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Biodiversity components mediate the response to forest loss and the effect on ecological processes of plant–frugivore assemblages

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Abstract

1. Anthropogenic disturbances are jeopardizing ecosystem functioning globally. Yet, we know very little about the effect of human impacts on ecological processes derived from trophic interactions. By focusing on biodiversity components of consumer and resource organisms, such as the diversity of phylogenetic lineages and the diversity of traits that influence species interactions, it is possible to simultaneously address the responses to disturbances and their effects on processes.

2. Here, we evaluate the consequences of forest loss on the ecological process of frugivory between fleshy-fruited plants and frugivorous birds. For 2 years, and at 14 sites representing a gradient of forest cover in the Cantabrian Range (N Iberian Peninsula), we monitored fruit and bird abundance, and fruit consumption. We compared the response to forest loss of both plants and birds by assessing the changes in phylogenetic and trait-based functional diversity in relation to forest cover. We further evaluated how changes in these biodiversity components translate into functional changes by estimating the degree of functional complementarity of plant and bird species.

3. We found different responses of plants and birds to forest loss. The diversity of plant assemblages did not respond to changes in forest cover, whereas bird assemblages markedly lost phylogenetic and trait-based functional diversity at high levels of forest loss. Functional complementarity of birds was well predicted by phylogenetic and trait-based functional diversity, but functional complementarity of plants depended exclusively on the diversity of traits.

4. Forest loss filtered avian phylogenetic lineages and traits, and influenced how birds contributed to the frugivory process. These results show how the diversity decay of one trophic level may compromise ecological processes derived from trophic interactions. Therefore, we suggest that a multitrophic response-effect framework, which includes measures of functional traits, lineages and species functional contributions across trophic levels, may be required to fully understand the ecological consequences of biodiversity decays.

1 | INTRODUCTION

Anthropogenic disturbances can affect ecosystem functioning through their impact on biodiversity, particularly since species extinctions can lead to decays in ecological functions (Cardinale et al., 2012; Dirzo et al., 2014). Although early studies have evidenced ecosystem functioning declines along negative gradients of species richness (e.g. Tilman & Downing, 1994; Valiente-Banuet et al., 2015), the mechanisms determining how biodiversity losses affect the resilience of ecological processes, especially those derived from trophic interactions, are still unclear (Reiss, Bridle, Montoya, & Woodward, 2009). In this sense, the functional impact of disturbances has been studied by focusing on species traits, that is, by identifying those traits that simultaneously determine species response to disturbance (response traits) and their functional contributions (effect traits, Lavorel & Garnier, 2002; see also Suding et al., 2008). In the case of trophic processes, that is those derived from interactions across trophic levels, functional decays are expected when processes depend on matching traits (i.e. traits determining interaction occurrence; Schleuning, Fründ, & García, 2015), and such traits also render species across trophic levels vulnerable to disturbance (Moretti et al., 2013; Schleuning et al., 2015). Nevertheless, trait-based approaches may be insufficient to comprehend the current and future vulnerabilities of trophic processes, and the explicit consideration of species phylogenetic relationships has been called for (Díaz et al., 2013). Thus, it is necessary, first, to assess the response to the disturbance of consumer and resource organisms in terms of both the phylogenetic and trait-based functional diversity, and second, to discern the effects of these two biodiversity components on trophic processes estimated from ecological interactions (Figure 1).

Phylogenetic diversity (i.e. the variety of lineages in a species assemblage; Cadotte, Dinnage, & Tilman, 2012) represents the evolutionary history of co-occurring species. Under the assumption that closely related species share similar characteristics in their phenotypic traits (Cadotte et al., 2012), it can be used as a proxy of the variability of ecological roles played by species within a community. Therefore, closely related species can be expected to share similar ecological interactions (Brousseau, Gravel, & Handa, 2017; Rezende, Lavabre, Guimarães Jr., Jordano, & Bascompte, 2007), and also similar sensitivity to disturbance (Helmus et al., 2010; Lososová et al., 2015). Trait-based functional diversity, in contrast, directly describes the dispersion of phenotypic traits within species assemblages (Laliberté & Legendre, 2010; Villéger, Mason, & Mouillot, 2008). It is therefore an important indicator of potential filtering effects of anthropogenic disturbances, since such filtering will alter trait distributions (Bregman et al., 2016). Also, trait-based functional diversity could be considered as a determinant of ecosystem

functioning, since it represents the functional contribution of the different species within communities (Gagic et al., 2015; Pigot et al., 2016).

Frugivory, the ecological interaction emerging from the consumption of fruits by animals, is a trophic process accounting for a substantial portion of energy flow in temperate and tropical ecosystems (Fleming, 1991; Jordano, 2000). Frugivory may drive plant population and community dynamics, through the demographic outcomes of seed predation and seed dispersal (Simmons et al., 2018), but it also affects the fitness of animals through the varied nutritional or toxical values of fruits (Quintero, Pizo, & Jordano, 2020). Plant and frugivore assemblages are known to show variable levels
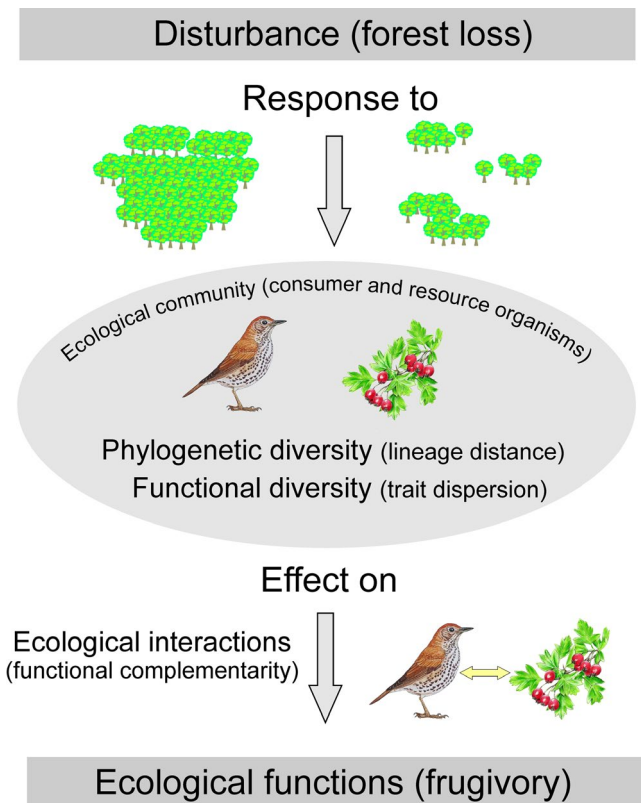

FIGURE 1 Conceptual model relating ecological processes to anthropogenic disturbance through the response to and the effect of biodiversity components applied to frugivory under forest loss. The response of consumer (frugivore) and resource (plant) organisms to disturbance may be addressed by integrative biodiversity components beyond taxonomic diversity, such as phylogenetic and trait-based functional diversity. These two components are also the predictors of ecological function, which can be estimated as the combination of the functional contributions of different species to interaction networks. Artwork by Daniel García (song thrush) and Víctor González (hawthorn)

of phylogenetic and trait-based functional diversity across environmental gradients (e.g. Dehling, Fritz, et al., 2014) or levels of disturbance (e.g. Bregman et al., 2016; Ribeiro et al., 2016). Land use, and specifically forest loss, represents one of the main drivers leading to altered frugivory interactions due to the decline in, or even the extinction of plant and frugivore populations (Farwig, Schabo, & Albrecht, 2017; McConkey et al., 2012). Plant–frugivore communities therefore represent suitable systems for evaluating the decay of an ecological process under anthropogenic disturbance.

Here we focus on the fleshy-fruited plants and frugivorous birds of the Cantabrian woodland to assess the consequences of forest loss on frugivory (Figure 1). By using a gradient of forest cover, we first evaluate the responses of plants and frugivores through their phylogenetic and trait-based functional diversity. Second, we evaluate the effects of these biodiversity components in frugivory. For this, we used plant–frugivore interactions to measure how the species of each trophic level specialize on their interaction partners. We therefore regard this measure to represent species roles in terms of functional complementarity (Pigot et al., 2016) of both plants and birds. Our study represents a step beyond previous studies on frugivore biodiversity, which have evaluated responses to disturbance (e.g. Bregman et al., 2016) separately to effects on plant–frugivore interactions (e.g. Pigot et al., 2016). We also apply a multitrophic response-effect trait approach (Lavorel et al., 2013; Moretti et al., 2013), under which the same traits that influence the sensitivity of plants and frugivores to disturbance, may also influence the matching of species in plant–frugivore interactions. Specifically, we tested two hypotheses: (a) a loss of phylogenetic and trait-based functional diversity will occur along the forest loss gradient; and (b) the loss of phylogenetic and trait-based functional diversity will lead to losses in complementarity of species contributions to frugivory.

2 | MATERIALS AND METHODS

2.1 | Study system

This study was conducted in mid-elevation woodlands of the Cantabrian Range in the northern Iberian Peninsula. The main anthropogenic impact in this area is from deforestation, due to historical logging and the opening of rangeland for extensive livestock rearing, which has led to a highly fragmented forest landscape (García, Quevedo, Obeso, & Abajo, 2005). The remnant woodlands contain variable-sized patches of primary and secondary forest, embedded in an extensive matrix of pastures with stony meadows and heathland. The secondary forest is typically dominated by fleshy-fruited trees (e.g. hawthorn *Crataegus monogyna*, holly *Ilex aquifolium*, rowan *Sorbus aucuparia*, etc.) and shrubs (blackberry *Rubus fruticosus/ ulmifolius*, wildrose *Rosa* spp., etc.). Fruiting plant species have sequential ripening peaks (see Table S3.1). However, standing fruit crops of plant individuals can remain for several months, resulting in a wide overlap between species in their fruiting periods. The main frugivores in the study region are passerine birds, which can have

mutualistic and antagonistic effects on plants (Simmons et al., 2018). Many species swallow entire fruits, enabling the deposition of intact seeds after regurgitation or defecation (legitimate seed dispersers; e.g. thrushes *Turdus* spp., European robin *Erithacus rubecula*). Other species peel the fruits to feed on the seeds (seed predators; e.g. bullfinch *Pyrrhula pyrrhula*) or pick out the pulp and discard the seeds (pulp eaters; e.g. Great tit *Parus major*; Simmons et al., 2018). We focused here on frugivory as a trophic process, considering all frugivorous birds irrespective of their handling behaviour and any potential differences in terms of their demographic effect on plants.

2.2 | Sampling design

The study was conducted from 2012 to 2014 in two localities in Asturias: Sierra de Peñamayor (43°18′09.5″N, 05°30′32.6″W) and Bandujo-Puertos de Marabio (43°14′35.2″N, 6°05′41.6″W). In total, we delimited fourteen 150 × 150 m study plots with a minimum distance between plots within each locality of 350 m. The plots were chosen to represent similar vegetation composition, geomorphology (slope ≤25%, limestone substrate, altitude 990–1250 m a.s.l.) and anthropic management (extensive livestock), as well as to include a wide gradient of forest cover (3%–70%), interpreted here as a negative gradient of forest loss. Forest cover per plot was estimated as the proportion of area occupied by the canopy projection of all trees (DBH > 10 cm, height > 1.5 m), digitized in a Geographic Information System (ArcGIS9.3) based on 1:5,000-scale orthophotographs (2011).

2.3 | Plant and bird assemblages

At the beginning of the fruiting season (September–February) of 2012–2013 and 2013–2014, we recorded fleshy-fruit production as an estimate of the pool of fruits available annually to frugivores. In each plot, we mapped all individual fruiting trees and shrubs (for blackberry, bramble patches >50 cm diameter) and estimated individual crop sizes. We visually estimated the number of standing fruits (we considered the arilated seeds in yew *T. baccata* and blackberries as single fruits for counting) per individual tree or shrub, by means of a semi-quantitative scale with six intervals (0 = without fruits; 1 = 1 – 10 fruits; 2 = 11 – 100; 3 = 101 – 1,000; 4 = 1,001 – 10,000; 5 ≥ 10,001; Fruiting Abundance Index [FAI], Saracco, Collazo, & Groom, 2004). Individual crop sizes were extrapolated from FAI ranks considering an allometric fit between the actual crop size and FAI (actual crop size = $1.765^{1.9249FAI}$; R^2 = 0.80; N = 136 individual plants; Martínez & García, 2015). For each plot, we also estimated plant species richness as the number of fleshy-fruited plant species present.

In each plot, during the fruiting season, we conducted point-count bird censuses between 09.00 and 15.00 hr, avoiding the days of heavy rain and wind, from nine census points regularly distributed throughout a 36-cell grid (25 × 25 m cells; each point in the centre of a set of four adjacent cells). Nine census rounds were performed per

point-count, plot and annual fruiting season (1–2 censuses/month), with a total effort of 189 sampling hours. In each census point, all birds heard or seen (with the help of 8 × 30 binoculars) within a 5-min period were registered. Bird richness was estimated as the number of species detected across all censuses per plot.

We constructed plot-based matrices of species abundances (abundance matrices hereafter) for plants and for birds to represent local species assemblages. For this, we estimated the absolute abundance of each species based on the cumulative number of records (fruits or birds) per plot, pooling the data for the two annual fruiting seasons. Species rarefaction curves (Figure S7) indicate that our sampling effort was complete enough to detect maximum species richness in both plants and birds.

2.4 | Plant–frugivore interactions and regional network

In each plot during the fruiting season (September–February), we recorded fruit consumption of birds by monitoring bird activity in independent observation slots of the point-count census, between 09.00 and 15.00 hr. Observation rounds were carried out by a single observer per plot, moving around three to four strategic positions within a plot (vantage points, different to point-count positions) during a 1-hr period in each plot. These vantage points were chosen to visually cover the whole plot extent (and hence to include different fruiting plant species), and were positioned at distances >50 m from the individual fruiting plants. The observer approached the vantage points, through a low detectability zone, in order to minimize bird reluctance to their presence. Four different observers were involved in the observation rounds, alternating between plots. In each round, recordings of every feeding bout (a single bird handling a single fruit) were made with 8 × 30 binoculars at distances ranging from 50 to 100 m. Over the study period, we performed 17 observation rounds of 1-hr-per-plot (i.e. eight rounds in 2012–2013 and nine rounds in 2013–2014) with a total effort of 238 sampling hours. We estimated the cumulative number of fruits of each plant species consumed by each bird species so as to build a regional-level interaction network (Table S4.). Although present in the study site, no frugivory event was recorded for honeysuckle *Lonicera periclymenum*, wildrose or blackthorn *Prunus spinosa*, and therefore these plant species were excluded from further analysis.

2.5 | Biodiversity components

We aimed to estimate plot-scale measures of plant and bird biodiversity through different components. To do this, we considered the contributions of the different species present in each local assemblage of fleshy-fruited plants and frugivorous birds to (a) the variety of phylogenetic lineages (phylogenetic diversity); and the (b) variability in traits which are relevant for frugivory (trait-based functional diversity). In order to estimate each component, we constructed distance-based matrices of phylogenetic relationships and traits for plants and birds separately. Moreover, in order to account for the importance of species abundances in explaining ecological functions (Gagic et al., 2015), both biodiversity components were weighted by the abundance of species in each local assemblage (square-root transformed abundances).

2.5.1 | Phylogenetic diversity

We extracted the phylogenetic distances between the plant species studied here from the comprehensively dated phylogeny of the European flora 'Daphne' (Durka & Michalski, 2012). This phylogeny is based on the backbone family phylogeny of the Angiosperm Phylogeny group III (Bremer et al., 2009), but dated using more recent molecular studies. We extracted the plant tree using the *drop.tip* function of the APE package (Paradis & Schliep, 2018) in R. For birds, we built 10,000 time-calibrated trees from the BirdTree online tool (BirdTree.org), using Ericson method as a backbone for phylogenetic reconstruction (Ericson et al., 2006; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). We used TreeAnnotator (Drummond & Rambaut, 2007) to generate the Maximum Clade Credibility (Bayesian MCC) tree. We regard these approaches to provide the best information currently available for the phylogenetic relationships of the included plant and bird species respectively.

To assess phylogenetic diversity, we measured the phylogenetic distances (branch length) for plant and for bird species in their respective phylogenetic trees (Figure S2). Then, for each plot and trophic level, we estimated the phylogenetic divergence among the species present in each local assemblage by means of the Mean Pairwise Distance (MPD). To this end, we extracted the square root of the pairwise phylogenetic distance matrix (Letten & Cornwell, 2015) for both phylogenies using the *cophenetic* function in the R package APE (Paradis & Schliep, 2018). Finally, we estimated the abundance-weighted MPD values of each plot using the *mpd* function in the R package PICANTE (Kembel et al., 2010).

2.5.2 | Trait-based functional diversity

To estimate the functional diversity of plant and frugivore assemblages, we focused on four phenotypic traits related to three levels of matching involved in frugivory: (a) traits related to fruit handling, such as bird bill length and bill width, assumed to match with fruit length and diameter (Dehling, Jordano, Schaefer, Böhning-Gaese, & Schleuning, 2016; Dehling, Töpfer, et al., 2014); (b) traits related to consumer energy requirements and resource availability, such as bird body mass (Jordano, 2014) and plant crop mass (Dehling, Töpfer, et al., 2014); (c) traits related to consumer foraging behaviour and resource spatial structure, such as bird Kipp's index (Kipp's distance divided by wing length; Dehling, Töpfer, et al., 2014), which indicates wing pointedness and is related to mobility and preferred forest stratum (pointed wings are typical of canopy foragers), and plant

height (Dehling, Töpfer, et al., 2014). All plant traits were estimated from field sampling. Fruit measurements were based on 25 ripe fruits (five fruits from five different individuals) sampled in the study plots in 2012–2013. Crop mass was estimated by multiplying mean fruit mass by mean crop size for each plant species. Plant height was measured as the maximum height of each species in the study plots. For each bird species, we measured bill width and bill length, Kipp's distance and wing length on museum specimens (minimum four specimens per species, two male and two female, following Eck et al., 2011), and obtained body mass from Dunning Jr. (2008). With the four matching traits of each trophic level, we constructed species × trait matrices using the means of each species trait, and where plant crop mass and bird body size were log-transformed.

We measured trait-based functional diversity in terms of trait-based distances among species, that is, the magnitude of the differences of a set of species to the average trait value in each (plant or bird) assemblage. For this, we first combined all matching traits to build plant and bird multidimensional trait spaces, based on Euclidean distances, using Principal Coordinates Analysis (PCoA; Villéger et al., 2008), in which all species (i.e. the whole set of species from every local assemblage) were projected. Then, we calculated values of Functional Dispersion (FDis) separately for plants and for birds for each plot. This index reflects the average distance of the species present locally to the centroid of the multidimensional trait space of the species assemblage (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, Legendre, & Shipley, 2014).

2.6 | Species contributions to frugivory

We aimed to estimate the trophic process of frugivory based on the contributions of individual species to the plant–frugivore interaction network. We considered all interactions across plots to build a single, regional network in which species roles were estimated irrespective of the local conditions, avoiding potential biases determined by differences in network size among plots (Dormann, Fründ, & Schaefer, 2017). Thus, we built a regional network by pooling all observations of feeding bouts, corresponding to the different pairings of plant and bird species, across observation rounds, fruiting seasons and plots.

We estimated the contribution of each plant and bird species to the regional network from their degree of specialization on their respective interacting partners (Pigot et al., 2016), by means of standardized Kullback–Leibler divergence (*d'*; Blüthgen, Menzel, & Blüthgen, 2006). This is a measure of the specialization of a given species and also of the exclusiveness (non-overlap) in interactions relative to other species, representing thus the complementarity in the functional niche of species within the same trophic level (Blüthgen & Klein, 2011). Values of *d'*, which range from 0 to 1, were estimated from the regional network with the BIPARTITE package in R (Dormann, 2011). Afterwards, we calculated local values of niche partitioning for plant and bird assemblages separately (<*d'*>), as

the abundance-weighted mean *d'* values of the species present in each local assemblage (i.e. we used abundance matrices). High local values of <*d'*> thus characterize assemblages with a high degree of partitioning in their interaction niches, indicating a high degree of functional complementarity among species in the provision of frugivory.

2.7 | Data analysis

2.7.1 | Standardization of metrics

To account for the potential effects of differences in species abundances across plots on the estimates of biodiversity components (MPD, FDis) and the degree of functional complementarity (<*d'*>) of plants and birds, we calculated Standardized Effect Sizes (SES) for all metrics using null models. For this purpose, we compared observed values of local assemblages (i.e. those estimated through weighting by abundance matrices) to 1,000 sets of randomized assemblages generated using '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). To calculate SES of MPD, FDis and <*d'*>, we subtracted the mean of the randomized values from the observed local values, and divided this result by the standard deviation of the random values. For simplicity, henceforth all mentions of MPD, FDis and <*d'*> refer to the standardized form, which represents the units of standard deviation rather than units from the raw values. All SES estimates were tested for collinearity with species richness by means of pairwise Pearson's correlation coefficient (Table S1).

2.7.2 | Response to forest cover

First, we studied the effect of forest loss on two biodiversity components by checking the response of phylogenetic and trait-based functional diversity to forest cover. For this, we fitted a linear mixed effect model (LM4 package in R, Bates, Maechler, Bolker, & Walker, 2015) for plants and birds separately. The model considered plot-level values of standardized MPD and FDis as a single response variable. Forest cover (log-transformed) and the type of biodiversity component (MPD, FDis) were included as explanatory fixed factors. An interaction between the fixed factors was also included in order to test whether the effect of forest cover differed between components. Plot identity was incorporated as a random factor.

2.7.3 | Effects of biodiversity components on functional complementarity

Second, we studied the effects of the biodiversity components on the degree of functional complementarity in the trophic process

(frugivory). We fitted linear mixed effect models considering plot-level values of <*d'*> of both plants and birds as response variable, and MPD and FDis of plants and birds as predictors (separate models for MPD and FDis). In order to control for the differences between plants and birds, each model also incorporated the trophic level as a fixed factor (with two levels: plants and birds) and the interaction between trophic level and MPD or FDis. Thus, we test whether the relationship between biodiversity and functional complementarity differed between trophic levels. Plot identity was included as a random factor.

3 | RESULTS

Overall, we detected seven species of fleshy-fruited plants and 17 species of birds involved in plant–frugivore interactions. In each plot, the richness of fruiting plants ranged from three to six species, and was independent of forest cover (Figure S1). Two plant species, holly and hawthorn, were dominant and occurred in all plots (mean relative abundance: 45.7% and 40.1% respectively; Table S6.1). Richness of frugivorous birds per plot varied from 8 to 15 species, and was positively correlated with forest cover (Figure S1). Blackbird was the most frequent and abundant bird species, followed by redwing *T. iliacus* and European robin (mean relative abundances: 32.2%, 16.0% and 13.4% respectively; see Table S6.2). Frugivory observations rendered 3,158 consumed

fruits. We detected 56 pairs of plant–bird interactions, with hawthorn–blackbird and holly–blackbird being the most frequent (33.2% and 14.8% of fruits consumed respectively). Plants belonged to four families (Figure S2), with yew, the only gymnosperm, as the most distant species. Birds belonged to five passerine families, Eurasian jay *Garrulus glandarius* being the phylogenetically most unique species (Figure S2).

According to the multidimensional trait-spaces, plants showed lower trait variability than birds (Figure S3). PCoA identified two dimensions that accounted for 92.9% of the total variance of trait values across plant species. The first plant PCoA dimension (81.1% of variance explained) was negatively correlated with all single traits (Figure S3a). Bird PCoA also identified two main axes that accounted for 96.5% of variance. The first bird PCoA dimension (76.6%) represented a positive gradient of bill width, bill height and body mass (Figure S3b). The second bird PCoA dimension (19.9%) was positively correlated with Kipp's index.

3.1 | Response to forest loss

For plants, MPD and FDis were not affected by forest cover (Figure 2a; Table 1). In contrast, both MPD and FDis of birds showed a significant decrease with declining forest cover (Figure 2b; Table 1), but with a steeper slope in MPD (β_{st} = 1.03) than in FDis (β_{st} = 0.51). For both plants and birds, MPD was positively correlated with local
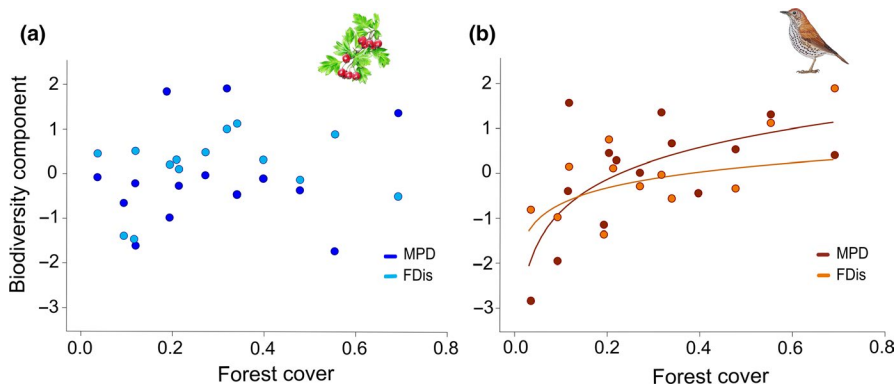

FIGURE 2 Relationship between components of biodiversity (phylogenetic diversity mean pairwise distance [MPD], darker shades; trait-based functional diversity FDis, lighter shades) and the proportion of forest cover for (a) plants and (b) birds. Dots represent standardized effect size values of metrics in different plots. Logarithmic trend lines indicate statistically significant relationships

Trophic level	Fixed effect	Estimate	SE	t-value	p
(a) Plants	Intercept	0.31	0.51	0.61	0.551
	Forest cover	0.27	0.30	0.91	0.377
	Biodiversity component (FDis)	0.17	0.64	0.26	0.794
	Forest cover × FDis	−0.02	0.37	−0.04	0.968
(b) Birds	Intercept	1.52	0.52	2.94	0.006
	Forest cover	1.03	0.30	3.42	0.002
	Biodiversity component (FDis)	−1.03	0.57	−1.81	0.081
	Forest cover × FDis	−0.52	0.33	−1.58	0.125

TABLE 1 Linear mixed effect models testing the response of biodiversity components (phylogenetic diversity mean pairwise distance [MPD], trait-based functional diversity FDis) of (a) plants and (b) birds to forest cover (log-transformed). The parameter estimates are given in standardized form. The type of biodiversity component and its interaction with forest cover were also considered as fixed effects. Plot was incorporated as a random effect

FIGURE 3 Relationships between (a) phylogenetic diversity (mean pairwise distance [MPD]) and (b) trait-based functional diversity (FDis) and functional complementarity in plant–frugivore assemblages (<d'>). Dots represent standardized effect size values of metrics in different plots, and trend lines, statistically significant relationships between variables, for plants (blue) and birds (orange)
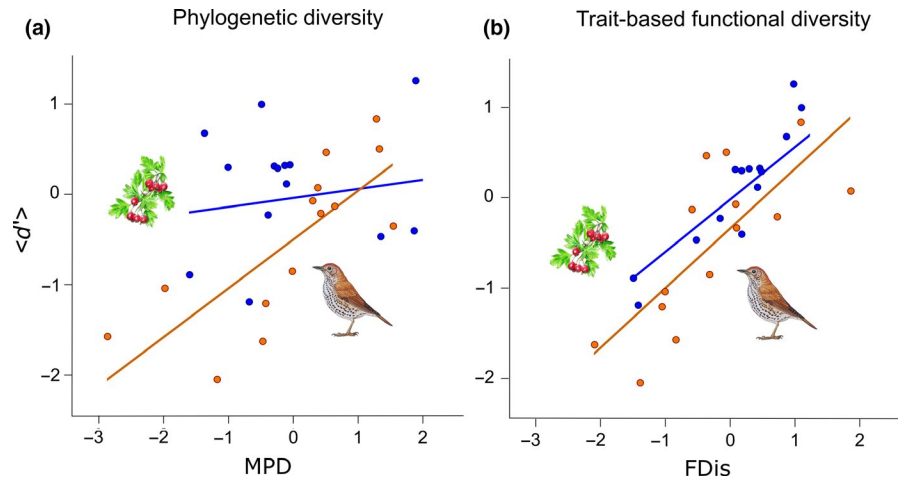

(a) Phylogenetic diversity

(b) Trait-based functional diversity

TABLE 2 Linear mixed effect models testing the effect of (a) phylogenetic diversity (mean pairwise distance [MPD]) and (b) trait-based functional diversity (FDis) on functional complementarity (<d'>) of two trophic levels (plants and birds). The parameter estimates are given in standardized form. Models included trophic level and its interaction with MDP or FDis as fixed effects. Plot identity was incorporated as a random effect

Fixed effects	Estimate	SE	t-value	p
(a) Phylogenetic diversity				
Intercept	−0.50	0.16	−3.14	0.005
Trophic level (plant)	0.60	0.23	2.66	0.014
MPD	0.54	0.13	4.14	<0.001
MPD × Plant	−0.44	0.20	−2.21	0.038
(b) Trait-based functional diversity				
Intercept	−0.34	0.12	−2.83	0.009
Trophic level (plant)	0.36	0.14	2.53	0.018
FDis	0.66	0.11	5.87	<0.001
FDis × Plant	0.08	0.18	0.43	0.670

species richness (Table S1). FDis, in contrast, was positively correlated with local species richness for birds, but not for plants.

3.2 | Effects of biodiversity components on functional complementarity

The local values of functional complementarity <d'> were, on average, higher for plants than for birds (Figure 3; Table 2). Individual plant and bird species showed similar ranges of variation in their specialization on interaction partners (d' = 0.06–0.65, Figure S4).

The relationships between <d'> and the biodiversity components varied depending on the component and the trophic level (Table 2). MPD showed a positive effect on <d'>, but only in the case of birds (Figure 3a; Table 2). However, FDis was positively related to <d'> for both plants and birds (Figure 3b; Table 2).

4 | DISCUSSION

Here, we focus on different biodiversity components to understand the response of species assemblages to anthropogenic disturbance, and the effect of these components on ecological processes derived from trophic interactions. Specifically, we account for phylogenetic lineages and interaction-related matching traits of fleshy-fruited plants and frugivorous birds. Our results suggest a decoupled response of plant and bird assemblages: while plants did not respond to forest loss, birds suffered a decrease in phylogenetic and trait-based functional diversity in response to forest loss. Moreover, functional complementarity of birds in plant–frugivore networks was closely associated with phylogenetic and trait-based functional diversity. In contrast, functional complementarity of plants depended on the diversity of plant matching traits, but not on phylogenetic diversity. Forest loss, therefore, filtered bird phylogenetic lineages and traits, leading to frugivore assemblages with reduced functional complementarity.

4.1 | Response to forest loss

Our analysis across the regional gradient reveals that plant and bird assemblages differed in their response to forest cover. In our study system, forest cover did not affect plant diversity, contrasting with other studies where disturbance had a negative impact on plant trait-based functional diversity and led to an impoverishment in the variety of phylogenetic lineages (Laliberté et al., 2010; Ribeiro et al., 2016). Here, the studied forest cover gradient entailed a change in local total fruit abundance (Pearson's correlation coefficient: r = 0.61, p = 0.02; N = 14 plots), but did not affect plant richness (Figure S1). In fact, most fruit resources were provided by the almost ubiquitous hawthorn and holly (ranging from 73% to 99% of total fruit availability across plots), together with the frequent blackberry (Table S6.1). Because these plants are able to recolonize deforested land and form secondary successional patches (Martínez & García, 2017), the composition of the fleshy-fruited plant assemblages seems resilient in the face of loss of forest cover. Besides, other

fleshy-fruited tree species, such as yew, could have escaped logging and cattle browsing, owing to low, but persistent recruitment at safe sites for establishment (García & Obeso, 2003).

In contrast with plants, birds suffered a loss of diversity with decreasing levels of forest cover (Figure 2), as also shown by previous studies regarding the impact of land use (Bregman et al., 2016; Petchey, Evans, Fishburn, & Gaston, 2007). This decay was nonlinear, suggesting some robustness in bird assemblages from high to medium levels of forest availability, but a quickly accelerating loss of biodiversity at the threshold of low forest cover (*c*. 20%). Such robustness was probably related to the persistence of a core of common species, like the small-sized great tit (Paridae) and European robin (Turdidae), together with the occurrence of medium-sized thrushes and blackbird (Turdidae). The occurrence of these species would maintain both high degrees of phylogenetic and trait-based functional diversity (Figures S2 and S3; Table S3.2). Our results suggest that the traits measured here are related to the ability of bird species to cope with forest loss; such traits could be defined as *response traits* to forest loss (Schleuning et al., 2015). For example, avian body and bill size, as well as a pointed wing shape, seem beneficial to the exploitation of the fruits of varied sizes spatially scattered across the landscape (Plein et al., 2013). Moreover, our results suggest that other traits not measured here, but related to phylogenetic differences among species, were also probably acting as response traits. For example, some lineages (e.g. Turdidae) have behavioural traits (e.g. flocking behaviour, winter frugivorous diet) which are important in tracking and exploiting fruit resources across fragmented landscapes during winter (García, Zamora, & Amico, 2011). Despite the ability of bird assemblages to cope with forest loss up to a certain extent, reductions below this threshold filtered frugivore assemblages, resulting in the loss of species that were of distant lineages and with morphologically distinct traits (e.g. Eurasian jay and blackcap *Sylvia atricapilla*; Figures S2 and S3). The high distinctness of these species may, in fact, represent higher levels of specialization in other niche requirements (as suggested by Coux, Rader, Bartomeus, & Tylianakis, 2016), which are probably only fulfilled in areas of high forest cover (complementary dietary components, such as acorns for jay or insects for blackcap; e.g. Carnicer, Jordano, & Melián, 2009; Selås, 2017).

4.2 | Effects of biodiversity components on functional complementarity

We found large differences across plots in frugivory, measured as functional complementarity of plant and bird species within plant–frugivore networks. We found substantial variation from high specialization (i.e. high niche segregation) to high generalization (i.e. high niche overlap) among species in both plants and birds (see also Pigot et al., 2016). For both trophic levels, these differences were related to the changes in trait-based functional diversity, with greater trait dispersion encompassing higher functional complementarity in

frugivory (see also Dehling et al., 2016). This pattern seems related primarily to the inclusion of small-sized fruits and their specialized frugivores in interaction networks (García, Donoso, & Rodríguez-Pérez, 2018). Namely, small-sized drupes, like elder *Sambucus nigra* and blackberry, are mostly eaten by small birds such as blackcap, but also by other, larger species, such as bullfinch and Eurasian jay, which increase the degree of trait-based functional diversity in local bird assemblages. Interestingly, tropical systems have shown the opposite pattern in that specialized interactions were mostly driven by large fruits (Naniwadekar, Chaplod, Datta, Rathore, & Sridhar, 2019).

The positive correlation shown here between trait-based functional diversity and functional complementarity in both birds and plants may be interpreted from two perspectives. Firstly, the diversity of matching traits influences the variety of possible interactions in a community. A high diversity of matching traits thus increases niche differentiation, and thereby functional complementarity, among species (e.g. complementarity in resource use, Gagic et al., 2015). This perspective highlights that trait matching is an important mechanism that conditions forbidden links and the occurrence of plant–bird interactions (e.g. birds of small gape size are not able to feed on large fruits; Dehling et al., 2016). Secondly, it suggests that the contribution of individual bird and plant species to the functional complementarity among species in interaction networks depends on specific functional traits. Here we pinpoint phenotypic traits such as bird body size and fruit size as important effect traits (sensu Suding et al., 2008), which imply that large bird species contribute more to frugivory (see also Schleuning et al., 2015). For birds, functional complementarity was also positively related to phylogenetic diversity. This correlation may partially result from the fact that the bird phenotypic matching traits measured here are known to show a significant phylogenetic signal (e.g. Rezende et al., 2007). Also, it suggests that functional complementarity among frugivorous birds may respond to some unmeasured traits represented by lineage differences, like foraging and spatial behaviour (Schleuning et al., 2014). In contrast, for plants, the variety in phylogenetic distances was not a proxy of functional complementarity among species in interaction networks. In fact, phylogenetically unrelated species (e.g. rowan and yew) showed a similar low degree of specialization in interactions, whereas highly related species (e.g. rowan and whitebeam *Sorbus aria*) differed markedly (Figure S4). Because we found that functional complementarity was related to matching traits of plants, our results suggest the existence of ecological convergence among different lineages of fleshy-fruited plants sharing phenotypic traits such as fruit size and plant height and similar interaction partners (Rezende et al., 2007).

Our study was on a relatively species-poor plant–frugivore system. We therefore argue that our findings may also be applied to other species-poor systems affected by similar processes of historical forest loss (e.g. Farwig et al., 2017; González-Varo, 2010). However, they could also be relevant for species-rich systems where fleshy-fruited plants may show resilience to anthropogenic impact (e.g. Pires et al., 2014), but significant loss of frugivore diversity has

been found in responses to forest loss (e.g. Morante-Filho, Arroyo-Rodríguez, Pessoa, Cazetta, & Faria, 2018).

4.3 | Concluding remarks

The present work shows how a decay in diversity within one trophic level (e.g. consumers) may compromise ecological processes, when the phylogenetic lineages and the traits determining species susceptibility to disturbance are also driving the matching of trophic interactions. Indeed, a cascade effect is to be expected, by which the response of one trophic level to disturbance will impact on the fitness of the other trophic level involved. In our specific case, from the point of view of plants, we might also assume that some indirect, negative consequences will emerge from bird functional decay, as the loss of specialized seed dispersers has been found to decrease the magnitude of seed deposition in this study system (García et al., 2018). We therefore argue that our findings can be extended to different trophic processes (e.g. pollination, herbivory, seed predation) performed by plant and animal assemblages harbouring diverse lineages and phenotypic traits which are involved in interaction matching, and confronted by common scenarios of anthropogenic disturbance.

AUTHORS' CONTRIBUTIONS
D.G., M.S. and R.P. conceived and designed the study; D.G., J.R-P. and I.D. collected field data; R.P. and M.S. collected phylogenetic and trait data and performed analyses; R.P. and D.G. wrote the manuscript. All authors reviewed the manuscript and approved the final version.

DATA AVAILABILITY STATEMENT
Original data associated with this article are deposited in Dryad Digital Repository https://doi.org/10.5061/dryad.08kprr500 (Peña et al., 2020).

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SUPPORTING INFORMATION

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