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Diversity and Distributions WILEY

Trait-habitat associations explain novel bird assemblages mixing native and alien species across New Zealand landscapes

Jean-Yves Barnagaud[1] 🔵 | Eckehard G. Brockerhoff[2,3] 🔵 | Raphaël Mossion[1] |
Paul Dufour[4] | Sandrine Pavoine[5] | Marc Deconchat[6] | Luc Barbaro[5,6] 🔵

[1]CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France

[2]Scion (New Zealand Forest Research Institute), Christchurch, New Zealand

[3]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[4]Laboratoire d'Écologie Alpine, CNRS, Univ. Savoie Mont Blanc, CNRS, LECA, Univ. Grenoble Alpes, Grenoble, France

[5]Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum national d'Histoire naturelle (MNHN), Centre National de la Recherche Scientifique (CNRS), Sorbonne Université, Paris, France

[6]DYNAFOR, INRA, Université de Toulouse, Castanet-Tolosan, France

Correspondence
Jean-Yves Barnagaud, CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Montpellier, France.
Email: jean-yves.barnagaud@ephe.psl.eu

Abstract

Aim: Species introductions have reshaped island faunas for the last 200 years, often threatening native biodiversity. Approximately equal numbers of native and alien species currently co-occur in the New Zealand avifauna, but they show distinct habitat use. Antagonistic interactions, habitat affinities and legacies of introduction history may concur to explain their segregation along habitat gradients. To investigate these processes, we explored how habitat, ecological traits and introduction history relate with the current composition of bird assemblages.

Location: New Zealand

Taxon: Birds

Methods: We analysed 917 bird point counts spread along habitat and elevation gradients in the Canterbury region, South Island and related 10 ecological traits to landscape composition using a three-table ordination method known as "RLQ analysis", accounting for spatial autocorrelation and phylogeny. We tested whether alien species' positions in the RLQ were related to proxies of introduction history.

Results: Eighteen endemic, 11 native and 19 alien species were distributed along a gradient from forest to open-habitat assemblages, in relation to foraging mode, nesting site and body size. A second gradient segregated species between native and exotic forests according to territoriality, sedentarity and diet. Traits accounted for the separation of native and alien bird species in forests, but not in open habitats. Phylogenetic signals emerged from the separation of native and alien species by forest type, and spatial structures suggested a landscape-level, rather than regional or local determinism. These correlations were independent of introduction history, although open-habitat assemblages tended to host alien species introduced later in time.

Main conclusions: Habitat type and resource availability explain the spatial partitioning of New Zealand bird assemblages between native and alien species more consistently than competitive exclusion. We conclude that trait-mediated ecological differences among species have likely played a predominant role in species'

segregation among landscapes, while maintaining endemic bird assemblages in native forests.

1 | INTRODUCTION

Avifaunas of oceanic islands are amongst the most distinctive in the world, with disproportionate rates of endemism and narrow distributions (Newbold et al., 2018). Island bird species and assemblages exhibit unique combinations of ecological traits and evolutionary pathways with few equivalents on continental landmasses (Pavoine et al., 2017). These unique features make them sensitive to changes in their abiotic or biotic environment, and ultimately more prone to extinctions as compared to mainland species (Blackburn et al., 2004; Sanchez-Ortiz et al., 2019).

Worryingly, island bird assemblages face the synergistic impacts of climate change, habitat loss and human-mediated introductions of alien species—including predators, pathogens and competitors (Blackburn et al., 2004; Parlato et al., 2015; Walker et al., 2019). The latter threat is exacerbated on oceanic islands where long-term isolation has limited native species' capacity to accommodate novel biotic interactions (Traveset et al., 2013). As a consequence, introductions of alien species, usually coinciding with modifications of island habitats for human land use, have dramatically altered native island avifaunas and disrupted irreplaceable ecosystem processes and services provided by endemic species, such as seed dispersal, pollination and pest control (Anderson et al., 2011; Foster & Robinson, 2007; Şekercioğlu et al., 2016). In New Zealand, for instance, predation of endemic species by introduced mammals is a key factor in the decline of several obligate bird-pollinated or bird-dispersed plant species, ultimately contributing to the impoverishment of native plant assemblages on top of direct habitat destruction (Carpenter et al., 2018; Kelly et al., 2010; Wotton & Kelly, 2012).

The composition of island bird assemblages could result from species' idiosyncratic responses to habitat, land use and abiotic features, but may also arise from niche-based exclusion between native and alien species. Because these processes can hardly be tested experimentally, a comprehensive way to explain patterns of native and alien species' co-occurrence within assemblages relies on correlative methods to analyse the spatial distribution of ecological traits and compare their influence with that of other possible drivers (Allen et al., 2013; Kennedy et al., 2010; Vandewalle et al., 2010). Ecological traits encompass species characteristics, such as diet, mobility or reproductive traits and are organized into syndromes that emerge from evolutionary strategies in response to environmental conditions (Díaz et al., 2016; Jeliazkov et al., 2020). Directional variations of these syndromes along environmental gradients allow inferences on species co-occurrence or exclusion patterns over large regional extents, although the exact processes involved necessarily

remain uncertain (Mouillot et al., 2013; Pavoine et al., 2011; Violle et al., 2014). To be robust, this approach requires well-defined spatial gradients (e.g., elevation or forest-open habitat continuums) and carefully chosen traits that reflect species' resource use while avoiding circularity with environmental variables (e.g., in birds, dietary preferences, foraging modes or breeding locations; Jeliazkov et al., 2020; Kennedy et al., 2010). With these conditions in mind, patterns of trait-habitat correlations may be a fruitful way to infer processes explaining patterns of alien and native species' exclusion.

Anthropogenic alteration of native island habitats favours alien species that can thrive in urban areas, cultivated fields or planted forests (Barnagaud et al., 2014; Cardador & Blackburn, 2019; Sol et al., 2017). Accordingly, many successful introductions involved species that shared ecological traits associated with synanthropy, such as dietary generalism, investment in reproduction or small size (Allen et al., 2017; Capellini et al., 2015; Sol et al., 2012). It is often unclear whether the success of some alien species is attributable to human-created resources or to adaptation to their novel environment. For instance, large-scale studies suggest that signals of introduction events remain prevalent long after species' establishment in many islands irrespective of local habitat suitability (Blackburn et al., 2020; Case, 1996). However, niche-related processes also explain invasion success, especially the association between alien species and anthropogenic habitats worldwide (Cardador & Blackburn, 2019). Separating the relative roles of traits and introduction history is therefore a critical step to explain differences in habitat use between native and alien species, especially in island ecosystems (Blackburn et al., 2020; Duncan et al., 2019; Pipek et al., 2020).

New Zealand's avifauna has been altered substantially by species extinctions following Maori and European settlement. The current avifauna is also affected by species introductions, most of which occurred in the second half of the 19th century (e.g., Diamond & Veitch, 1981; Pipek et al., 2020; Veltman et al., 1996). Today, New Zealand's bird assemblages are therefore typically novel, mixing native and introduced species in various proportions according to habitats (Robertson et al., 2007). However, in larger native forests, assemblages are dominated by native bird species with comparatively fewer aliens (Barbaro et al., 2012; Clout & Gaze, 1984; Deconchat et al., 2009; MacLeod et al., 2008). New Zealand bird assemblages therefore represent an excellent opportunity to investigate the habitat-related sorting of native and alien species.

New Zealand native and alien birds are partitioned across habitat types both at the landscape and local scales, at least in forested landscapes. Contrary to other remote islands, however, this habitat

segregation is not fully consistent with direct competition between alien and native bird species (Barnagaud et al., 2014). Credible, non-mutually exclusive explanations lie in limited niche overlap, the use of niches left vacant by extinct native species, or distinct distributions in space (van Heezik et al., 2008). These multiple processes may leave an identifiable signal in trait-habitat relationships. Differing or opposite trait-environment correlations in native and alien species would support the hypothesis that niche differences play a role in the spatial segregation among assemblages through environmental filtering (Cadotte & Tucker, 2017). Conversely, species segregation along ecological gradients associated with similar trait-environment relationships among natives and aliens would indicate either competitive exclusion or a limited role of environmental preferences (e.g., if the distributions of alien species are mainly related to their introduction history, Blackburn et al., 2020; Cardador & Blackburn, 2020). Finally, the co-occurrence of native and alien birds in assemblages in spite of trait differences may be indicative of vacant niche filling, especially if alien species exhibit some of the traits known to have played a role in the decline or extinction of native species (e.g., exposure to predators when breeding on ground or in low vegetation, Diamond & Veitch, 1981; Parlato et al., 2015).

We explored the composition of bird assemblages of the South Island of New Zealand to assess the extent to which ecological traits and introduction history may explain previously reported habitat separations between native and alien birds. Traits differ markedly between native species, which tend to be frugivore, carnivore or insectivore and alien species that exhibit a strong tendency towards granivory (Barnagaud et al., 2014; Soares et al., 2021). However, these studies did not test whether these ecological differences can explain their segregation among habitats, nor did they explore the role of introduction history on these trait and habitat patterns. We thus used a multivariate framework to establish an explicit link between traits, species and environment, while accounting for the role of spatial proximity and phylogeny in these patterns (Pavoine et al., 2011). We also investigated possible legacy effects of introduction history on trait-habitat associations.

2 | MATERIALS AND METHODS

2.1 | Study area

The study was carried out in the Canterbury Region of the South Island, New Zealand and included Banks Peninsula in the east, the Canterbury Plains and part of the Southern Alps in the west (Figure 1). Elevation ranged from 0 to 1,205 m (mean 316 ± 240 m, all variation in standard deviation units). The climate is seasonal and temperate and varies with elevation under the influences of mountains and coastal areas. The landscapes are mainly composed of exotic grasslands, modified natural grasslands, some shrubland, native forest and plantation forests. Exotic plantation forests (57% of total forest cover on sampled points) are dominated by *Pinus radiata* while native forests account for 43% of total forest cover, mainly in the
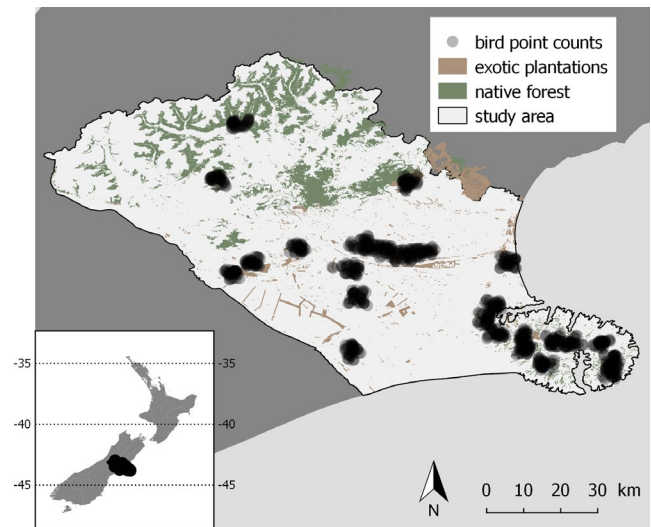

FIGURE 1 Study region (light grey, insert) extending from Banks Peninsula in the East to the Southern Alps in the West and the location of the 917 point counts within the study region. Points are grouped in clusters; dot density depicts the number of adjacent points

Southern Alps and on Banks Peninsula. Together, forests account for 59% of the landscape on sampled points, with high heterogeneity (from open to forested landscapes). While the native forests studied in the Southern Alps are mainly old growth, those on Banks Peninsula are mainly regenerating forests after clearance had occurred since the mid-1800s (with the primarily native forest cover on the peninsula having declined to about 1% forest cover in 1900 and subsequent growth to about 15% in 2008, Wood & Pawson, 2008). Open habitats mainly consist of exotic grassland and mixed native and exotic grassland used as pasture, with locally substantial remnants of native tussock grasslands and occasional shrubs. Some grassland areas are interspersed with more or less substantial areas of regenerating native, exotic or mixed shrubland.

2.2 | Bird sampling

A set of 917 point counts was surveyed once during two field campaigns by the same observers (Austral summer 2005–06:402 points in 50 days; 2006–07:515 points in 64 days; 1–36 points per day, mean = 16 points per day, standard deviation = 9 points per day). This study builds on two previous surveys and publications that were more limited in scope and extent (Deconchat et al. (2009) analysed 238 point counts that were restricted to Banks Peninsula only; and Barnagaud et al. (2014) analysed a total of 501 point across all the regions but limited to forests, i.e., excluding non-forest habitats). Points were grouped into clusters (34 to 44 points per cluster) located to cover both forests and grassland areas within each cluster, but excluding urban and suburban areas (Figure 1). Forest cover within the clusters varied from a minimum of about 1% to over 90%. Points were located at least 200 m apart from each other to avoid

double-counting; all birds heard or seen within 100 m around each point were recorded and counted during 15 min by a single experienced observer among a team of six observers; preliminary data exploration revealed no observer effect. Points were assigned randomly to observers, but all observers covered all areas and habitats. All point counts were performed in suitable weather conditions with low wind, between 7 a.m. and 1 p.m. (hence excluding nocturnal species; bird sampling beyond the early morning is standard practice in New Zealand, e.g., Spurr & Ralph, 2006).

We retained all recorded species in our analyses to obtain the most comprehensive representation possible of bird assemblages occurring in all point counts (n = 48 species for 917 point counts, species list and abbreviations used in figures in Appendix S1). We classified birds according to their origin, distinguishing 18 New Zealand endemics, 11 New Zealand natives (non-endemic species that also occur elsewhere as native species) and 19 alien species mostly introduced in the 19th century from Europe and North America (Robertson et al., 2007).

2.3 | Environmental variables

We characterized landscape composition in 500 m buffers centred on each point count, using the most biologically relevant classes among the 43 land use categories of the New Zealand Land Cover Database V2 (Table 1, based on Terralink International, 2004). We specifically selected the land use types targeted in the setting of the bird sampling protocol, which aimed to contrast at best native and exotic habitats along a gradient ranging from native forests to open pastures. The trait diversity of both native and alien species within bird assemblages tends to increase with habitat diversity in a landscape (Méndez et al., 2018); we therefore quantified landscape heterogeneity using Shannon-Wiener's index based on the polygon surfaces of these classes within each buffer. We also used observers' field recordings of elevation and vegetation height within a 100 m radius around each point to obtain a more local characterization of habitats (Table 1).

2.4 | Ecological traits

We compiled 10 ecological traits known to influence habitat selection in birds (see Table 2 for a synthesis and justification and more details in Appendix S1). Five traits (foraging behaviour, diet, nest location, social behaviour, migration behaviour, thermal preference) represented the functional link between species and their habitat (Mac Nally, 1994; Robinson & Holmes, 1982). Five other traits (clutch size, brood number per year, age at fledging and body weight) represented ecological niches and interspecific interactions (Brandle et al., 2002). In addition, we recorded three variables characterizing introduction effort at the scale of New Zealand for the 19 alien species (no finer-grained data are currently available): date of first introduction, number of successive introduction events and total

number of individuals released during these events (retrieved from Duncan, 1997).

2.5 | Phylogeny

We constructed a phylogeny of the 48 species (Appendix S2) with a composite of bird phylogeny established by Prum et al. (2015) and a maximum clade credibility tree computed from 10,000 iterations of the Hackett backbone (Jetz et al., 2012, downloadable at www.birdtree.org, "Stage 2 Hackett Backbone"), following the method of Cooney et al. (2017). This approach provided more reliable divergence times and topology of the earliest branching events (especially for separating major non-passerine taxa) than previously published phylogenies (Thomas, 2015).

2.6 | Trait-environment relationships

We characterized the spread of bird traits along habitat gradients with a RLQ analysis, a three-table multivariate ordination linking a sites * environment table (matrix R, here summarized in a principal component analysis, PCA) to a species * traits table (matrix Q, here a Hill & Smith analysis, HS) through a site * species table (matrix L, here a correspondence analysis [CA] based on species' counts on the 917 points). We weighted the PCA and Hill & Smith analyses by the sites and species weights computed in the CA to ensure homogeneity among tables, as described in Thioulouse et al. (2018). We added two supplementary tables following Pavoine et al. (2011). First, we accounted for the spatial arrangement of the survey through the eigenvalues of a sites * sites binary Gabriel neighbours matrix based on point count coordinates (table S), synthesized through a PCA (Thioulouse et al., 2018). We then concatenated the PCA axes of tables R and S to obtain table E, which thus formed a synthesis of environmental and spatial gradients. Similarly, we incorporated phylogenetic autocorrelation with a species * species square-root transformed pairwise phylogenetic distance matrix (table P; phylogenetic distance defined as the sum of branch lengths on the shortest path between two species in the phylogenetic tree), summarized by a principal coordinate analysis (PCoA). We concatenated this PCoA and the PCA axes of table Q to associate trait and phylogenetic information (table T). Following the basic structure of a RLQ analysis, we subsequently related tables E and T through the link table L. The resulting trait-environment ordinations accounted for the spatial proximity among point counts and the phylogenetic relatedness among species. For semantic simplicity, we refer to this analysis as "RLQ".

2.7 | Impact of introduction effort

We investigated the impact of introduction history on trait-habitat associations through a MANOVA relating species' coordinates in the

TABLE 1 Environmental variables used in the study

Variable	Acronym	Resolution	Data source	Definition	Mean ± SD
% exotic grassland	exgr	Landscape	New Zealand Land Cover Database 2	Mainly exotic herbaceous vegetation, either seeded or under spontaneous dynamics	34.53 ± 28.49
% exotic scrub	exsc	Landscape	New Zealand Land Cover Database 2	Shrubland of mainly exotic plants that invaded modified grassland under spontaneous dynamics	3.39 ± 8.52
% young plantation forest	yopl	Landscape	New Zealand Land Cover Database 2	Mature planted forest of exotic trees under silvicultural management	3.14 ± 9.02
% mature plantation forest	mapl	Landscape	New Zealand Land Cover Database 2	Mature forest of exotic trees under silvicultural management	17.20 ± 22.94
% native herbaceous vegetation	nagr	Landscape	New Zealand Land Cover Database 2	More or less native grassland under spontaneous dynamics	5.77 ± 15.83
% native scrub	nasc	Landscape	New Zealand Land Cover Database 2	Native shrubland vegetation under spontaneous dynamics	3.41 ± 8.26
% native forest (all stages)	nafo	Landscape	New Zealand Land Cover Database 2	Native forest without silvicultural management	10.28 ± 18.62
Landscape heterogeneity	s500	Landscape	Calculated from previous variables	Shannon-Wiener's index on habitat polygon size within buffers, reflects the heterogeneity of habitats and resources	0.66 ± 0.41
Mean elevation (m)	elev	Local	Recorded on field	Elevation of a point count; key for the regional distribution of habitats and correlated with temperature and precipitation gradients	316.1 ± 240.1
Mean vegetation height (m)	vegh	Local	Recorded on field	Proxy of the local vegetation structure. High vegetation height is usually associated with older stands and more complex understorey	8.0 ± 7.7

Note: Resolutions: landscape: 500 m buffer around each point; local: 100 m around each point.

TABLE 2 Summary of ecological traits and proxies of introduction effort used in the study (*n* = 48 species)

Ecological trait	Categories	Justification
Foraging (categorical, 7 classes)	aerial (f.aer), bark forager (f.bkf), canopy gleaner (f.cag), foliage gleaner (f.fog), ground gleaner (f.grg), ground prober (f.grp), understorey gleaner (f.grp)	Foraging mode affects directly the resources and habitat structures accessible to a species. It is therefore related to the distribution of species among habitats, and across vegetation strata within habitats
Main diet (categorical, six classes)	Fruits (d.fru), invertebrates (d.inv), nectar (d.nec), omnivorous (d.omn), seeds (d.see), vertebrates (d.ver)	Diet often conditions the extent to which species co-occur within an assemblages or exclude each other due to competition. The distribution of diets is related to habitat composition and therefore contributes to species' habitat affinities
Nest location (categorical, four classes)	rock cavities (n.cav), tree cavities (n.cat), ground (n.ogr), open in trees (n.opt)	The availability of nest sites differs among habitats. Nest site also modulate species' exposure to predation (e.g., ground-nesting species were largely eliminated by rats, boars and cats) and contributes to interspecific competition within habitats
Social behaviour (categorical, three classes)	territorial (s.ter), non-territorial (s.nter), gregarious (s.gre)	Social behaviour directly affects relative species' abundances within a habitat. It affects both pressure over food resources, nest sites and space. If related to habitat, social behaviour may also inflate species turnover along environmental gradients (when bird distributions are expressed in counts of individuals per location, as is the case here)
Movements (categorical, two classes)	sedentary (m.sed), local migrant (m.loc)	Migration is often associated to higher specialization, philopatry and ability to cope with seasonal habitats/resources
Thermal preference (continuous, °C)	temp	Thermal preference, computed as the thermal centroid of a species' distribution, is related to habitat and elevation affinities
Clutch size (continuous)	c_siz	A critical trait for reproductive strategies, clutch size is usually under strong selection pressure as a response to environmental constraints and stability
Brood number per year (continuous)	n_brd	The number of broods per year evolves partly as a response to the phenology and seasonality of resources, which varies among habitats
Age at fledging (continuous, days)	fledg	Reflects colonization speed and evolves partly as a response to resource stability
Weight (continuous, g)	wght	Integrative proxy of ecophysiological demands, resource use, life history, tolerance to disturbance and dispersal ability
Date of first introduction event (year)		Time since the first settlements of propagules (assuming that the first event was successful)
Number of introduction events (continuous)		Introduction pressure: recurrence of propagules arrival
Total number of individuals released (continuous)		Introduction pressure: intensity of the immigration flow

RLQ to the three variables quantifying each species' introduction effort (*n* = 19). No phylogenetic structure appeared in the number of introduction events (Pagel's $\lambda = 7.3 \times 10^{-5}$, $p = 1$) and total number of individual released (Pagel's $\lambda = 6.6 \times 10^{-5}$, $p = 1$), but date of first introduction was clustered (Pagel's $\lambda = 0.99$, $p = 4.2 \times 10^{-5}$). This structure was explained by the late introductions of two *Anatidae* (Canada Goose, *Branta canadensis* and Mallard, *Anas platyrhynchos*, respectively, introduced in 1905 and 1910) and two other non-passerines (Sulphur-crested Cockatoo, *Cacatua galerita*, in 1900 and Little Owl,

Athene noctua, in 1906). To check whether our results were robust to this phylogenetic structure, we re-estimated the MANOVA, imposing a phylogenetic covariance matrix estimated with a linear-time algorithm, and assuming a Brownian motion model (Ho & Ané, 2014; a Pagel's lambda model returned similar results).

All data processing and data analyses were performed using the ade4 (Thioulouse et al., 2018), adiv (Pavoine, 2020), phylolm (Ho & Ané, 2013) and phytools (Revell, 2012) packages of R version 3.6.1 (R Core Team, 2016). Maps were constructed in QGIS 3.6.

3 | RESULTS

We recorded 1–59 birds per point (mean = 17.3 ± 7.9 birds, all uncertainties in standard deviations unless otherwise stated), belonging to 1–17 species per point (7.3 ± 2.7 species). Native and endemic species accounted for 0 to 85% of species within an assemblage (mean = 30.6 ± 19.7%).

3.1 | Structure of trait-environment relationships

The RLQ analysis builds principal component axes that reflect the co-variation of traits and environmental variables as revealed by assemblage composition, also accounting for space and phylogeny. The two first axes of the RLQ accounted for 74% (RLQ1) and 25% (RLQ2) of total variance (third axis: 0.3%; not retained). The negative side of RLQ1 was dominated by native forests at higher elevations, hosting typically small-bodied species with invertebrate diets, canopy gleaning, high territoriality and sedentarity (Figure 2, lower row). The positive side of RLQ1 was associated with low-elevation exotic grasslands hosting larger-bodied species, but also including a guild of granivorous, understorey-gleaning passerines. This first RLQ axis discriminated high-elevation assemblages consisting mainly of native forest species from lower-elevation assemblages dominated by open-habitat species and some understorey-gleaning generalist granivores. The latter species group was associated with plantation forests on the negative side of RLQ2, while the positive side of this second axis encompassed both native forest birds and mixed assemblages of open-habitat natives and aliens with a relatively wide range of traits (Figure 2, upper row). Consistently, the projection of species (Figure 3a) and points (Figure 3b) on these two axes confirmed that RLQ1 summarized a gradient ranging from birds associated with native forests

at higher elevations to exotic open habitats at lower elevations, while RLQ2 isolated alien seed-eating passerines living predominantly in plantation forests.

Three partly overlapping assemblages emerged from this two-dimensional space. Native forest assemblages (negative side of RLQ1, positive side of RLQ2) consisted mostly of endemic and native passerines such as bellbird (*Anthornis melanura*) and rifleman (*Acanthisitta chloris*), with the exception of two European thrushes (blackbird [*Turdus merula*] and song thrush [*T. philomelos*], Figure 3a). These species are territorial, sedentary and predominantly insectivorous. Avian assemblages occurring in plantation forests (positive side of RLQ1, negative side of RLQ2) were distinct on both taxonomic and functional grounds (Figure 3b), being dominated by European finches (goldfinch [*Carduelis carduelis*], greenfinch [*C. chloris*] and redpoll [*C. flammea*], Figure 3a), a group of abundant small tree-nesting granivorous passerines. The last assemblage (positive sides of RLQ1 and RLQ2) consisted of a less defined mixture of native and alien species exhibiting traits associated with ecological generalism and open or wetland habitats, such as gulls, introduced wildfowl or Australasian swamphen (*Porphyrio melanotus*; Figure 3a). This asymmetry implies that while native/endemic and alien forest species have distinct trait suites, native and alien open-habitat or wetland species are less functionally distinct from forest bird assemblages.

3.2 | Spatial distribution of trait-environment relationships

A spatial structure appeared when mapping point count scores on RLQ1: negative values were located in the north-western, higher elevation parts of the study area and positive values were mainly in the foothills and inland Canterbury Plains (Figure 4a), with the
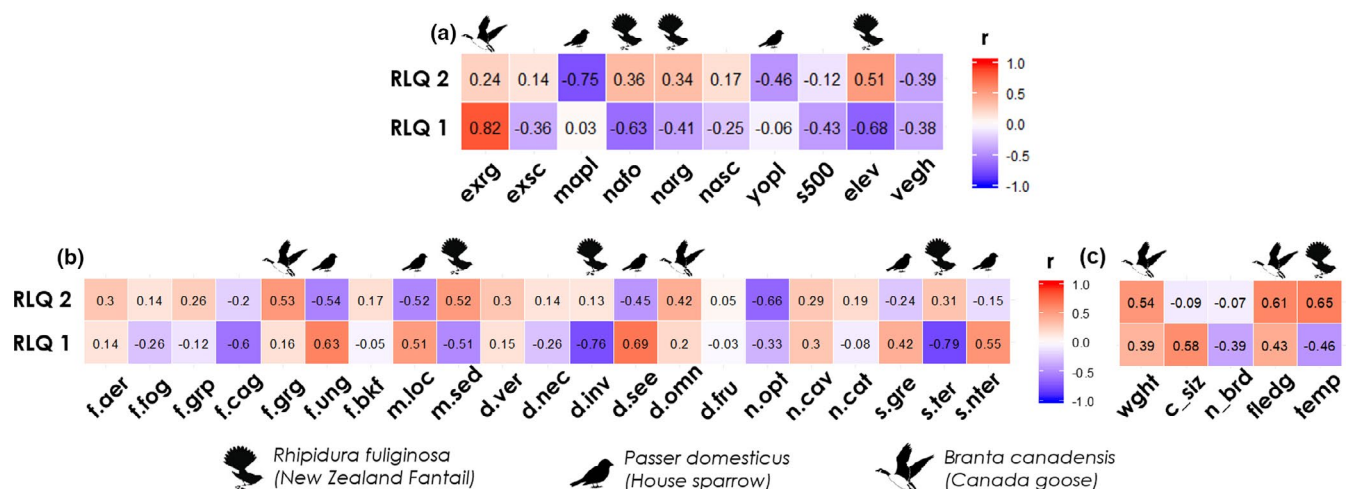

FIGURE 2 Pearson's correlation coefficients (*r*) of the two components of the RLQ with habitat variables (a), ecological traits (b) and life history traits (c). Trait acronyms are explained in Table 2. Silhouettes depict representative species of the three main groups of trait-environment relationships found in the RLQ (species associated with native forests, species associated with plantation forests and open-habitat species)

FIGURE 3 Projections of species (a) and point counts (b) in the bivariate RLQ space controlled for phylogeny and space (species acronyms are explained in Appendix S1, silhouettes in Figure 2). The length of empirical ellipse axes equals 1.5 * the standard deviation of projection coordinates on RLQ1 and RLQ2. Silhouettes depict representative species of the three main groups of trait-environment relationships found in the RLQ (species associated with native forests, species associated with pl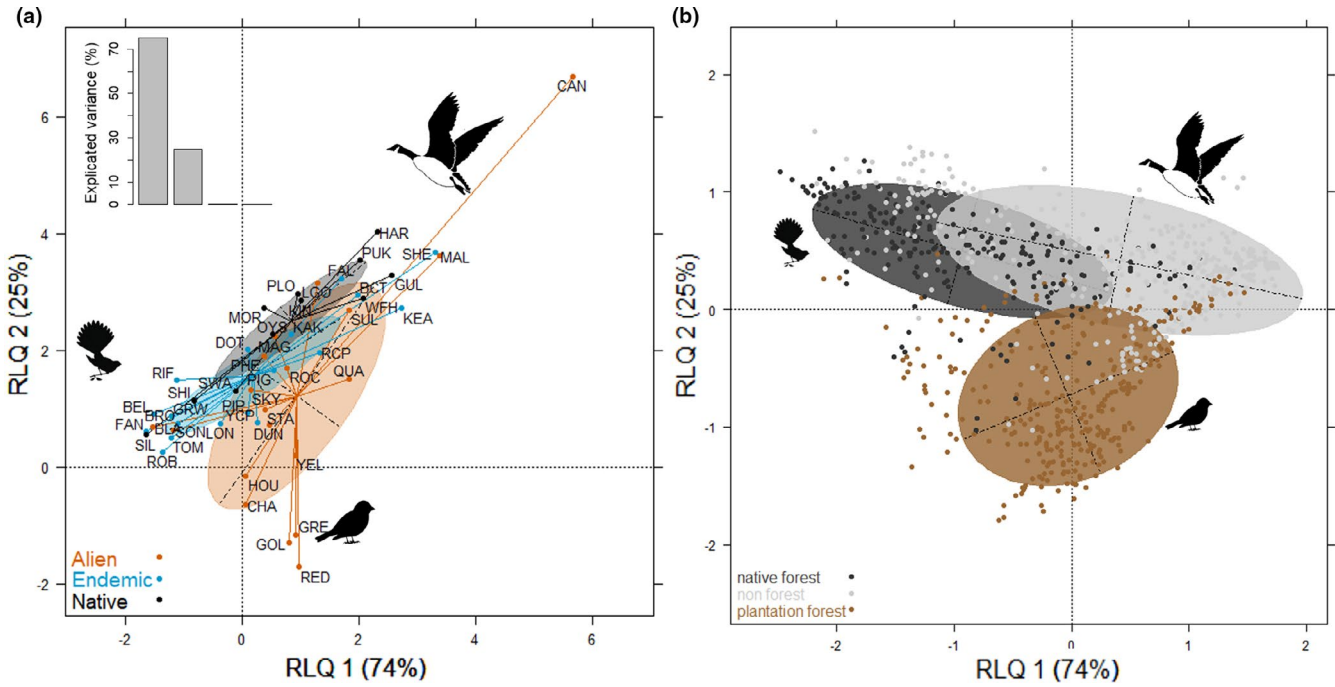antation forests and open-habitat species). Three extreme points (one in plantation forest and two in non-forest) are not represented for ease of reading
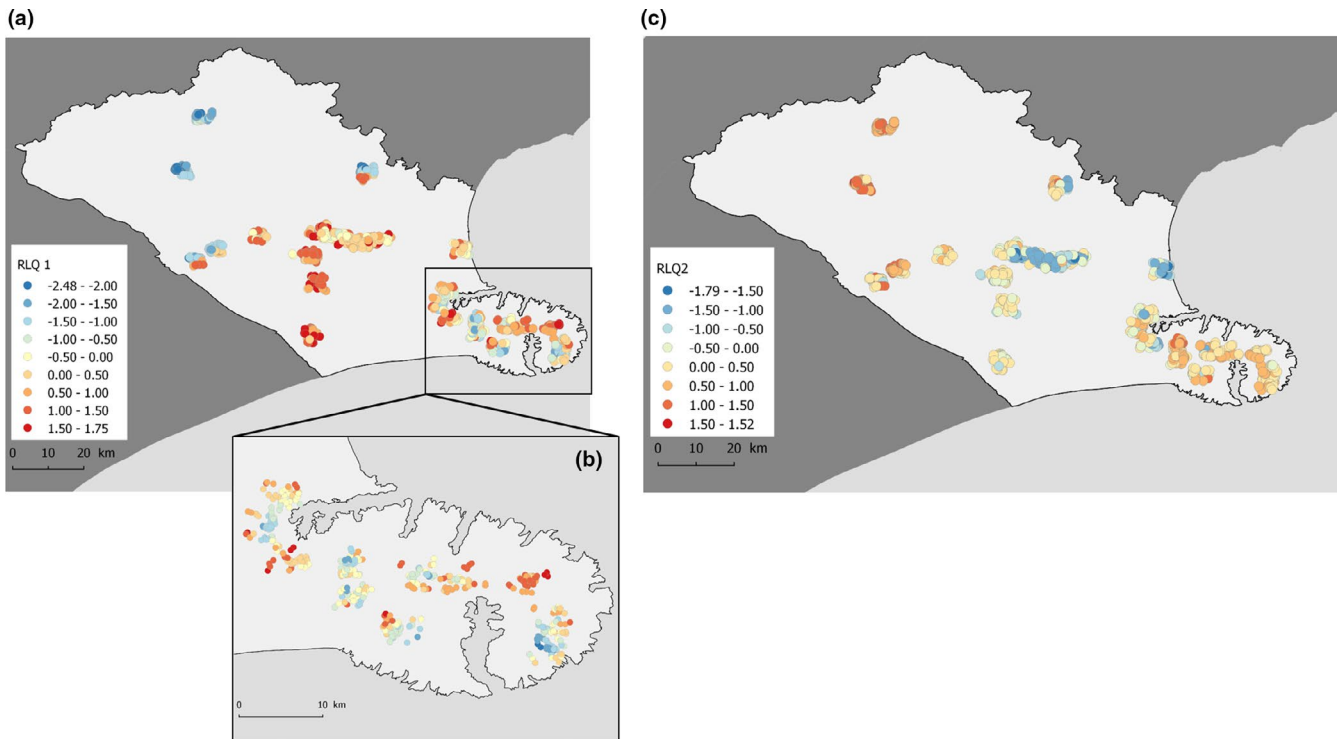

FIGURE 4 Spatial distribution of the scores of RLQ1 (a; b: RLQ1 in the Banks Peninsula) and RLQ2 (c) in the study area

exception of Banks Peninsula which encompassed all the variability along this axis (Figure 4b). Because of this elevational gradient, most open-habitat assemblages were located closer to the sea than forest ones. Intermediate assemblages, close to the centroid of RLQ1 and corresponding to mixed native-alien assemblages living in open or mosaics habitats, were located in the middle of the study area (Figure 1). The geographic structure of RLQ2 opposed a cluster of negative values (assemblages dominated by alien species) in the plantation forests of the foothills to positive values (assemblages dominated by native species) in high-elevation native forests and in parts of Banks Peninsula (Figure 4c). RLQ2 scores were close to 0 in most of the lower elevation lowlands, indicative of less demarcated assemblages mixing native and alien species, especially within the Banks Peninsula habitat mosaics.

The ordination of point counts on RLQ axes (Figure 3b), their mapping (Figure 4) and the particular pattern of the Banks Peninsula assemblages (Figure 4b) revealed that the structure of the ordination was not a consequence of the regional elevation gradient. The alien forest species guild overlapped little with the two others, although most plantation forests were located at low or intermediate elevations, close to open habitats (Figure 4b). Conversely, the native forest guild and the open-habitat guild overlapped substantially (Figure 4b), although they were mainly located at the two extremes of the elevation gradient (Figure 4a).

3.3 | Influence of phylogeny

RLQ1 and RLQ2 were phylogenetically structured (Figure 5), as expected from the RLQ mapping in Figure 4. Negative values of RLQ1 were mostly associated with three closely related families of endemic passerines (e.g., *Petroicidae*, *Mohouidae* and *Acanthisittidae*), and the only two European *Turdidae* successfully introduced in New Zealand), revealing some evolutionary conservatism in the trait-habitat relationships of forest species (Figure 5a-c, RLQ1). The positive side of RLQ1 (open habitat assemblages) was less structured and included distant clades, including all wetland species and several passerines (Figure 5a, RLQ1). The main phylogenetic structure in RLQ2 was the concentration of negative values associated with exotic granivorous species living in plantations (finches, yellowhammer and house sparrow, Figure 5b, RLQ2), confirming that these European species share trait-habitat relationships that have no equivalent within the regional bird assemblage.

3.4 | Effect of introduction history

Alien forest species (negative sides of RLQ1 and RLQ2) tend to have been introduced earlier than open-habitat ones, but this pattern was mainly driven by the late introduction of a few large non-passerines
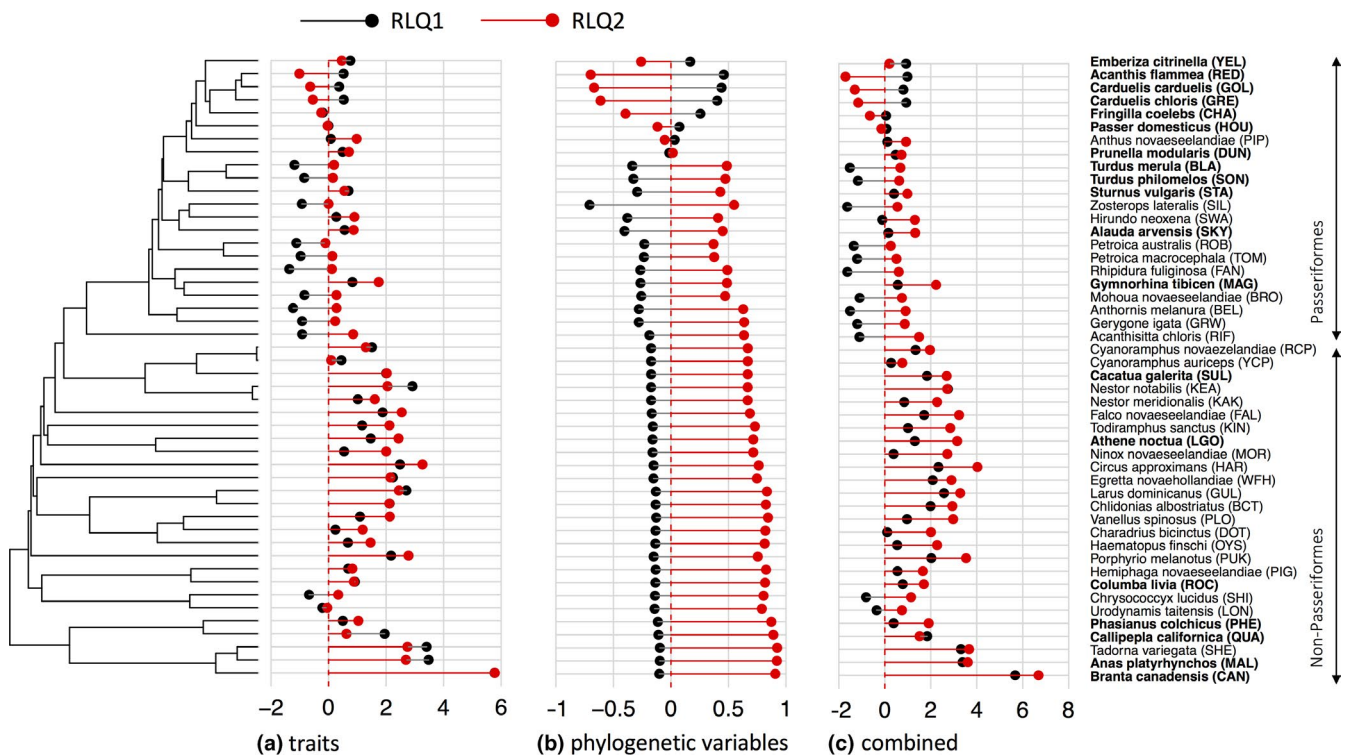

FIGURE 5 (a) Distribution of the RLQ scores in the phylogenetic tree of the 48 bird species encompassed by the study (alien species in bold, see Appendix S1 for acronyms). The mapping uses an interpolation of the RLQ scores along each edge following the default behaviour of the function contMap in the R package phylotools. (b) projections of trait variables (the components of a Hill & Smith analysis on the species x trait matrix) on the RLQ axes (black: RLQ1, red: RLQ2). (c) projection of phylogenetic variables (the components of a principal coordinate analysis on a phylogenetic dissimilarity matrix) on the RLQ axes. (d) combined projection of traits and phylogeny on the RLQ axes

(Figure 6a–c, F2,14 = 8.66, *p* = .004; with phylogenetic correction: *t* value = 2.57, *df* = 13, *p* = .021, not shown on figure). Neither the number of introduction events (Figure 6c–d, F2,14 = 0.72, *p* = .50; with correction: *t*-value = −1.84, *df* = 13; 0.09) nor the number of released individuals (Figure 6e–f, F2,14 = 0.39, *p* = .68; with correction: *t*-value = 0.46, *df* = 13, *p* = .65) had any effect on the ordination, suggesting that the predictors used to account for introduction history had little impact on current trait-environment associations.

4 | DISCUSSION

Previous studies on New Zealand bird assemblages showed that native and alien species are segregated along gradients of anthropogenic land use. However, they did not investigate the role of species' ecological traits in these patterns and were either restricted to forests (Barbaro et al., 2012; Barnagaud et al., 2014; Clout & Gaze, 1984), agricultural (MacLeod et al., 2008) or urban habitats (van Heezik et al., 2008). Others used functional diversity metrics based on occurrence-only data from the New Zealand breeding bird atlas (Méndez et al., 2018; Robertson et al., 2007). In this work, we showed that such niche partitioning within bird communities is stronger in forests than in open habitats and is related to distinct trait syndromes, consistent with those found at broader spatial scales (Soares et al., 2021). Furthermore, we found that these trait-habitat associations are largely independent of the introduction history of alien species.

Native and alien species were more clearly partitioned by their traits in forests than in open landscapes, where they exhibited more similar ecological trait suites. Open habitats at lower elevations in New Zealand were historically restricted to wetlands and smaller areas of grassland or scrub. The conversion of these habitats for agriculture and urbanization restrained the range of open-habitat native specialists to only a few species such as fernbird (*Megalurus punctatus*) and New Zealand pipit (*Anthus novaeseelandiae*, Heather et al., 2005). Large-scale modifications of open habitats also involved the replacement of native vegetation by European (or related North American) herbaceous and woody species. These conversions further facilitated the colonization of European birds, which were released into habitats that greatly resembled those modified habitats from which they originated and for which their traits had evolved to be adapted to. The majority of open habitat endemics had become extinct even before these habitat changes, soon after colonization by humans from the 14th century onwards (including at least North and South Island geese [*Cnemiornis* spp.], Finsch's duck [*Chenonetta finschi*], Eyle's harrier [*Circus eylesi*], New Zealand quail [*Coturnix novaezelandiae*], adzebills [*Aptornis* spp.], rails [*Rallus* spp.], snipes [*Gallinago* spp.] and Laughing owl [*Sceloglaux albifacies*]; Blackburn et al., 2004; Holdaway, 2001, as well as large-bodied forest moas [*Dinornithidae*, Blackburn et al., 2004; Holdaway, 2001]). These selective extinctions and introductions may in turn have increased contrasts in trait composition among habitats and inflated the role of traits indirectly related to habitat preference, such as body size

or diet preferences, in explaining current bird assemblages (Parlato et al., 2015).

In our ordination analysis, RLQ scores showed a gradient from open areas in lowlands to the native forests of the Southern Alps and Banks Peninsula. This reflects the fact that many native species were largely relegated to native forest remnants after the conversion of lowland habitats to agricultural land uses (Deconchat et al., 2009). Nevertheless, the transition from native forest to open-habitat species assemblages in the RLQ space was not a smooth gradient of habitat preferences—for instance, several species located close to the origin of RLQ1 were open-habitat specialists (oystercatcher [*Haematopus unicolor*], New Zealand dotterel [*Charadrius obscurus*] and skylark [*Alauda arvensis*]). Furthermore, assemblages remained well differentiated in the RLQ space within Banks Peninsula (Figure 4), in association with a complex topography and diverse landscape mosaics where native forests and all types of open habitats were located close together. The persistence of trait partitioning across adjacent habitats within a landscape suggests that strong trait-habitat associations, rather than geographic distance, inhibited the invasion of native bird assemblages by alien species in indigenous forests (Duncan, 1997; Veltman et al., 1996). Larger-scale spatial and temporal data would be necessary to infer the influence of environmental filtering per se (Méndez et al., 2018; Ruffell & Didham, 2017), but a landscape-level determinism in trait distributions matches the separation of native and exotic species within habitat mosaics, as previously observed in the same region (Barbaro et al., 2012; Barnagaud et al., 2014). Our results are therefore consistent with the hypothesis that native and exotic species are rarely in direct interaction in these novel bird assemblages because their trait differences (especially foraging ecology and diet) maintain a segregation across the boundaries between patches of different habitat types.

Birds in landscapes dominated by native forests tended to be smaller-sized, insectivorous and territorial (e.g., tomtit [*Petroica macrocephala*], rifleman [*Acanthisitta chloris*] and fantail [*Rhipidura fuliginosa*]), while alien colonizers of exotic plantations were on average more social and granivorous (e.g., finches or buntings). These results are consistent with a recent study comparing alien and native species' traits among species from 73 oceanic islands (Soares et al., 2021; New Zealand was not included). The strong imprint of body size on the RLQ pattern is likely inflated by the extinction of large flightless forest species following the introduction of mammalian predators (Holdaway, 1989). However, diet, body size and territoriality also range amongst the traits that explain the winner/ loser dynamics observed in European and Nearctic bird assemblages (Baiser & Lockwood, 2011; Devictor et al., 2008; Newbold et al., 2018). Species that cope well with anthropogenization in their area of origin are common in landscapes dominated by exotic plantations in New Zealand (e.g., greenfinch [*Carduelis chloris*], chaffinch [*Fringilla coelebs*] and goldfinch [*Carduelis carduelis*]), as also observed in European plantation forests (Pedley et al., 2019). This similarity suggests that trait-based winner/loser dynamics could also have confined ecologically specialized native species in their native habitats,
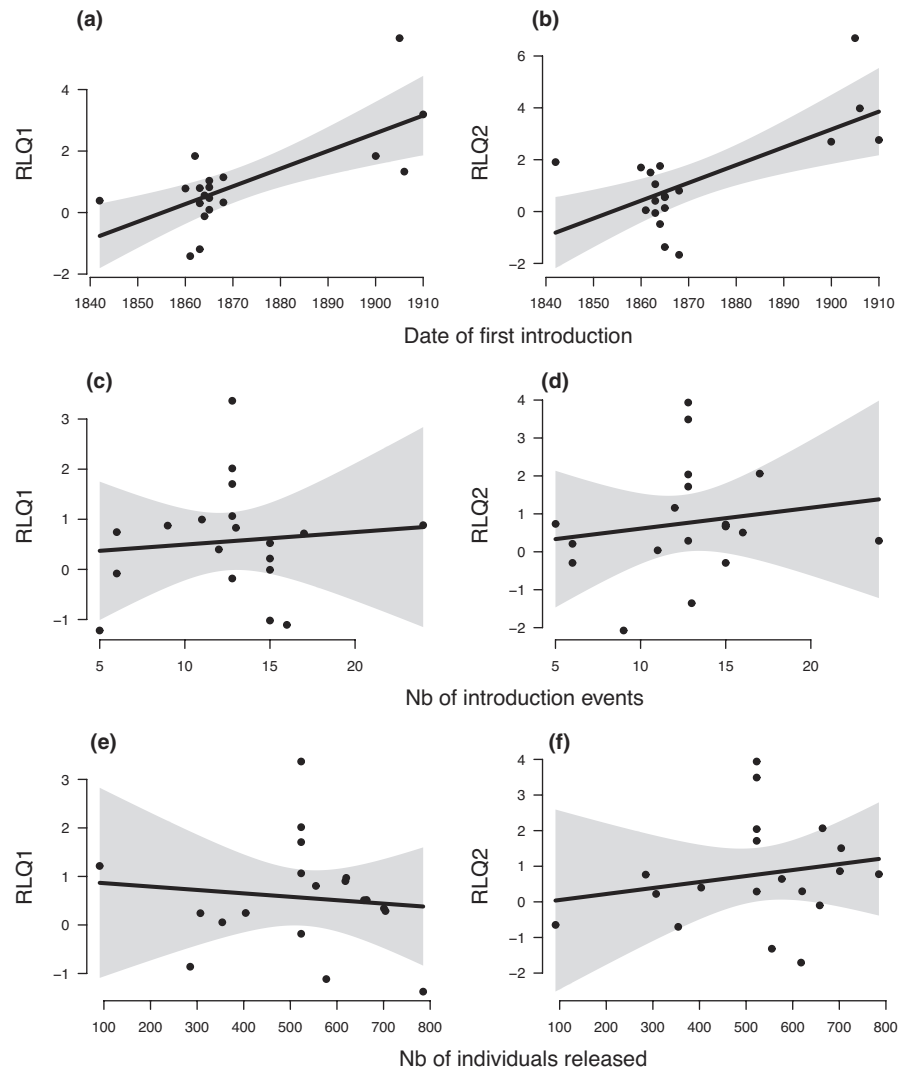
while generalism would have permitted some alien colonizers to invade novel man-created landscapes, which remained largely free of competition from native species (Cardador & Blackburn, 2019).

Unique among alien species in our analysis, song thrush and blackbird exhibited a strong association with native forest, and a trait suite dominated by insectivory, sedentariness and territoriality (Barbaro et al., 2012; Clout & Gaze, 1984; MacFarlane et al., 2016). As a result, they were associated with native forest specialists in our RLQ, although these two thrushes are found in a wide range of landscapes both in New Zealand and in their native areas, including old-growth forest, shrubland and various types of plantations (Samaš et al., 2013) as well as suburban areas (not assessed in our study). European thrushes are ground foragers that frequently feed on ground invertebrates and breed in lower vegetation strata (Martay & Pearce-Higgins, 2020), a niche left partly vacant as a result of the extinction of numerous native ground bird species under the pressure of mammalian predators (Duncan & Blackburn, 2004). Our results are therefore consistent with competitive release allowing alien ground-nesters and foragers to colonize lower forest strata, although demonstrating the exact role of competition is not possible because of the extinction or severe decline of many native ground-nesters.

These trait-based interpretations are an advancement on previous studies which showed habitat partitioning between alien and native forest birds along a gradient of vegetation height within New Zealand forests (Barnagaud et al., 2014). Similar patterns would also arise if the two thrushes were the remnants of a wider pool of alien species sharing similar traits as native forest birds (relatively small size, insectivory and territoriality), most of which failed to establish long-term populations for reasons unrelated to habitat (Pipek et al., 2020). Thus, dedicated monitoring and experimental protocols would probably be needed to separate the relative roles of habitat, competition and introduction success further, because they often translate into similar patterns of species distributions (Cadotte & Tucker, 2017; Germain et al., 2018).

We did not detect any signal of introduction history on trait-habitat associations, suggesting that ecological processes have taken over the initial human imprint on alien species distributions (consistent with findings of Soares et al., 2021, although they did not explicitly test variables representing introduction effort). The proxies used here are non-exhaustive compared with studies investigating introduction effort directly (Pipek et al., 2020) but they have the merit of being integrative and equally documented

for all species. It may seem intuitive, on ecological grounds, that traits overtake other drivers of species distributions among habitats once populations are sufficiently settled on an island. Nevertheless, our result contrasts with studies on various island avifaunas throughout the globe which still bear a detectable imprint of early colonization dynamics (Blackburn et al., 2013; Duncan et al., 2019). These multi-island studies were performed at coarser spatial grains or were based on species richness variations, which are less sensitive to local habitat variations than our fine-grained study of individual species. Furthermore, according to available archives, relatively few forest-related species were introduced to New Zealand in the initial colonization events. Forest species were also scarce among introduced species that failed to establish, some of which were insectivorous (e.g., Robin [*Erithacus rubecula*] or Nightingale [*Luscinia megarhynchos*], Pipek et al., 2020). These selective failures may have contributed to set an environmental filter-like pattern for reasons unrelated to habitat preference. However, introduction history alone cannot explain why European finches remain well demarcated from native species in the "exotic forest" side of the RLQ—which does not imply that they never enter native wood patches, but that they barely invaded landscapes entirely dominated by native forest. Discrepancies in the spatial distribution of resources within landscapes, between native and introduction areas, could explain this trait-mediated separation and contribute to explain introduction success. This hypothesis remains to be tested through macroecological-level comparative analysis (Blackburn et al., 2013; Duncan et al., 2019; MacLeod et al., 2009; Redding et al., 2019).

Overall, although the introduction history played a major role in early colonization events, our results indicate that the establishment success of most alien birds in New Zealand is the most substantially attributable to the anthropogenic conversion of habitats, against direct competition with native birds (Cardador & Blackburn, 2019; Veltman et al., 1996). Novel resources likely permitted the coexistence between alien and native birds within novel species assemblages in transformed New Zealand landscapes, while alien species' trait syndromes are consistent with their restriction to anthropogenic habitats 150 years after their introductions. Local adaptation, the expression of behavioural plasticity or fine-grained habitat changes may still lead to future colonization of native habitats by exotic species under the influence of gradual processes or unpredictable regime shifts (Gaüzère et al., 2018). However, our results suggest that trait-habitat relationships currently act as a strong filter to direct, competitive interactions between alien and native birds in New Zealand forests. Our results also reveal the originality of endemic bird assemblages' trait composition in native forests. Given the multiple pressures of global change, the unique bird diversity of New Zealand should be preserved especially because these assemblages may see their ranges restricted more in the future as a result of a warming climate (Walker et al., 2019).

The mitigation of global change pressures, especially the effects of biological invasions, land cover change and climate change, further pose major challenges to New Zealand avifauna. Predation by introduced mammals is considered to be the most important factor in ongoing declines, and also impeding the recovery of many endemic New Zealand birds (Innes et al., 2010). Although considerable progress has been made in controlling introduced predators using trapping and pesticides (Peltzer et al., 2019), more research is needed to investigate how managing the landscape matrix could potentially mitigate predation pressure on native species. In addition, several studies have shown that the configuration of woody elements in a mosaic landscape can help mitigate the large-scale decline of birds adapted to cooler climates, either by direct microclimatic effects or by indirect resource provisioning (Barnagaud et al., 2013; Walker et al., 2019). Thus, managing the landscape matrix is potentially also beneficial for both climate change mitigation and the maintenance of high-quality habitat patches (small or large) that provide key resources to native forest birds displaying high trait specialization. For instance, cavity nesters are the birds most prone to decline as a result of global change in New Zealand (Parlato et al., 2015; Walker et al., 2019), while they can be easily favoured by preserving old-growth patches or isolated trees within previously unfavourable landscape matrices. Enhancing coexistence among natives and aliens at the landscape level based on their distinct trait syndromes is therefore a potential key mechanism for bird conservation in changing land use mosaics of island ecosystems worldwide.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ddi.13432.

DATA AVAILABILITY STATEMENT

Trait and phylogenetic data are provided as supplementary materials. Bird counts (in a partially blinded and aggregated format to comply with the privacy policy of the owner) and environmental data are available at https://doi.org/10.5061/dryad.ghx3ffbq2 together with all scripts to replicate the analyses.

ORCID

Jean-Yves Barnagaud 🄳 https://orcid.org/0000-0002-8438-7809
Eckehard G. Brockerhoff 🄳 https://orcid.org/0000-0002-5962-3208
Luc Barbaro 🄳 https://orcid.org/0000-0001-7454-5765

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BIOSKETCH

The BIOTA project aims to explore the imprint of climate, land use and alien species on the bird faunas of oceanic islands through a functional biogeography approach. J.Y.B focuses his research on the processes underlying spatial variations in the composition and diversity of vertebrate assemblages at multiple spatial scales. He uses a combination of ecoinformatics methods coupling standardized data and opportunistic records from citizen sciences.

Author contributions: J-Y.B. and L.B. conceived the idea and supervised the study, L.B., M.D. and E.B. collected bird data, P.D. computed the phylogenetic tree, R.M. and J-Y.B. gathered the trait data, R.M. performed the statistical analyses with support of J-Y.B. and S.P., J-Y.B. led the writing. All the authors contributed substantially to all stages of the writing.

SUPPORTING INFORMATION

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