

Low functional richness and redundancy of a predator assemblage in native forest fragments of Chiloe Island, Chile

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Summary

1. Changes in land use and habitat fragmentation are major drivers of global change, and studying their effects on biodiversity constitutes a major research programme. However, biodiversity is a multifaceted concept, with a functional component linking species richness to ecosystem function. Currently, the interaction between functional and taxonomic components of biodiversity under realistic scenarios of habitat degradation is poorly understood.
2. The expected functional richness (FR)–species richness relationship (FRSR) is positive, and attenuated for functional redundancy in species-rich assemblages. Further, environmental filters are expected to flatten that association by sorting species with similar traits. Thus, analysing FRSR can inform about the response of biodiversity to environmental gradients and habitat fragmentation, and its expected functional consequences.
3. Top predators affect ecosystem functioning through prey consumption and are particularly vulnerable to changes in land use and habitat fragmentation, being good indicators of ecosystem health and suitable models for assessing the effects of habitat fragmentation on their FR.
4. Thus, this study analyses the functional redundancy of a vertebrate predator assemblage at temperate forest fragments in a rural landscape of Chiloe island (Chile), testing the existence of environmental filters by contrasting an empirically derived FRSR against those predicted from null models, and testing the association between biodiversity components and the structure of forest fragments.
5. Overall, contrasts against null models indicate that regional factors determine low levels of FR and redundancy for the vertebrate predator assemblage studied, while recorded linear FRSR indicates proportional responses of the two biodiversity components to the structure of forest fragments. Further, most species were positively associated with either fragment size or shape complexity, which are highly correlated. This, and the absence of ecological filters at the single-fragment scale, rendered taxonomically and functionally richer predator assemblages at large complex-shaped fragments.
6. These results predict strong effects of deforestation on both components of biodiversity, potentially affecting the functioning of remnants of native temperate forest ecosystems. Thus, the present study assesses general responses of functional and taxonomic components of biodiversity to a specific human-driven process.

Key-words: carnivores, environmental filters, raptors, South America, temperate forests

Introduction

Changes in land use, and subsequent habitat fragmentation, constitute major drivers of global change (Sala *et al.* 2000). Although reduction in original habitat, edge effects and

disruption of individuals' movements threaten the more specialized and space-demanding organisms (Crooks 2002; Fahrig 2003; Kuussaari *et al.* 2009), they promote the invasion of the remnant fragments by opportunistic and domestic species associated with the surrounding matrix (Crooks 2002; Fahrig 2003; Tschardtke *et al.* 2005; Hobbs *et al.* 2006; Devictor *et al.* 2010). This phenomenon impairs issuing

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accurate predictions of the overall response of biodiversity, particularly by considering its multifaceted nature including taxonomic, genetic and functional components in space and time. The former two components of biodiversity are reasonably well known, but functional diversity has been receiving increasing attention only recently (Diaz & Cabido 2001; Diaz *et al.* 2006; Petchey & Gaston 2006).

Functional diversity is the variability of roles played by species in relation to an ecosystem process or ecological interaction of interest, usually approached from the diversity of their functional (morphological, physiological, behavioural) traits, and it is believed to play a role linking species richness to ecosystem functioning (Diaz & Cabido 2001; Loreau *et al.* 2001; Naeem & Wright 2003). However, the response of functional diversity to global change in general, and habitat fragmentation in particular, has received much less attention than that of its taxonomic component (Diaz & Cabido 2001; Loreau *et al.* 2001; Naeem & Wright 2003; Tscharrntke *et al.* 2005; Petchey & Gaston 2006).

Biodiversity components are complementary though not necessarily independent of each other, and their responses to environmental gradients can covary (Diaz & Cabido 2001; Naeem & Wright 2003; Petchey & Gaston 2006). In particular, species tend to differ to some extent on their functional traits, and functional richness (FR) (i.e. the number and range of functional trait values present in an assemblage; Mason *et al.* 2005) is thus expected to associate positively with species richness (S) [the FR–species richness relationship (FRSR); e.g. Diaz & Cabido 2001; Petchey & Gaston 2002a, 2006; Petchey *et al.* 2007]. Nevertheless, the probability of species resembling each other in their functional traits increases with S . Therefore, functional redundancy is predicted to attenuate FRSR in species-rich assemblages (Fig. 1a; Naeem & Wright 2003; Petchey *et al.* 2007). In natural settings, where the composition and richness of species assemblages can vary with local conditions, FR will ultimately depend on both initial S and how much it changes in response to environmental fluctuations, with stronger effects in less-redundant species-poor systems (Fig. 1a).

Growing empirical evidence suggests that environmental effects are not independent of species' functional traits (e.g. Tscharrntke *et al.* 2005; Farias & Jaksic 2007, 2009; Heino *et al.* 2007), potentially affecting the form of the expected FRSR (Petchey & Gaston 2002b). Particularly, local conditions may act as environmental filters sorting species according to their phenotype (e.g. functional traits; Keddy 1992; Naeem & Wright 2003), making functionally similar species to co-occur more often than expected by chance, and rendering a flatter FRSR (Petchey *et al.* 2007; Mason *et al.* 2008; Fig. 1b). As FRSR translates species responses into functional consequences, assessing functional redundancy and environmental filters in fragmented landscapes may allow to foresee the effects of changes in land use on biodiversity and the provision ecosystem goods and services (Fig. 1c; Tscharrntke *et al.* 2005; Diaz *et al.* 2006; Cumming & Child 2009; Flynn *et al.* 2009; Moretti *et al.* 2009; Devictor *et al.* 2010).

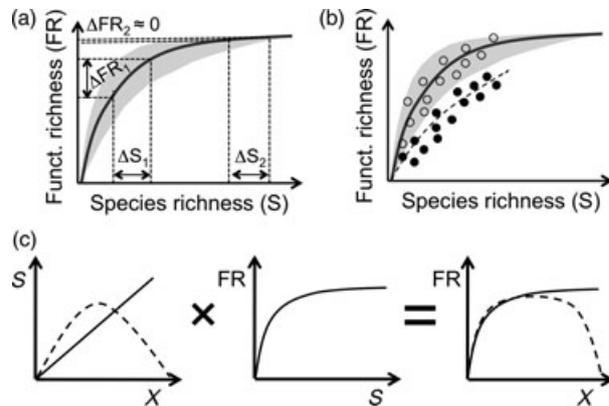


Fig. 1. Functional richness (FR)–species richness relationship (FRSR). (a) Functional richness is expected to be positively associated with species richness (S) in a decelerating fashion as a result of the effects of functional redundancy in species-rich assemblages. Thus, similar changes of S in poorer and richer assemblages (ΔS_1 and ΔS_2 , respectively) may have contrasting effects on FR (ΔFR_1 vs. ΔFR_2). (b) In addition, environmental filters may act sorting species according to their functional traits and reducing the overall functional differentiation among species in a given place and time. Accordingly, the resulting assemblages will be nonrandom samples of the species pool, showing lower FR values (filled dots) than predicted from a random FRSR (open dots) for any given level of S . (c) Finally, the resulting form of the FRSR determines the way in which the response of S to a given environmental factor translates into FR. The sketch exemplifies how an asymptotic FRSR may attenuate the functional richness consequences of two alternative hypothetical responses of S to an environmental gradient X , where the association between FR and X results from the interaction between the FRSR and the association between S and X .

One of the important ways in which top predators affect ecosystems is through prey consumption, mediating biological interactions and energy-nutrient flows through the food web (Duffy 2002; Casula, Wilby & Thomas 2006; Farias & Jaksic 2007, 2009). This way, they can control pests and disease vectors (Cardinale *et al.* 2003; Ostfeld & Holt 2004; Diaz *et al.* 2006), or conflict with human activities for their impact on livestock, poultry and game species (Graham, Beckerman & Thirgood 2005). Accordingly, the FR of a predatory assemblage can be estimated as the diversity of diet compositions shown by predator species (i.e. FR in prey consumption), which summarizes the range of energy-nutrient paths and biotic interactions they affect (Cardinale *et al.* 2003; Casula, Wilby & Thomas 2006; Farias & Jaksic 2007, 2009). Moreover, because of their high energy and space requirements, top predator species are sensitive to habitat loss and fragmentation, particularly those ecologically more specialized (Purvis *et al.* 2000; Duffy 2003). Therefore, highly degraded habitats are expected to have more generalist predators, resulting in lower FR and higher functional redundancy (Purvis *et al.* 2000; Ryall & Fahrig 2006). This makes predators such as avian raptors and mammalian carnivores good indicators of habitat degradation (Sergio, Newton & Marchesi 2005) and suitable models for investigating the effects of habitat fragmentation on FR.

In south-central Chile, a large fraction of the native temperate rain forest has been cleared for timber extraction and

silvo-agricultural activities (Armesto *et al.* 1998; Smith-Ramirez 2004; Willson, Sieving & De Santo 2005). Vertebrate predator assemblages in this region comprise species closely associated with native forests along with several habitat generalists and exotic species, responding differentially to habitat fragmentation (Acosta-Jamett & Simonetti 2004; Grez, Simonetti & Bustamante 2006) with unknown consequences for FR and ecosystem function within remnant forest patches.

The aims of this study were (i) to assess the extent of functional redundancy (Fig. 1a) for a vertebrate predator assemblage (raptors and carnivores) in a rural landscape of Chiloe island, southern Chile, (ii) to test the existence of environmental filters affecting their resulting FRSR (Fig. 1b), and (iii) to assess how the response of their S to habitat fragmentation translates into FR within remnant forest fragments (Fig. 1c). This was accomplished by contrasting an empirically derived FRSR for raptors and carnivores occurring in forest fragments against those predicted from null models, and testing the association between predicted S and FR values with the structure (i.e. size, shape complexity and connectivity) of such fragments.

Materials and methods

STUDY AREA

The study area is located in northeastern Chiloe island (Ancud Department, X Region of Chile), comprising remnant fragments of native temperate rain forest around Senda Darwin Biological Station (SDBS: 45°53'S, 73°40'W, approximately 27-m elevation; Fig. 2). Climate is wet temperate (mean annual precipitation and temperature: 2090 mm and 12°C, respectively), with most precipitation occurring between April and September (Aravena *et al.* 2002). This area was formerly located in the confluence between Valdivian and North-Patagonian forests (Veblen, Schlegel & Oltremari 1983). Currently, native forests are highly fragmented by clearing for livestock raising and timber extraction (most fragments being < 50 ha and few > 1000 ha; Jaña-Prado *et al.* 2006), and the open-matrix corre-

sponds mainly to pastures and secondary shrublands (Aravena *et al.* 2002). Previous studies in Chiloe island have documented the effects of habitat fragmentation on local plant communities (Jaña-Prado *et al.* 2006), nonraptorial birds (Armesto *et al.* 2005; Willson, Sieving & De Santo 2005) and small mammals (e.g. *Dromiciops gliroides* Thomas 1894; Jimenez 2005). Little is known about the ecology of avian raptors and mammalian carnivores inhabiting rural areas, and their response to forest fragmentation is anecdotal (Diaz 2005; Willson, Sieving & De Santo 2005) or known from single-species studies (Elgueta, Valenzuela & Rau 2007). Habitat use was previously assessed only for *Leopardus guigna* Molina 1972 (Sanderson, Sunquist & Iriarte 2002), *Lycalopex fulvipes* Martin 1837 (Jimenez 2006) and *Milvago chimango* (Vieillot 1816) (Morrison & Phillips 2000).

QUANTIFICATION OF FOREST FRAGMENTS STRUCTURE

All the forest fragments in the study area ($n = 6660$) longer than 20 m along their longest axis were digitalized from aerial photographs (1 : 20 000) (Fig. 2; see Appendix S1, Supporting information). Three patch structure metrics were computed for digitized fragments using FRAGSTATS 3.3 (McGarigal *et al.* 2002): (i) area (A) as estimator of fragments size, which in Chiloe island is positively correlated with horizontal and vertical forest habitat structure (Jaña-Prado *et al.* 2006); (ii) shape index ($SI = 0.25 \times p/\sqrt{A}$, with p and A being fragment perimeter and area, respectively) as estimator of fragment shape complexity and edge effects, describing the extent to which fragments depart from a geometrically simple compact configuration of the same area (for raster maps, square: $SI = 1$); (iii) proximity index ($PROX = \sum_i A_i/h_i^2$, A_i and h_i being area of, and distance to, patch i within a 1000-m buffer, respectively) as estimator of fragment connectivity.

PREDATOR SURVEY

During January–May of 2009 and of 2010, a representative subset of forest fragments was surveyed for the occurrence of raptors and carnivores (Fig. 2), sampling effort being proportional to patch size as long as permitted by accessibility to private lands. Carnivores were surveyed at 50 forest fragments, with 97 stations placed along transects equipped with Tomahawk live traps (1–14 per patch) and 73

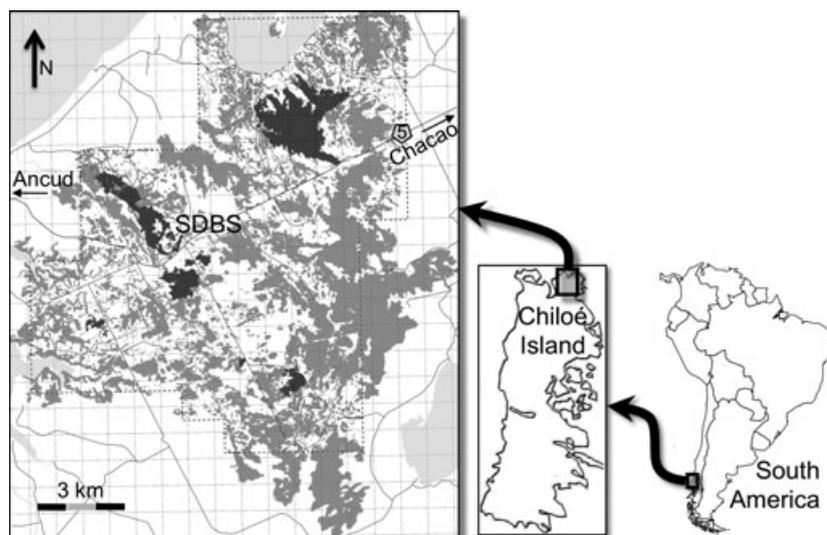


Fig. 2. Location and schematic representation of the fragmented rural landscape in northeastern Chiloe Island, X Region, Chile. The largest map shows the extent of the study area (dotted lines) and the 6660 forest fragments digitized (grey polygons), with those surveyed for vertebrate predators highlighted in darker grey. Lines represent roads and Route 5 connecting Ancud and Chacao. SDBS: Senda Darwin Biological Station and reserve.

camera-trap stations (1–10 per patch) along transects, spaced 250 and 500 m, respectively. Sampling stations were baited with raw chicken parts, lured with bobcat urine and remained active during five consecutive days (sampling effort: 485 and 365 stations-nights, respectively). Tomahawk traps were held open during the first two nights allowing individuals' familiarization with the devices and minimizing 'trap-shyness'. Nocturnal raptors were surveyed at 54 forest fragments using owl vocalization playbacks at 36 stations; some stations comprising several adjacent fragments, while the largest patches required up to seven stations. At each station, two to three playback sessions were performed within 4 h after dusk every two or three nights, depending on weather conditions and avoiding playback in rainy nights (sampling effort: 81 station-nights). Finally, all fragments were exhaustively scouted for direct observations and spontaneous vocalizations of diurnal and nocturnal raptors, and carnivores, along with indirect signs of their presence (e.g. fresh tracks, faeces and pellets). The survey was designed to assess the probability of occurrence of predators at a given time and forest fragment, so that sampling period for any set of species was constrained to be always < 1 week.

ASSESSMENT OF THE FRSR OF THE PREDATOR ASSEMBLAGE

The FRSR of the predator assemblage (Fig. 1a) was assessed by regressing empirical estimates of species richness (S) and FR. Because of logistical constraints, surveys of diurnal raptors, nocturnal raptors and carnivores could not be carried out simultaneously. Then, actual values of S and FR at each forest fragment could not be quantified directly from recorded simultaneous occurrences of predator species. Therefore, their expected values for each fragment were estimated from predictions of an empirical model (EM) obtained using a randomization procedure.

First, a binary vector was obtained for each predator species describing its presence-absence at surveyed forest fragments, and logistic regression models (McCullag & Nelder 1989) were used to construct incidence functions for species showing five or more positive records (approximately $\geq 10\%$ forest fragments). Incidence functions represent the occurrence probability of predators conditional on the structure (i.e. size, shape and connectivity) of forest fragments. Patch structure metrics were normalized through natural logarithmic transformations to attain more stable solutions. Further, there was a high colinearity between $\log(A)$ and $\log(SI)$, indicating that largest patches were also structurally more complex for both the surveyed fragments and the entire landscape (Pearson's $r = 0.82$, $P_{(t = 10.5, \text{d.f.} = 52)} < 0.01$ and $r = 0.68$, $P_{(t = 75.4, \text{d.f.} = 6658)} < 0.01$, respectively). This is a consequence of largest fragments including long-narrow forest strips associated with riparian habitats, ravines and linear human structures (e.g. roads and fences), and comprising several private lands with different management strategies, thus yielding higher habitat heterogeneity. Accordingly, only univariate or bivariate models adding the effect of connectivity to that of either size or shape complexity, were tested. In each case, the performance of models alternatively including one or more patch structure metrics was contrasted using the Bayesian information criterion (i.e. BIC; Burnham & Anderson 2002; Bolker 2008), which tends to be more conservative and less prone to over-parameterization than either the Akaike's information criterion or its version corrected for small sample size (i.e. AIC and AICc, respectively; Burnham & Anderson 2002), because of more stringent penalization on the number of model parameters to be estimated (Bolker 2008, pp. 210–211).

Then, EM was obtained by relocating 5000 times the observed number of occurrences of each predator species among the surveyed patches according to their incidence functions. The occurrence probability for species with fewer than five positive records was conservatively assumed independent of patch structure (i.e. irrespective of size, shape, complexity and connectivity), except for the forest specialist hawk *Buteo albigula* Philippi 1899 and the river otter *Lontra provocax* (Thomas 1908). The single occurrence of the former was randomly relocated among patches equal or larger than the one where the species was recorded, while occurrences of the latter were only among patches comprising or bordering permanent streams.

Iteratively, S was obtained for the forest fragments summing the simulated predator occurrences, and FR was estimated using the index proposed by Petchey & Gaston (2002a) as the sum of the branches of a dendrogram of functional dissimilarity among predator species, connecting the species subsets of interest. The dendrogram was obtained applying a hierarchical cluster analysis, using the unweighted pair group with arithmetic mean (UPGMA) clustering algorithm (Legendre & Legendre 2003) on a functional dissimilarity matrix constructed from published information on relative consumption of prey categories by species in the regional pool (see Appendix S2; Table S1, Supporting information). Accordingly, in this study, FR means the variety of patterns of prey consumption shown by the predator assemblage.

Finally, the resulting expected FR values for each level of S and its 95% confidence interval were obtained from the mean and 2.5–97.5% quantiles of the distribution of simulated values. Then, the form of the FRSR predicted by EM was assessed regressing the expected FR values and S using general linear models (Neter *et al.* 1996). Exponential models (i.e. $FR = a \times S^b$) linearized on log-log scale (i.e. $\log(FR) = \log(a) + b \times S$) were fitted, and nonlinearity in FRSR was assessed from estimates of parameter b (\pm SE), the null hypothesis being $b = 1$ for linear association. On the contrary, $b < 1$ will indicate some degree of functional redundancy in the vertebrate predator assemblage.

TESTING ENVIRONMENTAL FILTERS

To assess the existence of environmental filters (Fig. 1b), the FRSR predicted by the EM was contrasted against those predicted by two null models: one (R0) accounting only for species' functional traits; another (R1) also accounting for the observed number of positive records of each recorded species, thus breaking the spatial structure of the assemblage while preserving the actual profile of species rarities and functional redundancy at the rural landscape level. From these comparisons, we assessed whether the empirical FRSR can be attributed to environmental filters acting at the single-patch scale or above (e.g. landscape or regional scales).

R0 was obtained by simulating 5000 random extinction trajectories, each one performed by deleting predator species one by one from the entire assemblage recorded at the study area until a single one is left, and recalculating each time the corresponding FR value. Thus, R0 represents the expected distribution of plausible FR values for each level of S resulting from the set of functional traits present in the assemblage, all being possible combinations of S -species equally probable. Accordingly, the resulting FRSR represents the degree of intrinsic functional redundancy (cf. Petchey *et al.* 2007) of the assemblage for each S -level.

R1 was obtained by relocating randomly (5000 times) the observed number of positive records of species among the surveyed fragments, and recalculating each time the corresponding FR and S values

(totalling 270 000 simulated values for each variable). Thus, R1 represents the FRSR expected from environmental filters acting above the patch level (e.g. landscape or region level), determining the relative abundance of species in the assemblage, with species occurrences at forest fragments being independent of their size, shape and connectivity.

Then, for each null model and S -level, the expected FR values and their 95% confidence interval were obtained analogously to EM and contrasted to assess significant differences between the FRSR predicted by the different models. Further, by definition, $FR = 0$ for $S = 1$; thus, environmental filters, resulting in lower than expected FR for $S > 1$, should render shallower slopes for FRSR (Fig. 1b). Accordingly, for R0 and R1, a general linear model (Neter *et al.* 1996) was fitted between expected FR values and S (log-log transformed, see above), and the resulting estimates of parameter a (\pm SE) were compared among the three models, testing the predictions $a_{EM} < a_{R1} \leq a_{R0}$ and $a_{EM} = a_{R1} < a_{R0}$ for environmental filters acting at or above the single-patch scale, respectively.

TESTING FRAGMENTATION EFFECTS ON S AND FR

The resulting effects of forest fragmentation on the two diversity components (Fig. 1c) were assessed by regressing the FR and S predicted by EM for each surveyed fragment against patch structure metrics. Given that the combination of the individualistic response of species may result in a variety of functional forms for S and FR, order-two polynomial terms were included to account for accelerating, decelerating and unimodal responses (Neter *et al.* 1996). Model selection followed the Bayesian information criterion (BIC; Burnham & Anderson 2002). All simulation and modelling procedures were performed using R software (R Development Core Team 2006).

Results

PREDATORS' INCIDENCE FUNCTIONS

Overall, 14 species were recorded at the study area, ranging from forest specialist to matrix-associated and to domestic species. Eight species attained the minimum number of positive records required to assess their incidence functions (Appendix S3; Table S1, Supporting information). All of them responded positively to patch size or shape complexity

(Fig. 3), most being clearly associated with one of these variables (i.e. Δ BIC > 2 between alternative models; Table S1, Supporting information). This likely resulted from a combination of habitat selection by forest specialists and a combination of sampling area and edge effects (i.e. incidence probability increasing with fragment area or closeness to the surrounding matrix). Surprisingly, no significant response to patch connectivity was detected for any of these species, nor their inclusion in the incidence functions was supported by its BIC criterion (Δ BIC < 2 ; Table S1, Supporting information).

FRSR OF THE PREDATOR ASSEMBLAGE

The 25 predator species in the regional species pool encompass a wide variety of foraging habits (Table S2; Fig. S1, Supporting information), from species highly specialized in the consumption of small mammals, birds or aquatic prey to generalized predators that also include carrion, arthropods and plant material in their diet (Appendix S2, Supporting information). Using this information and the obtained incidence functions to assess FR, expectations from the EM suggest a linear association between this variable and S (FRSR) for the 14 species recorded in the study area, indicating low levels of functional redundancy among species ($b \approx 1$, Table 1; Fig. 4b,e).

Table 1. Form of the functional richness–species richness relationship predicted by three models (see text)

Model	a [$\log(a) \pm$ SE]	$b \pm$ SE
Random (R0)	0.12 [−2.14 \pm 0.03]	0.82 \pm 0.01
Random (R1)	0.06 [−2.88 \pm 0.03]	0.97 \pm 0.02
Empirical (EM)	0.05 [−2.91 \pm 0.03]	0.98 \pm 0.02

Values are estimates of parameters for the exponential association functional richness ($FR = a S^b$), fitted by means of general linear models after linearizing the association as $\log(FR) = \log(a) + b \log(S)$; with $\log(x)$ being natural logarithm transformations.

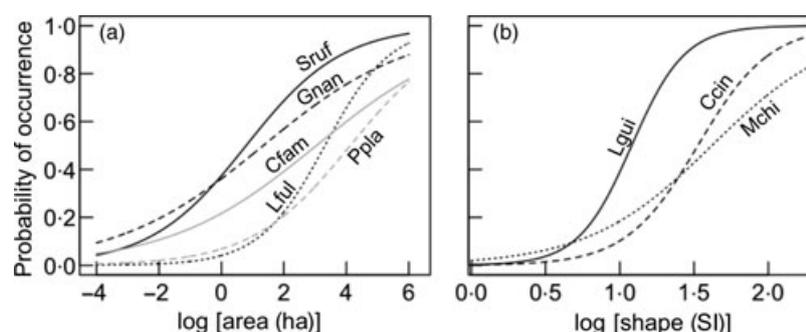


Fig. 3. Predicted incidence function for vertebrate predators recorded at five or more surveyed forest fragments, in relation to their (a) size (= area) and (b) shape complexity (= shape index). Sruf: *Strix rufipes*, Gnan: *Glaucidium nanum*, Cfam: *Canis lupus familiaris*, Lful: *Lycalopex fulvipes*, Ppla: *Polyborus plancus*, Lgui: *Leopardus guigna*, Ccin: *Circus cinereus*, Mchi: *Milvago chimango*. $\log(x)$ are natural logarithm transformations of predictor variables.

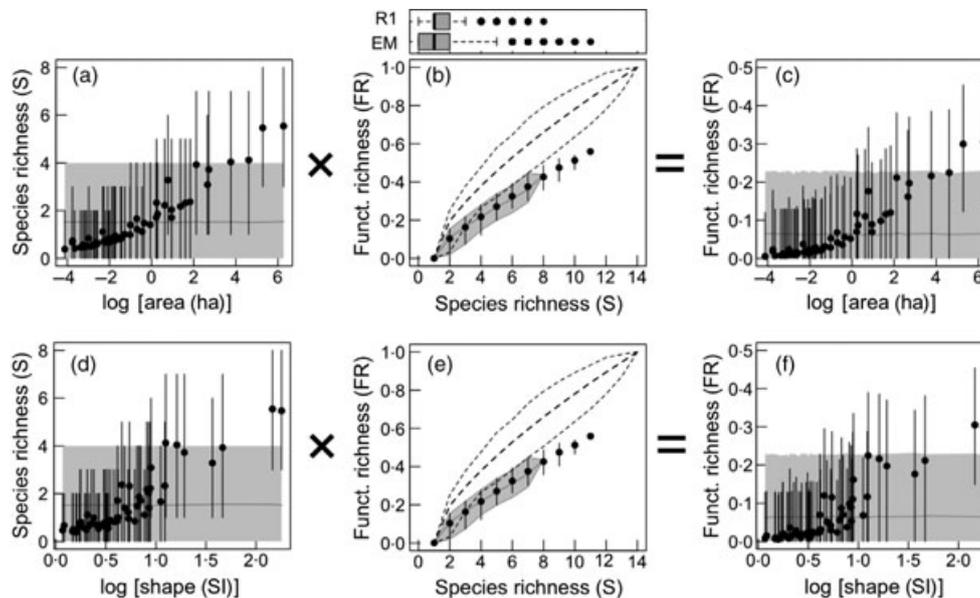


Fig. 4. Results of simulations showing the expected functional richness (FR)–species richness relationship (FRSR) for the vertebrate predator assemblage in Chiloe. This figure follows the organization of Fig. 1c, representing FR response to fragment structure (a–c: fragment size, d–f: fragment shape; $\log(x)$ are natural logarithm transformations) as resulting from the interaction of the FRSR and the association between species richness (S) and fragment structure. Each plot shows the mean (filled dots) and 95% confidence intervals (bars) of response variables predicted by an empirically derived model (EM). Further, the grey line and shaded areas represent the mean and 95% confidence intervals of the same variables predicted by a neutral model accounting only for the observed number of occurrences of predator species (R1). (b,e) segmented lines represent the FRSR predicted by a null model (R0) accounting only for species in the study area. Upper panel in (b): box-plot showing distribution of S resulting from EM and R1.

ENVIRONMENTAL FILTERS

When the FRSR was evaluated according to expectations from R0, there was a steep and slightly nonlinear FRSR for the 14 predators observed at the study area (i.e. $b < 1$, Table 1), suggesting little (intrinsic) functional redundancy in the assemblage (cf. Petchey *et al.* 2007). However, for most S -levels, FR values predicted by R0 tended to be significantly higher than expected from EM (Fig. 4b,e), indicating the action of environmental filters. The FRSR became shallower and linear after accounting for species rarities (R1), resulting in lower FR values than those predicted by R0 but not from EM expectations (Fig. 4b,e). Accordingly, estimations of parameters a and b suggest that the overall form of the FRSR predicted by EM and R1 did not differ significantly (Table 1). This suggests the lack of environmental filters on predators' functional traits at the single-fragment scale. Thus, differences in the shape of the FRSR predicted by EM and R0 may have resulted from environmental filters acting on a higher spatial scale, resulting in the numerical dominance of the whole assemblage by (and thus a higher co-occurrence of) species similar in their moderate to high consumption of small mammals (< 1 kg; Table S1; Fig. S1, Supporting information). Nonetheless, EM predicted a broader range of S -values than R1. Given that most species show similar incidence functions (Fig. 3), there is a higher probability of several species co-occurring in some fragments according to EM than R1. Further, the recorded positive association with the size and shape complexity of forest fragments resulted in very low incidence of species in small

fragments, which are numerically dominant in the landscape. As a result, this rendered a more biased distribution of S -values, with most fragments showing none up to two species and null to low FR, and a few of them showing relatively high values of both variables (Fig. 4b).

FRAGMENTATION EFFECTS ON S AND FR

Finally, the positive association with fragment size or shape complexity found for all modelled species (Table 1; Fig. 3), together with the strong correlation between these two patch metrics, rendered a positive linear and polynomial association between expected S and both $\log(A)$ and $\log(SI)$, respectively (Fig. 4a,d; Table S4, Supporting information). Then, for the range of fragment sizes in this rural landscape, a higher number of predator species is predicted to occur at the largest forest fragments owing to both habitat selection by species and sample area and edge effects. These are conservative results given the low number of records for a subset of the assemblage at the study area. Further, the resulting linear FRSR and the subsequent lack of functional redundancy indicate that changes in S are tracked by proportional changes in FR, explaining the similar form taken by the association between both biodiversity components and fragment structure (Fig. 4c,f; Table S4, Supporting information).

Discussion

In this study, the form of the FR–species richness relationship (FRSR) for vertebrate predators was first assessed to test

the existence of functional redundancy (Fig. 1a). The observed steep FRSR indicates low redundancy at our study area (Fig. 4), typical of species-poor assemblages (Diaz & Cabido 2001; Petchey & Gaston 2002a,b, 2006; Naeem & Wright 2003; Farias & Jaksic 2007, 2009; Petchey *et al.* 2007). Top predators are expected to show lower species richness than taxa at other trophic levels, and consequently less intrinsic functional redundancy (cf. Petchey *et al.* 2007), being particularly vulnerable to species loss in terms of FR (Purvis *et al.* 2000; Duffy 2002, 2003; Cardinale *et al.* 2003; Fahrig 2003; Casula, Wilby & Thomas 2006; Ryall & Fahrig 2006).

Southern temperate rain forests are relatively poor in top predator species when compared to other rain forests in South America, owing to historical and biogeographic factors (Meserve & Jaksic 1991; Trejo, Figueroa & Alvarado 2006). Their long-lasting isolation from physiognomically similar ecosystems at lower latitudes by the South American arid diagonal, impaired faunal exchanges and promoted high levels of faunal endemism (Smith-Ramirez 2004). Further, predators at Chiloe island constitute a subset of those in continental forests. Thus, the assemblage studied seems to have an intrinsically impoverished vertebrate predator fauna, with most of their elements representing habitat generalists and cosmopolitan species – a pattern likely reinforced by deforestations and land conversion.

Functional richness is not only affected by species richness and the overall patterns of functional differentiation in the species pool. It also depends on how environmental filters affect FR at a given time and place by sorting species according to their functional traits (Fig. 1b; Keddy 1992; Naeem & Wright 2003; Heino *et al.* 2007; Petchey *et al.* 2007; Mason *et al.* 2008). In our study area, the expected FR of vertebrate predators at forest fragments was lower than predicted solely from the functional structure of the whole assemblage (Fig. 4), implying the action of environmental filters (Fig. 1b; Naeem & Wright 2003; Petchey *et al.* 2007; Mason *et al.* 2008). However, those differences disappeared after accounting for the observed number of occurrences for each predator species at the study area (Table 1; Fig. 4). This suggests that environmental filters did not act on the relative abundance of predator species at the scale of single fragments, but at a higher spatial scale, being responsible for the overall profile of commonness and rarity of predator species at our study area.

Previous studies encompassing broader spatial scales show that changes in species richness may notoriously affect the functional diversity of arthropods, birds and mammals, in association with biogeographic gradients (Cumming & Child 2009; Moretti *et al.* 2009; Devictor *et al.* 2010) or agricultural habitat simplification and human disturbance (Tscharntke *et al.* 2005; Flynn *et al.* 2009; Moretti *et al.* 2009). Rather than contrasting localities differing on land use, this study focused on a smaller scale, assessing whether fragment structure in a rural area affects the taxonomic and FR of predators, and the extent to which fragments may still be functional representatives of the originally continuous land-

scape. A natural extension should be to compare the FR of this and other rural landscapes against those of more pristine temperate forests, to dissect the ultimate effects of anthropogenic and biogeographic environmental filters.

Both the response of species richness to environmental gradients and the FRSR will ultimately determine how FR responds to disturbance (Fig. 1c). For the range of forest fragment sizes analysed in this study, the shared positive response of most predators to the size and shape complexity of forest fragments (Fig. 3), and the positive correlation between these two patch structure metrics, explained the response of species richness (Fig. 4). Then, the low functional redundancy of the predator assemblage and the resulting linear FRSR determined parallel responses of the two components of biodiversity (Fig. 4), as both forest-specialists and matrix-associated species tended to co-occur in largest fragments regardless of their functional traits.

On the other hand, the occurrence of matrix-associated species at forest fragments and their putative functional effects there, even if occasional, should increase with the extent of the contact zone between the alternate habitat types (Crooks 2002; Fahrig 2003; Tscharntke *et al.* 2005), thus explaining their higher incidence in the largest and more complex-shaped fragments. Accordingly, several opportunist and open-matrix avian raptors (cf. Trejo, Figueroa & Alvarado 2006) occurred at forest edges and on the canopy (Appendix S3, Supporting information), while domestic dogs were recorded far inside the largest fragments. This indicates that all surveyed forest fragments are small enough for being frequented by a taxonomically enriched predator assemblage. Further, the expected functional consequences of such enrichment suggest that even large forest fragments at the study area may actually function as novel ecosystems (cf. Hobbs *et al.* 2006) instead of being representative remnants of the original landscape.

Previous studies in the same area highlighted the relevance of connectivity of forest fragments and matrix quality for several small birds (Armesto *et al.* 2005). However, connectivity was not included in the incidence functions of local vertebrate predators (Fig. 3), and consequently it does not seem to affect their species richness or FR. On the one hand, connectivity of forest fragments may be irrelevant for most predators in the study area, which are habitat generalists or matrix-associated species. On the other hand, the high number and proximity of small fragments scattered over the study area, the strips of riparian forest along creeks and rivers (Fig. 2), and the presence successional scrub in the matrix (Aravena *et al.* 2002; Jaña-Prado *et al.* 2006), may render the surrounding open matrix relatively permeable for species with large home ranges, such as mammalian carnivores and avian raptors. Accordingly, connectivity of remnant large forest fragments may still be high enough so that none is isolated from the viewpoint of forest-associated predator species (Crooks 2002; Fahrig 2003).

The latter situation contrasts with rural areas in the continent, particularly along the Chilean central valley, with a longer deforestation history and higher levels of isolation

among forest fragments (Armesto *et al.* 1998; Aravena *et al.* 2002; Smith-Ramirez 2004; Grez, Simonetti & Bustamante 2006). Thus, the scenario in our study area could represent an earlier stage of the deforestation process when compared to continental counterparts, and its study thus enables understanding the initial response of forest ecosystems to changes in land use (Aravena *et al.* 2002). However, studying landscapes currently affected by ongoing habitat degradation implies dealing with transient states and considering that 'unpaid extinction debts' may affect our conclusions (Kussaari *et al.* 2009). It is likely that connectivity will increase its relevance in our study area in the future, because fragments are expected to become more isolated by increased degradation of the surrounding matrix (Aravena *et al.* 2002).

In conclusion, factors acting at or above the scale of the entire landscape determine low levels of FR and redundancy of vertebrate predators at forest fragments in Chiloe island. Accordingly, the resulting linear FRSR yielded proportional responses of the two biodiversity components to changes in the structure of forest fragments. Further, the high colinearity between fragment size and shape complexity and the absence of ecological filters at the scale of single fragments determine a positive correlation in the response of both forest specialists and matrix-associated species, with large complex-shaped fragments showing a taxonomically and functionally richer predator assemblage. This foretells strong effects of deforestation on biodiversity, potentially affecting the functioning of any remnant of original forest ecosystems within the range of fragment sizes recorded here. Our study assesses general local patterns in the response of functional and taxonomic components of biodiversity to a specific human-driven process. Understanding such responses, by considering different facets of biodiversity as well as their interaction in real-world settings, should help predict the effects of human activities on ecosystems (Tschardt *et al.* 2005; Diaz *et al.* 2006; Cumming & Child 2009; Flynn *et al.* 2009; Devictor *et al.* 2010), complementing ongoing research on causes and consequences of the biodiversity and ecosystem functioning relationship (Diaz & Cabido 2001; Loreau *et al.* 2001; Naeem & Wright 2003; Petchey & Gaston 2006).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Digitalization of forest fragments.

Appendix S2. Functional diversity estimation.

Appendix S3. Predator's incidence functions and functional traits.

Table S1. Incidence functions for predator species

Table S2. Relative biomass consumption of prey categories by predator species

Table S3. PCA analysis on predators prey consumption

Table S4. Response of biodiversity components to forest fragment structure

Fig. S1. PCA-biplot and dendrogram (UPGMA) representing the functional structure of the assemblage.

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