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# Habitat filtering by landscape and local forest composition in native and exotic New Zealand birds

JEAN-YVES BARNAGAUD,<sup>1,2,3,8</sup> LUC BARBARO,<sup>1,2</sup> JULIEN PAPAÏX,<sup>4,5</sup> MARC DEONCHAT,<sup>6</sup>  
AND ECHEHARD G. BROCKERHOFF<sup>7</sup>

<sup>1</sup>INRA, BIOGECO, UMR1202, 69 Route d'Arcachon, 33612 Cestas, France

<sup>2</sup>Université de Bordeaux, BIOGECO, UMR1202, Avenue des Facultés, 33405 Talence, France

<sup>3</sup>Centre for Informatics Research on Complexity in Ecology, Aarhus University, Department of Bioscience, NyMunkegade 114, 8000 Aarhus C, Denmark

<sup>4</sup>UR BIOGER, INRA, Avenue Lucien Brétignières, BP01, 78850 Thiverval-Grignon, France

<sup>5</sup>UR MIAJ, INRA, Domaine de Vilvert, 78352 Jouy-en-Josas CEDEX, France

<sup>6</sup>INRA, UMR 1201 DYNAFOR, F-31326 Castanet Tolosan, France

<sup>7</sup>Scion (New Zealand Forest Research Institute), P.O. Box 29237, Christchurch 8540 New Zealand

**Abstract.** Untangling the relative influences of environmental filtering and biotic interactions on species coexistence at various spatial scales is a long-held issue in community ecology. Separating these processes is especially important to understand the influences of introduced exotic species on the composition of native communities. For this aim, we investigated coexistence patterns in New Zealand exotic and native birds along multiple-scale habitat gradients. We built a Bayesian hierarchical model, contrasting the abundance variations of 10 native and 11 exotic species in 501 point counts spread along landscape and local-scale gradients of forest structure and composition. Although native and exotic species both occurred in a wide range of habitats, they were separated by landscape-level variables. Exotic species were most abundant in exotic conifer plantations embedded in farmland matrices, while native birds predominated in areas dominated by continuous native forest. In exotic plantation forests, and to a lesser extent in native forests, locally co-occurring exotic and native species were segregated along a gradient of vegetation height. These results support the prediction that exotic and native bird species are segregated along gradients related to anthropogenic disturbance and habitat availability. In addition, native and exotic species overlapped little in a multivariate functional space based on 10 life history traits associated with habitat selection. Hence, habitat segregation patterns were probably mediated more by environmental filtering processes than by competition at landscape and local scales.

**Key words:** *Bayesian hierarchical models; biological invasions; bird introductions; exotic plantations; habitat filtering; interspecific interactions; native forest.*

## INTRODUCTION

Species introductions have generated much interest from ecologists and conservationists in the last two decades. Introduced species can profoundly affect local community processes (Didham et al. 2005) and thus may modify the various facets of ecological diversity at various spatial scales (Sanders et al. 2003, Lessard et al. 2009), sometimes with negative consequences for ecosystem services (Vilà et al. 2010, Ladle and Whittaker 2011, Simberloff et al. 2013).

The concern for community-level effects of species introductions arose within a long-held debate about the determinants of species diversity in space and time (e.g., Ricklefs 1987). Abiotic conditions, resource gradients, dispersal limitations, and biotic interactions shape species distributions and assemblages, from continental

to local spatial scales (Pearson and Dawson 2003). Whether or not species introductions impact community structure therefore depends on the extent to which environmental filtering prevents local interferences between exotic and native species (Maitner et al. 2012). Exotic species may be related to resources and habitats modified by man, which are inaccessible to, or unused by, native species. Niche conservatism may also cause exotic species to fill only partially native habitat niches in the invaded range (Strubbe et al. 2013). This is the essence of the “opportunism hypothesis,” which is expected to result in strong environmental filtering patterns at landscape and local scales (Diamond and Veitch 1981, Case 1996). Alternatively, when exotic and native species occupy similar ecological niches, they may be displaced by interspecific competition for local resources (Mack et al. 2000, Levine et al. 2003). The relative importance of niche-based filtering processes and biotic interactions on the coexistence of native and exotic species, and their scales of influence, have thus become a primary focus of community-oriented conser-

<sup>8</sup> E-mail: jeanyves.barnagaud@gmail.com

vation biology (Shea and Chesson 2002, Melbourne et al. 2007).

Bird introductions have sometimes resulted in dramatic changes in the diversity and composition of local avifaunas, particularly on islands (Case 1996). However, it is unclear whether these changes were due to direct interactions with introduced exotic species, or were the indirect consequence of habitat alteration. Habitat fragmentation and matrix permeability driven by anthropogenic land use might indeed limit species' coexistence at a landscape scale, by altering population persistence and exchanges within native species' metapopulations, or preventing exotic species' dispersal and settlement (Case 1996). Habitat filters may also act at local scales, as generalist, behaviorally flexible, exotic birds tend to replace specialized, less tolerant, native species along a gradient of man-made alteration from undisturbed indigenous habitats to highly urbanized areas (e.g., van Heezik et al. 2008, Sol et al. 2012). It has therefore been proposed that native and exotic species rarely interact directly, because habitat partitioning and human disturbance prevent their local co-occurrence (Sol et al. 2012). However, this prediction lacks support from regional studies focused on non-urban gradients. The high conservation value of native forest, even as small remnants within an agricultural matrix (Lindenmayer et al. 2002), suggests indeed that native and exotic species could regularly co-occur. In addition, the abundance-habitat relationships of native and exotic bird species sharing similar ecological requirements have rarely been directly addressed (e.g., Acevedo and Restrepo 2008, Lugo et al. 2012; both from Caribbean Islands). Yet, such comparative studies are essential for assessing whether exotic and native bird species with similar habitat preferences interact over shared resources.

We tested whether landscape and local-scale forest gradients segregate forest-related exotic and native birds in New Zealand. By focusing on forests and forest birds, we contrasted the responses of species with overlapping habitat requirements, which therefore might be expected to co-occur and possibly interact over resources. New Zealand forests are an ideal study area to address this aim. Human activities since the mid 19th century involved the replacement of large areas of mature native forests by farmland and, in some cases, plantations of exotic trees (Wilson 2008). In the late 19th century, numerous exotic bird species were introduced by European settlers in these modified landscapes (Duncan 1997), and most successfully established species spread across much of the country. These exotic bird species currently occur in New Zealand with similar or higher abundances than native species (Cassey 2001, Robertson et al. 2007, Barbaro et al. 2012). Hence, any habitat filtering patterns could not merely be related to species' rarity or to species staying at their initial location of introduction. We investigated habitat segregation patterns by testing the following predictions:

- 1) Native and exotic species' abundances are mainly filtered by landscape-level gradients of forest cover and composition (Case 1996). If, as in urban areas, habitat disturbance had a dominant influence on bird community structure (Sol et al. 2012), we expected native species to be more abundant in large, continuous native forests, and exotic species to occur mostly in fragmented forests.
- 2) Echoing landscape-level patterns, we expected local forest structure and composition to separate native and exotic birds. We expected native species to be dominant in undisturbed native forest stands in which they evolved, while exotic species should be more abundant in exotic plantations in which resources for native birds are scarcer and/or more disturbed (Didham et al. 2007).
- 3) Vegetation height separates native and exotic birds when they co-occur locally, either because of competitive exclusion, or because species' ecological preferences lead them to use different strata. Specifically, in exotic forests, we expected native species to occur mostly in mature stands, which are more similar in structure and understorey composition to native forests than are younger plantations (Brockerhoff et al. 2003).

We further explored the overlap of native and exotic species in a multivariate functional trait space, as an indication of the relative roles of niche separation and competitive exclusion in generating habitat segregation patterns at the local scale.

## METHODS

### *Study area*

A total of 501 point counts separated by at least 200 m and clustered into 25 regions (11–32 points per region) were conducted in the Canterbury Region of the South Island, New Zealand. The study covered a gradient of landscape fragmentation ranging from farmland dominated by grasslands, crops, and urban areas with forest remnants, to mainly forested areas (Fig. 1; Deconchat et al. 2009). All points were located in forests (any habitat dominated by contiguous mature trees), between sea level and ~1200 m above sea level. Forests consisted of regenerating or old native forest remnants (75% of the total forest cover) and planted, exotic stands (25%), which covered together 15% of the study area (i.e., 85% non-forest). Historically, forest cover was even lower than today in some parts of the study area. For example, on Banks Peninsula, natural forest had declined to as little as 1% in the mid 1900s but today regenerating and old growth forest remnants account for ~15% of the area (Wood and Pawson 2008).

### *Landscape and local habitat variables*

New Zealand forest birds' local abundances are mostly affected by landscape composition below a 500-m radius (Deconchat et al. 2009). Hence, local and

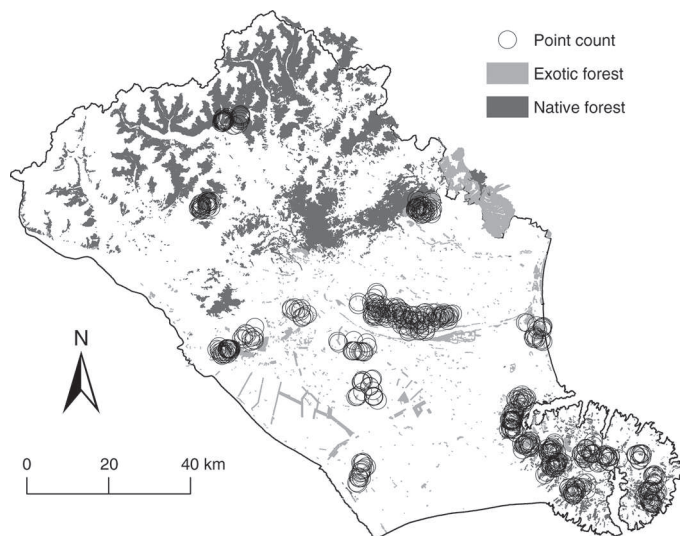


FIG. 1. Distribution of sampling plots and forested habitats in South Island, New Zealand.

landscape-scale forest structure and composition were quantified, respectively, in buffers of 100 and 500 m radii centered on each point count.

Field observers characterized local habitat structure and composition by means of two main parameters. The height of the dominant vegetation stratum (vegetation height, VH) was visually estimated and assigned to one of eight categories (0–0.5 m, 0.5–1 m, 1–2 m, 2–5 m, 5–10 m, 10–20 m, 20–30 m, >30 m) as a proxy of habitat structure. For analyses, the midpoint of each vegetation class was used, and VH was considered as a continuous variable. The composition of local habitat (local habitat type [ $h$ ]) was classified as native forest (including *Kunzea ericoides* and other native trees and shrubs,  $n = 280$  points) or exotic forest (all mature or young plantations of exotic trees;  $n = 221$  points).

Forest composition was quantified at the landscape scale according to the New Zealand Land Cover Database 2 (Terralink 2004). From the relative total forest cover (FOR, including mature stands and shrubland of >2 m height, ranging from 0.9% to 78.6% of total buffer area,  $49.36\% \pm 23.40\%$  [mean  $\pm$  SD]), we extracted the proportion of native forest (NATFOR, ranging from 0% to 100% of total forest cover,  $42.68\% \pm 44.49\%$ ). Nonnative forest consisted of managed stands of exotic trees, but could include areas with native understorey plants, although this cannot be assessed through remote sensing land cover data.

#### *Bird sampling*

Each of the 501 breeding bird communities was sampled once in the austral summers of 2005–2006 ( $n = 307$  points) and 2006–2007 ( $n = 194$  additional points). All birds heard or seen within 100 m were mapped and counted by one of six observers during three consecutive 5-minute replicates, which limited the risk of double counting and ensured community closure during the sampling (MacKenzie et al. 2005). A few points were

performed by several observers to ensure methodological consistency; we thus considered seven different possible observer identities (six individuals plus multiple individuals).

We retained 21 bird species (Appendix A: Table A1) qualified as at least partly forest dependent in the relevant literature (Heather et al. 2005, Robertson et al. 2007). We did not consider non-forest birds (mostly waterbirds and a few ground-nesting birds of open habitats) as they exploit distinct habitat and trophic resources, and are not expected to co-occur with forest species. The small number of non-forest species recorded during point counts concerned nonresident individuals. These were removed from the data set to avoid spurious habitat filtering patterns (list of excluded species in Appendix A: Table A2). We thus retained 10 native species (including endemic subspecies of more widespread species) and 11 exotic species introduced by humans in the 19th century (Appendix A: Table A1; following Heather et al. 2005, Robertson et al. 2007).

To explore how the functional composition of native and exotic guilds can account for habitat response patterns, we compiled data on 10 life history traits for the 21 species (Table 1). We selected five traits likely to be directly related to species' habitat selection (Robinson and Holmes 1982, Mac Nally 1994, Martin 1998): habitat specialization, nest location, foraging method, diet, and territoriality. We also included migratory status, body size, mass, and annual productivity (mean annual egg and brood number), as they affect species' ecological niches and interspecific interactions (Brandle et al. 2002).

#### *Statistical analyses*

We related bird species' abundances to landscape and local habitat composition in a multispecies  $N$ -mixture hierarchical model, accounting for imperfect detections during the sampling process (Royle and Dorazio 2008,

TABLE 1. Life history traits and their loadings on the two first components (C1 and C2) of a Hill and Smith analysis ( $N = 21$  species).

Class and variable	Native species	Exotic species	C1	C2
<b>Habitat (cat)</b>				
Forest related	8	3	0.378	0.067
Generalist	2	8	-0.416	-0.073
<b>Foraging method (cat)</b>				
Canopy gleaner	7	1	0.377	0.217
Ground gleaner	1	4	-0.630	0.008
Ground prober	0	3	-0.025	0.445
Understorey gleaner	2	3	0.043	-0.622
<b>Biometry (cont)</b>				
Size (cm)	18.5 ± 12.0	20.0 ± 8.5	-0.217	0.506
Weight (g)	82.7 ± 200.1	81.7 ± 102.2	-0.186	0.469
<b>Movements (cat)</b>				
Migratory	4	6	-0.149	-0.015
Sedentary	6	5	0.136	0.014
<b>Diet (cat)</b>				
Herbs, seeds, fruits, nectar	2	6	-0.299	-0.268
Carnivorous-insectivorous	8	3	0.343	0.026
Omnivorous	0	2	-0.694	0.928
<b>Nesting site (cat)</b>				
Cavity on rock	1	1	-0.521	0.337
Cavity on tree	2	0	0.660	-0.462
Open on ground/rock	0	3	-0.670	-0.509
Open on tree	7	7	0.124	0.127
<b>Reproduction (cont)</b>				
Clutch size (no. eggs/clutch)	3.0 ± 1.2	4.6 ± 2.8	-0.315	-0.324
Brood number (no. broods/yr)	2.2 ± 0.4	1.9 ± 0.5	0.356	-0.074
<b>Social behavior (cat)</b>				
Non territorial	0	5	-0.512	-0.512
Territorial	10	6	0.160	0.160

*Note:* The number of native and exotic species per class is given for categorical traits (cat); the mean and SD is given for continuous traits (cont).

Schaub and Kéry 2011). The model included an observation process to estimate unobserved parameters (species' detectability and abundance) from replicated counts, and a latent ecological process relating species' abundance to landscape and habitat variables (Fig. 2). We assumed that the effects of landscape and habitat differed between individual species, but were shared among exotic and native species, respectively.

*Abundance model (latent ecological process).*—The abundance of a species  $i$  at a site  $j$  ( $N_{i,j}$ ) was modeled as a Poisson distribution with mean  $\lambda_{i,j}$ :

$$N_{i,j} \sim \text{Poisson}(\lambda_{i,j}). \quad (1)$$

The mean  $\lambda_{i,j}$  was linearly related to site-specific habitat and landscape covariates through a log link:

$$\log(\lambda_{i,j}) = \alpha_{i,h(j)} + \beta_{1,i} \times \text{FOR}_j + \beta_{2,i} \times \text{NATFOR}_j + \beta_{3,i,h(j)} \times \text{VH}_j + \beta_{4,i} \times \text{ALT}_j + \varepsilon_{i,j}. \quad (2)$$

The parameters  $\beta_{1,i}$ ,  $\beta_{2,i}$ , and  $\beta_{4,i}$  were species-specific slopes for total forest cover, native forest cover, and altitude. The slope for local vegetation height,  $\beta_{3,i,h(j)}$ , and the intercept  $\alpha_{i,h(j)}$ , differed between local habitats dominated by exotic or native forest. A normally

distributed latent random effect  $\varepsilon_{i,j}$  was added to account for over-dispersion in the Poisson process (Schaub and Kéry 2011). Twenty-five region-level priors were assigned to  $\varepsilon_{i,j}$  to account for spatial dependencies between point counts. In addition, separate means were assigned to each of these 25 priors for each of the two survey years.

Species-level slopes and intercepts were random effects drawn from separate normal hyper-prior distributions for exotic and native species. For instance,  $\beta_{1,i}$  had two distinct hyper-prior normal distributions, according to species' guild [ $G(i)$ , native or exotic species]. The hyper-parameters describing this distribution were the guild-level mean  $\mu_{1,G(i)}$  and variance  $\sigma_{1,G(i)}$  of individual species' responses to the percentage of forest cover (Sauer and Link 2002). Similar hyper-priors were defined for  $\beta_{2,i}$  and  $\beta_{4,i}$ . For  $\alpha_{i,h(j)}$  and  $\beta_{3,i,h(j)}$ , separate hyper-priors were defined for exotic and native species, and for exotic and native local habitats (hence four hyper-priors for these two parameters). The mean  $\mu_{0,G(i),nf}$  (for native forests) was set to 0 to make the model identifiable; hence, the effect of local habitat type was expressed as the difference between species abundances in native and exotic habitats.



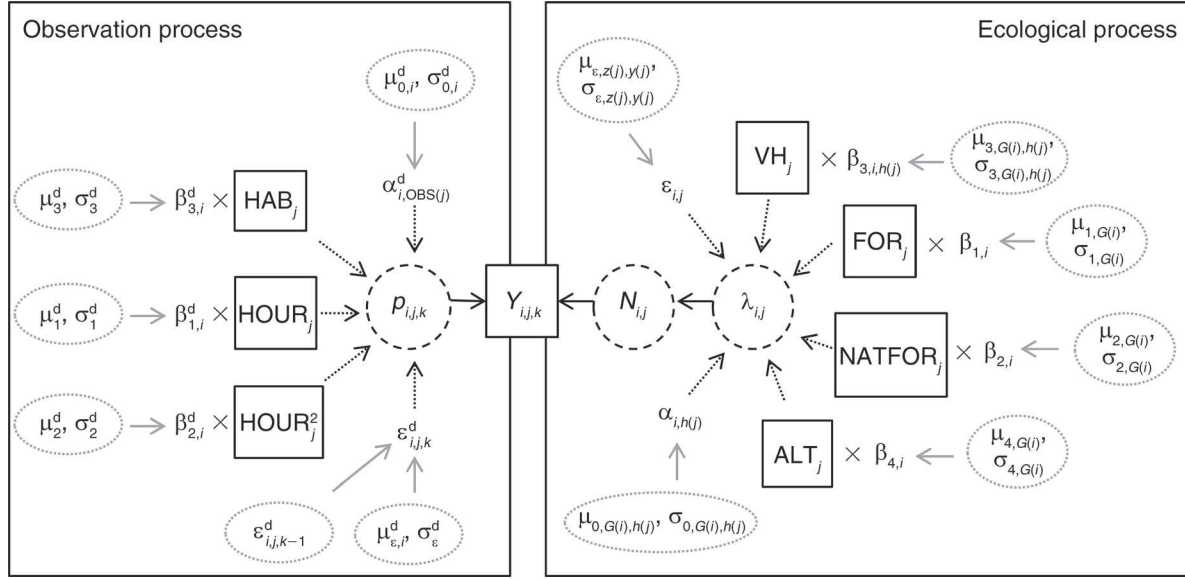


FIG. 2. Schematic representation of the model (refer to *Methods* for definitions of abbreviations and indices). Solid squares and dashed circles represent respectively observed and latent variables. Solid and dashed arrows represent stochastic and deterministic relationships. Hyper-priors are in gray dotted circles. Species' point-level abundances ( $N_{i,j}$ ) are modeled as a Poisson distribution with mean  $\lambda_{i,j}$ , related to landscape (NATFOR<sub>j</sub>, FOR<sub>j</sub>) and local habitat (VH<sub>j</sub>) variables. Species-level parameters ( $\alpha_{i,h(j)}$ ,  $\beta_{1,i}$ ,  $\beta_{2,i}$ ,  $\beta_{3,i,h(j)}$ ,  $\beta_{4,i}$ ) are drawn from hyper-priors, structured per guild [ $G(i)$ ] and/or local habitat type [ $h(j)$ ], with means  $\mu_{0,G(i),h(j)}$ ,  $\mu_{1,G(i)}$ ,  $\mu_{2,G(i)}$ ,  $\mu_{3,G(i),h(j)}$ ,  $\mu_{4,G(i)}$  and associated variances  $\sigma_{0,G(i),h(j)}$ ,  $\sigma_{1,G(i)}$ ,  $\sigma_{2,G(i)}$ ,  $\sigma_{3,G(i),h(j)}$ ,  $\sigma_{4,G(i)}$ . The parameter  $\epsilon_{i,j}$  models overdispersion, and is drawn from a hyper-prior for each of 25 geographical regions  $z$  and the two survey years  $y$ , with mean  $\mu_{e,z(j),y(j)}$  and variance  $\sigma_{e,z(j),y(j)}$ . Replicated counts,  $Y_{i,j,k}$ , are modeled as a binomial distribution depending on  $N_{i,j}$  and the detection probability  $p_{i,j,k}$ , which varies as a function of observers (OBS<sub>j</sub>), habitat structure (HAB<sub>j</sub>), and daytime (HOUR<sub>j</sub>). The parameter  $\alpha_{i,OBS(j)}^d$  is drawn from a species-level hyper-prior with mean  $\mu_{0,i}^d$  and variance  $\sigma_{0,i}^d$ . The other species-level parameters  $\beta_{1,i}^d$ ,  $\beta_{2,i}^d$ , and  $\beta_{3,i}^d$  are drawn from hyper-priors common to all species, with mean  $\mu_1^d$ ,  $\mu_2^d$ ,  $\mu_3^d$  and variance  $\sigma_1^d$ ,  $\sigma_2^d$ ,  $\sigma_3^d$ . The parameters  $\epsilon_{i,j,k}^d$  and  $\epsilon_{i,j,k-1}^d$  model overdispersion in counts and their temporal autocorrelation among consecutive replicates.

*Detection model (observation process).*— $Y_{i,j,k}$ , the number of individuals of species  $i$  observed at site  $j$  during replicate  $k$ , was modeled as a binomial distribution with parameters  $N_{i,j}$  and  $p_{i,j,k}$ :

$$Y_{i,j,k} \sim \text{Binomial}(N_{i,j}, p_{i,j,k}). \quad (3)$$

The species/site/replicate-specific probability of detection,  $p_{i,j,k}$ , was a logit function of two site-specific covariates, hour (HOUR<sub>j</sub>) and habitat structure (HAB<sub>j</sub>, forest or shrubland):

$$\begin{aligned} \text{logit}(p_{i,j,k}) = & \alpha_{i,OBS(j)}^d + \beta_{1,i}^d \times \text{HOUR}_j + \beta_{2,i}^d \\ & \times \text{HOUR}_j^2 + \beta_{3,i}^d \times \text{HAB}_j + \epsilon_{i,j,k}^d \end{aligned} \quad (4)$$

where  $\alpha_{i,OBS(j)}^d$  is the species-specific intercept that varies among observers, and  $\beta_{1,i}^d$ ,  $\beta_{2,i}^d$ , and  $\beta_{3,i}^d$  are the species-specific estimates of time of day and habitat effects, which accounted for the main factors that influence bird detectability, i.e., species identity, observer effect, daytime, and habitat structure (Link and Sauer 2002). The intercept and the effects of daytime and habitat on detectability were drawn from common normal hyper-prior for all species. The variable  $\epsilon_{i,j,k}^d$  was a latent random effect with an autoregressive structure (Johnson and Hoeting 2003; details in Appendix B), aimed to account for possible learning effect arising from the

temporal contiguity of the three replicates at each point. Its distribution was common across sites and within species (consistent with Kéry 2010).

*Analysis.*—Noninformative priors were specified for all parameters (Royle and Dorazio 2008, Kéry 2010). Three Monte Carlo Markov chains were run under R 2.15 (R Development Core Team 2012) and JAGS (Plummer 2003; code in Supplement). Chain mixing and convergence were measured by the Gelman and Rubin statistic ( $\hat{R}$ ; Gelman et al. 2004), and were acceptable after 125 000 iterations of burn-in and 125 000 additional iterations, thinned by 100, for inference ( $\hat{R} < 1.1$  for all parameters). Goodness of fit was assessed with a posterior predictive check based on a  $\chi^2$  discrepancy measure ( $p$ ; Gelman et al. 2004, Kéry 2010).

Testing predictions in a Bayesian model is particularly straightforward (Kéry 2010). For instance, we tested the prediction that the proportion of native forest had a positive effect on native species' abundances by computing the probability  $p(\mu_{2,nat} > 0)$ , as the proportion of MCMC iterations in which  $\mu_{2,nat}$  was above 0. Similarly, we tested the prediction that native species are more abundant in native habitats than exotic species by computing the probability  $p(\mu_{2,natives} > \mu_{2,exotics})$ . A probability close to 0.5 implies no difference between the hyper-parameters of each guild, while values close to 0

(1) suggest that native species are less (more) abundant than exotic species in native habitats.

*Functional differences in exotic and native species.*— Functional differences among native and exotic species were investigated with a Hill and Smith multivariate analysis (Hill and Smith 1976) based on a 21 species  $\times$  10 traits matrix (Table 1). We retained the two first components of the analysis, which accounted for 39.1% of the total variance, and investigated the distribution of species in this functional space using ellipses centered on the centroids of exotic and native species, with axes representing  $1.5\times$  the standard deviation of species' coordinates on each principal component.

## RESULTS

The posterior predictive check indicated adequate fit ( $p = 0.67$ ) and hyper-parameters were not correlated, which confirmed that the model was well supported by the data. Most species were observed at less than one-half of the points ( $194 \pm 142$  points [mean  $\pm$  SD]) and at low estimated abundances ( $1.15 \pm 1.51$  individuals/point, as assessed by the hierarchical model, posterior summaries in Appendix A: Table A1).

Native species abundances increased with total forest area ( $p(\mu_{1,\text{nat}} > 0) = 0.99$ ) and proportion of native forest ( $p(\mu_{2,\text{nat}} > 0) = 0.99$ ), while exotic species were more abundant in smaller forest patches embedded within non-forest matrices ( $p(\mu_{1,\text{ex}} > 0) = 0.08$ ) and dominated by exotic plantations ( $p(\mu_{2,\text{ex}} > 0) = 0.03$ ). The two guilds overlapped little along the gradients of forest cover (Fig. 3a,  $p(\mu_{1,\text{nat}} > \mu_{1,\text{ex}}) = 0.99$ ) and composition (Fig. 3b,  $p(\mu_{2,\text{nat}} > \mu_{2,\text{ex}}) = 1$ ).

The proportion of native forest was not correlated with total forest cover (Pearson's  $R^2 = 0.03$ ), which confirmed that the two landscape-level variables were not surrogates of a single ecological gradient. Abundances decreased with altitude similarly for native and exotic species ( $p(\mu_{4,\text{nat}} > \mu_{4,\text{ex}}) = 0.43$ ).

Both native and exotic species occurred in native and exotic habitats at the local scale, albeit in variable proportions, and thus, habitat composition separated species little at the local scale (Fig. 4a). Native species were slightly more abundant in native habitats ( $p(\mu_{0,\text{nat,nf}} > \mu_{0,\text{nat,ef}}) = 0.64$ ) and exotic species, in exotic habitats ( $p(\mu_{0,\text{ex,ef}} > \mu_{0,\text{ex,nf}}) = 0.55$ ). However, exotic species were more abundant than native species in exotic ( $p(\mu_{0,\text{ex,ef}} > \mu_{0,\text{nat,ef}}) = 0.94$ ) and, to a lesser extent, in native stands ( $p(\mu_{0,\text{ex,nf}} > \mu_{0,\text{nat,nf}}) = 0.88$ ). The two guilds were more separated by local forest height than composition (Fig. 4b), especially in exotic stands ( $p(\mu_{3,\text{nat,ef}} > \mu_{3,\text{ex,ef}}) = 0.89$ ), less in natives ( $p(\mu_{3,\text{nat,nf}} > \mu_{3,\text{ex,nf}}) = 0.67$ ). In exotic forests, native species occupied tall, mature stands in exotic local vegetation ( $p(\mu_{3,\text{nat,ef}} > 0) = 0.84$ ), but were rather ubiquitous in native stands ( $p(\mu_{3,\text{nat,nf}} > 0) = 0.44$ ). Inversely, exotic species were more abundant in lower

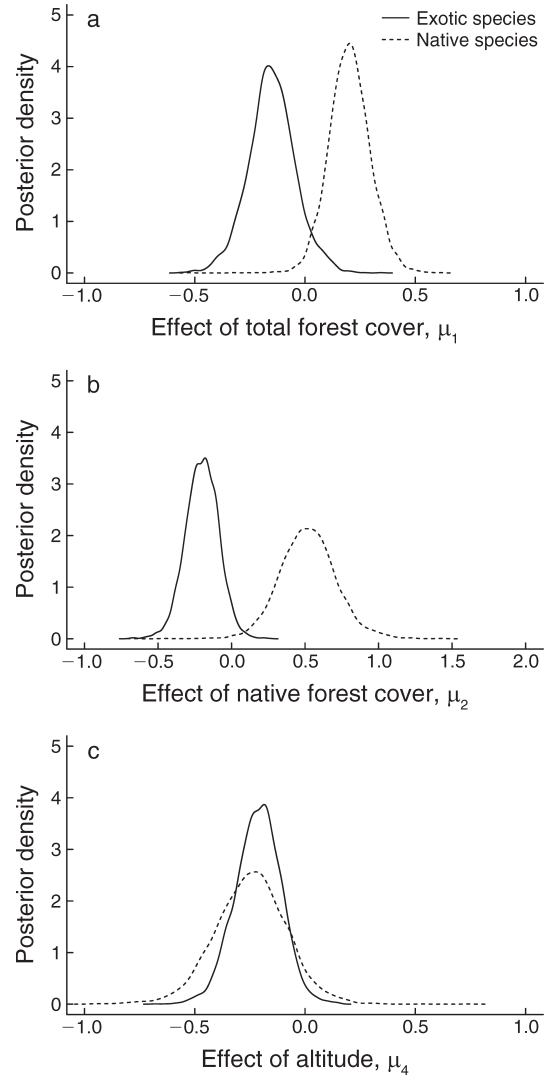


FIG. 3. Posterior densities of species' responses to landscape composition for (a) percent forest cover, (b) percentage of native forest relative to total forest cover and (c) altitude, per guild (solid lines show exotic species; dashed lines show native species).

and younger vegetation in both habitats ( $p(\mu_{3,\text{ex,ef}} < 0) = 0.78$ ;  $p(\mu_{3,\text{ex,nf}} < 0) = 0.74$ ).

Detection probabilities were similar for native and exotic species (Fig. 5a; for posterior summaries per species see Appendix A: Table A1), and were positively autocorrelated among the three consecutive replicates of each point count ( $p(\rho > 0) = 1$ ). Detection probabilities varied weakly during the day (Fig. 5b) and were lower in scrub-dominated vegetation than in taller mature forest (Fig. 5c,  $p(\mu_{3,\text{shr}}^d < \mu_{3,\text{for}}^d) = 1$ ).

The two first components of the Hill and Smith analysis were dominated by nesting site, diet, biometry, and territoriality, while migratory status and reproduction had a comparatively lower influence (Table 1). Exotic species tended to be less territorial, had

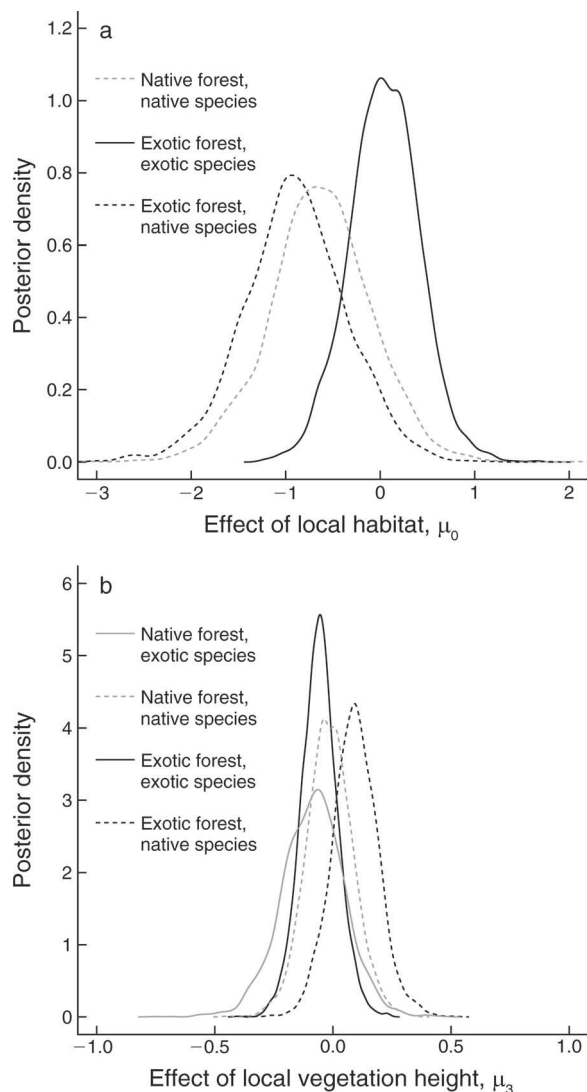


FIG. 4. Posterior densities of species' responses to (a) local habitat composition and (b) vegetation height. In panel (a), exotic species in native habitats are set to 0 as the reference level.

omnivorous or herbivorous diets, and foraged or nested closer to the ground or in the understorey. The native guild was dominated by insectivorous species nesting and foraging higher in trees. Remarkably, only two exotic species (Blackbird, *Turdus merula*, and Song Thrush, *Turdus philomelos*) overlapped with the native guild in this functional space (Fig. 6).

#### DISCUSSION

Exotic and native birds were partly segregated along habitat gradients ranging from exotic plantation forests to continuous native forests, sparse to dense landscape-level forest cover, and lower to taller local vegetation. The two guilds overlapped little in a functional multivariate trait space; supporting the hypothesis that

environmental filtering contributes more to species co-occurrence patterns than competition. In our study area, most forest loss and fragmentation resulted from the long-term conversion of past native forests to farmland, while naturally open habitats were rare or absent (Brockerhoff et al. 2008, Deconchat et al. 2009). Our results are thus consistent with the prediction that landscape-scale habitat disturbance contributes to the coexistence of exotic and native species.

Case (1996) predicted that landscape-level features are stronger filters than local habitat differences, because they influence exotic species' access to resources and native species' long term persistence. Accordingly,

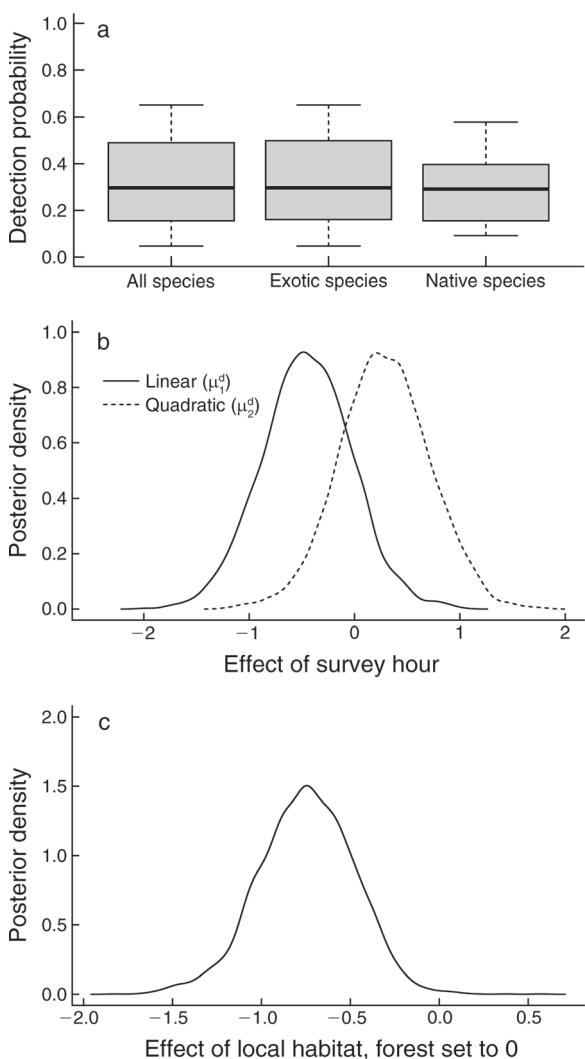


FIG. 5. (a) Estimated detection probabilities for the 21 bird species (11 exotic and 10 native) included in our model. The heavy black bar indicates the median detection probability, the upper and lower edges of the box indicate the 25% and 75% quartiles, and the bars include extreme values until a maximum of  $1.5 \times$  the interquartile distance. (b, c) Posterior densities of the mean response of 54 detection probability to (b) hour and (c) local habitat type (forest taken as the reference level).



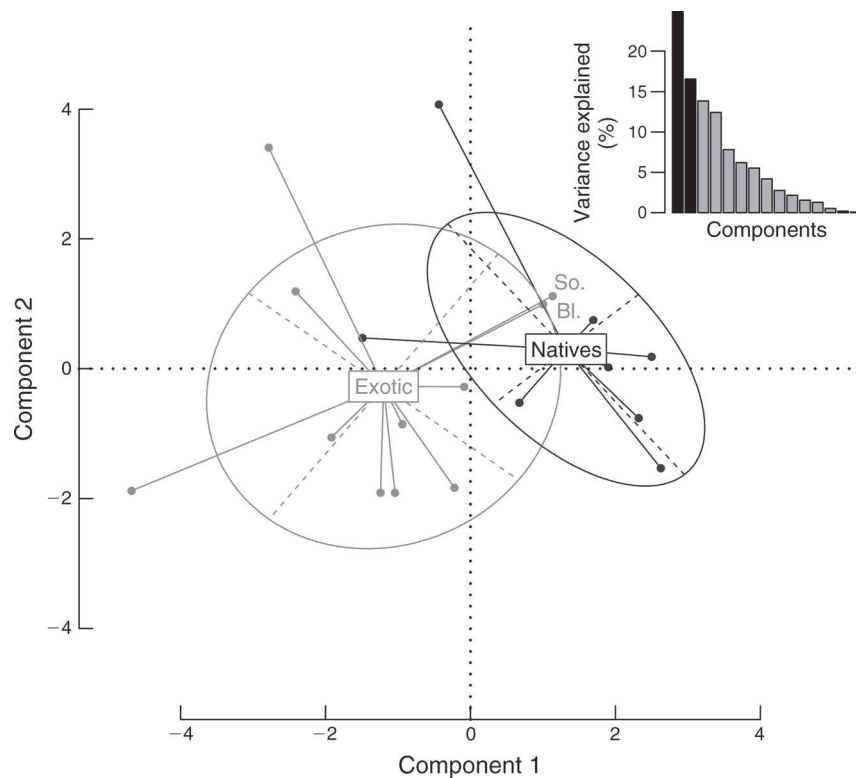


FIG. 6. Distribution of the 21 species along the two first components of a Hill and Smith analysis built on 10 life history traits related to species' habitat and resource use. The inset shows the percentage of variance explained by each component (components 1 and 2 are black, subsequent components are gray). Ellipses are built on the centroids and 1.5 SD of native (black) and exotic (gray) species' coordinates on each component. The positions of Blackbird (Bl.) and Song Thrush (So.) are indicated.

matrix composition influences the persistence of native species (Deconchat et al. 2009, Kennedy et al. 2010), although explicit comparisons with exotic species' response to landscape patterns are scarce (but see Gardiner et al. 2009). Many forest-dependent exotic birds use both forest and adjacent farmland because of complementary resource needs throughout the year (Macleod and Till 2007), which may enhance their ability to thrive in small forest patches within mostly open matrix landscapes. Furthermore, exotic species prefer forest edges and rarely enter interior forest patches with the notable exception of *Turdus* spp. (Barbaro et al. 2012), which are precisely the ones that overlap most with native species in our multivariate analysis of functional traits. By contrast, increased disturbance, reduced resource availability, and limitations in metapopulation processes could explain why native species tend to avoid landscapes dominated by farmland matrices and exotic plantations (Case 1996).

Local habitat composition did not strongly influence abundances within each guild, suggesting that the separation between exotic and native birds does not occur mainly at that scale. In fact, exotic species were more abundant than natives, even in native stands, once landscape composition was accounted for. This pattern

could result from differences in combinations of life history traits between exotic and native species. Ecological generalism, partial niche filling and high productivity are known characteristics of successfully introduced species (Cassey 2001, Blackburn et al. 2009, Strubbe et al. 2013), and appear to be important factors that distinguish them from native species in our multivariate functional trait space. Furthermore, studies along urban gradients tend to conclude that life history traits influence habitat filtering patterns through responses to resource availability rather than interspecific competition (Sol et al. 2012).

Native and exotic species were segregated in the functional space consistent with their respective preferences for high and low exotic vegetation, which rules out direct interference for resource use between the two guilds. Because they do not share any long-term evolutionary history, this separation is also unlikely to be an adaptive output of interspecific competition (Araujo et al. 2011). Competitive exclusion may have happened earlier, preventing the settlement of canopy-dwelling exotic species or driving extinctions in ground or shrub-related native species shortly after introductions. This hypothesis, however, is not supported by an examination of species introduction records (Duncan

1997, Duncan et al. 2003). It is therefore likely that the separation of native and exotic species among forest strata is dominated either by a direct response to resource availability, or indirect consequences of other processes, such as mammal predation on ground-dwelling native species (Holdaway 1989).

Studying variation in predation, demographic rates, and competition along habitat gradients would be necessary to finely assess the contribution of biotic interactions to species coexistence. However, the correlative nature of our study does not necessarily weaken our inferences, as processes shaping large-scale patterns can rarely be directly monitored (McGill and Nekola 2010). More importantly, the multiple scales at which species assemblages are shaped by environmental and biotic influences are still rarely encompassed in a single modeling framework. In this respect, our multiscale approach revealed that niche differences acting at a landscape scale structure bird assemblages more than local influences, including biotic interactions. This pattern suggests that native birds have been little affected by species introductions in New Zealand, and, more generally, that community ecologists and invasions biologists should pay more attention to landscape-level processes that may drive local community composition.

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