

Intermediate levels of wood extraction may facilitate coexistence of an endemic arboreal marsupial and Indigenous communities

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Abstract Land-use change is a major driver of biodiversity loss. Large-scale disturbances such as habitat loss, fragmentation and degradation are known to have negative consequences for native biota, but the effects of small-scale disturbances such as selective logging are less well known. We compared three sites with different regimes of selective logging performed by Indigenous communities in the South American temperate rainforest, to assess effects on the density and habitat selection patterns of the Near Threatened endemic arboreal marsupial *Dromiciops gliroides*. We used structured interviews to identify patterns of wood extraction, which was 0.22–2.55 m³ per ha per year. In the less disturbed site only two tree species were logged, in the intermediately disturbed sites eight species were logged at low intensity, and in the most disturbed site seven species were logged intensively. The site with intermediate disturbance had the highest fleshy-fruited plant diversity and fruit biomass values as a result of the proliferation of shade-intolerant plants. This site also had the highest density of *D. gliroides*. These findings are consistent with Connell's intermediate disturbance hypothesis, suggesting that coexistence of people with nature is possible if wood extraction volumes are moderate, increasing plant diversity. Indigenous communities have sustainably used natural resources for centuries, but current rates of land-use change are becoming a significant threat to both them and their natural resources.

Keywords Chile, *Dromiciops gliroides*, habitat selection, Indigenous community, intermediate disturbance hypothesis, sustainability, temperate rainforest, wood extraction

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Introduction

Land-use change is a major driver of biodiversity loss (Chapin et al., 2000). As a consequence of human activities, natural habitats have been fragmented and degraded, posing a major threat to wildlife through marked reductions in habitat quantity and quality (Didham et al., 2012; Tschardt et al., 2012; Haddad et al., 2015). Developments such as forestry plantations, croplands, cattle-raising grasslands and urban areas have encroached on natural habitats, posing a major threat to wildlife (Echeverría et al., 2006; Newbold et al., 2015). Although habitat disturbance is usually associated with biodiversity loss, intermediate levels of disturbance may be beneficial, as was demonstrated by Connell (1978), who proposed the intermediate disturbance hypothesis. The proposal that high diversity can be maintained by intermediate disturbance events that limit strong competitors and allow more species to coexist has been widely examined. In forest ecosystems, intermediate disturbance events are usually associated with forest gaps that allow shade-intolerant understorey plants to thrive (Dalling & Hubbell, 2002). These shade-intolerant plants usually have flowers and fruits that are important food resources for native animals (Fontúrbel et al., 2017).

Historically, Indigenous communities have obtained natural resources from native forests (Smith-Ramirez, 2007), but these traditional uses are being replaced by large scale land-use changes, resulting in habitat fragmentation and degradation, such as in the temperate rainforest of southern South America (Echeverría et al., 2006). Those forests are a biodiversity hotspot with high levels of endemism (Myers et al., 2000) and plant–animal mutualism. They are being affected by large-scale deforestation and subsequent replacement by other land uses (mainly forestry plantations; Nahuelhual et al., 2012) and by small-scale disturbance associated with selective logging (Smith-Ramirez, 2007). Selective logging causes less marked effects than habitat loss and fragmentation but can reduce habitat quality by removing large trees that provide resources such as nesting cavities (Lindenmayer et al., 2008) and habitat for other species (Tejo & Fontúrbel, 2019), ultimately altering forest composition and ecological processes (Asner et al., 2005).

Forest-dependent animals are good models for examining the effects of disturbance from selective logging (Castellón & Sieving, 2006). A charismatic example is

the monito del monte *Dromiciops gliroides*, a small arboreal marsupial (Hershkovitz, 1999) categorized as Near Threatened on the IUCN Red List (Martin et al., 2015). Although *D. gliroides* depends on forest habitats (Fontúrbel & Jiménez, 2011), it is tolerant of disturbance and capable of persisting in disturbed habitats if some structural features are retained (Salazar & Fontúrbel, 2016). Although the effects of large-scale disturbance on this species have been assessed (Fontúrbel et al., 2010, 2015; Uribe et al., 2017), the potential consequences of the small-scale disturbance associated with selective logging are poorly known. As fleshy fruits are an important component of the diet of *D. gliroides*, their abundance can influence its occurrence, abundance and behaviour (García et al., 2009; Morales et al., 2012; Tiribelli et al., 2017). Fleshy fruit abundance may increase in selectively logged forest, where light reaching the understorey results in the proliferation of shade-intolerant plants (Fontúrbel et al., 2017), a factor that could explain the presence of *D. gliroides* in disturbed habitats (Salazar & Fontúrbel, 2016). Forest-dependent species also coexist with Indigenous communities that traditionally extract native wood for their livelihoods (Smith-Ramirez, 2007).

To examine this issue, we compared the density and occupancy of *D. gliroides* in three native forest stands experiencing different intensities of selective logging. Following Connell's (1978), we hypothesized that the density of *D. gliroides* would be higher at an intermediate logging intensity as a result of a higher diversity of fleshy-fruited plants, which are associated with *D. gliroides* occupancy.

Study area and species

We conducted this study in Pucatrihue in southern Chile, at 150 m altitude (Fig. 1). The mean annual temperature is 12 °C and mean total annual precipitation is 2,500 mm. We defined three study sites, 1, 2 and 3, separated by 1–4 km to ensure independence, as the maximum movement range of *D. gliroides* is c. 500 m (Fontúrbel et al., 2010). Pucatrihue is a rural locality inhabited by Indigenous communities of the Huilliche branch of the Mapuche ethnic group. The Huilliche people (meaning 'people from the south' in Mapudungun) traditionally exploit marine resources for food but also extract wood from the surrounding native forests. Given the low population density of the area, most of the wood extraction is for subsistence.

Dromiciops gliroides is a small arboreal marsupial, endemic to the temperate rainforests of southern South America, the only extant species of the order Microbiotheria, which is closely related to the Australian marsupials (Hershkovitz, 1999). D'Elia et al. (2016) proposed there are three *Dromiciops* species, but this has been refuted based on morphological and genetic evidence (Valladares-Gomez et al., 2017; Martin, 2018; Suárez-Villota et al., 2018). *Dromiciops gliroides* is

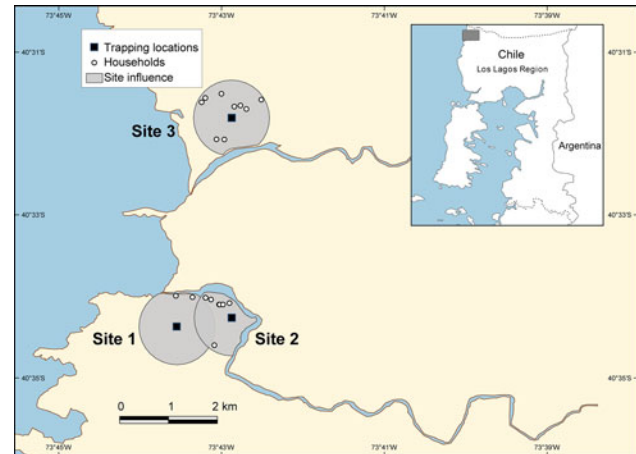


FIG. 1 Location of study sites 1, 2 and 3 in the temperate rainforest region of Pucatrihue, southern Chile, indicating the trapping locations, area of influence of each trapping location, and households where we interviewed Indigenous people regarding their use of the forest.

one of the few hibernating marsupials of South America (Hadj-Moussa et al., 2016), and a seed dispersal agent for at least 16 native plant species (Amico et al., 2009). Although formerly considered to be restricted to old-growth forests (Hershkovitz, 1999), it also occurs in secondary forests (Fontúrbel et al., 2010) and abandoned exotic plantations (Fontúrbel et al., 2014; Uribe et al., 2017). Despite being tolerant of habitat disturbance, *D. gliroides* depends on habitat structure and heterogeneity (Salazar & Fontúrbel, 2016), and feeds on fleshy fruits (its primary food source) and animal protein (invertebrates and eggs; Cortés et al., 2011).

Methods

Habitat characterization

At each trapping location we measured per cent canopy cover, with a spherical crown densiometer (as this variable is associated with occurrence of *D. gliroides*; Salazar & Fontúrbel, 2016), plant diversity (using the Shannon entropy index, H' ; Jost, 2006) by counting individuals of all plant species within a 2.5 m radius, and quantified the number of fleshy fruits per plant and estimated their biomass from a sample of 10–20 ripe fruits of each species (Fontúrbel & Medel, 2017). From the latter, we estimated fruit biomass density and diversity, and the diversity of fleshy-fruited plants, using H' (Goenster et al., 2011). As there are no meteorological stations near the study site, we obtained daily temperature and precipitation records from meteoblue (2016) and YR (2016), averaging the values from the two sources. We selected these sources because of their high data resolution and precision.

Wood extraction and use assessment

As selective logging is the main disturbance in the study area, we conducted an assessment of how local people extract and use native wood from each of the three survey areas. We defined a 700-m buffer of influence around each area so as to include all households involved in local wood extraction. We used structured interviews (Amare et al., 2017) to assess which tree species were logged, and the approximate wood volume extracted. Respondents were assured anonymity, and no personal data or information other than wood use and extraction were stored or analysed. Interviews were limited to permanent Pucatrihue residents and were conducted by HGA. We interviewed only the head of the household, asking about the family's economic activities, household characteristics, land ownership and wood use (Cinner et al., 2010). We used these data to estimate how often tree species were logged and the wood volume extracted.

Trapping

We conducted live trapping surveys at the three sites. As *D. gliroides* is an arboreal marsupial, we used custom-made wire-mesh traps (26 × 13 × 13 cm) placed 1.5–2.5 m above the ground, baited with fresh banana slices (Fontúrbel, 2010). At each site, we set 40 traps in an 8 × 5 array with 10 m between traps. We opened traps at 19.00 and checked them at 7.30 the next day. We measured, weighed and sexed all captured individuals, and marked them using fur cuts in unique patterns, for identifying any recaptures, and released them in the capture location. Live trapping was conducted during November 2015–April 2016, the time of year during which *D. gliroides* is most active (Fontúrbel et al., 2014). We operated traps for 4–5 consecutive nights bimonthly, giving a total of 1,680 trap-nights.

Data analysis

We used a non-parametric multivariate analysis of variance (MANOVA) using the *adonis* function of the *vegan* package (Oksanen et al., 2013) in R 3.6 (R Development Core Team, 2019) to assess habitat differences between the three sites. We used canopy cover, plant diversity, fruit biomass, fruit biomass diversity, and diversity of fleshy-fruited plants as the response variables, and site as a factor. As we found significant differences, we conducted individual ANOVA tests for each response variable to examine differences among sites. We used factor analysis to describe the variability among the five response variables. Data variability comprises communality (variability explained by linear combinations of potential factors) and uniqueness (variability not explained by these linear combinations). We performed factor analysis using the function *factanal* in R, with two factors, regression

scores, and a Promax rotation (Long & Teeter, 2019). We used a principal component analysis to visualize differences. We compared plant species composition among sites using a non-parametric analysis of similarities (ANOSIM; Clarke, 1993) with a Bray Curtis similarity measure and 9,999 permutations to estimate significance. We visually represented differences using non-metric multidimensional scaling (nMDS) (Fontúrbel & Jiménez, 2014). We used a Bray Curtis similarity measure for nMDS and optimized the result to maximize the variance explained by the two components. We estimated nMDS components using the function *metaMDS* in the package *vegan* in R (Oksanen et al., 2013).

We used capture–recapture to estimate *D. gliroides* abundance and density at the three sites (Fontúrbel et al., 2010, 2012). As this marsupial has a mean home range of 1.6 ha (Fontúrbel et al., 2012), we assumed a closed population model; no individuals were recaptured at a different site from where they were originally captured. As *D. gliroides* populations may extend beyond the area covered by the trap arrays, we estimated abundance using a reversible jump algorithm in a Monte Carlo Markov chain, which is able to simulate individual distributions over undefined surfaces (Green, 1995). We performed abundance estimations using the package *multimark* (McClintock, 2015; McClintock, 2019) in R. To estimate population densities, we calculated effective sampling areas using the area of the trap array plus a buffer corresponding to the mean recapture distance (Parmenter et al., 2003). We then calculated population densities by dividing the estimated abundance by the effective sampling area (following Parmenter et al., 2003).

We used occupancy models to assess habitat selection patterns (MacKenzie et al., 2002). Occupancy models are a useful approach to estimate a species' distribution, by taking detection probability into account and reducing the probability of obtaining false negatives (Royle, 2006). We used the R package *unmarked* (Fiske & Chandler, 2011) to estimate occupancy models. Firstly, we assessed correlation among all climate and habitat variables, to discard any highly correlated variables ($r \geq 4$). Then, we used model-based recursive partitioning (Zelleis et al., 2008) to perform a selection process. This method is based on multivariate recursive partitioning (Cook & Goldman, 1984), which is built upon a parametric regression model. The advantages of this approach are the ease with which the results can be interpreted and the identification of those variables causing model distortion (Zelleis et al., 2008; Strobl et al., 2009). We conducted model-based recursive partitioning using the R package *partykit* (Hothorn et al., 2006; Zelleis et al., 2008), using a generalized linear model (GLM). We included the densities of all plant species, and retained plant diversity, biomass diversity and fruiting plant diversity in all models as we consider them fundamental for the feeding and forest structure preferences of *D. gliroides*, to reduce the variable subset and keep only those significant

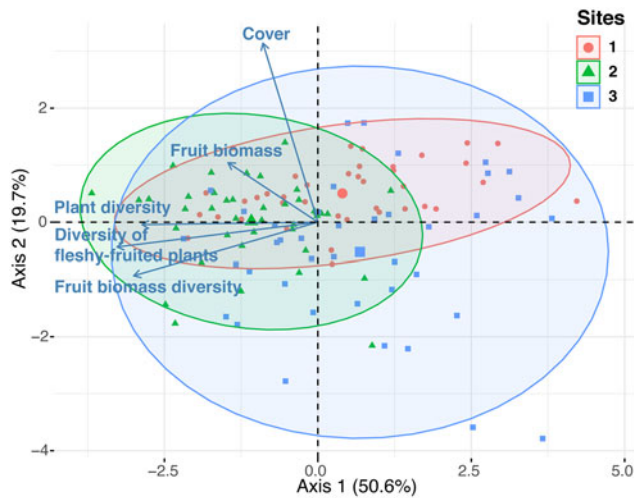


FIG. 2 Comparison of habitat characteristics of *Dromiciops gliroides* among the three study sites (1–3; Fig. 1) using a principal component analysis. Ellipses depict 95% confidence intervals for each habitat type, and arrows represent the five measured variables.

for *D. gliroides* habitat selection (Zelleis et al., 2008). We fitted 25 potential occupancy models (Supplementary Material 1). After removing the non-convergent models, the 17 candidate models were compared using the Akaike information criterion (AIC; Burnham & Anderson, 2002). We retained three models within the $\Delta\text{AIC} \leq 5$ subset (representing a cumulative model weight of 0.95). We plotted occupancy probabilities (ψ) and the 95% confidence intervals for each variable using the *R* package *ggplot2* (Wickham, 2016).

Results

We found significant differences in habitat characteristics among the three sites (non-parametric MANOVA $F_{2,117} = 13.67$, $P < 0.001$; Fig. 2), which were explained by significant variations in canopy cover (Supplementary Fig. 1a), fruit biomass (Supplementary Fig. 1b), fruiting plant diversity (Supplementary Fig. 1c) and fruit biomass diversity (Supplementary Fig. 1d), but not by variations in plant diversity (Supplementary Fig. 1e). Site 1 had a more closed canopy than the other sites. Site 2 had some canopy openings and the highest fruit biomass, plant diversity, fruiting plant diversity and fruit biomass diversity (Table 1). Site 3 had a relatively open canopy, and the lowest fruit biomass,

TABLE 1 Per cent canopy cover, fruit biomass, plant diversity, fruiting plant diversity and fruit biomass diversity at the three study sites (Fig. 1). All figures are mean \pm SE.

Site	% canopy cover	Fruit biomass (g/m ²)	Plant diversity (H')	Fruiting plant diversity (H')	Fruit biomass diversity (H')
1	88.5 \pm 0.9	280.87 \pm 30.37	1.72 \pm 0.04	1.18 \pm 0.06	0.82 \pm 0.07
2	85.2 \pm 1.7	376.97 \pm 28.51	1.84 \pm 0.03	1.22 \pm 0.05	1.22 \pm 0.05
3	74.6 \pm 2.6	209.51 \pm 40.06	1.77 \pm 0.05	1.10 \pm 0.07	0.81 \pm 0.08

TABLE 2 Factor analysis results for the five habitat variables (Table 1, see text for details; factor correlation = -0.462 ; model goodness of fit: $\chi^2 = 2.14$, $\text{df} = 1$, $P = 0.143$). Community is the variability explained by linear combinations of the five variables, and uniqueness is the variability not explained by these linear combinations.

Variable	Community	Uniqueness
% canopy cover	0.037	0.966
Fruit biomass	0.294	0.764
Plant diversity	0.320	0.532
Fruit biomass diversity	0.802	0.138
Fruiting plant diversity	0.662	0.033

fruiting plant diversity and fruit biomass diversity (Supplementary Fig. 1). Factor analysis showed that these five variables made differential contributions to the variability between the three sites (Table 2). Plant species composition was significantly different among the three sites (ANOSIM $R = 0.374$, $P = 0.001$; Fig. 3).

We identified 18 households whose occupants were extracting wood: two, seven and nine households within the influence of sites 1, 2 and 3, respectively (Fig. 1). There were wood extraction activities at all three sites, but with a large variability in intensity and number of tree species used (Table 3). Wood extraction was lowest in site 1 (a mean of 0.22 m³/ha/year; three species logged), intermediate in site 2 (0.33 m³/ha/year; eight species logged) and highest in site 3 (2.55 m³/ha/year; nine species logged). The tree species logged in site 1 were also the most commonly logged species in sites 2 and 3, but extraction intensity varied between sites (Table 3).

In the live trapping survey, we captured *D. gliroides* 36 times, corresponding to 28 individuals (recapture rate was 33%). We estimated a mean abundance of $8.26 \pm \text{SE } 0.01$, $35.29 \pm \text{SE } 0.13$ and $13.38 \pm \text{SE } 0.07$ at sites 1, 2 and 3, respectively, and mean population densities of $8.10 \pm \text{SE } 3.83$, $27.89 \pm \text{SE } 11.59$, and $13.57 \pm \text{SE } 6.46$ individuals/ha, respectively.

We captured *D. gliroides* at 29 of the 120 trap locations. The recursive partitioning model indicated that the trees *Luma apiculata* and *Drimys winteri* were significantly associated with detection of *D. gliroides* (Supplementary Fig. 2). The density of these two plant species along with the estimated diversity indices and the climatic variables produced 16 convergent models, from which we retained three models based on their AIC ranking (Table 4). Detection probability did not vary with temperature (Fig. 4a), but increased with

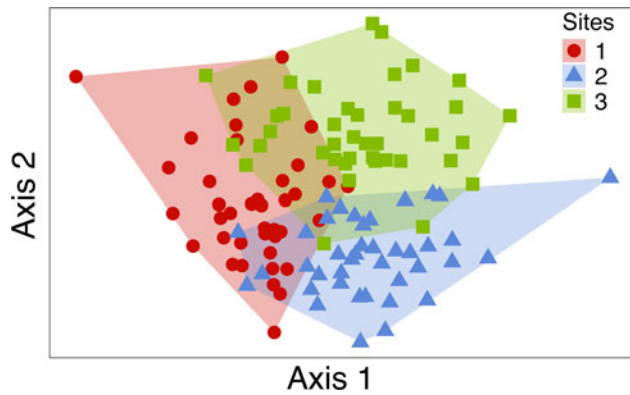


FIG. 3 Plant composition differences among the three study sites illustrated using a non-metric multidimensional scaling ordination (stress = 0.125).

increased precipitation (Fig. 4b) and decreased with increased fruit biomass (Fig. 4c). Occupancy increased with density of *L. apiculata* (Fig. 4d) and *D. winteri* (Fig. 4e), fruit biomass diversity (Fig. 4f) and fruiting tree diversity (Fig. 4g), but decreased with overall species diversity (Fig. 4h).

Discussion

The different intensities of selective logging at our three study sites could have been responsible for the habitat differences that influenced *D. gliroides* abundance and habitat selection. Differences in habitat factors between the three sites (canopy cover, fruit biomass, and fruiting plant and fruit biomass diversity) could be a result of the increasing level of small-scale wood extraction disturbance from sites 1 to 3, with site 2

having an intermediate level of disturbance. This would be consistent with the intermediate disturbance hypothesis (Connell, 1978), as *D. gliroides* was most abundant at site 2. Low levels of wood extraction can increase fruiting plant diversity, mainly as a result of the proliferation of shade-intolerant plant species (Fontúrbel et al., 2017) and the consequent increase in fruit biomass density and diversity.

Previous studies of the response of *D. gliroides* to habitat disturbance have focused on habitat fragmentation (Rodríguez-Cabal et al., 2007; Fontúrbel et al., 2010), degradation, and transformation by exotic plantations (Fontúrbel et al., 2014; Uribe et al., 2017), all of which are large-scale disturbances. As far as we are aware, this is the first study that explicitly assesses the responses of *D. gliroides* to different intensities of small-scale selective logging. For small-bodied arboreal animals such as *D. gliroides*, habitat structure plays a major role in determining occurrence, as they need a structurally complex habitat that provides movement pathways, nesting sites and shelter (Bro-Jørgensen, 2008). Unlike large-scale deforestation, selective logging does not have area or edge effects (Didham et al., 2012), but non-random tree removal (larger trees are usually logged first) alters characteristics (Asner et al., 2005) such as availability of nesting cavities (Reem & Löhmus, 2011). Nevertheless, low to medium levels of selective logging can create forest gaps, allowing shade-intolerant plants to thrive that would not usually grow beneath a dense canopy (Dalling & Hubbell, 2002). These shade-intolerant plants often have large flowers and fruits, an important food source for frugivores (Fontúrbel et al., 2017).

TABLE 3 Wood use and extraction patterns by local people at the three sites. Per cent indicates the number of households responding affirmatively to each question. Wood extraction volumes were calculated based on data provided by the respondents.

	Site 1 (2 households)	Site 2 (7 households)	Site 3 (9 households)
Firewood origin and sale			
Logging own land (%)	100.0	28.6	100.0
Purchased elsewhere (%)	0.0	57.1	0.0
Collection of fallen wood (%)	0.0	14.3	0.0
Firewood sale (%)	100.0	14.3	33.3
Tree species logged for firewood			
<i>Amomyrtus luma</i> (%)	100.0	85.7	77.8
<i>Aextoxicon punctatum</i> (%)	100.0	42.9	44.4
<i>Eucryphia cordifolia</i> (%)	100.0	42.9	33.3
<i>Laureliopsis philippiana</i> (%)	0.0	28.6	66.7
<i>Drimys winteri</i> (%)	0.0	14.3	55.6
<i>Nothofagus dombeyi</i> (%)	0.0	0.0	55.6
<i>Tepualia stipularis</i> (%)	0.0	0.0	33.3
<i>Amomyrtus meli</i> (%)	0.0	14.3	11.1
<i>Gevuina avellana</i> (%)	0.0	14.3	11.1
Other	0.0	14.3	0.0
Firewood volume extracted			
Annual total extraction (m ³)	34.0	51.5	392.0
Mean extraction (m ³ /ha/year)	0.2	0.3	2.6

TABLE 4 The three top occupancy models (for all 25 models, see Supplementary Material 1) fitted for the detection of *Dromiciops gliroides*, representing a 95% cumulative AIC weight ($c\omega$ AIC).

Model ¹	AIC	Δ AIC	ω AIC	$c\omega$ AIC	R^2
$\psi(\text{div} + \text{fpdiv} + \text{biom} + \text{Lapic} + \text{Dwint}), d(\text{pp} + \text{ffbm})$	182.8	0.00	0.75	0.75	0.35
$\psi(\text{div} + \text{fpdiv} + \text{biom} + \text{Lapic} + \text{Dwint}), d(\text{pp} + \text{temp})$	186.9	4.04	0.10	0.85	0.32
$\psi(\text{div} + \text{fpdiv} + \text{biom} + \text{Lapic} + \text{Dwint}), d(\text{ffbm})$	187.0	4.15	0.10	0.95	0.30

¹Occupancy (ψ) variables: div, plant species diversity; fpdiv, fleshy-fruited plant diversity; biom, dry fruit biomass; Lapic, *Luma apiculata* density; Dwint, *Drimys winteri* density. Detection (d) variables: pp, precipitation; temp, temperature; ffbm, fleshy fruit biomass density.

Our estimates of the density of *D. gliroides* are similar to those for other locations in southern Chile (Celis-Diez et al., 2012; Fontúrbel et al., 2012). The density at site 1 is similar to that on Chiloé island (Celis-Diez et al., 2012), and the densities at sites 2 and 3 are similar to those at continental sites in Chile and Argentina (Fontúrbel et al., 2012; Balazote-Oliver et al., 2017). Differences in density between sites could be related to differences in plant species composition, which may be influencing habitat selection. For example, common shade-intolerant species such as *Aristotelia chilensis* and *Rhaphithamnus spinosus* were absent from site 1 but were

abundant at sites 2 and 3. *Gevuina avellana*, a shade-tolerant species, was present only at site 1. Such plant species turnover is consistent with a light-incidence gradient as a result of habitat disturbance (Gianoli et al., 2010; Fontúrbel et al., 2017), and *D. gliroides* seems to be responding to these changes. The low density at the least disturbed site could be related to the lower diversity of fleshy-fruited plants (there were few shade-tolerant plant species with fleshy fruits), with individuals needing to move longer distances to forage (Salazar & Fontúrbel, 2016; Fontúrbel et al., 2017).

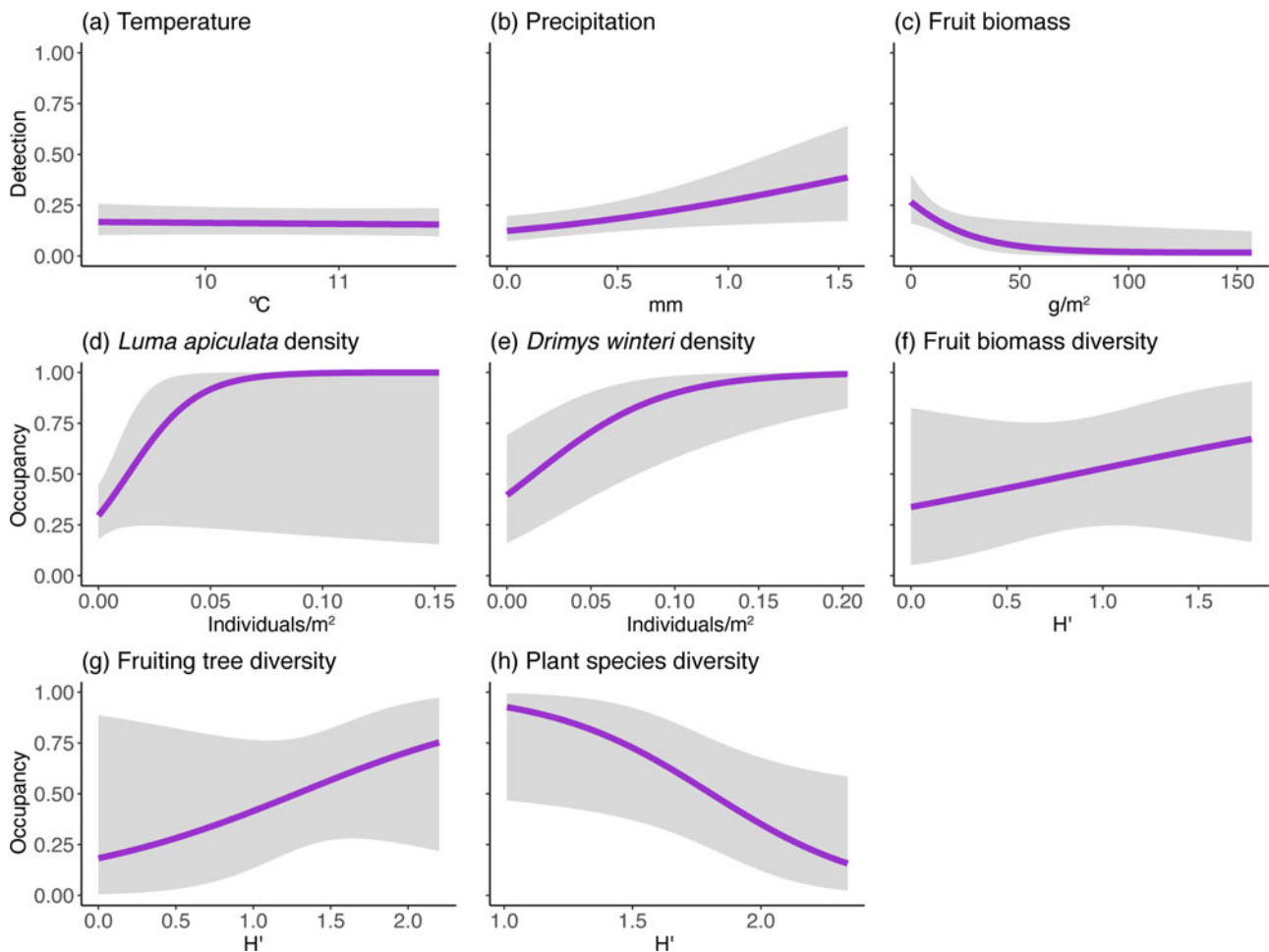


FIG. 4 The relationship between detection of *D. gliroides* and (a) temperature, (b) precipitation and (c) fruit biomass, and occupancy and density of the trees *Luma apiculata* (d) and *Drimys winteri* (e), and fruit biomass (f), fruiting tree (g) and plant species (h) diversity. Mean values and their 95% confidence intervals are presented.

As expected, given its frugivorous habit (Amico et al., 2009), the probability of *D. gliroides* occupancy increased with plant species diversity and fleshy-fruited plant species diversity. The availability of fleshy fruits increases after disturbance following establishment of fast-growing secondary vegetation (Greenberg et al., 2011). Despite being considered an old-growth forest species (Hershkovitz, 1999), *D. gliroides* selects secondary forests with a high diversity of fleshy-fruited plants. The presence of the native bamboo *Chusquea quila* and hemiparasitic mistletoe *Tristerix corymbosus* were the best predictors of the occurrence of *D. gliroides* in a fragmented landscape (García et al., 2009; Rodríguez-Cabal & Branch, 2011), but small-scale disturbance such as selective logging, fruit diversity and abundance appear to influence habitat selection. The fact that the densities of *L. apiculata* and *D. winteri*, common species of secondary forests, had significant effects on the probability of occupancy, indicates that *D. gliroides* is able to use secondary forest, and even abandoned exotic plantations, as long as there is some landscape heterogeneity to provide nesting sites (Salazar & Fontúrbel, 2016).

The Indigenous community is a crucial part of this story. Their houses, tools and fishing boats are constructed mainly from the wood of native species, and wood from native trees is used for heating and cooking (Smith-Ramirez, 2007). These communities have inhabited this area for centuries, using these natural resources sustainably (Herrmann, 2006; Molares & Ladio, 2012). Our findings show that small-scale local wood extraction and biodiversity conservation can coexist, with intermediate levels of disturbance producing beneficial conditions for *D. gliroides*. This could also be the case for other forest-dependent species with habitat needs similar to those of *D. gliroides* (e.g. understory birds; Fontúrbel & Jiménez, 2011). However, any increase in wood extraction could threaten *D. gliroides* and other native animals. In southern Chile, mean wood extraction volumes from old-growth forests are 2.5–8.5 m³/ha/year, and in secondary forests 7.5–15.0 m³/ha/year (Nahuelhual et al., 2007), well above the wood volumes extracted from our study area. Extraction of wood from site 3, where we recorded the highest extraction rate, increased during 2017–2019 as economic activities related to tourism increased. Approximately 60% of the native forest in site 3 was cleared during April 2018–January 2019 (F.E. Fontúrbel, unpubl. data).

Despite being a forest-dependent species, *D. gliroides* appears to be able to persist in logged habitats if wood extraction volumes are low, and intermediate disturbance could result in an increase in the species' density in response to the increase of fleshy-fruited plant diversity. Responses to small-scale disturbance are important for understanding how biodiversity is responding and adapting to a changing world (Armesto et al., 2010). Indigenous communities play a key role in conserving native forests, but increasing extraction pressure is harming this balance between people and nature. The evidence presented here could be used as a

guideline to establish a wood extraction quota, to protect the extant remnants of the declining temperate rainforests of Chile and its many endemic species, and the sustainable use of these forests by Indigenous communities.

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Author contributions Study design: HG-A, MS, JMM-B, JCS; field-work: HG-A, FEF; social survey: HG-A, AP; data analysis: HG-A, MS, FEF; writing: HG-A, FEF.

Conflicts of interest None.

Ethical standards Animal trapping and handling followed the guidelines of the American Society of Mammalogists (Sikes et al., 2011), captures were authorized by the Chilean Agriculture and Livestock Bureau (licence 302/2015 to FEF and HG-A), interviews with people were approved by the ethics committee of the Instituto Internacional en Conservación y Manejo de Vida Silvestre (FCTM-ICOMVIS-CGA-TA-091-2014), and this research otherwise abided by the *Oryx* guidelines on ethical standards.

Data availability Data for this article are available at doi.org/10.6084/m9.figshare.11451267

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