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Effects of landscape configuration on the occurrence and abundance of an arboreal marsupial from the Valdivian rainforest

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Abstract

Background: Habitat fragmentation and degradation processes affect biodiversity by reducing habitat quantity and quality, with differential effects on the resident species. However, their consequences are not always noticeable as some ecological processes affected involve idiosyncratic responses among different animal groups. The Valdivian temperate rainforests of southern Chile are experiencing a rapid fragmentation and degradation process despite being a biodiversity hotspot. Deforestation is one of the main threats to these forests. There inhabits the arboreal marsupial *Dromiciops gliroides*, an iconic species from the Valdivian rainforest, it is the only extant representative of the ancient Microbiotheria order, and it is currently threatened by habitat loss. Here we tested the effects of habitat configuration on *D. gliroides* occurrence and abundance along 12 landscapes of southern Chile with different disturbance levels.

Methods: We estimated *D. gliroides* occurrence and abundance using camera traps and related those metrics with landscape configuration indices obtained from FRAGSTATS (i.e., forest %, connectivity, patch number, contiguity, and distance to the nearest patch) using Bayesian linear mixed models.

Results: We found that *D. gliroides* occurrence was not influenced by landscape configuration, while its abundance was positively influenced by forest contiguity.

Conclusions: Although this arboreal marsupial is present in disturbed forests, its restricted movement capabilities and high dependency on the forest three-dimensional structure may affect its long-term persistence. We urge to rethink native forest conservation and management policies to improve habitat connectivity with possible positive consequences for native fauna.

Keywords: Abundance, *Dromiciops gliroides*, Habitat degradation, Habitat fragmentation, Landscape, Occurrence

Background

Habitat fragmentation process involves the subdivision of a continuous habitat in several smaller fragments, altering its spatial configuration and increasing edge effects [1–3]. Those habitat fragments are surrounded by a contrasting matrix that may preclude animal dispersal, reducing functional connectivity [4, 5]. Smaller fragments experience area and edge effects (i.e., due to larger

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edge / interior habitat ratios), exposing them to edge species (e.g., exotic herbivores) and human activities [6, 7]. As fragmentation process advances, the extant habitat fragments become smaller and more isolated [8]. The combined effects of area reduction and isolation would negatively affect forest-dependent species that cannot exploit other habitats and are unable to disperse through non-forested habitats, as it happens, for example, with Rhinocryptid birds [9–11], which are threatened by the loss of functional connectivity (i.e., the actual connectivity from the species' perspective, considering specific interactions with landscape structures) among forest fragments [12]. Furthermore, habitat fragmentation is usually accompanied by habitat degradation [13], which implies a reduction in habitat quality due to the scarcity of key structures, such as perches or tree cavities, usually limiting in disturbed habitats [14].

Alterations in habitat structure can change forest-dependent species composition and compromise their reproductive success [15, 16]. However, these species can be differentially affected by habitat fragmentation depending on their response to different landscape features [17]. That is why quantifying the effects of habitat fragmentation on biodiversity is important to understand how landscape-level anthropogenic changes alter the ecological scenario for the resident animal species [18]. Several landscape metrics have been developed to quantify landscape configuration (i.e., area, edge, shape, isolation, contagion, and connectivity), providing a comprehensive framework useful to assess the effects of habitat fragmentation on different focal species [19, 20]. In this regard, FRAGSTATS [21] offers a complete toolkit of landscape configuration metrics for ecologists, which can be used to assess how sensitive species are to habitat fragmentation [22]. Therefore, landscape configuration (i.e., the number of fragments, their size distribution, their shape, and spatial arrangement), which changes due to habitat fragmentation, provides a comprehensive framework to assess its effects on any focal species.

Valdivian temperate rainforests are located in the occidental margin of southern South America (from 37° to 44°S), and they are considered as a biodiversity hotspot due to their high level of endemism and the presence of relict species [23, 24]. However, these rainforests are among the most threatened ecosystems as a result of anthropogenic pressures, experiencing a rapid fragmentation and degradation due to the expansion of human activities [25, 26]. Deforestation is one of the main causes of habitat fragmentation, resulting in heterogeneous landscape mosaics, in which the extant native forest remnants are immersed in a contrasting matrix composed of degraded habitats and productive lands, confining most forest species to small and isolated fragments [27, 28].

This is the case of many small mammals and understory birds of these forests, which cannot disperse through non-forested matrices [29–31]. Nevertheless, as most species present idiosyncratic responses [17, 32], it may be very difficult to sort out broad generalizations to make informed decisions and elaborate appropriate management practices.

One of the iconic species of the Valdivian rainforest is the arboreal marsupial *Dromiciops gliroides*, which is the sole extant living representative of the ancient Microbiotheria order [33], and also the main seed disperser agent at these forests [34]. Due to the high dependence of the forest's three-dimensional structure, *D. gliroides* could be one of the most affected species by habitat fragmentation and degradation. This marsupial is unable to disperse through non-forested habitats [31], and its local abundances are negatively affected by habitat fragmentation and degradation [35, 36]. This species was considered to be restricted to old-growth forests [33], but recently has been found in secondary forests and abandoned forestry plantations [31, 37, 38] as long as they retain some structural elements that provide movement pathways, shelter, and nesting sites [39]. However, *D. gliroides* presence at disturbed habitats imply changes in abundance and behavior [40], related to resource availability and vegetation structure [39, 41]. Due to its habitat requirements, *D. gliroides* may be considered as an umbrella species, as its conservation would benefit many other species of the Valdivian rainforests [42], such as small understory birds.

In this study, we assessed the effects of landscape configuration on *D. gliroides* occurrence and abundance along 12 landscapes of southern Chile, with different disturbance levels. Considering *D. gliroides*' arboreal habits and its limited movement capabilities through non-forested habitats, we hypothesized that forest cover in the landscape, patch connectivity, and contiguity would be positively related to its occurrence and abundance, while a high number of patches and patch isolation will be negatively related to its occurrence and abundance.

Methods

Study area

We conducted this study at a 450-km latitudinal gradient (from 37°S to 41°S), covering ca. 80% of the Valdivian rainforests in Chile. Along this gradient, we selected 12 landscapes representative of four different levels of habitat disturbance: (1) old-growth native forests (Nahuelbuta National Park, Peumayén Park, and Puyehue National Park), (2) second-growth native forests (Oncol Park north, Huilo Huilo Reserve, and Katalapi Park), (3) native forests under selective logging (Moncopulli, Pucatrihue, and Cascadas), and (4) abandoned forestry plantations of *Pinus radiata* or *Eucalyptus globulus* (Forestal

Mininco, Oncol Park south, and Reserva Costera Valdiviana). We had a balanced design with three landscapes for each habitat disturbance condition (Table S1, available online as Supplementary Material). Those 12 sites were distributed along the Valdivian rainforests (Figure S1), comprising coastal, Andean, and intermediate depression zones. Sampling sites were separated at least 25 km from each other, except for the two sites at the Oncol Park (representing secondary forest and forest plantation conditions), which were 2 km apart. A detailed description of the structure and species composition of these 12 study landscapes can be found in Rodríguez-Gómez and Fontúrbel [40].

In Chile, *Dromiciops gliroides* inhabits the Valdivian forests from the southern end of the Maule Province (35°S) to the Palena Province (44°S), as its northern and southern limits were just expanded [43, 44]. Furthermore, Quintero-Galvis et al. [45] recently supported the presence of two *Dromiciops* species based on genomic

analyses, partially confirming the proposal of D'Elia et al. [46]. Therefore, in the light of these new findings, the northern sites (Mininco and Nahuelbuta) would correspond to the new species, *D. bozinovici*. However, both *Dromiciops* species are arboreal and depend on forest habitats. For those reasons, we will treat them as a single species for the purposes of this work.

Camera trap assessment

We used camera traps for estimating *D. gliroides* occurrence and relative abundance at the 12 landscapes. We monitored *D. gliroides* for two consecutive austral summers (December–April) from 2017 to 2019. We deployed 36 infra-red camera traps (Browning Strike Force HD Pro), which were operated in photographic mode with 1-min delay between shots to avoid capturing the same individual multiple times. We installed the camera traps at a height of 1–2 m above the ground on tree stems, and spaced at least 100 m from each other. We randomly

Table 1 *Dromiciops gliroides* occurrence and abundance data obtained from a two-year (2017 and 2018) camera-trap survey. Occurrence values represent the number of camera traps (of a total of 12) with at least one *D. gliroides* record; occurrence index represents the ratio between occurrence values and the number of camera traps installed. *Dromiciops gliroides* individuals (Dg ind) were estimated from camera traps after applying a 1-h independence interval. Relative abundances are expressed as the number of *D. gliroides* individuals per day

Year	Site	Condition	Occurrence	Occ index	Dg ind	Dg ind/day
2017	PNN	Native	8	0.667	9	1.179
2017	PNP	Native	9	0.750	78	0.696
2017	PPY	Native	9	0.750	101	0.902
2017	HHL	Secondary	4	0.333	64	0.571
2017	ONS	Secondary	10	0.833	82	0.732
2017	PKT	Secondary	10	0.833	141	1.259
2017	CAS	Logging	11	0.917	90	0.804
2017	MCP	Logging	6	0.500	34	0.304
2017	PUC	Logging	11	0.917	95	0.848
2017	FMP	Plantation	10	0.833	87	0.777
2017	ONP	Plantation	5	0.417	56	0.500
2017	RCV	Plantation	6	0.500	34	0.304
2018	PNN	Native	10	0.833	194	1.732
2018	PNP	Native	10	0.833	188	1.679
2018	PPY	Native	12	0.999	297	2.652
2018	HHL	Secondary	9	0.750	228	2.036
2018	ONS	Secondary	11	0.917	197	1.759
2018	PKT	Secondary	10	0.833	201	1.795
2018	CAS	Logging	9	0.750	148	1.321
2018	MCP	Logging	6	0.500	63	0.563
2018	PUC	Logging	10	0.833	155	1.384
2018	FMP	Plantation	11	0.917	179	1.598
2018	ONP	Plantation	6	0.500	50	0.446
2018	RCV	Plantation	8	0.667	78	0.696

PNN Nahuelbuta National Park, PNP Puyehue National Park, PPY Peumayén Park, HHL Huilo Huilo Reserve, ONS Oncol Park (secondary forest), PKT Katalapi Park, CAS Cascadas, MCP Moncopulli, PUC Pucatrihue, FMP Forestal Mininco, ONP Oncol Park (plantation), RCV Valdivian Coastal Reserve

located camera traps within each site (covering ~1 ha), placing three cameras per landscape at each monthly rotation (we conducted four rotations each summer). For each sampling year, we had 12 camera-trap points at each sampling site (making a total of 144 camera trap points per year). Our sampling effort consisted of 774,144 monitoring hours in 288 sampling points in both years. We used the information collected by the camera traps to obtain *D. gliroides* occurrence and relative abundance estimations.

We examined camera trap images looking for *D. gliroides*, pooling the data of both sampling years. As we cannot distinguish individuals from the photographs, we applied a 1-h independence interval to minimize the chance of counting the same individual more than once [37, 47]. After filtering the information, we estimated *D. gliroides* occurrence as the number of camera-trap points with at least one presence record of this species, divided by the number of camera traps installed. This occurrence index ranges between 0 (i.e., *D. gliroides* was not recorded at any camera trap) and 1 (i.e., *D. gliroides* was present on all camera traps). Then, relative abundance was estimated as the number of *D. gliroides* individuals per day.

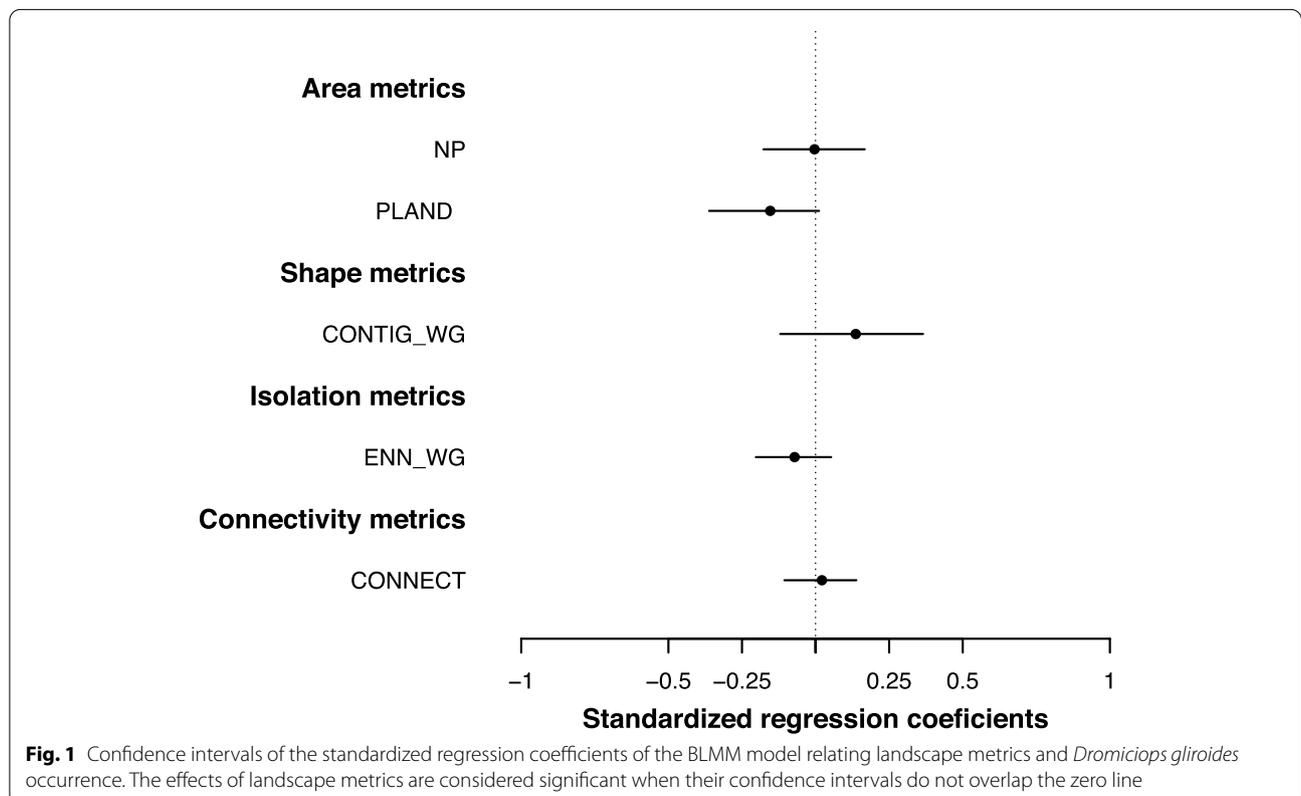
Landscape characterization

We assessed landscape configuration at the 12 study landscapes using Google Earth aerial images. We plotted

a circular buffer of 4-km radius from the centroid of the camera-trap monitoring area at each landscape and characterized the different land uses within this buffer in ArcGIS 10.6 (ESRI, Redlands CA). We distinguished the following land uses: native forest, forestry plantations, scrubland, prairie, and households. After that, we used the FRAGSTATS 4 software [21] to calculate landscape-level metrics (mean values for each site are presented in Table S2). From all the available metrics in FRAGSTATS, we selected five metrics based on biological criteria of *D. gliroides* [35, 39]. From those, we chose two area metrics: PLAND (% of native forest within the landscape) and NP (number of patches), one shape metric: CONTIG (contiguity index), one isolation metric: ENN (Euclidean distance to the nearest neighbor), and one connectivity metric: CONNECT (connectivity index). For CONTIG and ENN we used the weighted mean estimators. The connectivity index (CONNECT) depends on the threshold distance set a priori for its calculations. In this case, we used 250 m, which corresponds to the half of the maximum movement distance reported for *D. gliroides* [31, 48].

Data analysis

We related *D. gliroides* occurrence and abundance with the landscape metrics obtained with FRAGSTATS using Bayesian Linear Mixed Models (BLMM hereafter).

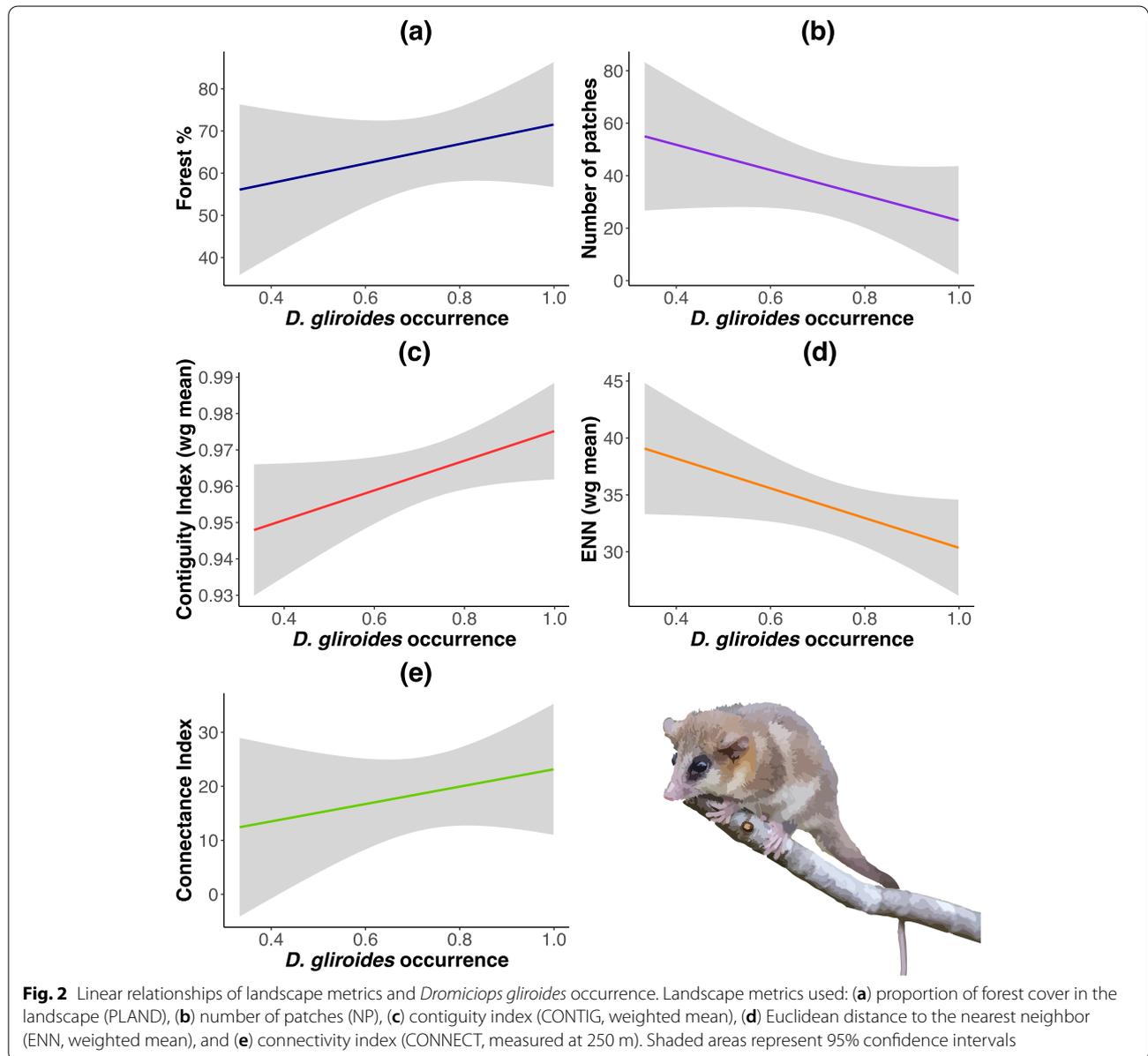


Before fitting the models, we centered and standardized landscape configuration data to make the coefficients comparable. We fitted separate BLMM models for occurrence and abundance data. We used a Gaussian error distribution for each model, including the five landscape metrics obtained from FRAGSTATS as fixed effects. Also, we included the sampling year and habitat disturbance condition as random effects to take temporal and disturbance level variability into account [49]. We performed BLMM analyses in R 4.0.4 [50] using the R packages ‘usdm’ [51] and ‘MCMCglmm’ [52] to implement Bayesian methods, and the ‘ggplot2’ package [53] for visualization data. We used the default priors in ‘MCMCglmm’ for fixed and random effects. To obtain a

minimum of 1000 posterior distributions, we ran 13,000 iterations for each model, with a burn-in period of 1000 iterations and a thinning interval of 3000 iterations. We considered landscape predictors significant if their 95% confidence interval did not overlap zero.

Results

We detected *D. gliroides* in all the sampling landscapes during the study. However, its abundance and occurrence were variable among sites, disturbance conditions, and years (Table 1). *Dromiciops gliroides* abundance decreased with habitat disturbance (i.e., old-growth forests > secondary forests > logged forests > plantations), and its occurrence at the sampling landscapes varied



between 5 and 11 cameras (out of 12) with at least one photographic record of this species. Mean occurrence index (with values ranging from 0 to 1) in the first year was 0.69 ± 0.06 (mean \pm SE), while in the second year was 0.78 ± 0.05 . The first year our camera trap survey recorded a total of 994 *D. gliroides* individuals (estimated after applying the 1-h independence interval to the raw dataset), and the second year the number of *D. gliroides* individuals was 1978. Thus, *D. gliroides* relative abundance in the first year was 0.74 ± 0.09 individuals / day, while in the second year was 1.47 ± 0.18 individuals / day.

Regarding landscape configuration effects on *D. gliroides* occurrence, none of these predictors was significant, but we detected a marginal effect on PLAND (Fig. 1 and Table S3). However, we observe positive trends with PLAND, CONTIG, and CONNECT metrics, and negative trends with NP and ENN (Fig. 2). Regarding landscape configuration effects on *D. gliroides* abundance, we found that CONTIG has a positive and significant effect on *D. gliroides* abundance (Fig. 3 and Table S4). In this case, we also observe positive trends with PLAND, CONTIG and CONNECT metrics, and negative trends with NP and ENN (Fig. 4).

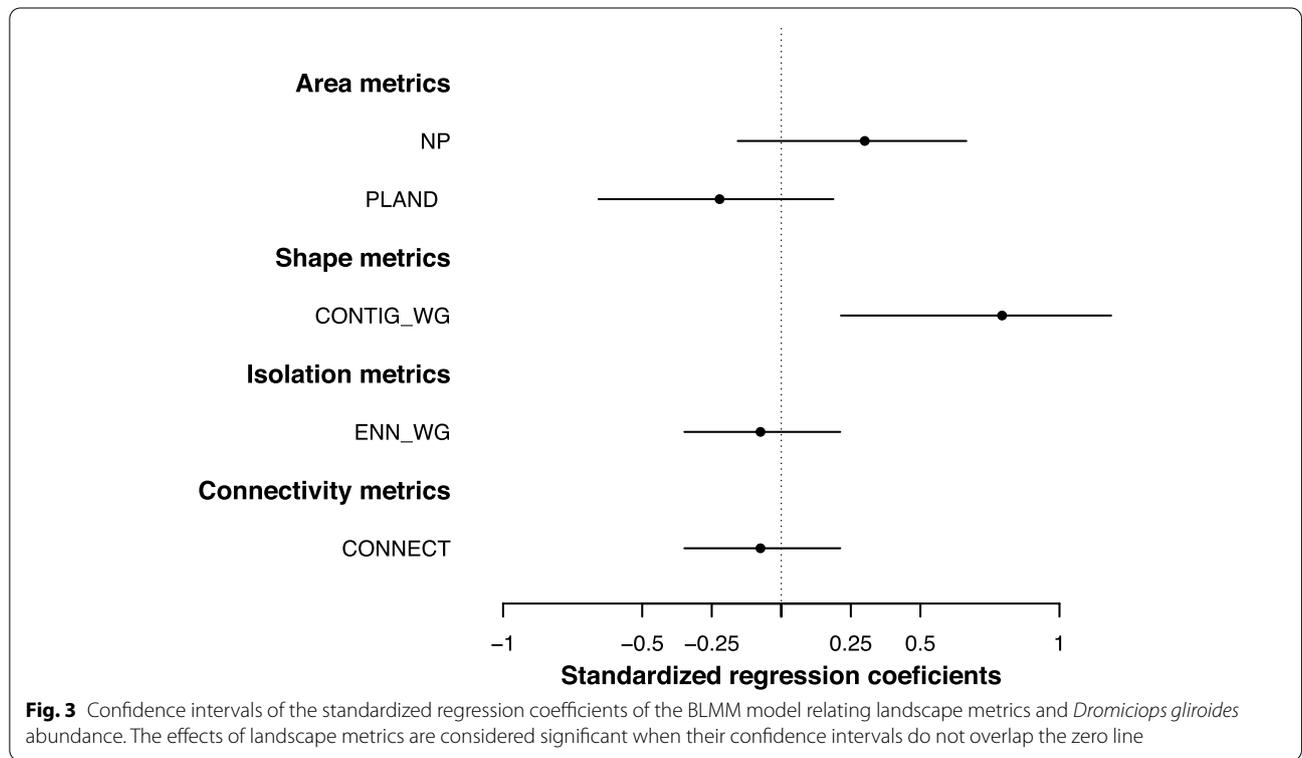
Discussion

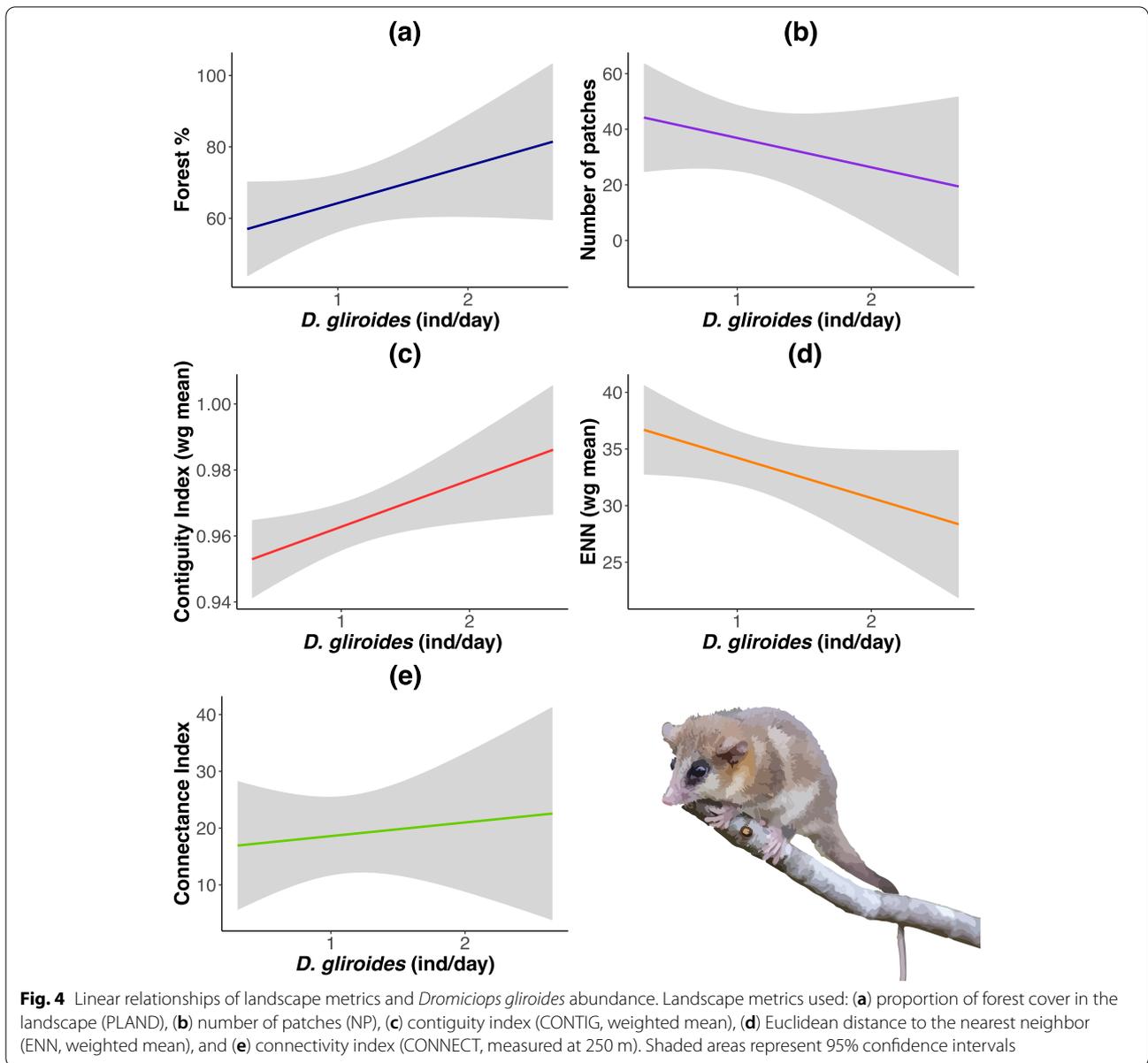
Our results showed that *D. gliroides* abundance is more sensitive to landscape configuration than its occurrence. Habitat contiguity was the most relevant factor, in this

case, explaining the abundance differences found in our camera-trap survey. However, forest proportion in the landscape had a marginal effect in explaining differences in occurrence as well. Therefore, the spatial configuration of the remaining forest patches within the landscape seems to be more relevant than habitat quantity for *D. gliroides*.

As *D. gliroides* is an arboreal marsupial, it largely depends on the three-dimensional structure of the forest, being unable to move across non-forested areas [31], as it happens with other forest species with restricted dispersal abilities, such as Rhinocryptids [11, 30]. Therefore, the proximity among forest patches (quantified using the CONTIG index) may be directly related to dispersal probability, as it reduces the resistance of contrasting matrices (e.g., a grassland). While disturbed habitat can offer complementary resources to *D. gliroides* (e.g., fruits from shade-intolerant plants; 39), also lack of certain key elements such as tree cavities that are central for nesting in *D. gliroides* and other bird species [54, 55], which may compromise their reproductive success [16, 56]. Thus, the limited availability of nesting sites in disturbed habitats may be related to lower abundances that we detected in this study. Despite *D. gliroides* is able to nest outside tree cavities when are scarce or absent [57], they are negatively affected by the lack of habitat complexity [36, 40] in disturbed habitats.

Besides tree cavities, *D. gliroides* is often associated with the native bamboo *Chusquea quila* [58], a major





component of its nests [59, 60]. Bamboo cover is also an important habitat feature for understory birds at these forests [56]. Therefore, the occurrence and abundance of *D. gliroides* across landscapes with different disturbance levels may depend on a multi-scale process, in which local vegetation structure and landscape configuration are relevant to explain the occurrence patterns observed in this study. A mild local disturbance may increase the availability of food resources, with a positive effect on *D. gliroides* occurrence and abundance [41, 61]. However, landscape-level processes are expected to have the opposite effect. For instance, if a fragmented landscape goes into an attrition process (i.e., forest fragments get smaller

and more isolated in time), it may outweigh the positive effects of increased resource availability. The challenging task in this regard, is to determine the ecological thresholds of landscape configuration that represent an inflection point from positive to negative effects on biodiversity [17, 62]. As a habitat become fragmented, positive effects are mainly related to local-scale processes that result in more diverse and abundant resources as a consequence of increased habitat heterogeneity (e.g., 41). On the contrary, negative effects are usually related to landscape-scale processes [63], mainly driven by edge-effects and the loss of functional connectivity among fragments [9, 12, 28, 36].

Effective conservation actions of forest-dependent animals, such as *Dromiciops gliroides*, require an integral approach to conserve species by conserving their habitats and interactions. Thus, landscape configuration should also be considered in conservation and management plans, promoting the restoration of functional connectivity among forest remnants. Due to its habitat requirements, *D. gliroides* is considered as an umbrella species of the Valdivian rainforests [42]. Therefore, managing the extant habitat remnants to fulfill *D. gliroides*' requirements will also protect other forest species (e.g., Rhinocryptid birds) that also benefit from forest contiguity and connectivity [11, 15, 30]. Also, it is important to stop deforestation as it may be leading to a non-return point for many forest-dependent species.

Conclusions

Landscape configuration matters. The abundance of the arboreal marsupial *Dromiciops gliroides* is affected by habitat contiguity, while forest proportion in the landscape had a marginal effect on its occurrence. As *D. gliroides* is a forest-dependent species, it cannot disperse through non-forested habitats. Therefore, maintaining the contiguity among forest fragments is the most relevant management practice to guarantee its long-term persistence. We urge to rethink native forest conservation and management policies, aimed to improve habitat conditions for native fauna by adequately managing landscape configuration to connect forest remnants.

Abbreviations

PLAND: % Of native forest within the landscape; NP: Number of patches; CONTIG: Contiguity index; ENN: Euclidean distance to the nearest neighbor; CONNECT: Connectivity index; BLMM: Bayesian Linear Mixed Models.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s40693-022-00107-9>.

Additional file 1: Table S1. Geographic coordinates and habitat condition of the sampled landscapes. **Figure S1.** Location of the sampling sites along the Valdivian rainforest, indicating the habitat condition of each site. **Table S2.** Mean values of landscape configuration metrics for each sampled landscape. **Table S3.** Detailed results of the Bayesian Linear Mixed Model fitted for *Dromiciops gliroides* occurrence and its relationship with landscape metrics. **Table S4.** Detailed results of the Bayesian Linear Mixed Model fitted for *Dromiciops gliroides* abundance and its relationship with landscape metrics.

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Data availability

R code and original data are freely available from the figshare digital repository: <https://doi.org/10.6084/m9.figshare.16649386>

Code availability

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Authors' contributions

F.E.F. and G.B.R.G. conceived the ideas and designed the methodology. G.B.R.G. and F.E.F. collected field data. V.P.F. and F.E.F. processed field data. V.P.F., D.A.M.M., G.J.C.V. and F.E.F. analyzed data. F.E.F. led manuscript writing with contributions of V.P.F., G.B.R.G., and G.J.C.V. The authors read and approved the final manuscript.

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Availability of data and materials

Figshare digital repository: <https://doi.org/10.6084/m9.figshare.16649386>

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

None.

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