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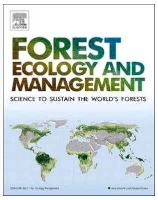

Bird taxonomic and functional diversity, group- and species-level effects on a gradient of weevil-caused damage in eucalypt plantations

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ABSTRACT

The relative contribution of bird communities to insect pest control has been seldom estimated using trait-based functional diversity indices, in opposition to the general usage of taxonomic indices simply based on the presence and abundance of species. Moreover, few studies attempted to quantify the explicit contribution of functional groups or species of birds to the control of insect pests. We investigated eucalypt plantations under a gradient of defoliation caused by the eucalyptus weevil *Gonipterus platensis* to assess how avian insectivory links with (1) taxonomic and (2) functional diversity indices, and with (3) groups and (4) species of functional insectivores. In agreement with our hypothesis, weevil-caused damage was negatively correlated to avian insectivory in the four studied approaches. Taxonomic diversity indices consistently presented a negative correlation with weevil-caused damage, but, contrary to our expectation, functional diversity indices were defective predictors of weevil-caused damage in eucalypt stands. Results were further explicit in the analyses conducted with groups and species of functional insectivores, wherein significant lower levels of weevil-caused damage in eucalypt stands were mainly associated with the higher abundance of canopy foragers, even though ground- and understory-gleaning species also provided competitive models at the species-level. This study establishes the importance of using multivariate trait-based approaches to understand how functional diversity drives ecosystem services, as it is here demonstrated for avian insectivory in eucalypt plantations. Top-down trophic control of the eucalyptus weevil by birds can reduce damage in areas where functional insectivorous birds aggregate.

1. Introduction

Among vertebrates, birds provide a number of essential and economically valuable ecosystem services to humans as a result of their taxonomic and niche diversity, acting as predators, seed dispersers, pollinators, scavengers, nutrient depositors, and ecosystem engineers, in addition to their recreational value (Whelan et al., 2015; Gaston et al., 2018). Although early studies related ecosystem functioning to taxonomic species richness and evenness as the only measures of diversity (Hillebrand et al., 2008; Kirwan et al., 2009), quantifying the relationship between ecosystem functioning and different community characteristics, commonly designated as traits, has produced more exact and suitable predictions of birds' role in ecosystems (Villéger et al., 2008; Laliberté and Legendre, 2010; Mouchet et al., 2010). Specific traits have been used to associate bird assemblages with greater contributions to ecosystem services and their subsequent summarisation using functional diversity indices has allowed to examine changes in the provisioning of ecosystem services across multiple land uses (e.g., Mayfield et al., 2010; Mouillot et al., 2013). The importance of trait complementarity in bird communities was demonstrated through the positive correlation of functional diversity indices with insect pest control (Philpott et al., 2009; Barbaro et al., 2014, Barbaro et al., 2017).

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However, the functional classification must include traits directly related to insectivory in order that bird functional diversity can be taken as a driver of avian insectivory (Zhu et al., 2017; Ikin et al., 2019). Moreover, the causes underlying the observed relationships between functional diversity indices and the function of interest, as, for example, insect pest control, may need further detail to answer problems at a scale relevant to management. In managed ecosystems where significant economic losses typically arise from the damage caused by a specific insect pest, quantifying the relative contribution of particular functional groups of birds to target pest control should be a key point to understand ecosystem functioning and enviably support pest management practices. In such cases, the abundance of functional insectivorous bird groups (Gaston et al., 2018; Ikin et al., 2019), or even single abundant species (Maas et al., 2015), could be a better predictor of targeted pest control services than functional diversity and taxonomic diversity indices.

The vast plantations of eucalypts (*Eucalyptus*, L'Hér. 1789) are a clear example of pest susceptibility in managed systems. Eucalypts are among the most widely planted tree species in the world, being the most important source of commercial cellulose fibre (Eldridge et al., 1994). Despite eucalypts have early benefited from the absence of insect pests by being established outside their native range, essentially in Australia, insect species that feed on eucalypts have been increasingly reported in eucalypt-growing regions worldwide (Hurley et al., 2016). Leaf-eating weevils in the *Gonipterus scutellatus* species complex (Gyllenhal 1883; Coleoptera: Curculionidae) have been accidentally introduced into eucalypt plantations around the world and are currently among the eucalypt pests of greatest concern (Jeger et al., 2018). Larvae and adults feed on buds, shoots and newly expanded leaves, causing eucalypts to lose apical dominance and decreasing wood productivity (Tooke, 1955; Loch and Matsuki, 2010). Eucalyptus weevil populations have been globally managed by means of biological control through the release of the egg parasitoid *Anaphes nitens* (Girault 1928; Hymenoptera: Mymaridae) but biological control programs were not completely successful in every country (Schröder et al., 2020). Although a release program of *A. nitens* was implemented in Portugal, which has the world's largest cultivated area of *Eucalyptus globulus* (Labill. 1799) (Cerasoli et al., 2016), the parasitoid has failed to control the eucalyptus weevil *Gonipterus platensis* (Marelli 1926; Coleoptera: Curculionidae) at higher altitudes (Reis et al., 2012). In these cases, weevil populations have been generally managed with neonicotinoids which, in addition to being more expensive, presenting contamination risks, and favouring the development of pest resistance (Holmes and MacQuarrie, 2016), were recently banned in the European Union (CJEU (Court of Justice of the European Union), 2023). Therefore, environmentally friendly control strategies are needed to reduce these hazards (Jactel et al., 2019) and sustain eucalypt-growing businesses.

Generalist predatory birds can have a top-down effect, reducing the abundance of their prey and thus their impacts (Mäntylä et al., 2011; Díaz-Siefer et al., 2022). This was demonstrated in forest systems where the density of predatory birds responded significantly to changes in prey density (Venier and Holmes, 2010; Bereczki et al., 2014), including in native eucalypt forests where the influx of generalist insectivores reduced the infestation of psyllids (Hemiptera: Psyllidae) (Loyn et al., 1983; Clarke and Schedvin, 1999). Similarly, outside of the native range of eucalypts, the local aggregation of insectivorous birds can potentially maintain sparse populations of the eucalyptus weevil or suppress emerging outbreaks. Even though eucalypt plantations are a poor habitat for birds in most areas where they have been introduced, especially if compared to native forests and monocultures of native tree species (Pina, 1989; Proençaet et al., 2010; da Silva et al., 2012; Calviño-Cancela, 2013), the unsuitability of eucalypt plantations for birds is mostly attributed to a shortage of feeding resources. On this basis, the eucalyptus weevil can represent an important food source for insectivorous birds. This hypothesis should have greater relevance considering recent results from molecular gut-content analyses of birds captured in eucalypt plantations that demonstrate that many native species feed on the eucalyptus weevil (da Silva et al., 2022).

In the present work, we investigated eucalypt stands in central Portugal to find support for the hypothesis that avian insectivory can mediate negative correlations between a gradient of weevil-caused defoliation, and bird diversity and abundance. We tested for variations in the strength of the diversity-insectivory relationship according to the specificities of (1) taxonomic diversity indices, based only on the presence and abundance of functional insectivores (i.e., bird species that exert insectivory services in eucalypt stands), and (2) functional diversity indices, that additionally used traits with functional significance for avian insectivory in their calculations. Concurrently, to obtain further evidence and clarification of the associations between avian insectivory and functional diversity, we tested if weevil-caused damage was correlated with the specific abundance of (3) functional groups of insectivorous birds, defined by the modalities of functional traits, and (4) functional insectivorous species. By combining these four approaches – taxonomic diversity, functional diversity, functional groups, and functional insectivorous species – we aimed to understand if tree condition in eucalypt plantations can be related to the diversity and abundance of functional insectivores, and, most particularly, whether the multiple facets of avian insectivory can reflect differences in the potential of birds to control the eucalyptus weevil.

2. Materials and methods

2.1. Study area

Fieldwork was conducted in 2019 within two areas dominated by eucalypt stands in central Portugal: one area with 50 km^2 near Sever do Vouga (centroid at 40°43′41.88″N 8°24′25.2″W; 78 to 482 m a.s.l.) almost continuously covered by eucalypt plantations, and other with 100 km^2 near Pampilhosa da Serra (centroid at 40°1′50.88″N 8°3′37.08″W; 335 to 728 m a.s.l.) where eucalypt stands were interspersed by pine plantations, shrublands, and subsistence farming (Fig. 1). Eucalypt plantations from the two areas were subjected to the same short-rotation management (10–12 years) and trees were 6 ± 3 and 5 ± 3 years-old and had a height of 10.9 ± 3.8 and 8.2 ± 4.0 m (mean ± SD), respectively, in Sever do Vouga and Pampilhosa da Serra. The study areas are characterized by a warm, dry summer temperate climate – the mean monthly temperature varies between 7.7 and 20.6 °C, and the mean accumulated annual precipitation varies between 461.1 and 1101.4 mm (IPMA (Instituto Português do Mar e da Atmosfera), 2019).

Random sampling points were generated within the study areas using QGIS version 3.4 software (QGIS Development Team, 2018). To simplify fieldwork logistics, additional sampling points were systematically created, corresponding to the four corners of 30 quadrats (~250 m × 250 m) centred on a randomly generated point. We discarded points located outside eucalypt stands, as well as points less than 150 m from their closest adjacent points, through the interpretation of 25 cm-resolution orthophoto imagery of 2018, accessed using the Web Map Service (WMS) on the website of the Direção-Geral do Território (https://cartografia.dgterritorio.gov.pt/wms/ortos2018?service = wms&request = getcapabilities). In total, 240 points were selected and subsequently visited during field surveys. Because pesticides were used to control eucalyptus weevil in part of the study areas, data collected at points up to 50 m from those sites were discarded to exclude any potential effects of pesticides on the samples. Overall, 215 sampling points were considered in this study.

2.2. Data collection

2.2.1. Weevil-caused damage

The eucalyptus weevil is typically bivoltine in the study areas, that is, it produces two generations in the same year. Adult insects are found throughout the year, although their emergence peak occurs in January

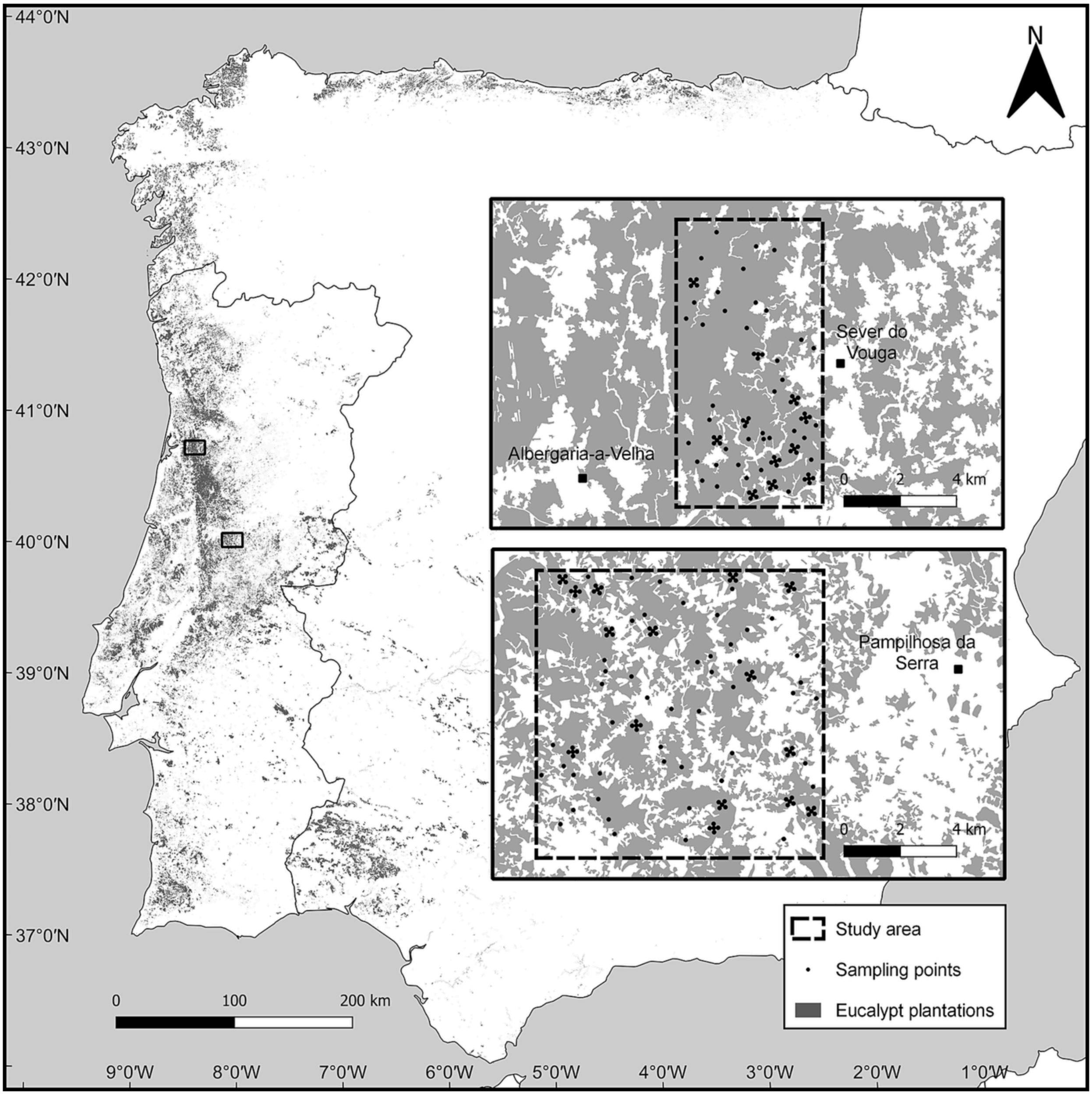

Fig. 1. Study area locations in central Portugal shown in the context of eucalypt distribution in the Iberian Peninsula. Distribution data for *Eucalyptus* spp. was obtained from the maximum actuality forest map of Spain (MFEMax) and the land use and occupation cartography of mainland Portugal for 2018 (COS2018), downloaded respectively from the websites of the Dirección General de Biodiversidad, Bosques y Desertificación (https://www.miteco.gob.es/es/cartografia-y-sig/ide/descargas/biodiversidad/mfe.aspx) and of the Direção-Geral do Território (https://mapas.dgterritorio.pt/DGT-ATOM-download/COS_Final/COS2018_v1/COS2018_v1.zip).

and August. Egg postures, containing an average of eight eggs, are laid in late winter and late summer with larval eclosion occurring two weeks after. Most damage to trees occurs in mid-spring and early-autumn during the abundance peaks of larvae. After complete development, larvae release from the tree and burrow into the soil, entering a 1–2-months pupal stage before adult emergence (Valente et al., 2004; Santolamazza-Carbone et al., 2006).

Two visits were made to evaluate weevil-caused damage in each point, in spring (May–June) and autumn (September–October), coinciding with the periods following the abundance peaks of first- and second-generation larvae, respectively. An imaginary cross of 20 m × 20 m was drawn according to tree rows at each point, and the closest eucalypt tree to each tip was sampled, totalling four trees per point which were not necessarily the same in the two visits. Because *E. globulus* is heteroblastic (i.e., during plant development, juvenile foliage is replaced by morphologically and physiologically distinct adult foliage) and the eucalyptus weevil prefers to feed on new adult leaves (Tooke, 1955; Branco et al., 2016), only trees that had transitioned, totally or partially, to adult foliage were sampled. Sampled eucalypt trees were neither affected by pests other than the eucalyptus weevil nor by pathogens in a conspicuous way. The upper third of the canopy, containing new flushing adult foliage, was inspected by a single observer (P.B.L.), using binoculars, and the damage caused by the eucalyptus weevil was scored according to the following scale: (0) no new leaves are damaged by adults or larvae; (1) <25% of new leaves are damaged; (2) 25 to 50% of new leaves are damaged; (3) 50 to 75% of new leaves are damaged; (4) more than 75% of the leaves are damaged, with at least ¼ of those showing damage in less than half of their leaf area; (5) more than 75% of the leaves are damaged, with at least ¼ of those showing damage in more than half of their leaf area; and (6) all new leaves are fully damaged (Ceia et al., 2021).

2.2.2. Bird community

Two point-counts were used to estimate the abundance of each bird species at the sampling points correspondingly during the nesting season of most bird species (May–June), and the post-breeding period and passage of migrant birds in the region (September–October). Counts were performed in the absence of rain or strong wind, in the period comprising the half hour preceding sunrise and the subsequent four hours. Counts started one minute after the observer arrived at the point to allow birds to settle down from any disturbance caused by his arrival. All birds heard or seen up to 50 m from the observer were recorded during a ten-minute period.

2.3. Data analysis

All data exploration, analyses, and modelling were performed with R version 4.2.2 software (R Core Team, 2022).

The maximum score obtained from the eight estimates of weevil-caused damage taken per point (four trees in two seasons) was used in the analyses as a proxy of the year-round highest abundance of the eucalyptus weevil at the points. Concurrently, bird abundance at each point was analysed as the sum of spring and autumn counts, so that our measures of avian insectivory covered the range of niches and periods associated with distinct life-cycle stages of the eucalyptus weevil in each of its two annual generations.

Analyses were conducted with a subset of the bird community concerning only functional insectivores (abbreviated as FI) to improve their potential to predict avian insectivory (Philpott et al., 2009; Barbaro et al., 2017, 2021; Lourenço et al., 2021). We classified as FI all the bird species that are insectivores or omnivores (Wilman et al., 2014) and regularly forage on eucalypt plantations. For this reason, following an exploratory analysis, we excluded rare species detected in <10% of the points (Supporting information: Table S1).

2.3.1. Taxonomic diversity indices

Taxonomic diversity indices consisted of the abundance and richness of FI (FI.N and FI.S, respectively), and Shannon's equitability index for FI (FI.EH), which was the normalization of the Shannon's diversity index based on the number of species of FI in the entire community, calculated using the function 'diversity' in the R package 'vegan' (Oksanen et al., 2022).

2.3.2. Functional diversity indices

Functional diversity indices consisted of functional richness (FRic; the amount of the multidimensional functional space filled by the community), functional evenness (FEve; regularity of abundance distribution in the filled functional space), functional divergence (FDiv; divergence of abundance distribution in the filled functional space) (Mason et al., 2005; Villéger et al., 2008), functional dispersion (FDis; mean distance of all species to the community mean trait value) (Laliberté and Legendre, 2010), and Rao's quadratic entropy (RaoQ; mean pairwise functional dissimilarity between species) (Botta-Dukát, 2005).

To calculate functional diversity indices, every FI species was assigned with a modality in 17 traits related to bird phenology, foraging substrate (Wilman et al., 2014) and morphology (Tobias et al., 2022) (Supporting information: Table S2). Traits were selected based on their significance to the particular function of avian insectivory, the accessibility to reliable information in literature, and the use of similar groupings for functional classification of birds in other studies (Philpott et al., 2009; Barbaro et al., 2014, 2017; Lourenço et al., 2021). Because the number of traits was too high compared to the number of FI species (species richness should be higher than 2^T with T being the number of traits; Mouchet et al., 2010), we reduced the information of the traits into independent axes using principal components analysis (PCA) (Laliberté and Legendre, 2010; Maire et al., 2015). Together with phenology, we used the first two axes from a PCA computed with the five foraging substrate traits in the original matrix (40.3%, and 23.3% of total variance, respectively), and the first axis from a PCA computed with the 11 morphological traits (79.9% of total variance). The resulting species-by-trait matrix (15 species × 4 traits) was used to calculate the five functional diversity indices using the package function 'dbFD' in the R package 'FD' (Laliberté and Legendre, 2010; Laliberté et al., 2014).

2.3.3. Functional groups

Functional insectivores were grouped according to the modalities of phenology (resident, and migrant), foraging substrate traits (ground, understory, mid-high, and canopy), and a representation of morphology traits using three body mass size classes: tiny (<15 g), small (15–30 g), and large (60–120 g) (Table 1). The size classes followed the classification of Philpott et al. (2009). Although 'air' was considered as a foraging substrate trait, it was not used to assemble a functional group for the reason that it was used by a single species in a minor percentage (Supporting information: Table S2). The nine functional groups assembled were thus assumed to evaluate the complementarity of insectivorous species in resource use in eucalypt plantations (Mouchet et al., 2010).

2.3.4. Modelling

Cumulative link mixed models ('clmm' procedure in the package 'ordinal'; Christensen, 2019) were used to model weevil-caused damage in the points (ordinal response variable), assuming unstructured thresholds. Univariate models were designed to include (1) taxonomic diversity indices (FI.N, FI.S, FI.EH), (2) functional diversity indices (FRic, FEve, FDiv, FDis, RaoQ), (3) the abundance of functional groups (nine groups), and (4) the abundance of functional insectivorous species (fifteen species) as single continuous explanatory variables. All models included the study area as a fixed factor and the quadrat as a random factor to account for spatial autocorrelation in the data sets. The strength of evidence for a model was evaluated by comparing the Akaike Information Criterion corrected for small sample size (AICc) with a null model, where all models with ΔAICc (AICc of null model - AICc of avian insectivory model) below -2.0 were considered as competitive models, and by determining if the 95% confidence intervals of the parameter estimates did not overlap with zero (Burnham and Anderson, 2002).

3. Results

3.1. General description of weevil-caused damage

Weevil-caused damage ranged from the absence of defoliation (level 0), recorded in 20% of the points, to the full defoliation of new leaves (level 6), recorded in 13% of the points. Intermediate damage symptoms were recorded in 15% (level 1), 5% (level 2), 6% (level 3), 17% (level 4), and 25% (level 5) of the points.

3.2. General description of the bird community

In total, 1676 individuals of 51 species were recorded in the two counts. A major percentage (76%) of total bird abundance corresponded to the fifteen bird species classified as FI in eucalypt stands (Table 1).

3.3. Relationship between weevil-caused damage and functional insectivores

There was a negative correlation between weevil-caused damage and most of the variables chosen to represent avian insectivory in the four studied approaches (Fig. 2; Supporting information: Fig. S1). The parameters for models computed in the four approaches are listed as

Table 1
List of the functional insectivorous bird species in eucalypt plantations and their correspondent assemblage in functional groups established according to the modalities of selected traits.

Species			Phenology	Foraging substrates				Body size
Common name	Scientific name	Code						
Tree Pipit	*Anthus trivialis*	ANTTRI	passage migrant	ground	–	–	–	small
Sardinian Warbler	*Curruca melanocephala*	CURMEL	resident	ground	understory	mid-high	–	tiny
Dartford Warbler	*Curruca undata*	CURUND	resident	–	understory	–	–	tiny
Great Spotted Woodpecker	*Dendrocopos major*	DENMAJ	resident	–	understory	mid-high	canopy	large
European Robin	*Erithacus rubecula*	ERIRUB	resident	ground	understory	–	–	small
European Pied Flycatcher	*Ficedula hypoleuca*	FICHYP	passage migrant	–	understory	mid-high	canopy	tiny
Eurasian Chaffinch	*Fringilla coelebs*	FRICOE	resident	ground	understory	mid-high	–	small
Crested Tit	*Lophophanes cristatus*	LOPCRI	resident	ground	understory	mid-high	canopy	tiny
Great Tit	*Parus major*	PARMAJ	resident	–	understory	mid-high	canopy	small
Coal Tit	*Periparus ater*	PERATE	resident	ground	understory	mid-high	–	tiny
Willow Warbler	*Phylloscopus trochilus*	PHYTRO	passage migrant	–	–	mid-high	canopy	tiny
Firecrest	*Regulus ignicapilla*	REGIGN	resident	–	understory	mid-high	–	tiny
Blackcap	*Sylvia atricapilla*	SYLATR	resident	–	–	mid-high	–	small
Eurasian Wren	*Troglodytes troglodytes*	TROTRO	resident	ground	understory	–	–	tiny
Eurasian Blackbird	*Turdus merula*	TURMER	resident	ground	understory	mid-high	–	large

Supporting information (Table S3).

From the three models computed with taxonomic diversity indices, only that using FI abundance was not competitive ($z = -1.99$, $p = 0.047$, $\Delta AICc = -1.8$). Weevil-caused damage showed a significant negative correlation with both FI richness ($z = -3.07$, $p = 0.002$, $\Delta AICc = -7.4$) and FI evenness ($z = -2.66$, $p = 0.008$, $\Delta AICc = -5.0$), and the model using FI richness was amongst the most competitive models overall.

Functional diversity indices were worse predictors of weevil-caused damage in the points ($\Delta AICc \geq 0.0$), except for functional richness which showed a significant negative correlation with the response variable ($z = -2.12$, $p = 0.034$, $\Delta AICc = -2.3$).

The best models for weevil-caused damage using the abundance of functional groups as explanatory variables were those computed with canopy foragers ($z = -3.30$, $p < 0.001$, $\Delta AICc = -9.3$) and tiny birds ($z = -2.59$, $p = 0.010$, $\Delta AICc = -4.6$). The first was the most competitive model overall and showed an extremely significant negative correlation with weevil-caused damage.

Significant relationships with weevil-caused damage were found in six of the fifteen models computed with the abundance of single functional insectivorous species (Fig. 2). The best models included the abundance of Great Tit (*Parus major*: $z = -2.96$, $p = 0.003$, $\Delta AICc = -7.6$), European Robin (*Erithacus rubecula*: $z = -2.92$, $p = 0.003$, $\Delta AICc = -7.1$) and Coal Tit (*Periparus ater*: $z = -2.85$, $p = 0.004$, $\Delta AICc = -6.3$), although significant negative correlations with the response variable were also found for Eurasian Wren (*Troglodytes troglodytes*: $z = -2.41$, $p = 0.016$, $\Delta AICc = -4.0$) and Great Spotted Woodpecker (*Dendrocopos major*: $z = -2.10$, $p = 0.036$, $\Delta AICc = -2.6$). The abundance of Eurasian Chaffinch (*Fringilla coelebs*) showed a significant positive correlation with weevil-caused damage ($z = 133.30$, $p < 0.001$), but the model was not competitive ($\Delta AICc = -1.9$).

4. Discussion

The four studied approaches – taxonomic diversity, functional diversity, functional groups, functional insectivorous species – fundamentally agreed that significantly lower levels of weevil-caused damage were associated with greater diversity and abundance of species that exert insectivory services in eucalypt stands, that is, functional insectivores. There were however important divergences between the four approaches, or within approaches between their respective models, here used to evaluate avian insectivory.

4.1. Relationship between weevil-caused damage and functional insectivores

In general, taxonomic diversity indices were better predictors of weevil-caused damage in eucalypt plantations than trait-based functional diversity indices. The abundance and richness of functional insectivores have been noted as indicators of insect pest control by birds in Mediterranean vineyards (Barbaro et al., 2017, 2021; Lourenço et al., 2021), tropical cacao and coffee agroforests (Philpott et al., 2009) and mosaic landscapes (Barbaro et al., 2014), but, in our study, weevil-caused damage only showed a significant negative correlation (which was competitive) with species richness. While the evenness of functional insectivores was not considered in previous studies, our results denoted its potential to predict avian insectivory, even though the relationship between weevil-caused damage and taxonomic diversity indices was better explained by species richness than by Shannon's equitability.

On the other hand, we found less robustness and consistency in the relationships between weevil-caused damage and functional diversity indices. Functional diversity indices are directly influenced by the selection of traits used in their calculation, which often varies between studies as well (Petchey and Gaston, 2006; Villéger et al., 2008). To account for this source of variability on functional responses, we selected studies that investigated avian insectivory through the calculation of functional diversity indices based on multiple bird traits, and chose the same specific traits (adult diet, phenology, foraging substrate, body size) to associate bird assemblages that may potentially contribute to insect pest control (Philpott et al., 2009; Barbaro et al., 2014, 2017; Lourenço et al., 2021). In addition, our study used similar trait selection procedures and the same combination of indices (i.e., functional richness, evenness, divergence, dispersion, and Rao's quadratic entropy) implemented in recent works (Matuoka et al., 2020; Baker et al., 2021; Barbaro et al., 2021; Lourenço et al., 2021). Nevertheless, while functional diversity indices were good indicators of avian insectivory and showed significant positive correlations with insect pest control services in previous studies (Philpott et al., 2009; Barbaro et al., 2017, 2014; Lourenço et al., 2021), in our case the models computed with functional diversity indices, except for functional richness, were not competitive. It is hardly conceivable that calculated functional diversity indices did not suit the purpose of testing avian insectivory in eucalypt plantations because of the small number of species in the bird community, since we took this limitation into account during species assembly and trait selection procedures. Also, functional richness is the only of the calculated indices that exhibits a strong relationship with species richness (Mouchet et al., 2010). The poor performance of functional diversity indices may be instead related with the low abundance of birds in eucalypt plantations, considering that the model computed with functional richness was the only satisfactory and, contrarily to the other functional diversity indices, functional richness does not include species relative abundances in its calculations (Laliberté and Legendre, 2010). Further studies using similar multivariate trait-based approaches to explore

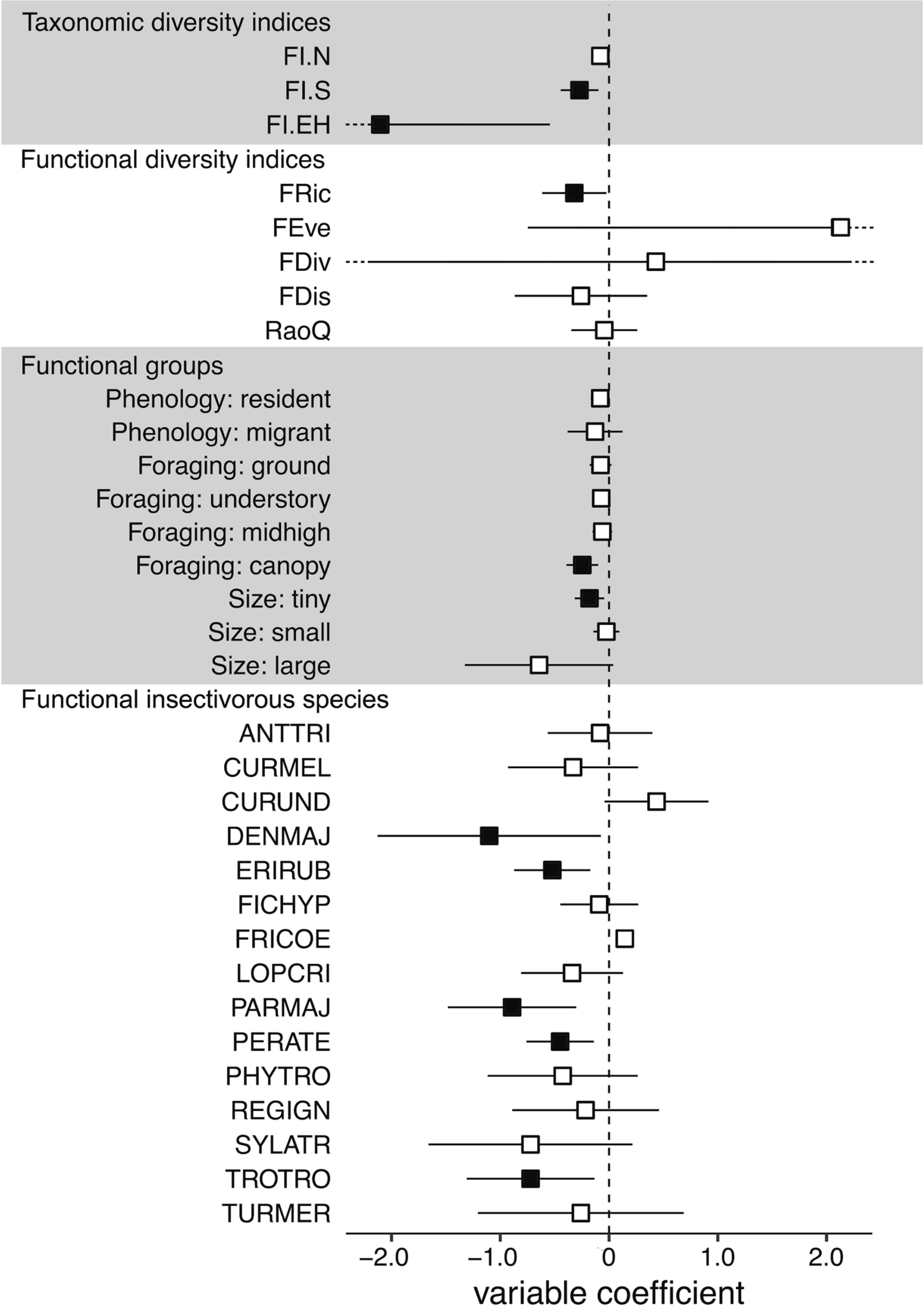

Fig. 2. Model coefficients for the explanatory variables used to predict weevil-caused damage in eucalypt plantations. Variables are grouped according to the four approaches to avian insectivory used in this study: taxonomic diversity indices (FI.N – abundance of functional insectivores; FI.S – richness of functional insectivores; FI.EH – Shannon's equitability index for functional insectivores), functional diversity indices (FRic – functional richness; FEve – functional evenness; FDiv – functional divergence; FDis – functional dispersion; RaoQ – Rao's quadratic entropy), functional groups, and functional insectivorous species (species assemblage and codes in Table 1). Error bars are 95% confidence intervals (dashed bar if the limit does not fit within the values indicated on the x-axis), and filled squares indicate competitive models, i.e., models with ΔAICc (compared to null model) < -2.0 in which weevil-caused damage was significantly related ($p < 0.05$) to the explanatory variable.

avian insectivory are required to better clarify and quantify these relationships, and attain a comprehensive understanding of how functional diversity drives pest control services.

A greater detail on the mechanisms underlying avian insectivory was reached through the abundance of multiple groups or species of functional insectivores. Groupings that included the foraging substrate tended to be more relevant than those formed according to body size or bird phenology. The foraging substrates used by birds should influence their ability to capture the eucalyptus weevil, and the extremely significant negative correlation found between weevil-caused damage and the abundance of canopy-foraging birds may implicate this functional group in the control of the eucalyptus weevil. Nonetheless, our approach at the species-level further enabled to discriminate the importance of functional insectivorous species against group assemblage. There were significant negative correlations between weevil-caused damage and the individual abundance of typical canopy-foraging species, namely Great Spotted Woodpecker, Great Tit and Coal Tit. At the same time, ground and understory gleaners, that would not necessarily be expected to capture defoliator larvae of the eucalyptus weevil in the canopy of eucalypt trees, were also associated with lower scores of weevil-caused damage. In effect, species such as the European Robin and the Eurasian Wren, that use predominantly the lower strata of eucalypt plantations, may also forage in the canopy of eucalypt trees, particularly in young plantations (5–8 years-old, as most ones in our study) where their abundance should be higher comparatively to that of canopy-foraging species (Calviño-Cancela, 2013). Additionally, such results may point to resource partitioning of prey life-cycle stages between functional insectivores. Because two generations of the eucalyptus weevil were produced during the study period, shallow-buried pupae and late-instar larvae descending from the canopy to pupate underground may have been taken by ground- and understory-gleaning birds. Recent molecular gut-content analyses of birds captured in eucalypt stands support weevil predation (at unidentified life-cycle stages) by functional insectivorous species that forage on different substrates (da Silva et al., 2022), thus validating their complementarity and joint potential for pest control in eucalypt plantations. However, da Silva et al. (2022) obtained no records of weevil predation for the Eurasian Wren, while it was amongst the functional insectivorous species whose abundance showed a significant negative correlation with weevil-caused damage in our study. Because only adult birds were sampled in da Silva et al. (2022), it could be that weevils are fed to developing chicks of Eurasian Wren but not being regularly eaten by the adult birds. Furthermore, our results do not provide support for the pest control potential of the Eurasian Chaffinch which had the highest detection rates of eucalyptus weevil in sampled birds' diet (da Silva et al., 2022). It is possible that functional insectivores were not exclusively related to direct predation of the eucalyptus weevil, but intraguild predation, as well as intraspecific and interspecific competition, also affected their association with weevil-caused damage (Schmitz, 2007; Pejchar et al., 2018). In any case, the net effects of birds on weevil-caused damage suggest that birds contribute positively to insect pest control in eucalypt stands.

4.2. Study limitations

One of the most common problems with assessing the impact of pests is that it is difficult to follow rules of good experimental design, such as randomization and replication, given that their occurrence is often temporarily and geographically patchy. To obtain a weevil-caused damage gradient that ranged from the absence of defoliation to the complete defoliation of new leaves, our study was set in two areas that covered 150 km^2. Our spatially correlated nested design was tentatively controlled using mixed models that included the quadrat as a random factor and the study area as a fixed factor, since this had only two levels, to adjust for their influence on the outcome of explanatory variables on weevil-caused damage. On the other hand, because all fieldwork was concentrated in a single year, we cannot exclude the possibility that the detected differences were simply correlational and that non-evaluated secondary relations (e.g., habitat quality) might have influenced bird abundances. For these reasons, although our models were consistent with tested hypothesis and sufficiently robust to denote individual correlations between weevil-caused damage and functional insectivorous birds, our results and conclusions should be taken cautiously as they do not provide evidence that birds are actively controlling the pest.

5. Conclusions

The provision of avian insectivory services in eucalypt plantations is likely supported by high levels of bird species richness, as it happens in most other ecosystems (Hooper et al., 2005; Cardinale et al., 2006), but our study showed that, for the particular control of the eucalyptus weevil, the presence and abundance of canopy-foraging insectivores, including keystone species as the Great Tit, may be more important than community taxonomic or functional richness. Introduced eucalypt plantations are a poor habitat for insectivorous birds given the low availability of insects, as eucalypt leaves have low palatability for the autochthonous entomofauna (Ohmart and Edwards, 1991), and the shortage of natural nest-sites (da Silva et al., 2012, da Silva et al., 2019). In this context, the bivoltine eucalyptus weevil can create a notorious food boost for insectivorous birds dwelling in eucalypt stands and the surrounding habitats. Considering that the five functional insectivorous species which delivered the best models (Great Spotted Woodpecker, European Robin, Great Tit, Coal Tit and Eurasian Wren) are basically resident in Portugal, it is required that measures to favour their breeding populations are integrated into management of eucalypt plantations. For example, the addition of nest-boxes in eucalypt plantations can attract populations of cavity nesters, namely Great Tit (da Silva et al., 2012), that may not only contribute positively to control the eucalyptus weevil but also enhance stand resistance in the face of potential attacks by other insects.

CRediT authorship contribution statement

Ricardo S. Ceia: Methodology, Formal analysis, Writing – original draft. **Nuno Faria:** Investigation, Writing – review & editing. **Pedro B. Lopes:** Investigation, Writing – review & editing. **Joana Alves:** Methodology, Writing – review & editing. **António Alves da Silva:** Methodology, Writing – review & editing. **Carlos Valente:** Resources, Writing – review & editing. **Catarina I. Gonçalves:** Resources, Writing – review & editing. **Vanessa A. Mata:** Writing – review & editing. **José P. Sousa:** Project administration, Writing – review & editing. **Luís P. da Silva:** Conceptualization, Methodology, Supervision, Project administration, Funding acquisition, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data and code supporting the results of this study are available from Figshare: https://doi.org/10.6084/m9.figshare.19326380 Ceia et al. (2022).

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Appendix A. Supplementary data

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