycling, insect predation; Fründ et al., 2013; Gagic et al., 2015). In general, it is assumed that greater trait diversity within animal assemblages, often measured by the dissimilarity in phenotypic trait values across species (Laliberté & Legendre, 2010; Villéger et al., 2008), leads to higher magnitudes of ecological functions due to complementarity among species in resource use (Fründ et al., 2013). Despite these advances, we are still far from having a comprehensive understanding of the relevance of trait diversity on animal ecological functions in real-world ecosystems (Bregman et al., 2016; Schleuning et al., 2015).

One key factor shaping the relationship between trait diversity and ecological functions is environmental variability (Flynn et al., 2009; Peña et al., 2020). Environmental factors modulate animal ecological functions, on the one hand, by filtering species richness and traits in local assemblages (Flynn et al., 2009). For instance, large-scale habitat disturbance (e.g., deforestation or land-use changes) can erode trait variability within animal assemblages (as some species are more vulnerable to disturbance depending on their traits; Luck et al., 2012) provoking decays in ecological functions (Bregman et al., 2016; Peña et al., 2020). Furthermore, other environmental factors, such as food resource availability, may shape trait variability in animal consumer assemblages, affecting ecological functions (Quitán et al., 2019). On the other hand, environmental factors may also drive ecological functions by affecting the per-capita functional role of animals through individual performance or behaviour (Díaz et al., 2013). For example, a higher temperature may increase the individual activity of insects, thus promoting pollination (Rader et al., 2013), and higher tree cover may foster longer stays of frugivorous birds in forest patches, thus increasing seed dispersal (García et al., 2010). Despite these findings, there remains debate on how environmental factors operating at different scales shape the relationship between animal trait diversity and ecological functions in nature (Cardinale et al., 2012). There is thus a need for studies that address the relationships between biodiversity

and ecological functions along environmental gradients in order to disentangle the direct and indirect (i.e., biodiversity-mediated) effects of environmental factors on ecological functions, as well as the specific relationships between biodiversity and ecological functions that emerge along such gradients.

Trait-based approaches enable comparative analyses across animal assemblages (Cadotte et al., 2011), but may be insufficient to explain the variability of ecological functions. One reason for this is that, despite the conceptual and methodological advantages of using traits, trait diversity estimates are limited to a chosen set of traits whose actual links to the performance of species may be diffuse (e.g., Bartomeus et al., 2018). This has encouraged the use of complementary measures of functional diversity based on phylogenetic approaches (Flynn et al., 2011). In this sense, phylogenetic diversity may provide further information about the potential role of species (Cadotte et al., 2012) since many ecological or behavioural properties of species may not be related to measurable functional traits, but can be approximated from their phylogenetic history (Cadotte et al., 2012; Flynn et al., 2011). Previous studies have shown that closely related species are ecologically more similar as a result of their shared evolutionary history (Cadotte et al., 2012; Tucker et al., 2018). Thus, measures of phylogenetic diversity may represent functional complementarity within animal assemblages better than trait diversity (Rezende et al., 2007). Another important predictor of ecological functions is species abundance (García et al., 2010; Gaston et al., 2018; Winfree et al., 2015), a biodiversity component related to other mechanisms underpinning BEF relationships, such as numerical effects of dominant species within assemblages (Mokany et al., 2008). Despite the importance of different biodiversity components for driving ecosystem functioning, integrative studies on the relative importance of traits and phylogenies, as well as abundance effects, on different animal-provided ecological functions are lacking (Llorente-Culebras et al., 2021).

Here, we focused on forest birds to assess the relevance of trait diversity, phylogenetic diversity and abundance on seed dispersal and insect predation. These are two major avian ecological functions provided by a similar pool of bird species that co-occur across large environmental gradients (e.g., Bregman et al., 2016; Hordley et al., 2021). We estimated biodiversity components for frugivorous and insectivorous birds, as well as the magnitude of their respective ecological functions, across gradients of forest cover and food availability in two agroecosystems (woodland pastures and apple orchards) in Asturias, Northern Spain. Both forest cover and food availability have been identified as main drivers of both biodiversity and bird-mediated functions (e.g., García et al., 2011; Hanz et al., 2019). To disentangle the relationships between environmental conditions, biodiversity and ecological functions, we used a hierarchical approach based on structural equation models. With

this model, we were able to quantify how (i) different biodiversity components were filtered along the environmental gradient, and (ii) the extent to which environmental factors imposed direct or indirect, that is biodiversity-mediated, effects on the two ecological functions studied in different agroecosystems. We expected (i) that larger environmental gradients of forest cover or resource availability would impose stronger filters on biodiversity components; (ii) that these environmental gradients would influence ecological functions independently of variation in biodiversity components, by affecting the per-capita role of birds; and (iii) that the effects of the biodiversity components on an ecological function would be consistent across ecosystems, but variable for different functions, due to the function-specific prevalence of different BEF mechanisms.

2 | MATERIALS AND METHODS

2.1 | Study design

The study was designed to evaluate seed dispersal and insect predation across environmental gradients of forest cover and food resources (fleshy-fruits and arthropods) in woodland pastures and apple orchards in the Asturias region (N Spain; Figure 1a). We set up a partially crossed design that enabled us to contrast both functions from a given agroecosystem (i.e., woodland pastures), and compare different agroecosystems for a given function (woodland pastures vs. apple orchards for insect predation; Figure 1a). We regard both agroecosystems as optimal for comparison because they occur in the same fine-grained variegated landscapes with remnant patches of seminatural forest, thus exhibiting sharp environmental gradients. In addition, the two ecosystems harbour a common regional pool of bird species.

As we studied ecological functions occurring in woody agroecosystems, we focused on forest-dwelling bird species belonging to two feeding guilds: frugivores and insectivores (Figure 1a). Previous work has demonstrated that avian frugivores drive forest regeneration and recovery in the Cantabrian range (Martínez & García, 2017), and that insectivorous birds are effective natural enemies of pest arthropods in Asturian apple orchards (García, Miñarro, et al., 2018). We considered species that use woody vegetation as their major foraging habitat, and excluded species that are typically ground-dwelling (e.g., pipits) or air-dwelling (swallows, raptors). Classification as frugivores or insectivores was based on knowledge of each species' seasonal diet (>30% fleshy-fruits or terrestrial invertebrates, respectively), based on direct observations and previous studies (García, 2016; García, Miñarro, et al., 2018; Wilman et al., 2014).

Firstly, mid-elevation woodland pastures, used as cattle range-land, contain variable-sized patches of primary and secondary forest embedded in a pasture-heathland dominant matrix. Forest patches are rich in fleshy-fruited woody species (e.g., hawthorn *Crataegus monogyna*, holly *Ilex aquifolium*; blackberry *Rubus fruticosus/ulmi-folius*), which represent a valuable resource for frugivorous birds, especially during fruit masting events (Martínez & García, 2015). Secondly, apple orchards are typically small plantations surrounded by patches of seminatural woody vegetation in the form of forest patches and hedgerows. Plantations are based on disease-tolerant local cultivars and low-input management, which allows for a high diversity and abundance of arthropods (García, Miñarro et al., 2018). Some of them are harmful and prevalent pests, such as the codling moth *Cydia pomonella*, which attacks apple fruits *Malus domestica* (Miñarro et al., 2011). Comprehensive descriptions of the studied agroecosystems may be found in previous studies (García, Donoso, et al., 2018; García, Miñarro, et al., 2018).

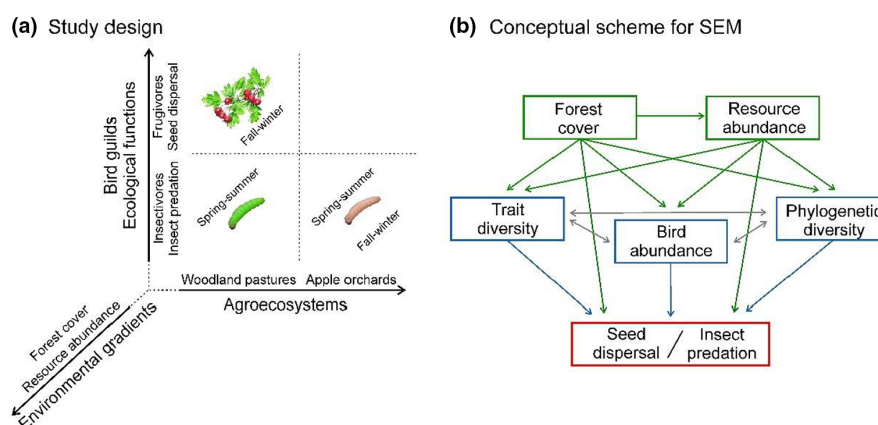


FIGURE 1 Representation of the partially crossed study design to contrast the performance of avian ecological functions across the environmental gradients of two agroecosystems in Asturias (N Spain): woodland pastures and apple orchards (a). Focusing on two guilds of forest-dwelling bird (i.e., frugivore and insectivore), two ecological functions were evaluated in woodland pastures (seed dispersal in fall–winter, and insect predation in spring–summer), and one function (i.e., insect predation) in apple orchards (i.e., fall–winter and spring–summer). Scheme of the Structural Equation Model (SEM) showing the hypothesized causal relationships between environmental gradients, bird diversity components, and ecological functions (b). The effect of environmental gradients (forest cover and resource abundance) are shown in green, and the effect of avian diversity components (trait diversity, phylogenetic diversity, and bird abundance) in blue. Additional fixed correlation structures were included for relationship among avian diversity components (grey). Artwork by Víctor González.

Our design consisted of twenty-five, 50-m radius circular sampling plots in each agroecosystem (Figure S1.1). Previous studies have shown that this spatial scale is the most suitable for representing the gradients of local environmental conditions in these systems (García et al., 2005), as well as being appropriate for detecting the effects of environmental gradients on bird assemblages and their ecological functions (García & Chacoff, 2007).

Woodland pasture plots were located, with a 200-m minimum distance between them, over a 30 km² extent in the Banduxu-Puertos de Marabiu area (43°14'35.2"N, 6°05'41.6"W). Plots were chosen to represent similar vegetation composition (altitude 990–1,250 m a.s.l.) and anthropic management (cattle rangeland), but covered a wide gradient of forest cover (Figure S1.2). Apple orchard plots were set up in different orchards distributed over 600 km² in central Asturias (43°21' to 43°30'N, 5°20' to 5°45'W), with a minimum distance between orchards of 1.3 km. Plots were established with their centres within the apple plantation, at 25-m distance from the plantation edge, in order to represent a gradient of variability of forest cover availability around orchards (Figure S1.2). Sampling was conducted from 2017 to 2019 in woodland pastures, and in 2015 and 2016 in apple orchards. Fieldwork was done under permission of apple owners to work within their private properties, and the Government of Asturias to work in Protected Areas.

2.2 | Environmental gradients

2.2.1 | Forest cover

We accounted for the abundance of seminatural temperate deciduous forest, as a measure of plot-level availability of source habitat for birds (or an inverse measure of human impact through farming). In each plot, we estimated the proportion of forest cover from a digitized layer of tree canopy projection in a Geographic Information System of the study plots (GIS, ArcGIS9.3) based on 1:5000 scale, 2014 orthophotographs (Figure S1.2). In woodland pastures, forest cover included trees and treelets (DBH > 10 cm, height > 1.5 m), and ranged from 6% to 77% of the plot area. In apple orchards, forest cover included hedgerows, small patches of forest, tall shrubs, and isolated remnant wild trees, ranging from 0% to 38% of plot area.

2.2.2 | Food resource abundance

We accounted for the availability of food resources for each avian guild: fleshy fruits for frugivores (woodland pastures) and arthropods for insectivores (both agroecosystems).

The abundance of fruits was sampled at the beginning of the ripening period of the fleshy-fruited plant assemblage (September–October) in 2017 and 2018. The crop of all individual plants of any fleshy-fruited species present in each plot was visually estimated

in the field using a semi-quantitative scale with six intervals (0 = without fruits; 1 = 1–10 fruits; 2 = 11–100; 3 = 101–1000; 4 = 1001–10,000; 5 ≥ 10,001; Fruiting Abundance Index, Saracco et al., 2004) transformed for individual crop sizes through allometric fit (Martínez & García, 2015). *Fruit abundance* was quantified as the cumulative number of fruits of all species per plot and sampling year.

The abundance of arthropods was assessed in July 2017 and 2018 in woodland pastures and in June 2016 in apple orchards, employing a beating sampling applied to 10 focal trees (hawthorn in woodland pastures and apple trees in apple orchards). Three taps were given with a stick to one branch of each focal tree and all falling arthropods were collected in a plastic tray (80 × 50 × 8 cm) held below the branch. Samples were inspected in the laboratory for arthropod collection and arthropod samples were kept frozen at –18°C. The total biomass of arthropods per tree was estimated from the wet weight of frozen samples, using a precision balance with 0.1 mg accuracy. *Arthropod abundance* was quantified as the sum of the total biomass of arthropods of all samples per plot.

2.3 | Frugivorous and insectivorous bird assemblages

Bird assemblages were evaluated by point-count censuses. In each plot, an observer at its centre registered all birds heard or seen (using 8 × 42 binoculars) over a 30-min period within the plot itself. Four different observers were involved in the census rounds, alternating between plots. Censuses were performed between 07:00 and 13:00 h, avoiding days of heavy rain and wind. Due to the small plot size, we did not expect any differences in detectability among bird species. To avoid double-counting of individuals, consecutive sightings of a given species were assumed as independent when recordings were separated by at least 5 min (Gregory et al., 2004). We also discarded repeated observations attributable to an individual bird which had remained in the plot throughout a given time slot (i.e., individuals that appear intermittently at the same perching site within short time periods). Censuses were performed every 2 weeks during fall–winter (September–January of 2015 in orchards; 2017 to 2019 in pastures) and spring–summer (April–August of 2016 in orchards; 2017 and 2018 in pastures), resulting in nine censuses per season. Data from different species were pooled across censuses per season, for each bird guild (i.e., total effort 225 h per avian guild). Data collection did not involve direct contact or interaction with animals, thus no ethical approval was required.

2.4 | Biodiversity components

We focused on birds to estimate three components of biodiversity, for each functional guild, and at the level of each plot: trait diversity, phylogenetic diversity and abundance.

2.4.1 | Trait diversity

We focused on a small set of morphological traits representing different aspects of avian foraging: body mass, bill length, gape width, Kipp's index (Kipp's distance divided by wing length), tarsus length and tail length. Body mass was obtained from Dunning (2008). The other traits were measured on at least four museum specimens (two male and two female, following Peña et al., 2020). Bill morphology relates to the size and type of food handled and consumed (Luck et al., 2012; Pigot et al., 2020). Body size is related to energy requirements and, thus, the magnitude of resource consumption (Luck et al., 2012). Kipp's index (*akin* hand-wing index) is an estimate of wing pointedness and is related to movement ability and locomotory behaviour, with high values related to greater ability for long-distance flights and low values to higher manoeuvrability in dense vegetation (Pigot et al., 2020). Tarsus and tail length are further proxies for locomotion and influence the type of foraging strategy (Luck et al., 2012; Pigot et al., 2020). We used all six functional traits for insectivorous birds, but excluded tarsus and tail lengths for frugivores, as the other four traits have been found particularly relevant to plant-frugivore interactions (Bender et al., 2018). Prior to analysis, we constructed species $\times$ trait matrices using the mean of each species trait and log-transformed body size and tail length.

We estimated trait diversity by quantifying the weighted average distance of all species to the weighted centroid of each bird assemblage (Laliberté & Legendre, 2010). For this, we first combined all traits to build bird multidimensional trait spaces, based on Euclidean distances, using principal coordinates analysis (PCoA; Villéger et al., 2008). Independent trait-spaces were built for frugivores in woodland pastures, insectivores in woodland pastures, and insectivores in apple orchards. Next, we calculated values of functional dispersion (FDis) for the bird assemblages of each plot, as a global measure of trait dispersion indicative of functional complementarity between species (Laliberté & Legendre, 2010; Villéger et al., 2008). Abundance-weighted FDis values and PCoA axes were estimated with the *dbFD* function in the R package *FD* (Laliberté et al., 2014).

2.4.2 | Phylogenetic diversity

We studied phylogenetic relationships between species with a complete dated phylogeny from BirdTree.org (Ericson et al., 2006; Jetz et al., 2012). We downloaded 10,000 backbone trees to generate the maximum clade credibility (Bayesian MCC) tree using *TreeAnnotator* (Drummond & Rambaut, 2007). We extracted the phylogenetic distance (i.e., branch length) matrix among all species in the pruned phylogeny using the function *cophenetic* implemented in the *ape* R package (Paradis & Schliep, 2019; Figure S3).

For each plot, we estimated the phylogenetic diversity (i.e., in terms of branch distances) among the species present in the local bird assemblage by means of the mean pairwise distance (MPD). We estimated the abundance-weighted MPD values of each plot from distance matrices (squared-root transformed; Letten &

Cornwell, 2015) using the *mpd* function in the *r* package *PICANTE* (Kembel et al., 2010).

2.4.3 | Abundance

We further quantified bird abundances for each species in the community. Thus, for each plot, we estimated the cumulative number of individuals recorded for each species, once summed across all frugivorous species and once across all insectivorous species recorded in a given plot.

2.4.4 | Standardization of metrics

In order to control potential effects of species abundance on the role of trait and phylogenetic diversity, we calculated standardized effect sizes (SES) of FDis and MPD. To this end, we compared observed values of local assemblages to 1000 sets of randomized assemblages, generated by using the function "quasiswap count" on the abundance matrices (Miklós & Podani, 2004; Oksanen et al., 2018). This permutation algorithm randomizes local abundance values by keeping both dimensions of the abundance matrix constant (marginal totals of species and plots). We subtracted the mean of the randomized values from the observed local values, and divided this by the standard deviation of the random values. For simplicity, henceforth all mentions of MPD and FDis refer to abundance-controlled parameters, which are measured as standardized effect sizes in standard deviation units.

2.5 | Seed dispersal and insect predation

Seed dispersal by birds was estimated in woodland pastures by quantifying the deposition of seeds of woody species handled by birds (i.e., depulped seeds regurgitated, defecated or discarded during pulp or seed predation by avian frugivores). Seeds were collected in 10 seed traps placed in different hawthorn trees in each plot in September–October 2017 and 2018. Seed traps consisted in a hanging plastic pot with a surface of 0.07 m² with bottom holes to allow rainwater drainage and covered by a wire mesh to protect seeds from rodent predation (Figure S1.3a). Seed traps were checked and seeds collected at the end of the fruiting season (February–March of 2017 and 2018). Seeds from fleshy-fruited species were identified with a seed reference collection from the study area and available literature (Balmori et al., 2013). We estimated *seed dispersal* magnitude per plot as the average density of seeds (seeds/m²) per seedtrap per plot.

We quantified insect predation in woodland pastures and apple orchards through observations of bird attack on lepidopteran larvae, mimicked by plasticine caterpillar models (see Peisley et al., 2015 for a similar procedure). Caterpillar models were 15-mm long and 3-mm in diameter, and imitated common species in each agroecosystem: *Aporia*

crataegi in woodland pastures and *Cydia pomonella* in apple orchards (Figure S1.3b). Each model was presented to birds in a posture imitating natural movement on a branch, pierced through its longitudinal axis with a green wire to attach it to the branch. Insect predation sampling was set up simultaneously in all plots, replicated twice in each agroecosystem: mid-October 2015 and mid-July 2016 in apple orchards, and mid-July 2017 and 2018 in woodland pastures. For each sampling session, we deployed 10 caterpillar models across 10 trees (hawthorn in woodland pastures, apple tree in apple orchards) within each plot. Models were examined 7 days after set up, recording whether they showed signs of bird attack (beak marks) on their surface or had been partially removed). The ground under the focal trees was inspected to avoid including “naturally” fallen models. For each tree in each plot, we estimated *insect predation* rate as the number of attacked or removed caterpillar models relative to those that remained unaffected.

2.6 | Statistical analysis

We used piecewise structural equation models (pSEMs) to address both biodiversity-driven and direct environmental effects on ecological functions, and to evaluate the differential relationships between biodiversity components and ecological functions along environmental gradients. pSEMs were based on a hierarchical conceptual scheme (Figure 1b) that accounted for direct and indirect relationships between environmental gradients (forest cover and resource availability), biodiversity (trait diversity, phylogenetic diversity and abundance), and ecological functions (seed dispersal or insect predation). We hypothesized that the magnitude of a given function is affected by environmental gradients and various biodiversity components, interpreting these direct links as follows: (a) Environmental gradients shape different biodiversity components (e.g., when forest cover or resource availability increases, trait variability may increase or species abundance decrease); (b) Environmental gradients have direct effects on ecological functions, independent of biodiversity components, which can be interpreted as the effects on the per-capita functional role of individual animal (e.g., when, birds spend more time in fruit-rich patches, or in a canopy area for protection); and (c) Each independent biodiversity component drives ecological functions (e.g., when higher phylogenetic diversity determines an increase in the number of dispersed seeds). Based on this conceptual scheme, we set up independent models for each ecological function (response variable) and their corresponding bird functional guilds in different agroecosystems (Figure 1a).

Piecewise SEMs (PIECEWISESEM package in R; Lefcheck, 2016) allow the fitting of generalized linear mixed models (GLMMs) considering non-Gaussian error distributions in response variables. Technically, SEMs were represented by a list of GLMMs (lme4 package in R; Bates et al., 2015) that considered seed dispersal and insect predation as response variables at the tree scale. Seed dispersal (the number of seeds per m²) was fitted assuming a Poisson error distribution (log-link function), after transforming the average density of seeds to integers, and insect predation (attacked vs. unattacked model caterpillars) was fitted assuming a binomial distribution (logit-link function). Plot

identity was incorporated in all models as random factor (Table S5.1). Additional fixed correlation structures were included for relationships among the three biodiversity components, reflecting that the relationship among components is not presumed to be causal and unidirectional (Lefcheck, 2016). For analyses, fruit and bird abundances were square-root transformed and arthropod abundance was log-transformed. All predictors (environmental gradients and biodiversity components) were scaled to zero mean and unit variance.

Models initially included all conceptually envisioned links (Figure 1b), from which we conducted a backward simplification by removing non-significant relationships until achieving the best model, characterized by the lowest AIC (Figures S5.1, S5.2 and S5.3). We also evaluated BIC values in the specific case of insect predation models in woodland pastures, where both saturated and simplified models showed similar AIC (Figure S5.2). The goodness of fit of the pSEM was assessed by evaluating the Fisher's C for conditional independence ($p > 0.05$ indicates there are no missing paths among variables, and thus models represent the data appropriately; Lefcheck, 2016). In the interest of parsimony, we did not control for sampling season (spring–summer/fall–winter) or year (2017/2018) in the models as their inclusion did not qualitatively change our findings (Figures S5.1, S5.2 and S5.3).

3 | RESULTS

3.1 | General overview of bird assemblages

We recorded a regional species pool incorporating 43 species (37 in woodland pastures; 34 in apple orchards; 28 common species; Table S2). Of these, 2 were classified as frugivores only, 16 as insectivores only, and 25 as omnivores (frugivore and insectivore; Table S2).

Both agroecosystems harboured comparable gradients of species richness in their local bird assemblages (Table S4.1). Bird abundance gradients were similar between functional guilds in woodland pastures (individuals per plot; 19–173 frugivores, and 47–136 insectivores), whereas apple orchards presented generally higher abundances and a wider gradient across plots (41–248 insectivores). Bird assemblages had highly heterogeneous distributions of relative abundances within each community (Figure 2), with a few dominant species, such as *Turdus merula* and *Erithacus rubecula*, and many rare species. The specific ranks of relative abundance of the different species were, however, similar between bird guilds and agroecosystems (Figure 2).

Trait spaces of bird assemblages were mostly determined by body size (and correlated bill, tail, and tarsus sizes) on the first axis and wing pointedness on the second axis (Figure 2). Bird species were clustered in certain areas of the trait space, differentiating between many clustered small-sized species, a group of large-sized birds that were more evenly distributed over the trait space (e.g., thrushes, *Turdus* spp.), and a few species with extreme trait combinations defining the extent of the avian trait space (e.g., *Garrulus glandarius*, *Cuculus canorus*, *Nannus troglodytes*). Generally, insectivore assemblages occupied a wider trait space than frugivores (Figure 2).

FIGURE 2 Multidimensional trait-space of frugivorous and insectivorous birds ($n = 43$ species) in two different agroecosystems. Here, the same six morphological traits (bill width, bill length, Kipp's index, tarsus length, tail length, and body mass) were considered for both avian guilds. Dots represent individual species, which are also indicated by their acronyms (Table S2). Dot size corresponds to the relative species abundance in the respective agroecosystem and avian guild. Artwork by Daniel García.

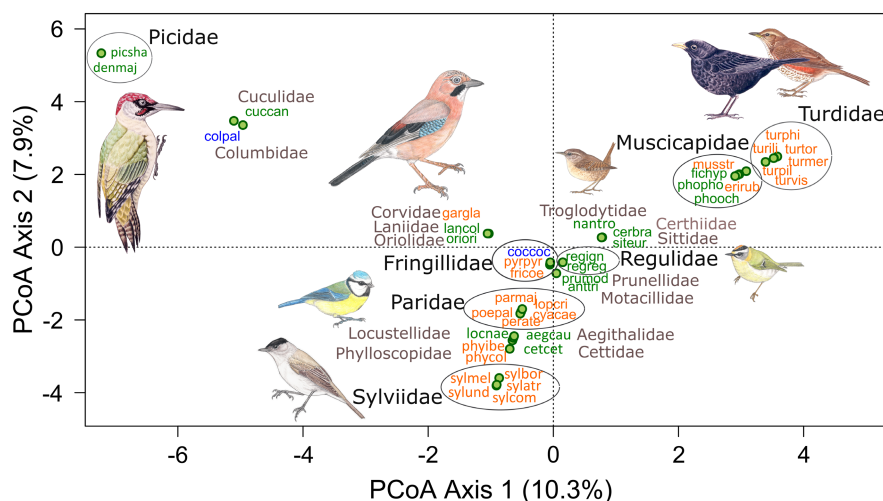
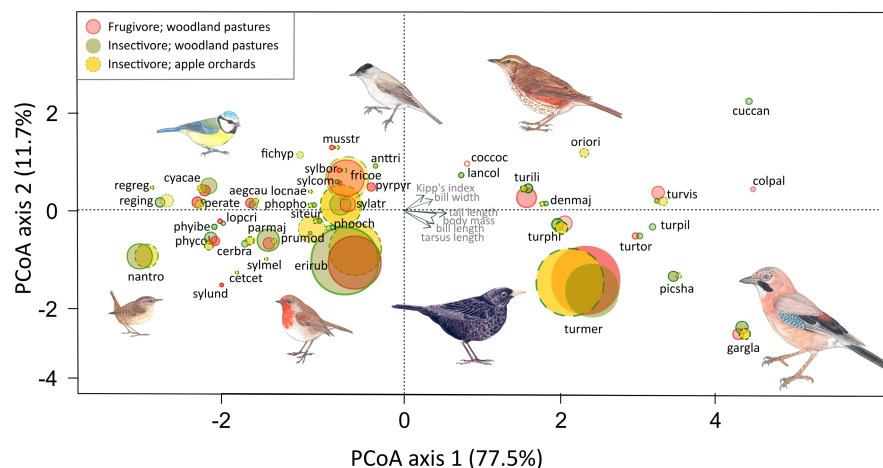


FIGURE 3 Multidimensional phylogenetic-space of the avian community ($n = 43$ bird species) in two agroecosystems in the Cantabrian range (northern Iberian Peninsula), considering the phylogenetic distance (i.e., branch length) between species (sqrt-transformed). Bird phylogenetic tree is based on published phylogeny (Jetz et al., 2012, see Methods). Dots represent bird species also indicated by their acronyms (Table S2) in blue for frugivores, green for insectivores, and orange for both. Families that are represented by only one bird species are in grey. Those families represented by at least two species are indicated in black and embedded within the corresponding circle. Artwork by Daniel García.

Phylogenetic variability within bird assemblages was high (Figure 3). Bird species belonged to twenty-one families, only three being non-passerine (Picidae, Cuculidae, and Columbidae), which were phylogenetically the most unique species (Figure 3). Overall, the core of frugivores comprised more closely related species belonging to fewer families (i.e., mostly thrushes) compared to insectivore assemblages (Figure 3).

3.2 | Effects of environmental gradients and biodiversity components on ecological functions

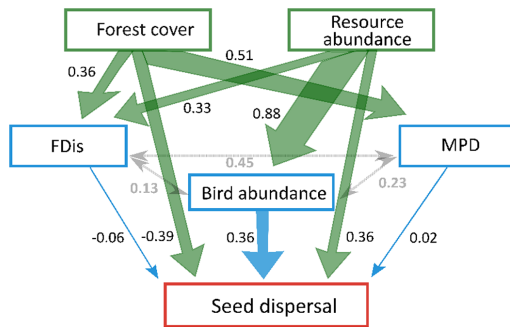
The pSEM-specific goodness-of-fit measure Fisher's C provided statistical support of the goodness-of-fit of all three models ($p > 0.1$ in Fisher's C tests in all models).

Following the hierarchical structure of our conceptual framework (Figure 1b), the piecewise SEM for seed dispersal in woodland

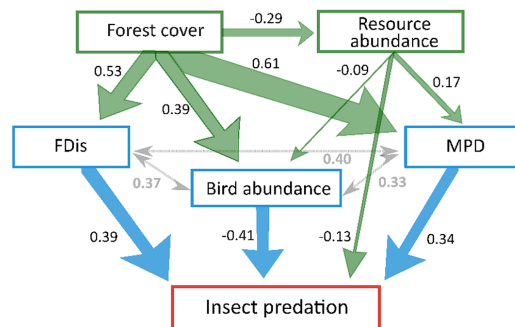
pastures revealed significant positive effects of forest cover on frugivore FDis and MPD (Figure 4a; Table S5.2). Higher fruit abundance also increased FDis, and to a greater extent bird abundance. Moreover, seed dispersal was directly related to environmental gradients, negatively to forest cover and positively to fruit abundance. Bird abundance showed a strong positive effect on seed dispersal, in contrast to weak effects of FDis and MPD on seed dispersal.

The piecewise SEM for insect predation in woodland pastures revealed a negative effect of forest cover on arthropod biomass, but strong positive effects on all biodiversity components of insectivorous birds (Figure 4b). Increased arthropod abundance was associated with higher MPD, but was negatively related to bird abundance and insect predation. Overall, the effects of the different biodiversity components on insect predation were comparable in magnitude, with positive effects of FDis and MPD, and a negative effect of bird abundance on insect predation (Figure 4b).

(a) Woodland pastures



(b) Woodland pastures



(c) Apple orchards

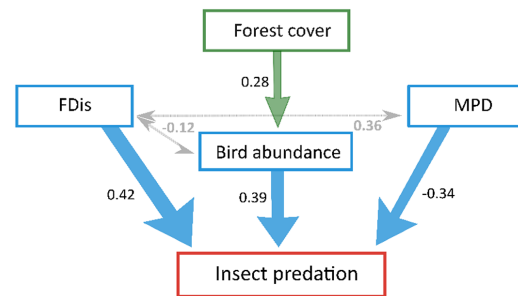


FIGURE 4 Summary of the piecewise Structural Equation Models (SEMs) testing the effects of environmental gradients and bird diversity components on seed dispersal in woodland pastures (a), and insect predation in woodland pastures (b) and apple orchards (c). Standardized path coefficients are given next to each path, and only significant relationships are shown. Effects of environmental gradients (forest cover and resource availability,) are shown in green, and effects of biodiversity components (trait diversity [FDis], bird abundance and phylogenetic diversity [MPD]) in blue. Arrow thickness is proportional to the relative strength of effects. Grey double headed arrows show correlated errors between biodiversity components. Value of Akaike's Information Criterion (i.e., AIC) was 46.1 for model (a); 53.6 for model (b); and, 22.9 for model (c).

Differently to woodland pastures, the SEM for insect predation in apple orchards suggested only weak environmental control on avian diversity and associated ecological function (Figure 4c). Namely, forest cover had an indirect positive effect on insect predation by increasing bird abundance (Table S5.2). Irrespective of the environmental gradients, FDis and bird abundance were positively related to insect predation across plots. In contrast, plots with higher MPD were characterized by decreasing insect predation.

4 | DISCUSSION

In this study, we simultaneously investigated the relationships between biodiversity components and ecological functions across the environmental gradients of two agroecosystems. Specifically, we followed a hierarchical framework to evaluate (i) the biodiversity-driven environmental effects on ecological functions, (ii) the direct effects of environmental gradients on ecological functions and (iii) the specific relationships between biodiversity components and ecological functions. Specifically, first, we found strong filtering effects imposed by the gradients of forest cover and food resources on biodiversity components of frugivorous and insectivorous assemblages. Second, environmental gradients showed direct effects on seed dispersal, in contrast to the lack of such direct effects on insect predation. Finally, we demonstrated that trait and phylogenetic diversity and the abundance of birds were related to the magnitude of both ecological functions. In particular, seed dispersal was exclusively affected by bird abundance, which was in fact strongly driven by gradients of resource availability, whereas trait-based and phylogenetic diversity affected insect predation largely independent of the environmental context. Our results therefore reveal that the functional effects of biodiversity depend on the environmental context and the ecological function considered.

4.1 | Effects of environmental gradients on biodiversity components and ecological functions

We found strong effects of environmental gradients as local filters of biodiversity for both frugivore and insectivore assemblages (see also Bregman et al., 2016). Overall, we found a positive effect of forest cover on both avian guilds, implying also a similar trend of response in trait and lineage distributions (see also Bregman et al., 2016; Petchey et al., 2007). As other studies have suggested, forest loss encompassed a decay of variability in terms of trait and phylogenetic diversity (i.e., bird assemblages with less divergent trait combinations and lower average phylogenetic distances; Barnagaud et al., 2014; Bregman et al., 2014). Similarities between guilds in their core species composition (most frugivores were also insectivores; Table S2) and the abundance distributions of assemblages (Figure 2) could explain the concordant responses to forest cover gradients (Figure 4a,b). While trait and phylogenetic diversity were primarily controlled by forest cover, frugivore abundance was exclusively related to fruit abundance. In fact, the high ability of fruit-resource tracking by flocking frugivores (e.g., thrushes) in these woodland pastures likely explains why fruit availability is the main determinant of bird abundance along this environmental gradient (Martínez & García, 2015). In contrast, insectivore abundance was primarily promoted by forest cover (see also Barbaro et al., 2014), since insectivores rely on a specific foraging substrate (Jankowski et al., 2013). Thus, our results reveal how the biodiversity of different avian guilds is distinctly shaped by several sets of environmental factors (Tscharntke et al., 2008).

We also found evidence for direct environmental effects on ecological functions, especially in woodland pastures. Specifically, we found strong effects of forest cover and fruit abundance on seed dispersal, but little indication of such direct effects on insect predation. Seed deposition by frugivores increased in low-cover plots (i.e., those with only isolated remnant trees) and in fruit-rich plots, irrespective of the effects of biodiversity. These patterns are probably explained by environmental effects on individual frugivore behaviour, with longer times spent (and consequently higher seed deposition) in patches offering protection (e.g., remnant trees in the open matrix) and high food concentration (Martínez & García, 2015).

4.2 | Comparison of seed dispersal and insect predation

By comparing avian-driven seed dispersal and insect predation, our study showed that different components of biodiversity are important in determining the magnitude of these two ecological functions. Furthermore, through identifying the effects of particular biodiversity components, we were able to approximate the mechanisms underpinning each biodiversity-ecosystem function link. Specifically, seed dispersal depended almost exclusively on variability in bird abundance, whereas insect predation was largely driven by trait and phylogenetic diversity within bird assemblages. The positive effect of frugivore abundance on seed dispersal is an expected result (see previous studies in this system, García, Donoso, et al., 2018; García et al., 2010), probably explained by the dominant role of species such as *T. merula* and *E. rubecula* (Figure 2). These species are characterized by high abundances and highly frugivorous diets (García, 2016). This suggests a dominance effect, driven by the disproportionate role of functionally effective and common species, as a major mechanism driving the relationship between animal biodiversity and ecosystem function (Winfree et al., 2015). This is consistent with the mass-ratio hypothesis (sensu Mokany et al., 2008) proposing that species abundances are the main driver of BEF relationships in nature. On the other hand, the positive effect of trait and phylogenetic diversity on insect predation suggests that more divergent trait values and more distant lineages increase the magnitude of avian insectivory, consistent with the complementarity hypothesis (Blüthgen & Klein, 2011; Gagic et al., 2015). In the specific case of insectivores, both trait and phylogenetic diversity may capture complementarity in foraging strategies and spatio-temporal segregation of trophic niches (Pigot et al., 2016).

The differences between seed dispersal and insect predation seem to be related to differences in the underlying resource variability. In fact, fruit abundance varied across plots by almost four orders of magnitude (ranged from 638 to 1.15×10^6 fruits per plot), a much sharper gradient than that observed in arthropod abundance (min-max biomass; 0.02–0.14 g arthropods per plot; Table S4.2). Previous work has suggested that environmental heterogeneity strengthens the link between biodiversity and ecosystem functioning by increasing the variability in species richness among assemblages and by fostering niche differences between coexisting species (Albrecht

et al., 2021; Tylianakis et al., 2008). In our study, the wide gradient of fruit availability across sites, rather than provoking a higher niche partitioning within the frugivore assemblage, resulted in a pronounced gradient in bird abundance leading to the emergence of dominance effects on seed dispersal (see also Winfree et al., 2015).

4.3 | Avian ecological function across agroecosystems

By comparing insect predation in two agroecosystems, we contrast the response of avian insectivores across environmental gradients, and the consistency of the biodiversity-ecosystem functioning relationship for insectivory.

We found filtering effects of forest loss on biodiversity components to be stronger in woodland pastures than in apple orchards. In fact, the stronger biodiversity response in woodland pastures could be related to the higher structural contrast represented by forest and non-forest habitat patches in this agroecosystem compared to apple orchards, where the canopy cover of apple trees also acts as avian shelter (García, Miñarro, et al., 2018; Martínez-Sastre et al., 2020).

Generally, all components of biodiversity jointly influenced insect predation in both agroecosystems. However, the direction of effects was variable and the only consistent effect across the two agroecosystems was that of trait diversity on insect predation. This suggests a consistency in the positive effect of divergent trait values and trophic niche partitioning on insectivory functions (see also Barbaro et al., 2014). Conversely, we found that the effects of both phylogenetic diversity and abundance components differed in sign between woodland pastures and apple orchards. Concerning phylogenetic diversity, we attribute the differences to specific compositional changes which may entail reductions in phylogenetic variability in apple orchards (e.g., the absence of *C. canorus* from the orchards, Figure 3; Table S4.1). Moreover, we hypothesized that these differences across agroecosystems may result from differential species contributions (i.e., insectivore role) and their correspondence to phylogenetic divergence. Positive effects of bird abundance on insectivory have been previously reported for apple orchards (García, Miñarro, et al., 2018; Martínez-Sastre et al., 2020), and could potentially be related to increased abundance of highly effective insectivores in this agroecosystem (e.g. tits, Paridae; García et al., 2021). Conversely, in woodland pastures, the most dominant species (e.g. *T. merula*, *Fringilla coelebs*) may not be particularly effective as insect consumers (Wilman et al., 2014). This could be explained by a negative relationship between specific abundances and functional effectiveness (Gaston et al., 2018), which could be tested through sensitivity analyses to address the influence of dominant species on the magnitude of ecological functions.

4.4 | Frontiers of trait-based BEF research in animal ecology

Animal traits are largely used as surrogates of animal ecological functions, and trait diversity is commonly assumed to underpin the

positive effects of biodiversity on ecosystem functioning by representing niche complementarity between species (Hillebrand & Matthiessen, 2009). Here, we seek to generalize the role of trait diversity on ecosystem functioning by comparing ecological functions across agroecosystems, but also by accounting for phylogenetic diversity and animal abundance as other important components of animal diversity. Although limited by the small range of functions and agroecosystems studied, we argue that generalities exist mostly within functions, with some—insect predation—being more trait-driven than others—seed dispersal. Consolidating these generalities for more functions, and identifying which functions are more driven by animal trait diversity than others will require extensive multi-function studies (such as those performed in relation to species richness, e.g., Albrecht et al., 2021). Moreover, our study suggests that environmental context conditions trait diversity effects on ecological functions, not only by filtering trait variability in a local assemblage, but also by regulating the strength of the relationship between biodiversity components and ecosystem functioning (Albrecht et al., 2021; Winfree et al., 2018). Integrative, large-scale studies comparing effects of trait diversity on animal-mediated ecosystem functions across large environmental gradients may, thus, be a frontier for future work. Such studies could form the basis for identifying the functions and environmental conditions where trait approaches are more relevant, and prospectively it should become possible to discern the general rules of how trait diversity drives ecosystem functions of different animal groups. A unifying framework, integrating different biodiversity components, environmental gradients and ecological functions is, thus, needed to fully harvest the potential—and to identify key limitations—of trait-based approaches in animal functional ecology. We see our study as a first step in that direction.

AUTHORS' CONTRIBUTIONS

D.G., M.M., M.S. and R.P. conceived and designed the study; R.P. and D.G. collected field data; R.P. and M.S. compiled trait and phylogenetic data; R.P. performed analyses; R.P. and D.G. wrote the manuscript with input from M.S. All authors reviewed the manuscript and approved the final version.

ACKNOWLEDGEMENTS

We thank Carlos Guardado, Rodrigo Martínez-Sastre, Alejandro Núñez, Jairo Robla, Luis Rodríguez, and Rubén Tarifa for technical support. We thank Anna Fantur, Christina Schultheiß, Mathias Templin and Till Töpfer for measuring bird specimens, and the following collections for providing bird skins: Zoologisches Forschungsmuseum Alexander König Bonn, Senckenberg Naturhistorische Sammlungen Dresden, Senckenberg Naturmuseum Frankfurt and Naturhistorisches Museum Basel. The research was funded by MinECo/FEDER CGL2015-68963-C2-2-R and Fundación BBVA 044-2019 ClaveSER to D.G., and MinECo/FEDER BES-2016-078260 to R.P. We thank all apple orchard owners for giving permission to work within their private properties, and the Government of Asturias for permissions to work in Protected Areas.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest. M.S. and D.G. are Associate Editors of Functional Ecology, but took no part in the peer review and decision-making processes for this paper.

DATA AVAILABILITY STATEMENT

Original data associated with this article are deposited in Dryad Digital Repository <https://doi.org/10.5061/dryad.xgxd254jr> (Peña et al., 2022).

ORCID

Rocío Peña  <https://orcid.org/0000-0002-7668-3472>

Matthias Schleuning  <https://orcid.org/0000-0001-9426-045X>

Marcos Miñarro  <https://orcid.org/0000-0002-5851-6873>

Daniel García  <https://orcid.org/0000-0002-7334-7836>

REFERENCES

- Albrecht, J., Peters, M. K., Becker, J. N., Behler, C., Classen, A., Ensslin, A., ... Schleuning, M. (2021). Species richness is more important for ecosystem functioning than species turnover along an elevational gradient. *Nature Ecology & Evolution*, 5, 1582–1593. <https://doi.org/10.1038/s41559-021-01550-9>
- Balmori, P. T., García, P. Z., & Lázaro, Á. H. (2013). *Semillas de frutos carnosos del norte ibérico: guía de identificación*. Ediciones Universidad de Valladolid.
- Barbaro, L., Giffard, B., Charbonnier, Y., van Halder, I., & Brockerhoff, E. G. (2014). Bird functional diversity enhances insectivory at forest edges: A transcontinental experiment. *Diversity and Distributions*, 20(2), 149–159. <https://doi.org/10.1111/ddi.12132>
- Barnagaud, J. Y., Daniel Kissling, W., Sandel, B., Eiserhardt, W. L., Şekercioglu, Ç. H., Enquist, B. J., ... Svenning, J. C. (2014). Ecological traits influence the phylogenetic structure of bird species co-occurrences worldwide. *Ecology Letters*, 17(7), 811–820. <https://doi.org/10.1111/ele.12285>
- Bartomeus, I., Cariveau, D. P., Harrison, T., & Winfree, R. (2018). On the inconsistency of pollinator species traits for predicting either response to land-use change or functional contribution. *Oikos*, 127(2), 306–315. <https://doi.org/10.1111/oik.04507>
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bender, I. M. A., Kissling, W. D., Blendinger, P. G., Böhning-Gaese, K., Hensen, I., Kühn, I., ... Schleuning, M. (2018). Morphological trait matching shapes plant-frugivore networks across the Andes. *Ecography*, 41(11), 1910–1919. <https://doi.org/10.1111/ecog.03396>
- Blüthgen, N., & Klein, A. M. (2011). Functional complementarity and specialisation: The role of biodiversity in plant-pollinator interactions. *Basic and Applied Ecology*, 12(4), 282–291. <https://doi.org/10.1016/j.baae.2010.11.001>
- Bregman, T. P., Lees, A. C., MacGregor, H. E. A., Darski, B., de Moura, N. G., Aleixo, A., ... Tobias, J. A. (2016). Using avian functional traits to assess the impact of land-cover change on ecosystem processes linked to resilience in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, 283(1844), 20161289. <https://doi.org/10.1098/rspb.2016.1289>
- Bregman, T. P., Sekercioglu, C. H., & Tobias, J. A. (2014). Global patterns and predictors of bird species responses to forest fragmentation: Implications for ecosystem function and conservation.

- Biological Conservation*, 169, 372–383. <https://doi.org/10.1016/j.biocon.2013.11.024>
- Cadotte, M., Dinnage, R., & Tilman, D. (2012). Phylogenetic diversity promotes ecosystem stability. *Ecology*, 93(8), S223–S233. <https://doi.org/10.1890/11-0426.1>
- Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services. *Journal of Applied Ecology*, 48(5), 1079–1087. <https://doi.org/10.1111/j.1365-2664.2011.02048.x>
- Cardinale, B. J., Duffy, J. E., Gonzalez, A., Hooper, D. U., Perrings, C., Venail, P., ... Naeem, S. (2012). Biodiversity loss and its impact on humanity. *Nature*, 486(7401), 59–67. <https://doi.org/10.1038/nature11148>
- de Bello, F., Lavorel, S., Diaz, S., Harrington, R., Cornelissen, J. H. C., Bardgett, R. D., ... Harrison, P. A. (2010). Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodiversity and Conservation*, 19(10), 2873–2893. <https://doi.org/10.1007/s10531-010-9850-9>
- Diaz, S., & Cabido, M. (2001). Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology & Evolution*, 16(11), 646–655. [https://doi.org/10.1016/S0169-5347\(01\)02283-2](https://doi.org/10.1016/S0169-5347(01)02283-2)
- Diaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., ... Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, 3(9), 2958–2975. <https://doi.org/10.1002/ece3.601>
- Drummond, A. J., & Rambaut, A. (2007). BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology*, 7(1), 214. <https://doi.org/10.1186/1471-2148-7-214>
- Dunning, J. B. J. (2008). *CRC Handbook of avian body masses*. (J. John B. Dunning, Ed., 2nd ed.). CRC Press.
- Ericson, P. G., Anderson, C. L., Britton, T., Elzanowski, A., Johansson, U. S., Kallersjö, M., ... May, G. (2006). Diversification of Neoaves: Integration of molecular sequence data and fossils. *Biology Letters*, 2(4), 543–547. <https://doi.org/10.1098/rsbl.2006.0523>
- Flynn, D. F. B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B. T., Lin, B. B., ... DeClerck, F. (2009). Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, 12(1), 22–33. <https://doi.org/10.1111/j.1461-0248.2008.01255.x>
- Flynn, D. F. B., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem–function relationships. *Ecology*, 92(8), 1573–1581. <https://doi.org/10.1890/10-1245.1>
- Fründ, J., Dormann, C. F., Holzschuh, A., & Tscharntke, T. (2013). Bee diversity effects on pollination depend on functional complementarity and niche shifts. *Ecology*, 94(9), 2042–2054. <https://doi.org/10.1890/12-1620.1>
- Gagic, V., Bartomeus, I., Jonsson, T., Taylor, A., Winqvist, C., Fischer, C., ... Bommarco, R. (2015). Functional identity and diversity of animals predict ecosystem functioning better than species-based indices. *Proceedings of the Royal Society B: Biological Sciences*, 282(1801), 20142620. <https://doi.org/10.1098/rspb.2014.2620>
- García, D. (2016). Birds in ecological networks: Insights from bird–plant mutualistic interactions. *Ardeola*, 63(1), 151–180. <https://doi.org/10.13157/arla.63.1.2016.rp7>
- García, D., & Chacoff, N. P. (2007). Scale-dependent effects of habitat fragmentation on hawthorn pollination, frugivory, and seed predation. *Conservation Biology*, 21(2), 400–411. <https://doi.org/10.1111/j.1523-1739.2006.00593.x>
- García, D., Donoso, I., & Rodríguez-Pérez, J. (2018). Frugivore biodiversity and complementarity in interaction networks enhance landscape-scale seed dispersal function. *Functional Ecology*, 32(12), 2742–2752. <https://doi.org/10.1111/1365-2435.13213>
- García, D., Miñarro, M., & Martínez-Sastre, R. (2018). Birds as suppliers of pest control in cider apple orchards: Bird biodiversity filters and insectivore effect. *Agriculture, Ecosystems & Environment*, 254, 233–243. <https://doi.org/10.1016/j.agee.2017.11.034>
- García, D., Miñarro, M., & Martínez-Sastre, R. (2021). Enhancing ecosystem services in apple orchards: Nest boxes increase pest control by insectivorous birds. *Journal of Applied Ecology*, 58(3), 465–475. <https://doi.org/10.1111/1365-2664.13823>
- García, D., Quevedo, M., Obeso, J. R., & Abajo, A. (2005). Fragmentation patterns and protection of montane forest in the Cantabrian range (NW Spain). *Forest Ecology and Management*, 208(1–3), 29–43. <https://doi.org/10.1016/j.foreco.2004.10.071>
- García, D., Zamora, R., & Amico, G. C. (2010). Birds as suppliers of seed dispersal in temperate ecosystems: Conservation guidelines from real-world landscapes. *Conservation Biology*, 24(4), 1070–1079. <https://doi.org/10.1111/j.1523-1739.2009.01440.x>
- García, D., Zamora, R., & Amico, G. C. (2011). The spatial scale of plant–animal interactions: Effects of resource availability and habitat structure. *Ecological Monographs*, 81(1), 103–121. <https://doi.org/10.1890/10-0470.1>
- Gaston, K. J., Cox, D. T. C., Canavelli, S. B., García, D., Hughes, B., Maas, B., ... Inger, R. (2018). Population abundance and ecosystem service provision: The case of birds. *Bioscience*, 68(4), 264–272. <https://doi.org/10.1093/biosci/biy005>
- Gregory, R. D., Gibbons, D. W., & Donald, P. F. (2004). Bird census and survey techniques. In *Bird ecology and conservation* (pp. 17–56).
- Hanz, D. M., Böhning-Gaese, K., Ferger, S. W., Fritz, S. A., Neuschulz, E. L., Quitián, M., ... Schleuning, M. (2019). Functional and phylogenetic diversity of bird assemblages are filtered by different biotic factors on tropical mountains. *Journal of Biogeography*, 46(2), 291–303. <https://doi.org/10.1111/jbi.13489>
- Hillebrand, H., & Matthiessen, B. (2009). Biodiversity in a complex world: Consolidation and progress in functional biodiversity research. *Ecology Letters*, 12(12), 1405–1419. <https://doi.org/10.1111/j.1461-0248.2009.01388.x>
- Hordley, L. A., Gillings, S., Petchey, O. L., Tobias, J. A., & Oliver, T. H. (2021). Diversity of response and effect traits provides complementary information about avian community dynamics linked to ecological function. *Functional Ecology*, 35(9), 1938–1950. <https://doi.org/10.1111/1365-2435.13865>
- Jankowski, J. E., Merkord, C. L., Rios, W. F., Cabrera, K. G., Revilla, N. S., & Silman, M. R. (2013). The relationship of tropical bird communities to tree species composition and vegetation structure along an Andean elevational gradient. *Journal of Biogeography*, 40(5), 950–962. <https://doi.org/10.1111/jbi.12041>
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, 491(7424), 444–448. <https://doi.org/10.1038/nature11631>
- Kembel, S. W., Cowan, P. D., Helmus, M. R., Cornwell, W. K., Morlon, H., Ackerly, D. D., ... Webb, C. O. (2010). Picante: R tools for integrating phylogenies and ecology. *Bioinformatics*, 26, 1463–1464.
- Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91(1), 299–305. <https://doi.org/10.1890/08-2244.1>
- Laliberté, E., Legendre, P., & Shipley, B. (2014). FD: Measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12.
- Lasky, J. R., Uriarte, M., Boukili, V. K., Erickson, D. L., John Kress, W., & Chazdon, R. L. (2014). The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. *Ecology Letters*, 17(9), 1158–1167. <https://doi.org/10.1111/ele.12322>
- Lefcheck, J. S. (2016). piecewiseSEM: Piecewise structural equation modelling in R for ecology, evolution, and systematics. *Methods in Ecology and Evolution*, 7(5), 573–579. <https://doi.org/10.1111/2041-210X.12512>
- Letten, A. D., & Cornwell, W. K. (2015). Trees, branches and (square) roots: Why evolutionary relatedness is not linearly related to functional distance. *Methods in Ecology and Evolution*, 6(4), 439–444. <https://doi.org/10.1111/2041-210X.12237>

- Llorente-Culebras, S., Molina-Venegas, R., Barbosa, A. M., Carvalho, S. B., Rodríguez, M., & Santos, A. M. C. (2021). Iberian protected areas capture regional functional, phylogenetic and taxonomic diversity of most tetrapod groups. *Frontiers in Ecology and Evolution*, 9(July), 1–15. <https://doi.org/10.3389/fevo.2021.634653>
- Luck, G. W., Lavorel, S., McIntyre, S., & Lumb, K. (2012). Improving the application of vertebrate trait-based frameworks to the study of ecosystem services. *Journal of Animal Ecology*, 81(5), 1065–1076. <https://doi.org/10.1111/j.1365-2656.2012.01974.x>
- Martínez, D., & García, D. (2015). Disentangling habitat use by frugivorous birds: Constant interactive effects of forest cover and fruit availability. *Basic and Applied Ecology*, 16(5), 460–468. <https://doi.org/10.1016/j.baae.2015.04.012>
- Martínez, D., & García, D. (2017). Role of avian seed dispersers in tree recruitment in woodland pastures. *Ecosystems*, 20(3), 616–629. <https://doi.org/10.1007/s10021-016-0043-6>
- Martínez-Sastre, R., Miñarro, M., & García, D. (2020). Animal biodiversity in cider apple orchards: Simultaneous environmental drivers and effects on insectivory and pollination. *Agriculture, Ecosystems and Environment*, 295(March), 106918. <https://doi.org/10.1016/j.agee.2020.106918>
- Miklós, I., & Podani, J. (2004). Randomization of presence-absence matrices: Comments and new algorithms. *Ecology*, 85(1), 86–92. <https://doi.org/10.1890/03-0101>
- Miñarro, M., Dapena, E., & Blázquez, M. D. (2011). *Guía ilustrada de las enfermedades, las plagas y la fauna beneficiosa del cultivo del manzano*.
- Mokany, K., Ash, J., & Roxburgh, S. (2008). Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, 96(5), 884–893. <https://doi.org/10.1111/j.1365-2745.2008.01395.x>
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., Ohara, R. B., ... Wagner, H. (2018). Vegan: Community ecology package. R Package Version 2. 4–6. <https://doi.org/10.1093/molbev/msv334>
- Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35(3), 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Peisley, R. K., Saunders, M. E., & Luck, G. W. (2015). A systematic review of the benefits and costs of bird and insect activity in agroecosystems. *Springer Science Reviews*, 3(2), 113–125. <https://doi.org/10.1007/s40362-015-0035-5>
- Peña, R., Schleuning, M., Donoso, I., Rodríguez-Pérez, J., Dalerum, F., & García, D. (2020). Biodiversity components mediate the response to forest loss and the effect on ecological processes of plant–frugivore assemblages. *Functional Ecology*, 34(6), 1257–1267. <https://doi.org/10.1111/1365-2435.13566>
- Peña, R., Schleuning, M., Miñarro, M., & García, D. (2022). Data from: Variable relationships between trait diversity and avian ecological functions in agroecosystems. *Dryad Digital Repository*. <https://doi.org/10.5061/dryad.xgxd254jr>
- Petchey, O. L., Evans, K. L., Fishburn, I. S., & Gaston, K. J. (2007). Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, 76(5), 977–985. <https://doi.org/10.1111/j.1365-2656.2007.01271.x>
- Pigot, A. L., Bregman, T., Sheard, C., Daly, B., Etienne, R. S., & Tobias, J. A. (2016). Quantifying species contributions to ecosystem processes: A global assessment of functional trait and phylogenetic metrics across avian seed-dispersal networks. *Proceedings of the Royal Society B: Biological Sciences*, 283(1844), 20161597. <https://doi.org/10.1098/rspb.2016.1597>
- Pigot, A. L., Sheard, C., Miller, E. T., Bregman, T. P., Freeman, B. G., Roll, U., ... Tobias, J. A. (2020). Macroevolutionary convergence connects morphological form to ecological function in birds. *Nature Ecology and Evolution*, 4(2), 230–239. <https://doi.org/10.1038/s41559-019-1070-4>
- Quitán, M., Santillán, V., Espinosa, C. I., Homeier, J., Böhning-Gaese, K., Schleuning, M., & Neuschulz, E. L. (2019). Direct and indirect effects of plant and frugivore diversity on structural and functional components of fruit removal by birds. *Oecologia*, 189(2), 435–445. <https://doi.org/10.1007/s00442-018-4324-y>
- Rader, R., Reilly, J., Bartomeus, I., & Winfree, R. (2013). Native bees buffer the negative impact of climate warming on honey bee pollination of watermelon crops. *Global Change Biology*, 19(10), 3103–3110. <https://doi.org/10.1111/gcb.12264>
- Rezende, E. L., Lavabre, J. E., Guimarães, P. R., Jr., Jordano, P., & Bascompte, J. (2007). Non-random coextinctions in phylogenetically structured mutualistic networks. *Nature*, 448(7156), 925–928. <https://doi.org/10.1038/nature05956>
- Saracco, J. F., Collazo, J. A., & Groom, M. J. (2004). How do frugivores track resources? Insights from spatial analyses of bird foraging in a tropical forest. *Oecologia*, 139(2), 235–245. <https://doi.org/10.1007/s00442-004-1493-7>
- Schleuning, M., Fründ, J., & García, D. (2015). Predicting ecosystem functions from biodiversity and mutualistic networks: An extension of trait-based concepts to plant-animal interactions. *Ecography*, 38(4), 380–392. <https://doi.org/10.1111/ecog.00983>
- Tscharntke, T., Sekercioglu, C. H., Dietsch, T. V., Sodhi, N. S., Hoehn, P., & Tylianakis, J. M. (2008). Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, 89(4), 944–951. <https://doi.org/10.1890/07-0455.1>
- Tucker, C. M., Davies, T. J., Cadotte, M. W., & Pearse, W. D. (2018). On the relationship between phylogenetic diversity and trait diversity. *Ecology*, 99(6), 1473–1479. <https://doi.org/10.1002/ecy.2349>
- Tylianakis, J. M., Rand, T. A., Kahmen, A., Klein, A. M., Buchmann, N., Perner, J., & Tscharntke, T. (2008). Resource heterogeneity moderates the biodiversity-function relationship in real world ecosystems. *PLoS Biology*, 6(5), 0947–0956. <https://doi.org/10.1371/journal.pbio.0060122>
- Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89(8), 2290–2301. <https://doi.org/10.1890/07-1206.1>
- Wilman, H., Belmaker, J., Jennifer, S., de la Rosa, C., Rivadeneira, M. M., & Jetz, W. (2014). EltonTraits 1.0: Species-level foraging attributes of the world's birds and mammals. *Ecology*, 95(October 2013), 2027. <https://doi.org/10.1890/13-1917.1>
- Winfree, R., Fox, J. W., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology Letters*, 18(7), 626–635. <https://doi.org/10.1111/ele.12424>
- Winfree, R., Reilly, J. R., Bartomeus, I., Cariveau, D. P., Williams, N. M., & Gibbs, J. (2018). Species turnover promotes the importance of bee diversity for crop pollination at regional scales. *Science*, 359(6377), 791–793. <https://doi.org/10.1126/science.aao2117>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Peña, R., Schleuning, M., Miñarro, M., & García, D. (2022). Variable relationships between trait diversity and avian ecological functions in agroecosystems. *Functional Ecology*, 00, 1–12. <https://doi.org/10.1111/1365-2435.14102>