Biotic homogenization: Loss of avian functional richness and habitat specialists in disturbed Andean temperate forests

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ABSTRACT

Habitat loss and degradation have the potential to alter the species richness–functional diversity relationship decreasing both species richness and functional richness, and increasing functional biotic homogenization. These anthropogenic disturbances may have strong impacts on species-poor systems with low functional redundancy. We tested the species richness–functional diversity relationship and the potential effects of deforestation and degradation on functional diversity of avian assemblages in a Biodiversity Hotspot, in southern Chile. For 101 sites established across a disturbance gradient, we conducted 505 point-transect surveys to measure avian community structure, 505 vegetation plots to quantify stand-level structure, and measured deforestation at the landscape-level. We used three functional diversity indices for avian assemblages (functional richness, functional evenness, and community-weighted specialization as a measure of functional biotic homogenization). We found a non-saturating relationship between species richness and both functional richness and community-weighted specialization, suggesting low functional redundancy. We also found a non-significant decline of functional evenness indicating that when adding new species to the initial pool, functional redundancy increases slightly. Deforestation led to a decrease in both functional richness and community-weighted specialization, particularly precluding the persistence of specialized species in disturbed forests. Functional evenness did not vary with deforestation suggesting that the regularity of density distribution in filled niche volume may be relatively resilient to disturbance. However, the fact that community-weighted specialization decreased linearly under deforestation serves as evidence of functional biotic homogenization processes ("loser" specialists being replaced by "winner" generalist species) in a Biodiversity Hotspot.

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1. Introduction

Anthropogenic disturbances of terrestrial habitats have triggered the sixth major extinction event in world history (Chapin et al., 2000; Dirzo et al., 2014). Habitat degradation and loss have specific patterns of negative impacts on local assemblages. Particularly, the reported trends of steep declines of specialist species and their replacement by generalist species may induce homogenization processes ("functional biotic homogenization hypothesis;" McKinney and Lockwood, 1999; Olden et al., 2004), which result from the inherently linked taxonomic and functional homogenization of local assemblages (Clavel et al., 2011). Taxonomic homogenization refers to the increase in species

similarity in space and time, while functional homogenization is the decrease in functional diversity among species in local assemblages (Devictor et al., 2008a). For its part, functional diversity is the value, range, and density of functional traits in local assemblages (Díaz et al., 2007). Although patterns of taxonomic homogenization are reasonably well known (Jetz et al., 2007; McKinney and Lockwood, 1999), functional homogenization has received attention only recently (Devictor et al., 2008a; Le Viol et al., 2012).

To understand how habitat degradation and loss might drive functional biotic homogenization, it is necessary to accurately measure relevant biodiversity parameters for ecosystem function. Approaches based on functional diversity have provided mechanistic links between diversity and ecosystem function (Petchey and Gaston, 2006; Díaz et al., 2007). The metrics used to quantify functional diversity is a major aspect for interpreting functional relationships. Two major indices for quantifying functional diversity of species distributed in a multidimensional functional niche volume include functional richness and

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functional evenness (Laliberté and Legendre, 2010; Mason et al., 2005; Villéger et al., 2008). These two indices are independent from each other and both measure different aspects of the distribution and complementarity of species in the functional niche volume (Naeem et al., 2012; Tilman et al., 2001). Functional richness (i.e. the volume of functional niche space filled by species in local assemblages) and species richness are predicted to be correlated from negligible to a positive one-to-one relationship (Cadotte et al., 2011). Species poor assemblages are expected to show a non-saturating species richness–functional richness relationship because of the absence of functional redundancy, the latter defined as the degree to which organisms resemble each other in their functional traits. On the contrary, functional evenness (i.e. the regularity of density distribution in filled niche volume) is not expected to show any a priori relationship with species richness (Mason et al., 2005; Villéger et al., 2008).

The relationship between species richness and functional diversity indices can further be altered by habitat degradation and loss. These processes act as "anthropogenic environmental filters" or conditions that selectively remove species according to their functional traits (Heino et al., 2007; Naeem and Wright, 2003). For example, anthropogenic environmental filters may reduce the density of habitat specialist species, which commonly have higher complementary or unique additional roles in the ecosystem than generalists, resulting in increased functional biotic homogenization (Clavel et al., 2011; Devictor et al., 2008a). The loss of only a few species can have strong impacts on ecosystem functioning in species-poor systems with low functional redundancy (i.e. functional diversity declines rapidly with habitat degradation and loss as a result of declining species richness) (Farias and Jaksic, 2011; Flynn et al., 2009). Therefore, using different functional diversity indices, including functional richness, evenness, and homogenization can help to elucidate why local assemblages subject to the same environmental filters may show contrasting patterns in functional diversity indices (Luck et al., 2013; Mason et al., 2008; Pakeman, 2011).

Recent functional diversity studies at large scales reported that changes in diversity across gradients of habitat disturbance result in the alteration of ecosystem functions provided by multiple taxa, including insects, birds, and mammals (Benton et al., 2002; Donald et al., 2001; Flynn et al., 2009; Luck et al., 2013; Pakeman, 2011). Most of these studies on changes in functional diversity across gradients of anthropogenic disturbance have used categorical habitat types. However, the relationships of continuous measures of disturbance (e.g. % habitat loss) with functional diversity and homogenization should be more informative than broad habitat categories, because functional trait variation is more likely to change continuously across environmental gradients (Cadotte et al., 2011; McGill et al., 2006). While these large-scale studies can inform agencies charged with prioritizing biodiversity globally (Brooks et al., 2006), conservation action is generally implemented within more limited geopolitical boundaries. Therefore, functional diversity studies are needed at operational local scales.

South American temperate forests, a Biodiversity Hotspot centered in south-central Chile (Myers et al., 2000), are globally exceptional for their high rates of endemic species despite supporting a relatively low avian richness (Rozzi et al., 1996; Vuilleumier, 1985). During the last decades, degradation and loss (deforestation) of these forest ecosystems have increased in extent with effects that are superimposed to the natural disturbance regime (Armesto et al., 1998). Rapid rates of deforestation, largely caused by an expansion of open areas for livestock, intensive agriculture, and plantation forestry may be increasing functional biotic homogenization at the landscape-level (Altamirano and Lara, 2006; Devictor et al., 2008a; Echeverría et al., 2006). Remnant patches of forests are frequently degraded after logging and burning, altering the availability of large-decaying trees, understory vegetation, and coarse woody debris at the forest stand-level, with potentially negative effects on habitat specialists persisting in these patches (Díaz et al., 2005; Ibarra and Martin, 2015; Ibarra et al., 2014c). However, no studies have examined the changes in patterns of functional diversity and homogenization of avian assemblages in southern temperate forests. Moreover, there are no studies that simultaneously test the influence of anthropogenic environmental filters on functional diversity indices while assessing if local assemblages become functionally homogenized as a result of habitat degradation and loss.

The aims of this study were to (i) assess the species richness–functional diversity relationship in avian assemblages in southern Chile, (ii) evaluate whether habitat degradation and deforestation act as environmental filters, (iii) test if the potential influence of deforestation on species richness alters functional diversity indices (richness and evenness) and increases functional biotic homogenization of avian temperate forest assemblages. We predicted that, being a species-poor system, southern temperate forests will show an accelerating species richness–functional richness relationship, and associated low functional richness and redundancy in avian assemblages. We also predicted that stand-level structural attributes of forests and landscape-level deforestation selectively remove species according to their functional traits (i.e. the density of specialist species is affected first), creating a pattern of functional biotic homogenization in this Global Biodiversity Hotspot.

2. Methods

2.1. Study area

We conducted our study in an area of 2585 km^2 within the Villarrica watershed in the Andean zone of the La Araucanía Region (39°16′S 71°W), southern Chile. Elevation ranges from 200 to above 2800 m above sea level (masl), with forests distributed from 200 to 1500 masl. Lowland areas (200–500 masl) are dominated by *Lophozonia obliqua*, *Nothofagus dombeyi*, and *Laurelia sempervirens*. Mid-elevation areas (500–900 m) are mixed forests dominated by *Saxegothaea conspicua*, *Laureliopsis philippiana*, and *N. dombeyi*. The deciduous *Nothofagus pumilio* and the coniferous *Araucaria araucana* dominate higher elevations from 900 to the tree line at 1500 m (Gajardo, 1993). The Villarrica watershed is characterized by steep, rugged geography with valley bottoms used mostly for agriculture, and small to medium-sized villages and towns. The area has a short dry season (<4 months), with a mean total annual rainfall of 1945 mm (Di Castri and Hajek, 1976).

We located 101 sites at a minimum distance of 1.5 km apart, ranging from 221 to 1361 masl. We used ArcGIS 10.1 (Environmental Systems Research Institute, Inc., Redlands, CA) to identify all the headwaters of smaller basins that were accessible by rural roads or hiking trails within the Villarrica watershed. We randomly selected 13 of these 19 basins and located the first site within all basins near the headwater (within 1 km of the tree line). We systematically established the remaining sites at every 1.5 km within drainages descending from the headwaters (see Ibarra et al., 2014b for details).

2.2. Avian surveys

We used birds because they are frequently monitored in biodiversity programs and are known to respond, taxonomically and functionally, to anthropogenic habitat disturbance (Donald et al., 2001; Flynn et al., 2009). We conducted point-transect surveys (Buckland et al., 2001). We surveyed each site once, from October to January, over two breeding seasons (2011–2013). In 2011–2012 we surveyed 81 (80.2%) sites while the remaining 20 (19.8%) were surveyed in 2012–2013 (Ibarra and Martin, 2015). Within each site, we established five point-transect surveys systematically separated by 125 m from adjacent point-transects, for a total of 505 point-transect surveys (101 sites × 5 point-transect surveys/site). Based on species accumulation curves, five point-transect surveys per site are considered an adequate number to completely describe bird species assemblages in southern temperate forests (Díaz et al., 2005; Jiménez, 2000). Each point-transect survey lasted 6 min during which every bird seen or heard within a 50 m radius was recorded (Bibby et al., 2000). We also used playbacks of

woodpecker and understory user calls at every second point-transect survey (three playbacks per site). After the initial 6 min count period, the call of each woodpecker (n = 3) and understory user (n = 4) species was played once, each call followed by 30 s of listening time, for a total of 14 min observation time (Drever et al., 2009). The distances to all birds detected were estimated and grouped into two distance intervals (0–25 and 26–50 m) for analysis. Using a hand-held weather monitor (Kestrel 4200, Kestrel-meters, Birmingham, MI), we recorded temperature (°C) and wind speed (m/s) at each point-transect survey. We assigned habitat class within 50 m of each point-transect to one of the following: old growth (>200 years old), mid-successional (35–70 years old) or early successional (<20 years old) forest, secondary shrubland, exotic forestry plantation, or cropland (Ibarra and Martin, 2015).

2.3. Vegetation and habitat measures

We used previous studies of bird–habitat relationships in South American temperate forests to identify potential structural habitat attributes that may be important for habitat specialist species (Díaz et al., 2005; Ibarra and Martin, 2015; Ibarra et al., 2014c; Reid et al., 2004). At every site, we located five vegetation plots (11.2 m radius; 0.04 ha; n = 505 plots) with each plot situated at the center of the previously described point-transect. For each plot we measured canopy cover, tree diameter at breast height (DBH) for all trees with DBH ≥12.5 cm, density of bamboo understory (number of contacts NC), and volume of coarse woody debris (see Ibarra et al., 2014c for details). For DBH we calculated the standard deviation (SD) for all trees in each plot, because SD (DBH) was considered a better indicator than the average of distribution of tree-age classes and stand structural complexity (Van Den Meersschaut and Vandekerkhove, 2000). Values of each habitat attribute for the five plots were averaged and a single value obtained for each of the 101 sites (Ibarra et al., 2014c).

Habitat specialist species are more prone to be negatively affected when habitat loss occurs rapidly (Clavel et al., 2011); therefore, we quantified the percentage of habitat loss (i.e. deforestation) as a measure of spatial instability of habitats within each site (Devictor et al., 2008a; Ibarra et al., 2014c). We measured deforestation within a 180 ha circle (750 m radius) around each site, which allowed us to characterize most of the area between neighboring sites. Deforestation (%) was obtained from a combination of three Landsat scenes (2012–2013). These scenes were corrected and processed to obtain a land-cover model for the study area using the IDRISI Selva (Eastman, 2012). The model included the following cover-types: forest, water bodies, snow or glaciers, cropland, and secondary shrublands. Commercial exotic tree-plantations covered only <2% of the study area so were considered marginal and included as forest. Cropland and secondary shrubland categories were integrated to obtain the percentage of deforested area for each site. We then used ArcGIS 10.1 to extract the circular area for each site and quantified % deforestation using Fragstat 4.1 (McGarigal et al., 2002).

2.4. Trait measures

We focused on eight traits of avian species, including five categorical and three continuous measures (Table 1). Categorical traits included habitat-use guild, nest guild, foraging guild, foraging substrate, and migratory status. Continuous traits included clutch size, body mass, and degree of habitat specialization. All trait measures selected relate to resource use relevant for ecosystem function (e.g. quantity, type, and temporality of resource used, and strategies for obtaining resources by each species, Table 1). For example, foraging guild has been used for testing "species-energy hypothesis" linking production of resources to avian diversity (Drever et al., 2009), migratory status relates to seasonality of resource use by species (Newbold et al., 2012), clutch size represents the range of potential fecundity values and the variety

of reproductive strategies for coping with environmental change (Luck et al., 2013), body mass is relevant for assessing food-web structure (Williams and Purves, 2011), and the degree of habitat specialization of species informs about both resource complementarity and functional biotic homogenization (Devictor et al., 2008a). Several traits including habitat-use guild, diet, migratory status, body mass, and degree of habitat specialization, have been associated with vulnerability of avian species to habitat disturbance in temperate forests (Cofré et al., 2007; Díaz et al., 2005) and elsewhere (Owens and Bennett, 2000).

2.5. Measuring homogenization

To assess current patterns of functional biotic homogenization, we followed Julliard et al. (2006) to quantify the degree of specialization of species (i.e. species specialization index, SSI) as the coefficient of variation (standard deviation/average) of their estimated densities across the six habitat classes identified within 50 m of each point-transect survey (described above) (Ibarra and Martin, 2015). SSI values were used to categorize species as specialist (SSI > 0.71), intermediate (SSI 0.31–0.70), or generalists (SSI < 0.3). We then used the community level weighted mean (Laliberté and Legendre, 2010) to obtain a community-weighted specialization index (CWSI) for every site. This index was calculated as the mean trait value (i.e. species specialization index, SSI) of all species occurring at a site, weighted by their densities (Shipley et al., 2006). The CWSI represents the density of less- or more-specialized species in avian assemblages per site, and is expected to decrease when there is a decline of species with relatively high species specialization index (SSI) values (Le Viol et al., 2012).

2.6. Data analysis

Many studies of functional diversity use species presence/absence rather than number of individuals as the unit of analysis, disregarding differences in density among species (Flynn et al., 2009; Stevens et al., 2003). Nevertheless, the density of individuals is likely more influential on ecosystem function than species presence/absence (Newbold et al., 2012; Petchey and Gaston, 2006).

We analyzed avian point-transect surveys using multinomial-Poisson mixture models in a distance sampling framework (Royle et al., 2004). We used the program R-Unmarked (Fiske and Chandler, 2011), which uses maximum-likelihood methods to estimate detection (p) and density (D) for each species across sites. We first used AIC to identify whether the half-normal or the hazard-rate was the most suitable distance function for each species (Royle et al., 2004). The half-normal function always received stronger support and thus it was used in all further analyses. To estimate detectability (p), we used four covariates potentially affecting the scale parameter of the detection function: date (number of days since start of surveys in October), time of survey (minutes since 5:00 h), wind speed (m/s), and temperature (°C). For each species, we used a stepwise covariate selection procedure (without parameterizing density, D) and then ranked each model by AIC to select top-ranked models for further modeling of density (D) (Ibarra and Martin, 2015).

To obtain the best models for D (covariates potentially influencing the Poisson mean), we created a candidate set of models based on model weights (w_i) and the precision of the estimated coefficients, using an information-theoretic approach (Akaike's Information Criterion [AIC]; Burnham and Anderson, 2002). Models within 2 AIC units of the top model were considered as the competitive set of best-supported models (Burnham and Anderson, 2002). We used canopy cover, SD of tree DBH, bamboo understory density, and volume of coarse woody debris for evaluating a range from 16 to 20 D models for each species. We averaged models with ΔAIC ≤ 4 in the final confidence set for each species (Burnham and Anderson, 2002). Averaged models were used to predict species D for each point-transect. D values for the five point-transect surveys conducted per site were averaged to obtain

Table 1
Traits used to assess avian functional diversity in Andean temperate forests, southern Chile.

Name	Habitat-use guild[a]	Nest guild[b]	Foraging guild[c]	Foraging substrate[d]	Migratory status[e]	Average clutch size[f]	Average body mass (g)[g]	Species specialization index (SSI)[h]
Chilean pigeon (*Patagioenas araucana*)	VPG	NCN	F(G)	G	P	1.5	200	0.12 (G)
Austral parakeet (*Enicognathus ferrugineus*)	LTU	SCN	F(G)	F(G)	P	7.5	200	2.68 (S)
Green-backed firecrown (*Sephanoides sephaniodes*)	VPG	NCN	N(I)	F(A)	M	2	5.98	0.23 (G)
Striped woodpecker (*Veniliornis lignarius*)	LTU	PCN	I	T(G)	R	3.5	39.97	1.21 (S)
Chilean flicker (*Colaptes pitius*)	LTU	PCN	I	T(G)	R	4	125	0.37 (I)
Magellanic woodpecker (*Campephilus magellanicus*)	LTU	PCN	I	T(G)	R	1.5	260	1.96 (S)
Thorn-tailed rayadito (*Aphrastura spinicauda*)	LTU	SCN	I(F)	T(F)	P	5	11.74	0.41 (I)
Des Murs's wire-tail (*Sylviorthorhynchus desmursii*)	UU	NCN	I	F	R	3	10.5	0.72 (S)
White-throated treerunner (*Pygarrhichas albogularis*)	LTU	PCN	I	T	R	3	25.6	0.38 (I)
Black-throated huet-huet (*Pteroptochos tarnii*)	UU	SCN	I(G)	G	R	2	144.33	0.96 (S)
Chucao tapaculo (*Scelorchilus rubecula*)	UU	SCN	I(G)	G	R	2	40.35	0.78 (S)
Magellanic tapaculo (*Scytalopus magellanicus*)	UU	SCN	I(G)	G(F)	R	2.5	11.67	0.57 (I)
White-crested elaenia (*Elaenia albiceps*)	VPG	NCN	I(F)	F(A)	M	2.5	15.62	0.16 (G)
Tufted tit-tyrant (*Anairetes parulus*)	SU	NCN	I(F)	F	R	3	7.2	0.32 (I)
Fire-eyed diucon (*Xolmis pyrope*)	SU	NCN	I(F)	A	P	2.5	30.45	0.11 (G)
Chilean swallow (*Tachycineta meyeni*)	LTU	SCN	I	A	M	4	16	0.23 (G)
Southern house wren (*Troglodytes aedon*)	SU	SCN	I	F	M	5	10.37	0.24 (G)
Austral thrush (*Turdus falcklandii*)	VPG	NCN	F(I)	G(F)	R	3	78.75	0.03 (G)
Patagonian sierra-finch (*Phrygilus patagonicus*)	VPG	NCN	G(H)	G	M	3.5	21.3	0.60 (I)
Austral black bird (*Curaeus curaeus*)	VPG	NCN	I(H)	G	R	4.5	90	0.25 (G)
Black-chinned siskin (*Carduelis barbata*)	SU	NCN	G(H)	G	M	4.5	15.83	0.09 (G)

[a] Based on its primary use of forest structure for nesting and/or feeding. SU = shrub user, VPG = vertical profile generalist, LTU = large tree user, UU = understory user (Díaz et al., 2005).

[b] Cavity nester considered species relying on tree cavities for more than 10% of their nests (Altamirano, 2014). NCN = non-cavity-nester, PCN = primary cavity-nester, SCN = secondary cavity-nester.

[c] I = insectivorous, G = granivorous, N = nectarivorous, F = frugivorous, H = herbivorous (Jaksic and Feinsinger, 1991). Secondary foraging guild in parentheses. Only the primary foraging guild was used for analysis.

[d] G = ground, A = air, F = foliage, T = timber (Jaksic and Feinsinger, 1991, complemented with our own field observations). Secondary foraging substrate in parentheses. Only the primary foraging substrate was used for analysis.

[e] M = migrant (the entire population leaves for some time), P = partial migrant (a fraction of the population leaves the site for some time), R = resident (the entire population remains on site year-round) (Jaksic and Feinsinger, 1991).

[f] Altamirano (2014), Altamirano et al. (2012).

[g] J. T. Ibarra, Unpublished data.

[h] Calculated using field data. Species Specialization Index (SSI) values (Julliard et al., 2006) were used to categorize species as G (generalist, SSI < 0.3), I (intermediate, SSI 0.31–0.70), and S (specialist, SSI > 0.71).

one estimated density per site for each species (Ibarra and Martin, 2015).

Functional richness (FRic) was calculated with the observed species richness per site. Then we combined species functional traits (Table 1) with the estimated species densities (*D*) per site, to calculate functional evenness (FEve). Community-weighted specialization index (CWSI) was calculated combining the species specialization index (SSI) values described above (Table 1) with the estimated species densities (*D*) per site. Prior to analyses, each trait measure was standardized to a mean of 0 and a standard deviation of 1. We used the program R-FD (Laliberté et al., 2011) for calculating all functional diversity indices (FRic, FEve, CWSI).

We used generalized linear models (GLMs) to assess the species richness–functional diversity relationship by regressing empirical observations of species richness and functional diversity indices. To assess the effects of deforestation, we regressed species richness and functional diversity indices against % deforestation (deforestation values were $\log_{10}[x + 1]$ transformed before statistical comparison). The combination of the responses of species may result in different functional forms for species richness and functional diversity indices; therefore, we included quadratic terms to account for decelerating, unimodal, or accelerating responses in all tests (Farias and Jaksic, 2011). To assess the strength of evidence for each tested model, we calculated the value of AIC for small sample sizes (AICc) and model weight (w_i). We used model weights to calculate evidence ratios (ERs) and compare the relative support of different models, including the null expectation (i.e. local assemblages comprise a random set of species and thus functional diversity indices are randomly distributed across functional niche volume) (Petchey et al., 2007).

3. Results

Twenty one species were included in all analyses because they used forest edges or forest interior (we did not consider species that generally do not use forests but may have been recorded incidentally during a survey). Six (28.6%) species were habitat specialists (species specialization index, SSI > 0.71), six were intermediate (SSI 0.31–0.70), and 9 (42.9%) were generalists (SSI < 0.30; Table 1). The highest degrees of specialization were observed for two endemic cavity-nesting species: *Enicognathus ferrugineus* (SSI = 2.68; estimated density *D* = 0.28 ind/ha), the southernmost parakeet of the world, and *Campephilus magellanicus* (SSI = 1.96; *D* = 0.06 ind/ha), the largest woodpecker in South America. The lowest degrees of habitat-specialization were observed for *Turdus falcklandii* (SSI = 0.03; *D* = 1.80 ind/ha), a habitat-generalist thrush, and *Sporagra barbata*, a habitat-generalist siskin (SSI = 0.09; *D* = 3.29 ind/ha; Table 1).

3.1. Species richness–functional diversity relationship

Empirical observations of avian species richness (mean ± SD) across sites ranged from 2.8 ± 1.3 to 10.6 ± 0.9. The patterns observed for the species richness–functional diversity relationship differed for the functional diversity indices assessed. Functional richness (FRic) was positively associated with species richness and did not even begin to saturate at the highest species richness (Table 2a, Fig. 1a). Functional evenness (FEve) showed no significant correlation with species richness, but the evidence ratio for the null model relative to the linear (negative) model was 2.86 (ER = 0.61/0.24), indicating that these two models had similar support (Table 2a, Fig. 1a). The

Table 2
Ranking of models relating a. Species richness and b. Deforestation, to functional diversity indices in Andean temperate forests.

	Model structure	K^a	AICc	$\Delta AICc^b$	W_i^c	$-2 * LL^d$	ER^e
a. Species richness							
Functional richness (Fric)	Species richness + species richness^2	4	−1624.36	0.00	0.60	−1632.78	1.53
	Species richness	3	−1623.51	0.85	0.40	−1629.76	
	Null model	2	−1568.26	56.11	0.00	−1572.38	
Functional evenness (FEve)	Null model	2	−246.25	0.00	0.68	−250.37	2.86
	Species richness	3	−244.15	2.10	0.24	−250.39	
	Species richness + species richness^2	4	−241.98	4.27	0.08	−250.40	
Community-weighted specialization index (CWSI)	Species richness + species richness^2	4	−207.70	0.00	0.70	−216.12	2.32
	Species richness	3	−206.02	1.68	0.30	−212.27	
	Null model	2	−170.23	37.47	0.00	−174.35	
b. Deforestation							
Functional richness (FRic)	Deforestation	3	−1582.83	0.00	0.70	−1589.08	2.38
	Deforestation + deforestation^2	4	−1581.10	1.73	0.30	−1589.51	
	Null model	2	−1568.26	14.57	0.00	−1572.38	
Functional evenness (FEve)	Null model	2	−246.25	0.00	0.68	−250.37	2.88
	Deforestation	3	−244.13	2.12	0.24	−250.38	
	Deforestation + deforestation^2	4	−241.97	4.28	0.08	−250.38	
Community-weighted specialization index (CWSI)	Deforestation	3	−191.89	0.00	0.73	−198.14	2.71
	Deforestation + deforestation^2	4	−189.90	1.99	0.27	−198.32	
	Null model	2	−170.23	21.66	0.00	−174.35	

[a] Number of parameters estimated.
[b] ΔAICc is the difference in AICc values between each model and the lowest AICc model.
[c] AICc model weight.
[d] $-2 *$ log likelihood.
[e] Evidence ratio among two most supported models.

community-weighted specialization index (CWSI) increased strongly as a function of species richness (Table 2a, Fig. 1a).

3.2. Environmental filter effects on functional diversity and homogenization

According to model selection results, 18 of the 21 species were associated with stand-level structural attributes (canopy cover, SD of tree DBH, density of bamboo understory, and volume of coarse woody debris; Table 3). Twelve species responded negatively and three

positively to canopy cover, nine species (including the six habitat specialists) responded positively to SD in tree diameter at breast height (DBH), three species (including two specialists) responded positively to bamboo density, two species responded negatively and one responded positively to volume of coarse woody debris (Table 3) (Ibarra and Martin, 2015).

At the community level, species richness was negatively associated with deforestation (Table 2b, Fig. 1b). The resulting consequence of deforestation on functional diversity indices differed. FRic was negatively
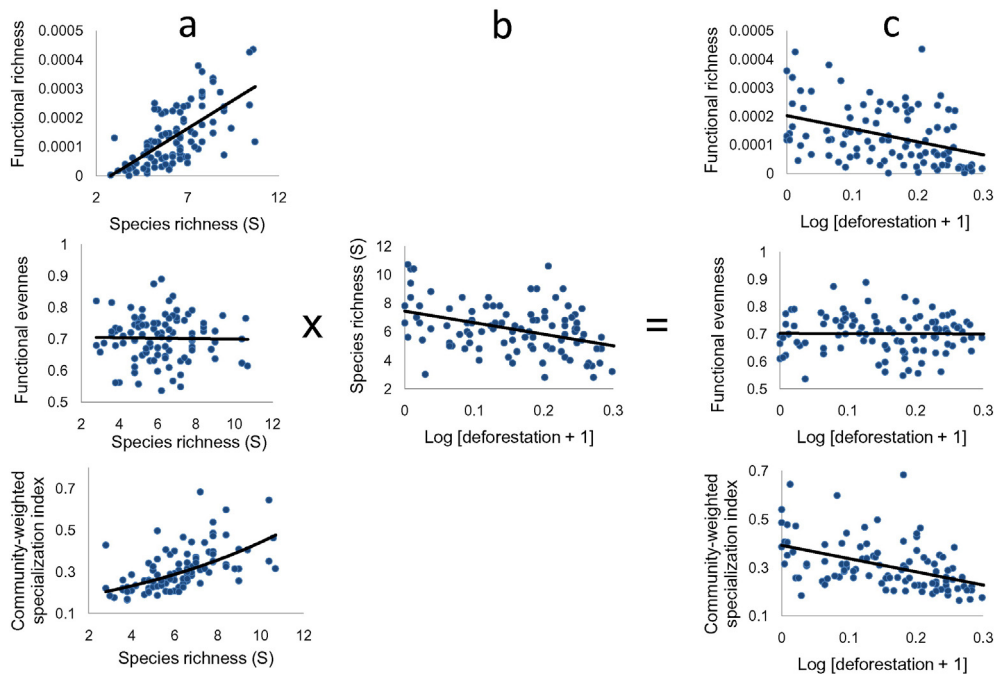
Fig. 1. (a) Estimated relationship between species richness and three functional diversity indices (Functional richness –FRic–, Functional evenness –FEve–, Community-weighted specialization –CWSI–) across 101 sites for 21 species in avian assemblages in Andean temperate forests, southern Chile. (b) Response of bird species richness to deforestation. (c) Response of three functional diversity indices (FRic, FEve, CWSI) to deforestation in Andean temperate forests. This figure depicts the differential responses of FRic, FEve, and CWSI to deforestation, resulting from the interaction of the relationship between species richness and the three functional diversity indices, and the association between species richness and deforestation.

Table 3

Forest stand-structural attributes associated with the estimated density (D) of avian species in Andean temperate forests, according to model selection statistics based on Akaike's Information Criterion (AIC). Parameter estimates [SE] for covariates present in the top model set with ΔAIC values <2 and with estimates of their 95% confidence intervals that do not overlap 0, are shown. + and − indicate the direction of the relation (more details in Ibarra and Martin, 2015).

English name	Forest stand-structural attributes			
	Canopy cover (%)	SD of diameter at breast height of trees (cm)	Bamboo understory density (NC)	Volume of coarse woody debris (m³)
Chilean pigeon				
Austral parakeet		+0.07 [0.03]		
Green-backed firecrown	−0.12 [0.03]			−0.21 [0.11]
Striped woodpecker	−0.64 [0.15]	+0.07 [0.02]		
Chilean flicker	−0.21 [0.08]			
Magellanic woodpecker	−1.51 [0.35]	+0.19 [0.09]		
Thorn-tailed rayadito	−0.23 [0.02]			
Des Murs's wire-tail		+0.04 [0.01]		+0.63 [0.31]
White-throated treerunner	−0.22 [0.04]			
Black-throated huet-huet	−0.44 [0.06]	+0.04 [0.01]	+0.13 [0.04]	
Chucao tapaculo	−0.44 [0.04]	+0.02 [0.01]	+0.05 [0.01]	
Magellanic tapaculo	−0.25 [0.05]	+0.03 [0.01]		
White-crested elaenia	−0.06 [0.01]			−0.25 [0.07]
Tufted tit-tyrant	+0.11 [0.04]			
Fire-eyed diucon				
Chilean swallow	−0.07 [0.03]	+0.02 [0.01]		
Southern house wren	+0.12 [0.03]			
Austral thrush				
Patagonian sierra-finch	−0.34 [0.05]			
Austral black bird	+0.09 [0.04]	+0.02 [0.01]		
Black-chinned siskin			+0.06 [0.03]	

associated with deforestation, with both the linear and the non-linear models receiving similar support (Table 2b, Fig. 1c). FEve showed no significant association with deforestation, with both the null model and the linear (negative) model receiving similar support (ER = 2.88; Table 2b, Fig. 1c). The community-weighted specialization index (CWSI) decreased strongly as a function of deforestation (Table 2b,
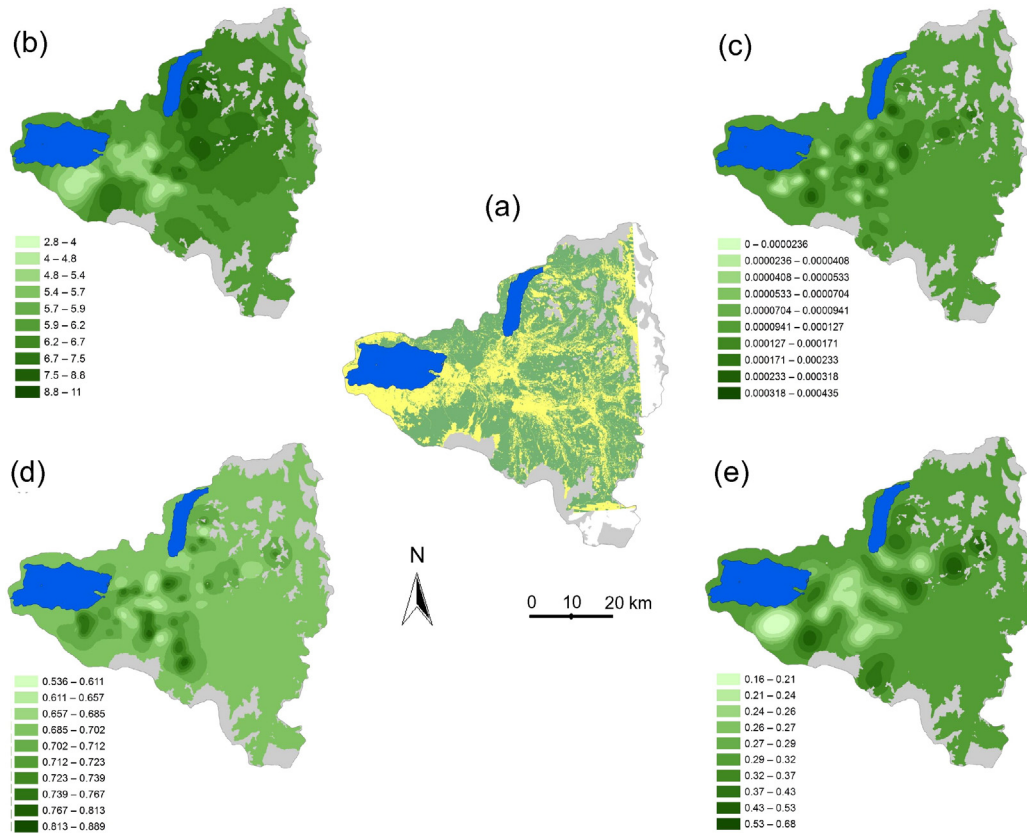
Fig. 2. Central map (a) shows forest cover (green) and deforested areas (yellow) in the Villarrica watershed for 2012–2013, Andean zone of the La Araucanía Region, Chile. Projection of (b) avian species richness, (c) functional richness (FRic), (d) functional evenness (FEve), and (e) community-weighted specialization (CWSI) in Andean temperate forests. In (b), (c), (d), and (e), darker green depicts areas of higher estimated values for either species richness or functional diversity indices (FRic, FEve, CWSI) whereas lighter green represents areas of lower estimated values. Alpine areas in gray and large lakes (Villarrica and Caburgua) in blue, are shown. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Fig. 1c). For easier interpretation of our results and for identifying taxonomically and functionally important areas for forest management and planning programs, the observed values for avian species richness and estimated functional diversity indices were projected using the spatial interpolation toolbar Kriging (Oliver and Webster, 1990), implemented in ArcGIS 10.1. The resulting projections show, graphically, an overlap between forested areas and areas of higher species richness and higher community-weighted specialization in the Villarrica watershed (Fig. 2).

4. Discussion

4.1. Species richness–functional diversity relationship

Our examination conducted in a global biodiversity hotspot extends earlier research on the relationship between biodiversity and ecosystem functioning (Cardinale et al., 2006; Díaz and Cabido, 2001; Farias and Jaksic, 2011; Gerisch et al., 2012). Our study elucidates some of the potential consequences of this altered relationship for functional biotic homogenization. We found that avian assemblages in Andean temperate forests showed relatively low functional richness (FRic) and functional redundancy, according to the observed steep relationship (relative to a random expectation) between species richness and functional richness that did not begin to saturate over the species richness values observed in our sites. Our findings of relatively low FRic and low redundancy in Andean forest avian assemblages are characteristic of species-poor systems (Díaz and Cabido, 2001; Farias and Jaksic, 2011; Petchey et al., 2007). Andean temperate forests are relatively impoverished in terms of avian species richness due to its history, climate, and geography. For example, during the last glacial maximum of the Pleistocene, the progression of glaciers generated contractions on the distribution of temperate forests, such that immigration of species from tropical ecosystems did not compensate for the extinction of local species (Villagrán and Hinojosa, 1997). Climatic change and geographic barriers (the Atacama Desert and the Andes range) resulted in a net loss of species during the Pleistocene, especially of faunal groups with tropical lineage (Vuilleumier and Simpson, 1971). As a result, Andean temperate forests have lower avian species richness than other temperate, subtropical, and Andean forest types (Jaksic and Feinsinger, 1991; Vuilleumier, 1985).

We also found a non-significant decline of functional evenness (FEve) as a function of species richness, contrary to what has been reported for lake fish assemblages in France (16–33 species), where FEve increased as species richness increased (Mason et al., 2008). FEve should decline with decreasing evenness on the distribution of both species and densities in the functional niche volume. A non-significant decline of FEve as a function of species richness has been reported for both artificial (simulated) data (Mouchet et al., 2010; Villéger et al., 2008) and empirical research on avian assemblages in land-bridge islands (Ding et al., 2013). Our result of a non-significant decline in FEve with increasing species richness suggests that when adding new species to the initial pool, functional redundancy may increase slightly if the functional niche volume is unsaturated in avian assemblages.

We used a continuous index for measuring the degree of community specialization, which is considered a robust and cohesive functional trait because it integrates species life history traits (e.g. dispersal ability, nest sites, diet) in a single cohesive parameter that facilitates an integration of community ecology with ecosystem ecology (McGill et al., 2006). This index, which has been applied across different ecological systems and countries, provides a predictive measure of the impact of anthropogenic disturbance on local assemblages (Devictor et al., 2008b, 2010; Le Viol et al., 2012). We found an accelerating relationship between the community-weighted specialization index (CWSI) and species richness, suggesting that increasing bird species richness in temperate forests is associated with accelerating niche complementarity (Clavel et al., 2011). Niche complementarity is a result of both positive species

interactions and differentiation in the spatial and temporal acquisition of resources between species (Mulder et al., 2001); it is expected to allow multispecies co-existence with greater stability and productivity at higher species richness levels (Lehman and Tilman, 2000; Tilman et al., 2001).

4.2. Environmental filters: toward a functional biotic homogenization in temperate forests?

We found strong evidence that deforestation at the landscape-level led to a decrease in both FRic and CWSI, a result in accordance with the few studies dealing with functional biotic homogenization of local assemblages when facing anthropogenic disturbance and global change (Clavel et al., 2011; Devictor et al., 2008a; Le Viol et al., 2012). FEve did not vary with increasing deforestation, suggesting that if the functional niche volume is unsaturated, as is the case in temperate forest avian assemblages, the regularity of density distribution in filled niche volume is relatively resilient to disturbance (Luck et al., 2013). However, the fact that CWSI decreased linearly under progressive deforestation suggests that habitat specialist species are "filtered" or lost first, increasing functional biotic homogenization.

Our results support the assertion that functional diversity is not merely affected by the initial pool of species occurring in local assemblages (first examination of this study: species richness–functional diversity relationship). Functional diversity is also influenced by the increasing pressure of anthropogenic environmental filters, which selectively remove species according to their functional traits, likely through shifting the intensity of competitive interactions in local assemblages (Clavel et al., 2011; Mason et al., 2008). Generalist species are expected to both benefit from competitive relaxation with specialists in disturbed environments, and to maintain relatively high densities across a wider range of habitats than specialists (Futuyma and Moreno, 1988). For example, Dueser and Hallett (1980) reported that one specialist rodent species showed stronger selection of one micro-habitat whereas two generalist rodents were able to exploit a range of micro-habitat types; however, the specialist species outperformed both generalist rodents in the habitat where it was specialized. In another study, the growth rate of generalist coral-reef fishes was more consistent between habitats than the growth of specialist fishes, but specialists grew faster than generalists in their single habitat (Caley and Munday, 2003). In Andean temperate forests, a habitat specialist owl species (Strix rufipes) was associated with a smaller subset of resources than a generalist owl (Glaucidium nana), and thus the specialist had lower densities across a disturbed landscape because there was a smaller number of habitats in which it was able to occur at high densities (Ibarra et al., 2014c).

The main anthropogenic environmental filters in southern temperate forests are deforestation and the degradation of remaining forest patches. Reported annual deforestation rates in South American temperate forests reach 4.5% per year in coastal areas (total cover loss of 67% by 2000) and 4.1% per year in some Andean locations (total cover loss of 44% by 2003) (Altamirano and Lara, 2006; Echeverría et al., 2006). Homogenization of avian assemblages in Andean temperate forests occurs across several spatial scales. The increasing homogenization of assemblages at the landscape-level, as a result of deforestation, has its counterpart at the stand-level where several remnant forest patches lack critical structural attributes (large-decaying trees, dense understory), affecting specialist species that eventually are locally extirpated from remaining forest patches (Díaz et al., 2005; Echeverría et al., 2007; Reid et al., 2004; Vergara and Armesto, 2009). Even those remaining forest patches showing suitable habitat for specialist species, such as sites with dense understory or large-decaying trees, are underused by specialist species in highly disturbed landscapes (Vergara and Armesto, 2009).

Our results can be interpreted as evidence for the functional biotic homogenization hypothesis, which addresses the question as to why

specialist, often endemic, species may be more vulnerable than generalists to anthropogenic disturbance (Clavel et al., 2011; Olden et al., 2004; Tabarelli et al., 2012). Our findings suggest that the increased deforestation may preclude the persistence and the coexistence of specialized "loser" species in highly disturbed forest sites. "Loser" species in Andean temperate forests such as the guilds of large tree users *E. ferrugineus*, *C. magellanicus*, *Veniliornis lignarius* and the understory users *Pteroptochos tarnii* and *Scelorchilus rubecula*, consist mostly of endemic species that rely on cavities available in large-decaying trees (DBH 61.3 to 193.8 cm; Altamirano, 2014). Likewise, the rapid decline of specialist primary cavity nesters in disturbed forest sites, such as *C. magellanicus* and *V. lignarius*, will likely affect the rates of cavity production (Altamirano, 2014; Ibarra and Martin, 2015). As a result, the density of secondary cavity nesters (e.g. owls, teals, parakeets, rayaditos, swallows, and wrens) that rely on cavities provided by these two primary cavity nesters and by tree decay processes, will decline as well (Altamirano, 2014; Beaudoin and Ojeda, 2011; Díaz and Kitzberger, 2013). The lack of cavities produced by *C. magellanicus* and *V. lignarius* may be buffered by cavities produced by the intermediate specialists *Colaptes pitius* and *Pygarrhichas albogularis* in sites with some disturbance and stand level degradation (Altamirano, 2014; Ibarra et al., 2014a). However, as forest patches continue to decrease in size and become degraded by both selective logging of large-decaying trees and understory removal, even intermediate specialist species will be lost (Ibarra and Martin, 2015; Vergara and Armesto, 2009).

Specialized species were also the largest (>body mass) in temperate forest assemblages. Body mass is related to species metabolic rates and ecosystem functioning as, for example, body mass of insectivorous birds is directly associated with the amount and type of invertebrates consumed in forest ecosystems (Luck et al., 2013). When studying the association between ecological variables and variation in extinction risk, Owens and Bennett (2000) found that the degree of habitat specialization was positively correlated with extinction risk via habitat loss. This highlights that some species that are taxonomically different can be both functionally similar and vulnerable to common mechanisms of extinction (Mason et al., 2008; Owens and Bennett, 2000).

The decline of specialist species is coupled with an increase in the density of generalist or "winner" species in local assemblages. "Winners" in temperate forests consist chiefly of species that are found mostly in secondary shrublands and degraded areas, but also use early successional forests characterized by a high canopy cover and simplified vertical structure (Díaz et al., 2005). Most of these are non-cavity nesting passerine species that have a similar morphology and belong to different foraging guilds (insectivorous or granivorous). These generalists join the list of other birds that were not considered in our study because they seldom occur in forest, such as *Callipepla californica*, *Vanellus chilensis*, *Diuca diuca*, *Mimus thenca*, *Sturnella loyca*, *Zonotrichia capensis*, *Sicalis luteola*, and *Molothrus bonariensis*, but that readily utilize anthropogenic croplands in Andean temperate forests (J. T. Ibarra. Unpublished data).

4.3. Implications for conservation

Functional diversity responses and homogenization patterns under anthropogenic disturbance offer the ability to understand how diversity is linked to ecosystem stability. Our index of community specialization indicates the degree to which species in an assemblage show wide or narrow niche widths (Le Viol et al., 2012), with more specialized assemblages spatially associated with more stable ecosystems and multi-aged forest stands (Clavel et al., 2011; Ibarra and Martin, 2015; Julliard et al., 2006). Our study predicts strong effects of deforestation on specialized biodiversity, potentially affecting the functioning of remnant forest stands, especially degraded stands that lack large-decaying trees and dense understory.

Recently, Ibarra and Martin (2015) provided specific recommendations to benefit habitat-specialist assemblages and species of conservation concern in southern temperate forests. These recommendations included the maintenance of multi-aged stands with a variety of tree sizes (SD of DBH = 19.9 ± 9 cm or mean DBH = 37.6 ± 12.5 cm), including large-decaying trees, with relatively high bamboo understory cover ($34.2 \pm 26.6\%$). However, in a manner analogous to many other countries (Cockle et al., 2011), forest policies in Chile specify the lower diameter of trees to be cut down. This specification protects young but encourages the harvest of large-decaying trees. Also, stands with a dense understory are commonly considered wasteful and indicative of "unhealthy and dirty forest conditions" by landowners and forest managers in Chile. The National Forestry Service (CONAF) and external forest certification agencies should make mandatory the maintenance of some understory, along with the continuous supply of large-decaying trees, to support forest biodiversity in Chile.

No specialist species inhabiting southern temperate ecosystems have received either national (except for *C. magellanicus*) or international conservation status or attention (Cofré et al., 2007). Furthermore, because many areas of southern temperate ecosystems and most species have not been sufficiently surveyed, current ecological knowledge of specialized species in temperate forest is rudimentary at best. Further research on species population trends, productivity, and specific habitat requirements is needed in order to establish reliable conservation status assignments and stewardship priorities for specialist species and assemblages. This research should help policy makers make informed conservation decisions for the maintenance of diverse and stable forest ecosystems in South American temperate landscapes.

Acknowledgments

References

Altamirano, T.A., 2014. Breeding Ecology of Cavity-nesting Birds in the Andean Temperate Forest of Southern Chile Dissertation Pontificia Universidad Católica de Chile, Santiago, Chile.

Altamirano, A., Lara, A., 2006. Deforestación en ecosistemas templados de la precordillera andina del centro-sur de Chile. Bosque 31, 53–64.

Altamirano, T.A., Ibarra, J.T., Hernández, F., Rojas, I., Laker, J., Bonacic, C., 2012. Hábitos de nidificación de las aves del bosque templado andino de Chile. Fondo de Protección Ambiental, Ministerio del Medio AmbienteSerie Fauna Australis. Pontificia Universidad Católica de Chile, Santiago.

Armesto, J.J., Rozzi, R., Smith-Ramírez, C., Arroyo, M.T.K., 1998. Conservation targets in South American temperate forests. Science 282, 1271–1272.

Beaudoin, F., Ojeda, V., 2011. Nesting of rufous-legged owls in evergreen Nothofagus forests. J. Raptor Res. 45, 272–274.

Benton, T.G., Bryant, D.M., Cole, L., Crick, H.Q.P., 2002. Linking agricultural practice to insect and bird populations: a historical study over three decades. J. Appl. Ecol. 39, 673–687.

Bibby, C.J., Burgess, N.D., Hill, D.A., Mustoe, S.H., 2000. Bird Census Techniques. 2nd ed. Academic Press, San Diego, California, U.S.A.

Brooks, T.M., Mittermeier, R.A., da Fonseca, G.A.B., Gerlach, J., Hoffmann, M., Lamoreux, J.F., Mittermeier, C.G., Pilgrim, J.D., Rodrigues, A.S.L., 2006. Global biodiversity conservation priorities. Science 313, 58–61.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, Oxford, U.K.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Inference: A Practical Information-theoretic Approach. 2nd ed. Springer-Verlag, New York, U.S.A.

Cadotte, M.W., Carscadden, K., Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48.

Caley, M.J., Munday, P.L., 2003. Growth trades off with habitat specialization. Proc. R. Soc. B Biol. Sci. 270, S175–S177.

Cardinale, B.J., Srivastava, D.S., Duffy, J.E., Wright, J.P., Downing, A.L., Sankaran, M., Jouseau, C., 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443, 989–992.

Chapin, F.S.I., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C., Díaz, S., 2000. Consequences of changing biodiversity. Nature 405, 234–242.

Clavel, J, Julliard, R., Devictor, V., 2011. Worldwide decline of specialist species: toward a global functional homogenization? Front. Ecol. Environ. 9, 222–228.

Cockle, K.L., Martin, K., Wesołowski, T., 2011. Woodpeckers, decay, and the future of cavity-nesting vertebrate communities worldwide. Front. Ecol. Environ. 9, 377–382.

Cofré, H., Böhning-Gaese, K., Marquet, P.A., 2007. Rarity in Chilean forest birds: which ecological and life-history traits matter? Divers. Distrib. 13, 203–212.

Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A., Couvet, D., 2008a. Functional biotic homogenization of bird communities in disturbed landscapes. Glob. Ecol. Biogeogr. 17, 252–261.

Devictor, V., Julliard, R., Jiguet, F., 2008b. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. Oikos 117, 507–514.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010. Defining and measuring ecological specialization. J. Appl. Ecol. 47, 15–25.

Di Castri, F., Hajek, E.R., 1976. Bioclimatología de Chile. Dirección De Investigación, Vice-Rectoría Académica, Universidad Católica De Chile, Santiago, Chile.

Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655.

Díaz, S., Kitzberger, T., 2013. Nest habitat selection by the austral parakeet in northwestern Patagonia. Austral Ecol. 38, 268–278.

Díaz, I.A., Armesto, J.J., Reid, S., Sieving, K.E., Willson, M.F., 2005. Linking forest structure and composition to avian diversity in successional forests of Chiloé Island, Chile. Biol. Conserv. 123, 91–101.

Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K., Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. Proc. Natl. Acad. Sci. 104, 20684–20689.

Ding, Z., Feeley, K.J., Wang, Y., Pakeman, R.J., Ding, P., 2013. Patterns of bird functional diversity on land-bridge island fragments. J. Anim. Ecol. 82, 781–790.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the Anthropocene. Science 345, 401–406.

Donald, P.F., Green, R.E., Heath, M.F., 2001. Agricultural intensification and the collapse of Europe's farmland bird populations. Proc. R. Soc. B Biol. Sci. 268, 25–29.

Drever, M.C., Goheen, J.R., Martin, K., 2009. Species-energy theory, pulsed resources, and regulation of avian richness during a mountain pine beetle outbreak. Ecology 90, 1095–1105.

Dueser, R., Hallett, J., 1980. Competition and habitat selection in a forest-floor small mammal fauna. Oikos 35, 293–297.

Eastman, J.R., 2012. IDRISI Selva. Clark University, Worcester, U.K.

Echeverría, C., Coomes, D., Salas, J., Rey-Benayas, J., Lara, A., Newton, A., 2006. Rapid deforestation and fragmentation of Chilean temperate forests. Biol. Conserv. 130, 481–494.

Echeverría, C., Newton, A.C., Lara, A., Rey-Benayas, J.M., Coomes, D.A., 2007. Impacts of forest fragmentation on species composition and forest structure in the temperate landscape of southern Chile. Glob. Ecol. Biogeogr. 16, 426–439.

Farias, A.A., Jaksic, F.M., 2011. Low functional richness and redundancy of a predator assemblage in native forest fragments of Chiloe Island, Chile. J. Anim. Ecol. 80, 809–817.

Fiske, I.J., Chandler, R.B., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Stat. Softw. 43, 1–23.

Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M., DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. Ecol. Lett. 12, 22–33.

Futuyma, D.J., Moreno, G., 1988. The evolution of ecological specialization. Annu. Rev. Ecol. Syst. 19, 207–233.

Gajardo, R., 1993. La vegetación natural de Chile: clasificación y distribución geográfica. Editorial Universitaria, Santiago, Chile.

Gerisch, M., Agostinelli, V., Henle, K., Dziock, F., 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. Oikos 121, 508–515. http://dx.doi.org/10.1111/j.1600–0706.2011.19749.x.

Heino, J., Mykrä, H., Kotanen, J., Muotka, T., 2007. Ecological filters and variability in stream macroinvertebrate communities: do taxonomic and functional structure follow the same path? Ecography 30, 217–230.

Ibarra, J.T., Martin, K., 2015. Beyond species richness: an empirical test of top predators as surrogates for functional diversity and endemism. Ecosphere 6, 142.

Ibarra, J.T., Altamirano, T.A., Martin, K., Vargas, F.H., Bonacic, C., 2014a. Tree-cavity nesting of austral pygmy-owls (Glaucidium nana) in Andean temperate forests of southern Chile. J. Raptor Res. 48, 82–85.

Ibarra, J.T., Martin, K., Altamirano, T.A., Vargas, F.H., Bonacic, C., 2014b. Factors associated with the detectability of owls in South American temperate forests: implications for nocturnal raptor monitoring. J. Wildl. Manag. 78, 1078–1086.

Ibarra, J.T., Martin, K., Drever, M.C., Vergara, G., 2014c. Occurrence patterns and niche relationships of sympatric owls in South American temperate forests: a multi-scale approach. For. Ecol. Manag. 331, 281–291.

Jaksic, F.M., Feinsinger, P., 1991. Bird assemblages in temperate forest of North and South America: a comparison of diversity, dynamics, guild structure, and resource use. Rev. Chil. Hist. Nat. 64, 491–510.

Jetz, W., Wilcove, D.S., Dobson, A.P., 2007. Projected impacts of climate and land-use change on the global diversity of birds. PLoS Biol. 5, e157.

Jiménez, J.E., 2000. Effect of sample size, plot size, and counting time on estimates of avian diversity and abundance in a Chilean rainforest. J. F. Ornithol. 71, 66–87.

Julliard, R., Clavel, J., Devictor, V., Jiguet, F., Couvet, D., 2006. Spatial segregation of specialists and generalists in bird communities. Ecol. Lett. 9, 1237–1244.

Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305.

Laliberté, E., Legendre, P., Shipley, B., 2011. FD: measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R Package Version 1.0-12. http://cran.r-project.org/web/packages/FD.

Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindstrom, A., Pearce-Higgins, J.W., Reif, J., Van Turnhout, C., Devictor, V., 2012. More and more generalists: two decades of changes in the European avifauna. Biol. Lett. 8, 780–782.

Lehman, C.L., Tilman, D., 2000. Biodiversity, stability, and productivity in competitive communities. Am. Nat. 156, 534–552.

Luck, G.W., Carter, A., Smallbone, L., 2013. Changes in bird functional diversity across multiple land uses: interpretations of functional redundancy depend on functional group identity. PLoS One 8, e63671.

Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. Oikos 111, 112–118.

Mason, N.W.H., Irz, P., Lanoiselée, C., Mouillot, D., Argillier, C., 2008. Evidence that niche specialization explains species-energy relationships in lake fish communities. J. Anim. Ecol. 77, 285–296.

McGarigal, K., Cushman, S.A., Neel, M.C., Ene, E., 2002. FRAGSTATS: Spatial Pattern Analysis Program for Categorical Maps. Amherst, Massachusetts, U.S.A.

McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21, 178–185.

McKinney, M.L., Lockwood, J.L., 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. Trends Ecol. Evol. 14, 450–453.

Mouchet, M.A., Villéger, S., Mason, N.W.H., Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. Funct. Ecol. 24, 867–876.

Mulder, C.P.H., Uliassi, D.D., Doak, D.F., 2001. Physical stress and diversity–productivity relationships: the role of positive interactions. Proc. Natl. Acad. Sci. 98, 6704–6708.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Naeem, S., Wright, J.P., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insormountable problem. Ecol. Lett. 6, 567–579.

Naeem, S., Duffy, J.E., Zavaleta, E., 2012. The functions of biological diversity in an age of extinction. Science 336, 1401–1406.

Newbold, T., Butchart, S.H.M., Sekercioğlu, C.H., Purves, D.W., Scharlemann, J.P.W., 2012. Mapping functional traits: comparing abundance and presence-absence estimates at large spatial scales. PLoS One 7, e44019.

Olden, J.D., LeRoy Poff, N., Douglas, M.R., Douglas, M.E., Fausch, K.D., 2004. Ecological and evolutionary consequences of biotic homogenization. Trends Ecol. Evol. 19, 18–24.

Oliver, M.A., Webster, R., 1990. Kriging: a method of interpolation for geographical information systems. Int. J. Geogr. Inf. Syst. 4, 313–332.

Owens, I.P., Bennett, P.M., 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc. Natl. Acad. Sci. 97, 12144–12148.

Pakeman, R.J., 2011. Functional diversity indices reveal the impacts of land use intensification on plant community assembly. J. Ecol. 99, 1143–1151.

Petchey, O.L., Gaston, K.J., 2006. Functional diversity: back to basics and looking forward. Ecol. Lett. 9, 741–758.

Petchey, O.L., Evans, K.L., Fishburn, I.S., Gaston, K.J., 2007. Low functional diversity and no redundancy in British avian assemblages. J. Anim. Ecol. 76, 977–985.

Reid, S., Díaz, I., Armesto, J., 2004. Importance of native bamboo for understory birds in Chilean temperate forests. Auk 121, 515–525.

Royle, J.A., Dawson, D.K., Bates, S., 2004. Modeling abundance effects in distance sampling. Ecology 85, 1591–1597.

Rozzi, R., Martínez, D.R., Willson, M.F., Sabag, C., 1996. Avifauna de los bosques templados de Sudamérica. In: Armesto, J.J., Villagrán, C., Arroyo, M.T. (Eds.), Ecología de Los Bosques Nativos de Chile. Editorial Universitaria, Santiago, Chile, pp. 135–152.

Shipley, B., Vile, D., Garmier, É., 2006. From plant traits to plant communities: a statistical mechanistic approach to biodiversity. Science 314, 812–814.

Stevens, R.D., Cox, S.B., Strauss, R.E., Willig, M.R., 2003. Patterns of functional diversity across an extensive environmental gradient: vertebrate consumers, hidden treatments and latitudinal trends. Ecol. Lett. 6, 1099–1108.

Tabarelli, M., Peres, C.A., Melo, F.P.L., 2012. The 'few winners and many losers' paradigm revisited: emerging prospects for tropical forest biodiversity. Biol. Conserv. 155, 136–140.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T., Lehman, C., 2001. Diversity and productivity in a long-term grassland experiment. Science 294 (80-.), 843–845.

Van Den Meersschaut, D., Vandekerkhove, K., 2000. Development of a stand-scale forest biodiversity index based on the State Forest Inventory. In: Hansen, M., Burk, T. (Eds.), Integrated Tools for Natural Resources Inventories in the 21st Century. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, U.S.A., pp. 340–350.

Vergara, P.M., Armesto, J.J., 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. Landsc. Ecol. 24, 25–38.

Villagrán, C., Hinojosa, L.F., 1997. Historia de los bosques del sur de Sudamérica, II : análisis fitogeográfico. Rev. Chil. Hist. Nat. 70, 241–267.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301.

Vuilleumier, F., 1985. Forest birds of Patagonia: ecological geography, speciation, endemism, and faunal history. Ornithol. Monogr. 36, 255–304.

Vuilleumier, F., Simpson, B., 1971. Pleistocene changes in the fauna and flora of South America. Science 173, 771–780.

Williams, R.J., Purves, D.W., 2011. The probabilistic niche model reveals substantial variation in the niche structure of empirical food webs. Ecology 92, 1849–1857.