



## Regional-scale variation on *Dromiciops gliroides* occurrence, abundance, and activity patterns along a habitat disturbance gradient

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Habitat structure may have a significant influence on the occurrence, abundance, and activity patterns of forest mammals. However, anthropogenic habitat disturbance changes habitat structure, which may alter those patterns of activity. We assessed occurrence, relative abundance, and activity patterns of *Dromiciops gliroides*, an arboreal marsupial endemic to the temperate rainforests of southern South America, contrasting four forest conditions at a regional scale: old-growth, second-growth, and logged forests, and abandoned exotic plantations. We conducted a camera-trap assessment in two consecutive austral summers across most of the Chilean range of *D. gliroides*, and compared habitat structure along a disturbance gradient. All structural features assessed differed among forest conditions. *Dromiciops gliroides* was present in all forest conditions, but its abundance decreased and activity got narrower as disturbance increased, being significantly lower in the exotic plantations. Activity patterns were variable among forest conditions and months, and were significantly more restricted temporally at exotic plantations. Although *D. gliroides* is tolerant to habitat disturbance, we show that structural alteration results in lower abundances and narrower activity patterns.

Key words: canopy cover, disturbance tolerance, habitat structure, nocturnal activity, population, selective logging

La estructura del hábitat ejerce un efecto importante sobre los patrones de presencia, abundancia y actividad de los mamíferos de bosque. Sin embargo, la perturbación antrópica puede alterar esos patrones al cambiar la estructura del hábitat. En este trabajo examinamos los patrones de presencia, abundancia relativa y actividad de *Dromiciops gliroides*, un marsupial arborícola endémico de los bosques lluviosos templados del sur de Sudamérica, comparando cuatro condiciones de bosque a escala regional: nativo maduro, secundario, talado, y plantaciones forestales exóticas. A tal fin, durante dos veranos australes, llevamos a cabo un monitoreo con trampas cámara a lo largo de este gradiente de perturbación, cubriendo casi la totalidad de la distribución de esta especie en Chile. Todas las características estructurales evaluadas difieren entre los distintos tipos de bosques estudiados. *Dromiciops gliroides* estuvo presente en todos los tipos de bosque, pero su abundancia y actividad disminuyeron conforme aumentó la perturbación, siendo significativamente menores en las plantaciones exóticas. Los patrones de actividad también variaron en función de las condiciones de tipo de bosque, así como también temporalmente (mes de estudio), siendo menores en las plantaciones exóticas. A pesar de que *D. gliroides* es tolerante a la perturbación del hábitat, nuestros resultados sugieren que una mayor alteración estructural del bosque resulta en menor abundancia y menor actividad de la especie.

Palabras clave: actividad nocturna, dosel arbóreo, estructura del hábitat, población, tala selectiva, tolerancia a perturbación

Occurrence, abundance, and activity patterns, of a given species are essential aspects of its ecology, reflecting physiological traits and ecological interactions, as well as the influence

of the local habitat and the surrounding landscape (Nupp and Swihart 1998; Gu and Swihart 2004; Tobler et al. 2009; Norris et al. 2010; Blake et al. 2012; Leuchtenberger et al. 2018). In

animals, these two parameters are determined by several factors, one of the most important of which is habitat structure (Myserud et al. 1999; Mancke and Gavin 2000; García et al. 2011; Albrecht et al. 2012). The combination of some important structural features such as canopy cover, tree density, and natural cavities (McElhinny et al. 2006) largely determines the availability of food resources, microclimate conditions, nesting sites, and movement pathways (McCoy and Bell 1991; Tews et al. 2004; Bro-Jørgensen 2008). Mammals, and particularly forest mammals, can respond to certain structural features by selecting specific plants or vegetation patches based on their structural features (Wiens 1989; Fedriani 2005), along with the availability, diversity, and aggregation of food resources (Morales et al. 2012; Fontúrbel et al. 2017). Those structural features can vary according to forest type, successional stage, and anthropogenic disturbance (Sala et al. 2000; Zenner 2005; Echeverría et al. 2007; Caviedes and Ibarra 2017). Thus, changes in habitat structure are likely to influence occurrence, abundance, and activity patterns (Kitchen et al. 2000; Asner et al. 2005; Martin and Realé 2008; Norris et al. 2010; Castaño-Villa et al. 2019a).

The temperate rainforests of southern South America are considered to be a biodiversity hotspot due to their high level of endemism (Myers et al. 2000; Mittermier et al. 2005), but due to anthropogenic impacts currently are among the most threatened ecoregions in the world. In Chile, this ecoregion extends from ca. 35°S to ca. 55°S. Despite their value for biodiversity, these rainforests are highly fragmented, degraded, and immersed within heterogeneous anthropogenic matrices as a result of different land uses, such as exotic tree plantations, agricultural crops, and livestock rising areas (Echeverría et al. 2006, 2007). Between 1975 and 2000, these human activities reduced the extent of native forest by 67% (Echeverría et al. 2006), and have resulted in substantial changes in forest composition and structure (Echeverría et al. 2007). Those changes can affect the occurrence, abundance, and activity, of forest-dependent small mammals, some species of which require dense forests with abundant woody debris, ferns, and bamboo (Patterson et al. 1990; Kelt 2000). Consequently, variation in mammal occurrence, abundance, and activity patterns, may occur as a consequence of habitat disturbance (Leuchtenberger et al. 2018). One iconic species of these forests is the monito del monte (*Dromiciops gliroides* Thomas 1894), a relict arboreal marsupial endemic to this habitat. As this marsupial is a forest-dependent species, it constitutes a good model to assess how forest disturbance will impact ecologically similar species (Fontúrbel and Jiménez 2011). However, our knowledge about responses to habitat disturbance by *D. gliroides* currently is fragmentary and limited to a few well-studied sites (Kelt 2000; Celis-Diez et al. 2012; Rodríguez-Cabal et al. 2013; Fontúrbel et al. 2014; Salazar and Fontúrbel 2016; Balazote-Oliver et al. 2017).

To gain insight into the effects of habitat disturbance on occurrence, abundance, and activity patterns, of *D. gliroides*, we conducted a 2-year camera-trap assessment along a habitat disturbance gradient at a regional scale, covering most of its distributional range in Chile. We hypothesized that anthropogenic

disturbance reduces habitat structure complexity, which decreases *D. gliroides* occurrence and abundance, and narrows its activity breadth at disturbed sites, compared to less disturbed sites, which have a more complex habitat structure.

## MATERIALS AND METHODS

**Study sites.**—The study was carried out along a latitudinal gradient of approximately 450 km (from 37°S to 41°S), covering ca. 85% of the range of *D. gliroides* in Chile. We gathered occurrence and relative abundance data at 12 sites (Supplementary Data SD1 and SD2) corresponding to four different forest conditions (in increasing order of disturbance): (1) protected native forests (not disturbed for at least 100 years); (2) second-growth forest that had been subject to commercial logging, with secondary regeneration at least 20 years old; (3) native forest sites subject to selective tree removal (e.g., for cooking and heating, typically by local subsistence farmers); and (4) sites in which the native vegetation was replaced by exotic tree species (*Pinus radiata* or *Eucalyptus globulus*), planted 15–25 years ago and currently abandoned. Study sites selected presented similar elevation, temperature, and precipitation values (Supplementary Data SD2). Hereafter, we refer to these forest conditions as “native,” “second-growth,” “logged,” and “plantation,” respectively. We sampled three replicates for each forest condition, and collected data during two sampling periods: one during the 2017–2018 austral summer, and the second during the 2018–2019 austral summer (Supplementary Data SD3).

**Study species.**—The monito del monte (*D. gliroides*) is a nocturnal, arboreal marsupial, endemic to the temperate rainforests of southern South America (Hershkovitz 1999). It is the only living representative of the order Microbiotheria, one of the oldest lineages of the australidelphian marsupials (Meredith et al. 2008; Nilsson et al. 2010; Duchêne et al. 2018; Eldridge et al. 2019). Its distribution in Chile ranges from the Maule Region (35°S) to Palena Province (44°S) of the Los Lagos Region (Oda et al. 2019), and it is found both in the Coastal and Andes mountain ranges, as well as in the intermediate depression (Kelt and Martínez 1989). It is often found in old-growth forests dominated by southern beeches (*Nothofagus* spp.) with dense understory vegetation and native bamboo (*Chusquea* spp.—Patterson et al. 1990), but it also occurs in second-growth forest stands and abandoned exotic tree plantations (Kelt 2000; Fontúrbel et al. 2012, 2014; Salazar and Fontúrbel 2016; Uribe et al. 2017). *Dromiciops gliroides* hibernates during winter or food shortages (Bozinovic et al. 2004; Cortés et al. 2011) and is more active during the summer (Kelt and Martínez 1989; Aizen 2003). It is a generalist species, feeding mainly on fleshy fruits, but also on eggs, insects, and other invertebrates, as protein sources (Cortés et al. 2011). In addition, *D. gliroides* has an important ecological role as a seed disperser of at least 16 native plant species (Amico et al. 2009).

**Camera-trap monitoring.**—We monitored *D. gliroides* at the 12 study sites described above using camera traps during two austral summer seasons (mid-December through mid-April). Camera traps are an effective and low-cost approach to

wildlife monitoring, with almost no observer interference (e.g., Gompper et al. 2006; Fontúrbel et al. 2014, 2015; Burton et al. 2015; Sollmann 2018). Accordingly, we used 36 georeferenced (GPS error  $\leq 3$  m) Browning Strike Force HD Pro camera traps, operated in photographic mode. We installed each camera trap to a tree stem between 1 and 2 m above the ground. Cameras were randomly located within forest vegetation (i.e., suitable habitat for *D. gliroides*) at three points within each sampling site, and rotated monthly through the 4 months of each season. Cameras were located  $\geq 100$  m from each other, such that three cameras across 4 months monitored a total area of  $\sim 1$  ha (288 sampling points across both years, and 774,144 h of monitoring effort). We used the information collected by the camera traps to obtain *D. gliroides* occurrence, relative abundance, and activity data.

**Habitat structure assessment.**—We assessed seven structural habitat features known to be relevant to *D. gliroides* (previously standardized by Salazar and Fontúrbel 2016). We visually estimated the following structural features within a radius of 2.5 m of each camera trap: (1) canopy cover (%); (2) stem density (number of stems with diameter at breast height  $\geq 2$  cm); (3) shrub cover (%); and (4) bamboo (*Chusquea* spp.) cover (%). In addition, we counted: (5) number of fallen logs; (6) number of stumps; and (7) number of natural cavities in the trees. Cover estimates were made by the same person, using visual estimates and photographs, to minimize potential bias. Percentage estimates were rounded to the nearest percent.

**Statistical analyses.**—We applied multivariate analysis of variance (MANOVA) to simultaneously compare all structural features measured in the field across the four forest conditions. We then used generalized linear models (GLMs) with a Gaussian error distribution to compare structural features individually across forest conditions. As forest condition is a factor with four levels, we used model outputs to perform pairwise comparisons between forest conditions in order to facilitate result interpretation, using the “glht” function from the “multcomp” R package (Hothorn et al. 2008). Such comparisons allow calculation of estimates and *P*-values for pairs of factor levels within the model (i.e., a modern version of planned comparisons for GLM).

To visualize differences in habitat structure among forest conditions, we applied nonmetric multidimensional scaling (hereafter NMDS—Minchin 1987) to the seven habitat structure variables measured in the field and described above. We used the “metaMDS” function of the “vegan” R Package (Oksanen et al. 2013). This function performs an NMDS analysis and tries to find a stable solution after several random starts, providing an optimal NMDS configuration for two axes defined a priori; this procedure iterates several configurations to find the optimal solution for the number of axes defined, maximizing variance explained. We used a Bray–Curtis dissimilarity index to compare structural variables among forest conditions. We used centering and principal component rotation (Varimax) to optimize visualization. Ordination stress indicates how well the two-dimensional visualization represents the actual data (the lower the stress, the better fit).

Before analyzing occurrence and activity of *D. gliroides*, we filtered raw camera-trap data by using an independence interval

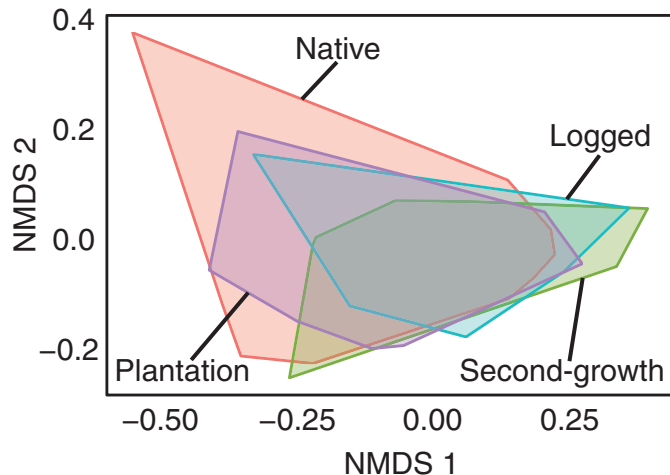
of 1 h between records to ensure independence. We used filtered camera-trap data as a proxy of the number of different individuals (i.e., relative abundance), as we are unable to distinguish them from the photos and to minimize the probability of counting the same individual twice (Oliveira-Santos et al. 2008; Fontúrbel et al. 2014). To compare abundance of *D. gliroides* (i.e., the number of independent camera-trap records) among forest conditions, we used generalized linear mixed-effect models (GLMMs) with a negative binomial error distribution (a discrete distribution, more accurate than Poisson distribution when there is data overdispersion) and a log link function. We included sampling site, sampling period (month), and year (first or second summer) as random factors to account for their variability (Zuur et al. 2009). For purposes of interpretation, we used the “glht” function to carry out pairwise comparisons among habitat condition levels, as explained above.

To assess activity patterns of *D. gliroides*, we first estimated *D. gliroides* activity density kernels for each habitat condition. For visualization purposes, we depicted activity patterns using circular plots (using data density as radius). We then compared *D. gliroides* activity kernels among habitats using the “compareCkern” function of the R package “activity.” This randomization test calculates the overlap between two activity kernels, calculating the  $\hat{\Delta}_5$  statistic as recommended by Ridout and Linkie (2009). This randomization procedure allows testing if the observed activity patterns are significantly different. We used 1,000 permutations for each pairwise comparison. All statistical analyses were conducted in R 3.6 (R Development Core Team 2019) using the packages “activity” (Rowcliffe et al. 2014; Rowcliffe 2019), “overlap” (Ridout and Linkie 2009), and “circular” (Agostinelli and Lund 2007).

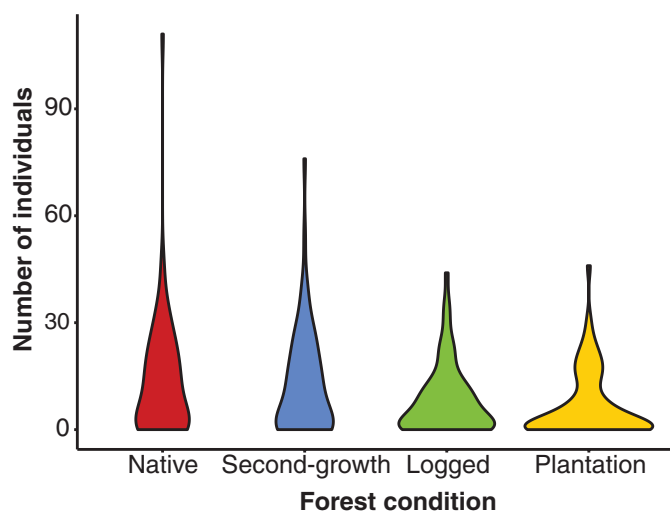
**Data availability.**—Original data associated with this article are available from the figshare digital repository: <https://doi.org/10.6084/m9.figshare.10312199>.

## RESULTS

Habitat structure was highly variable among forest conditions (MANOVA  $F = 7.77$ ,  $d.f. = 21$ ,  $P < 0.001$ ). We found significant differences in the seven structural features measured in the field. Canopy cover was different among all forest conditions except between native and second-growth forests (Supplementary Data SD4). Native and second-growth forests differed in stem density, bamboo cover, and natural cavities (Supplementary Data SD4). Logged forest stands differed in terms of canopy cover, stem density, shrub cover, bamboo cover, and the number of fallen logs. In contrast, abandoned exotic plantations differed from the other forest conditions in terms of bamboo cover and the number of logs, stumps, and natural cavities (Supplementary Data SD4). Visualizing those differences in the NMDS plot (Fig. 1) shows extensive overlap among the four forest conditions assessed. However, the overlap pattern observed suggests that each forest type has some unique habitat structure combinations. More interesting, perhaps, is the variation in area of these polygons (especially for native forests), which suggests differences in variability in habitat structure: in particular, native forests exhibit the greatest variation in forest



**Fig. 1.**—Nonmetric multidimensional scaling (NMDS) plot of the comparison of habitat structure among forest conditions (native forest, second-growth forest, logged forest, and exotic abandoned plantation). Ordination stress = 0.13.



**Fig. 2.**—*Dromiciops gliroides* relative abundance (expressed as individuals recorded by camera traps) among four different forest conditions.

conditions. Ordination stress was 0.13, which suggests that the NMDS ordination that we obtained explains well our habitat structure data (Supplementary Data SD5).

**Occurrence and relative abundance.**—We recorded *D. gliroides* at all sampling sites. We obtained 2,972 independent photographic records of *D. gliroides* across both sampling seasons ( $247.67 \pm 27.87$  records per sampling site). Of these, 990 records correspond to the native forest, 913 to the second-growth forest, 585 to the logged forests, and 484 to the abandoned exotic plantations (Fig. 2). Hence, assuming the number of images corresponds with the relative abundance of *D. gliroides*, the species decreases as the degree of disturbance increases (Fig. 2; Supplementary Data SD6), although this was significant only between logged forests and exotic plantations

**Table 1.**—Pairwise *Dromiciops gliroides* activity kernel comparison among (a) forest conditions, and (b) sampling months, using the  $\hat{\Delta}_5$  statistic. Bold *P*-values denote significant comparisons. Activity kernels for forest conditions and sampling months are depicted in Supplementary Data SD7 and SD8, respectively.

Comparison	$\hat{\Delta}_5$	<i>P</i> -value
(a) Habitat condition		
Logged–plantation	0.916	<b>0.042</b>
Logged–native	0.951	0.345
Logged–second-growth	0.969	0.825
Plantation–native	0.923	<b>0.018</b>
Plantation–second-growth	0.941	0.102
Native–second-growth	0.942	<b>0.037</b>
(b) Month		
December–January	0.908	0.054
January–February	0.909	<b>0.022</b>
February–March	0.914	<b>&lt;0.001</b>
March–April	0.938	0.363

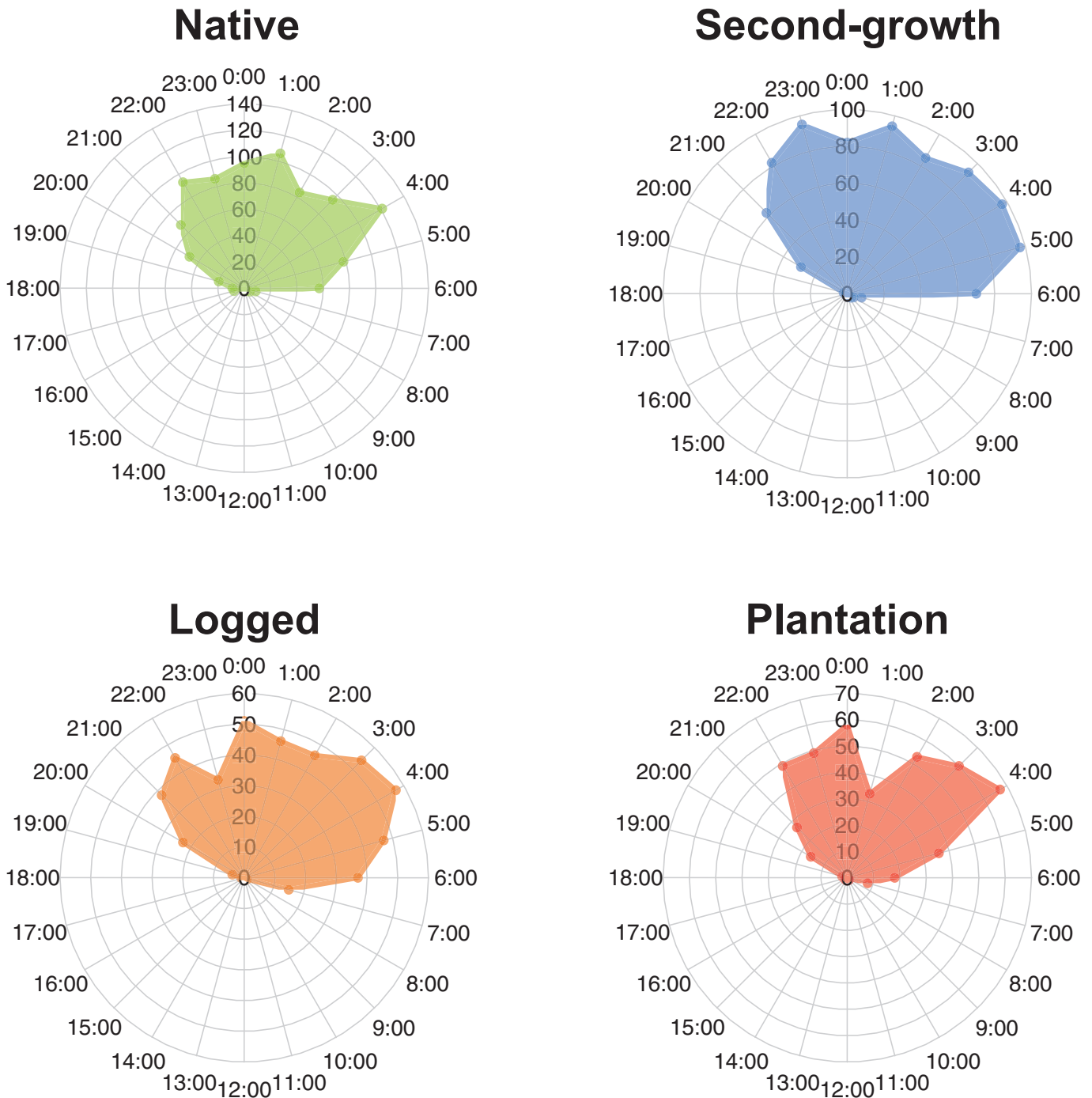
(GLMM estimate =  $-1.954 \pm 0.630$ ,  $P = 0.009$ ; details in Supplementary Data SD6).

**Activity.**—Activity of *D. gliroides* was entirely nocturnal and highly variable among forest conditions and sampling months (Table 1; Fig. 3). Overall, the activity period began at 2000 h and ended at 0600 h (Fig. 3). In the native forest, we observed a period of peak activity at 4:00 a.m., whereas in the second-growth forest, the period of peak activity extended from 4:00 to 5:00 a.m. On logged forests and exotic plantations, we observed periods of peak activity at 4:00 a.m., but recorded densities were much lower (Supplementary Data SD7). In pairwise comparisons of activity kernels (Supplementary Data SD8), we found significant differences between plantations and native forest, between native and second-growth forests, and between logged forests and plantations (Table 1a).

We also found substantial temporal variability in activity patterns, which was greatest in March (Fig. 4). In pairwise comparisons of sequential monthly activity kernels (Supplementary Data SD9), we found significant differences between January and February and between February and March (Table 1b).

## DISCUSSION

*Dromiciops gliroides* was present in all forest conditions, regardless of their differences in habitat. However, the number of records generally declined with disturbance, and was significantly lower in the most disturbed habitat, abandoned plantations of exotic trees (Fig. 2; Supplementary Data SD6). Historically, *D. gliroides* was considered an old-growth forest specialist (Hershkovitz 1999; Patterson and Rogers 2008), but it also occurs in second-growth forest (Kelt et al. 1994; Kelt 1996; Saavedra and Simonetti 2001; Fontúrbel et al. 2010) as well as in plantations of exotic trees (Fontúrbel et al. 2014, 2017; Uribe et al. 2017). This apparent tolerance to habitat disturbance may emerge from the increase in food resources available in disturbed habitats (Fontúrbel et al. 2017). The presence of some native vegetation with nesting sites seems to be a critical element for *D. gliroides* to tolerate disturbed habitats (Salazar and Fontúrbel 2016). Also, the presence of shade-intolerant fleshy-fruited

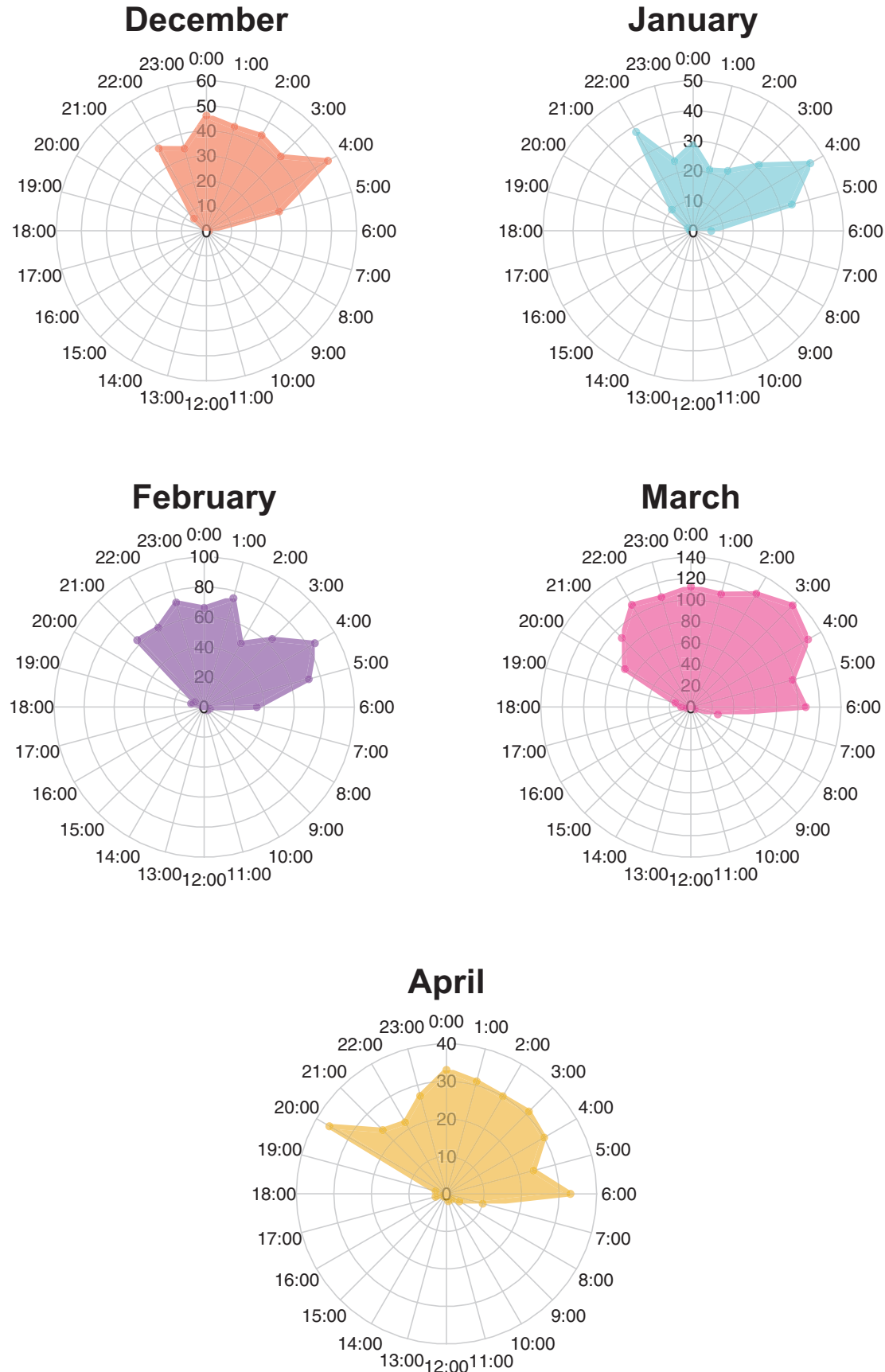


**Fig. 3.**—*Dromiciops gliroides* activity patterns among four different forest conditions. Each circular plot depicts a 24-h clock, with concentric circles that represent the number of individuals recorded by our camera traps at each 1-h time slot.

plants in disturbed habitat to some extent may compensate for structural differences (Fontúrbel et al. 2017). In old- or second-growth forests, a dense canopy may be favoring the presence of forest small mammals (Lindenmayer et al. 2008), and the presence of natural cavities (favored by the humidity and the closed canopy) increased the odds of occupancy by *D. gliroides* (Fontúrbel et al. 2012; Salazar and Fontúrbel 2016). Similarly, sites in Australian forests with large trees and canopy cover are preferred habitat for arboreal marsupials due to greater foraging

area (Recher et al. 1996; van der Ree et al. 2001). Applying this to Chile, although many native species may be present in disturbed forests, forest plantations can never replace native forests (Castaño-Villa et al. 2019b). However, based on our results, abandoned forest plantations may provide suitable habitat, albeit less complex, which may be further improved through informed forest management (McFadden and Dirzo 2018).

On the other hand, activity patterns were highly variable among forest conditions (see Table 1; Supplementary Data



**Fig. 4.**—*Dromiciops gliroides* activity patterns along the monitoring period (corresponding to the austral summer). Each circular plot depicts a 24-h clock, with concentric circles that represent the number of individuals recorded by our camera traps at each 1-h time slot.

SD8). *Dromiciops gliroides* activity was significantly narrower in abandoned exotic plantations compared to native forest stands, regardless of their degree of disturbance (Fig. 3; Supplementary Data SD8). This outcome can be related to the fact that nocturnal predators are favored in open habitats (Silva-Rodríguez and Sieving 2011; Moreira-Arce et al. 2015). *Dromiciops gliroides* therefore would avoid long exposure times in disturbed sites to avoid encounters with predators (Leuchtenberger et al. 2018). A similar situation may occur in logged sites, as large old trees are scarce or even absent (Clark and Clark 1996).

Monthly activity patterns were broader (in terms of time) at the end of the austral summer, significantly increasing from January to February, and again from February to March (see Supplementary Data SD9). This likely reflects the behavior of *D. gliroides* and the availability of fleshy fruits, which latter increases at the end of the summer (Fontúrbel et al. 2017). Fleshy-fruited plants respond to sunlight exposure, maturing earlier in low canopy cover sites, such as forest plantations, and later in less disturbed conditions, such as native forests (Fontúrbel et al. 2017). Consequently, activity levels increased at the end of the summer in less disturbed sites, probably due to higher food availability. This pattern is supported by patterns of abundance, which also were higher between February and March.

This study assessed the occurrence, abundance, and activity, of *D. gliroides* at a regional scale. Most of the information on this species and its responses to habitat disturbance comes from studies restricted to single sites rather than the regional perspective we used herein. Across this gradient, we contrasted four forest conditions. *Dromiciops gliroides* occurred in all our study sites, and although we documented lower levels of abundance and more temporally restricted activity in logged forests and abandoned exotic tree plantations, *D. gliroides* appears to be more resilient to habitat disturbance than we initially thought. However, the intertwined effects of habitat loss, fragmentation, and degradation may compromise the long-term persistence of this species in disturbed landscapes. Given the reductions in native forests in recent decades, further research should aim to quantify habitat requirements by *D. gliroides*, particularly so as to inform regional forest managers and wildlife ecologists. Depending on the outcome of these studies, the future of this “living fossil” (Palma and Spotorno 1999) may lie in the balance.

#### ACKNOWLEDGMENTS

We are grateful to Ignacio Orellana, Javier Cuadra, Valeria Gómez, and Valentina Riffo, who assisted us in the field. We are indebted to the Chilean Forestry Corporation (CONAF), Huilo Huilo Foundation, The Nature Conservancy, Oncol Park (Gustavo Escobar), Katalapi Park (Luis and Anita Corcuera), Peumayén Park (Joel Caiguan), Bernardo Eggers, David Carrasco, and Raúl Las Casas for granting us access to the sampling sites and support our research. Comments by Catalina González, Douglas A. Kelt, Marcus Vieira, and an anonymous reviewer improved an earlier version of this manuscript. This

study was funded by Fondo Nacional de Desarrollo Científico y Tecnológico project 11160152 (to FEF).

#### SUPPLEMENTARY DATA

Supplementary data are available at *Journal of Mammalogy* online.

**Supplementary Data SD1.**—Map of the study area.

**Supplementary Data SD2.**—Coordinates, forest condition, and environmental information of the sampling sites.

**Supplementary Data SD3.**—Dominant vegetation and landscape characteristics of the sampling sites assessed.

**Supplementary Data SD4.**—Pairwise generalized linear model (GLM) comparisons of structural features.

**Supplementary Data SD5.**—Nonmetric multidimensional scaling (NMDS) ordination stress plot.

**Supplementary Data SD6.**—Pairwise generalized linear mixed-effect model (GLMM) comparisons of *Dromiciops gliroides* abundance among forest conditions.

**Supplementary Data SD7.**—*Dromiciops gliroides* activity records by hour, forest condition, and month.

**Supplementary Data SD8.**—*Dromiciops gliroides* activity kernels per forest condition.

**Supplementary Data SD9.**—*Dromiciops gliroides* activity kernels per sampling month.

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Submitted 22 October 2019. Accepted 5 February 2020.

Associate Editor was Marcus Vieira.