

SHORT COMMUNICATION

Beyond habitat structure: Landscape heterogeneity explains the monito del monte (*Dromiciops gliroides*) occurrence and behavior at habitats dominated by exotic trees

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Abstract

Habitat structure determines species occurrence and behavior. However, human activities are altering natural habitat structure, potentially hampering native species due to the loss of nesting cavities, shelter or movement pathways. The South American temperate rainforest is experiencing an accelerated loss and degradation, compromising the persistence of many native species, and particularly of the monito del monte (*Dromiciops gliroides* Thomas, 1894), an arboreal marsupial that plays a key role as seed disperser. Aiming to compare 2 contrasting habitats (a native forest and a transformed habitat composed of abandoned *Eucalyptus* plantations and native understory vegetation), we assessed *D. gliroides*' occurrence using camera traps and measured several structural features (e.g. shrub and bamboo cover, deadwood presence, moss abundance) at 100 camera locations. Complementarily, we used radio telemetry to assess its spatial ecology, aiming to depict a more complete scenario. Moss abundance was the only significant variable explaining *D. gliroides* occurrence between habitats, and no structural variable explained its occurrence at the transformed habitat. There were no differences in home range, core area or inter-individual overlapping. In the transformed habitats, tracked individuals used native and *Eucalyptus*-associated vegetation types according to their abundance. Diurnal locations (and, hence, nesting sites) were located exclusively in native vegetation. The landscape heterogeneity resulting from the vicinity of native and *Eucalyptus*-associated vegetation likely explains *D. gliroides* occurrence better than the habitat structure itself, as it may be use *Eucalyptus*-associated vegetation for feeding purposes but depend on native vegetation for nesting.

Key words: behavior, fleshy fruits, southern Chile, spatial ecology, temperate rainforest

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INTRODUCTION

Habitat structure is a key factor influencing species occurrence and their ecological interactions (García *et al.* 2011; Albrecht *et al.* 2012). In this regard, dense habitats are usually associated with small body-sized ani-

mals, which can respond to habitat structure and its variation within the patch (e.g. Castaño-Villa *et al.* 2014). Moreover, thick vegetation offers shelter and movement pathways to small mammals and understory birds (Bro-Jørgensen 2008). Nevertheless, human activities such as selective logging, habitat fragmentation and the deliberate introduction of exotic species may change habitat structure and, consequently, alter the occurrence of native animals species and their behavior (Breitbach *et al.* 2012; Albrecht *et al.* 2014; Fontúrbel *et al.* 2015a). Those changes can derive from the clearance of dense habitats (e.g. understory vegetation removal) that may compromise the movement paths and increase the predation risk of small-bodied species (Bro-Jørgensen 2008) or the loss of key structural features such as natural cavities, commonly used by birds and small mammals for nesting (Kelm *et al.* 2008; Reem & Löhms 2011).

The South American temperate rainforest (SATR) is considered a biodiversity hotspot due to its high endemism levels (Myers *et al.* 2000; Mittermier *et al.* 2005). However, approximately 67% of the original SATR area was lost between 1975 and 2000, with a loss rate of 4.5% per year, because of the encroachment of human settlements and agricultural fields (Echeverría *et al.* 2006). As well as the most obvious effects of human activities, such as the loss of and fragmentation of the native SATR stands, there are other less evident effects, such as the degradation of the remaining forest patches (e.g. by dead wood extraction or cattle grazing) and the creation of more heterogeneous landscapes resulting from the combination of primary and secondary forests with productive lands, usually dominated by exotic species. Those effects together are likely to alter the habitat structure of the remaining forest patches, potentially compromising the persistence of many native animal species. This is relevant for arboreal small mammals, and particularly for the monito del monte (*Dromiciops gliroides* Thomas, 1894), a relict and endemic marsupial of the SATR that plays a key ecological role as a seed disperser (Amico *et al.* 2009; Fontúrbel *et al.* 2012). This marsupial is usually associated with dense forest habitats having abundant dead wood, ferns and bamboo (Kelt 2000; Rodríguez-Cabal & Branch 2011). Therefore, its occurrence and spatial ecology are expected to be altered within degraded habitats that may not provide enough nesting sites, movement paths or food resources. Although considered a primary forest specialist (Hershkovitz 1999), *D. gliroides* has recently been found in secondary forest stands (Fontúrbel *et al.* 2012)

and in abandoned productive lands dominated by exotic trees (Fontúrbel *et al.* 2014), but its occurrence in the latter remains unexplained.

Aiming to assess the occurrence and the spatial ecology of *D. gliroides*, we compared 2 contrasting habitats: a native forest and an abandoned *Eucalyptus* plantation with native understory vegetation. We asked the following questions. First, what habitat structural features influence *D. gliroides* occurrence? Second, does *D. gliroides* space use and movement behavior differ between those habitats?

MATERIALS AND METHODS

Study site

This study was conducted at the Valdivian Coastal Reserve (39°57'S, 73°34'W), a private protected area of The Nature Conservancy (Delgado 2010). This Reserve is one of the largest remnants (50 530 ha) of austral temperate rainforest in southern Chile. Our study site presents a complex habitat mosaic, comprising old-growth and secondary-growth native stands, and a transformed habitat involving exotic *Eucalyptus globulus* Labill. plantations (planted 12–20 years ago; currently abandoned) with abundant native understory vegetation.

Native forest and transformed (i.e. *Eucalyptus* plantation with native understory regrowth) habitats differ in terms of structure. There are larger shrub patches in the transformed habitat, whereas bamboo cover, stem density, fallen logs, natural cavities and relative humidity are larger in the native habitat; however, the number of stumps does not differ between habitats (for detailed information see Table S1). Such dissimilarities may emerge from the differences in vegetation composition between habitats: *Nothofagus dombeyi*, *Nothofagus pumilio* and *Eucryphia cordifolia* dominated the canopy at the native forest stands, whereas the exotic *E. globulus* was the only canopy species at the transformed habitat. Understory vegetation at the native forest is dominated by *Laurelia philippiana*, *Drimys winteri* and *Mitraria coccinea*, with sparse clumps of the native bamboo *Chusquea quila* and a few *Lapageria rosea* vines. In the transformed habitat, however, *Aristotelia chilensis*, *Rhaphithamnus spinosus*, *Ugni molinae*, *Luma apiculata* (all fleshy-fruited species with abundant fruits during the spring-summer period), thick *C. quila* clumps and abundant *L. rosea* vines climbing on the *Eucalyptus* stems dominate the understory vegetation.

Study species

We focused our research on the relict marsupial *Dromiciops gliroides* (Microbiotheriidae), the only extant species of the Microbiotheria order, and the only representative species of the Australidelphia Superorder in South America (Fontúrbel *et al.* 2012). This species was considered to be an old-growth forest specialist (Hershkovitz 1999), but it has been recently found in secondary-growth forest stands (Fontúrbel *et al.* 2010, 2012), and more recently at abandoned forest plantations with native understory (Fontúrbel *et al.* 2014). *D. gliroides* is a nocturnal and generalist species that feeds on fruits, eggs and insects (Cortés *et al.* 2011), and it is known to disperse the seeds of at least 16 species of native plants (Amico *et al.* 2009).

Occurrence and habitat structure

To determine the occurrence of *D. gliroides* in native and transformed habitats, we set 100 camera-trap sampling points placed randomly within each habitat type (50 points per habitat type), which were monitored simultaneously, covering a monitoring area of 1.28 ha (0.64 ha per habitat type). At each sampling point, we placed an infrared camera trap (Bushnell Trophy Cam 2011), which was set in photo mode and baited once with fresh banana slices, a bait highly effective for attracting *D. gliroides* (Fontúrbel & Jimenez 2009; Fontúrbel *et al.* 2014). Cameras were randomly placed at 10 locations per habitat (i.e. 20 cameras operating simultaneously at both habitats) and relocated every 28 days to a new location until 50 monitoring points per habitat type were reached. This procedure was repeated for 2 austral summer seasons: from December 2011 to April 2012, and from November 2012 to March 2013. At each camera-trap sampling point, we recorded a set of structural features that are known to be associated with *D. gliroides* capturing success (Kelt 2006). At a 2.5-m radius from each camera point, we measured the following structural features: (1) shrub cover (as percentage of area covered, estimated visually); (2) bamboo (*C. quila*) cover (estimated visually); (3) stem density, measured as the number of stems with DBH > 1 cm; (4) the number of fallen logs; (5) the number of stumps; (6) the number of natural cavities; (7) moss abundance (as a categorical variable with 3 levels: absent, scarce, abundant); and (8) fern abundance (categorical variable: absent, scarce, abundant).

Live trapping and telemetry tracking

To obtain live individuals for radio-tracking, we captured *D. gliroides* individuals using wire-mesh traps (Tomahawk-like, 26 × 13 × 13 cm, custom made). We placed the traps approximately 1.5-m above ground and baited with banana slices and a mix of mackerel and peanut butter (Fontúrbel & Jimenez 2009). At each habitat type, we set a 6 × 8 trapping grid with traps separated 10 m from each other. Trapping grids were operated for 7 consecutive nights, and checked on a daily basis at dawn. All captures were made by February 2014. All animal capturing and handling procedures followed the guidelines of the American Society of Mammalogists (Sikes *et al.* 2011) and were also approved and authorized by the Chilean Agriculture and Livestock Bureau (SAG; resolution 8291). For each captured individual, we recorded the following information: size, weight, sex and age (defined according to the body weight: adult [>24 g] or juvenile [≤24 g]). Individuals were marked using a haircut with a unique pattern to account for recaptures. Captured individuals were immediately released at the capture site.

Ten individuals (5 per habitat type) were fitted with telemetry glue-on transmitters (model A2415 from ATS, 0.5 g of weight [Isanti, MN, USA]). Transmitters were glued to animals' fur with non-toxic acrylic glue, carefully placed between scapulae. Only individuals weighing ≥18 g were used for telemetry tracking, to ensure that the transmitter represented less than 3% of the body weight. We did not remove transmitters after the tracking because they drop during molting (Fontúrbel *et al.* 2010). Given that the transmitter's battery lifespan is short (approximately 2 weeks), we conducted intensive tracking for 12 consecutive days (12 to 24 February 2014; when females had already weaned their offspring) from 2300 hours to 0500 hours, coinciding with *D. gliroides*' activity period (Fontúrbel *et al.* 2014) to obtain detailed information on *D. gliroides*' movement patterns.

At each habitat, we defined 6 fixed telemetry locations (with GPS error ≤4 m) to minimize location-associated error. Bearings were simultaneously taken from 2 fixed locations (location #1 and location #4, location #2 and location #5, or location #3 and location #6), to ensure that bearing angles were at least separated by 20°, and taken within 10-min intervals. For exploratory pur-

poses, we took some telemetry locations during daytime aiming to determine potential nesting sites. We used 2 ATS 3-element Yagi antennas, 2 R-1000 ComSpec receivers, and 2 digital compasses for acquiring telemetry data.

Data analyses

We used a logistic regression analysis to assess whether the occurrence of *D. gliroides* is determined by any of the structural features measured in field. Goodness-of-fit of logistic regressions was estimated using a Hosmer–Lemeshow test (Agresti 2007). For this analysis we only considered the 2012–2013 data because of the low number of occurrences detected in the 2011–2012 monitoring period, as few monitoring points concentrated most of the photographic records obtained.

Field telemetry data (i.e. bearings) were used to estimate actual locations by grouping 2 or 3 bearings taken within a 10-min interval and separated by at least 20°. Location estimations were performed using LOAS 4.0 software (Ecological Software Solutions, Switzerland). We tried 3 different bearing group combinations to choose the combination that presented the smaller cumulative ellipse error values (≤ 1 ha in any case). Based on these locations, we estimated *D. gliroides* core areas and home ranges using a fixed kernel estimator (FK) at 50 and 90%, respectively (Fontúrbel *et al.* 2010). Those estimations were performed using the software Biotas 2.0 (Ecological Software Solutions, Switzerland). Using the generated core area and home range layers (i.e. shapefiles), we estimated the overlap extent for each individual pair combination by intersecting layers using ArcGIS 10.1 (ESRI, Redlands, CA, USA) and estimating the amount of shared space with respect to the total core area or home range extent (Fontúrbel *et al.* 2010).

We used the Rao spacing test to determine whether tracked individuals fitted a random walk model. In addition, we assessed whether travel distances at each habitat type varied as a function of the time spent between locations, by calculating the distance between each location pair separated up to 60 min and conducting a linear regression of the travel distance as a function of the time (following Fontúrbel *et al.* 2012). Finally, we estimated habitat use and selection between native and *Eucalyptus*-associated vegetation at the transformed habitat, because both vegetation types co-exist at this habitat. To do this, we used the compositional analysis approach (Aebischer *et al.* 1993) following the procedures detailed in Fontúrbel *et al.* (2010).

RESULTS

Our camera trap survey provided 270 photos in the native habitat (63 in the 2011–2012 summer and 207 in the 2012–2013 summer) and 169 photos in the transformed habitat (46 in the 2011–2012 summer and 123 in the 2012–2013 summer). Examining this data by month, photographic records were more frequent in the transformed habitat during the early summer, whereas in the native habitat they were more frequent during the late summer (Fig. 1).

Throughout the live trapping, 7 individuals were captured at the native habitat and 5 individuals at the transformed habitat (see details in Suppl. Table S2). At the

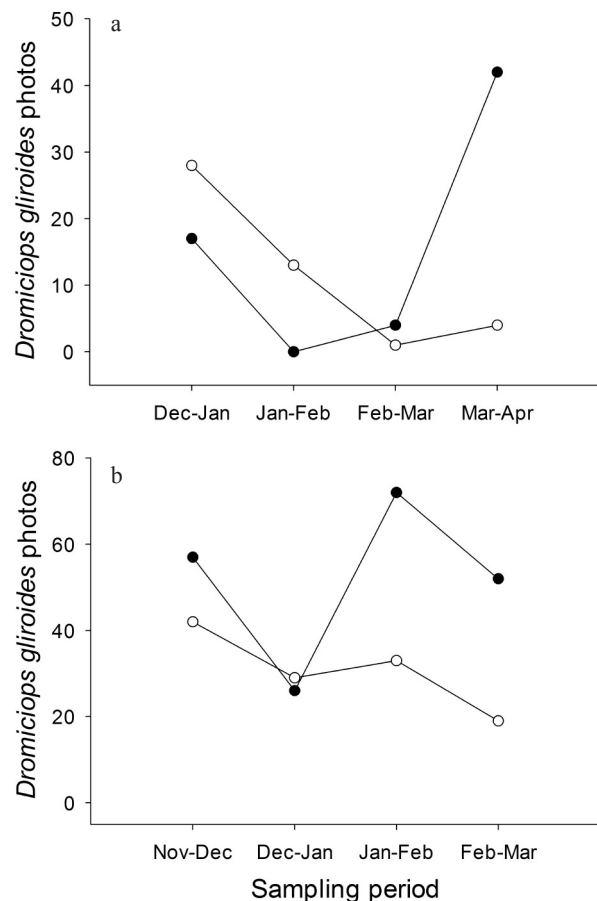


Figure 1 *Dromiciops gliroides* relative activity from camera-trap monitoring for (a) 2011–2012 austral summer (December to April) and (b) 2012–2013 austral summer (November to April). Closed symbols represent native habitat and open symbols transformed habitat.

native habitat we captured 4 juvenile males, 1 juvenile female and 2 adult females, whereas in the transformed habitat we captured 5 adult females. Overall, there was a difference in weight according to the sex (ANOVA $F_{1,10} = 18.156, P = 0.002$), with females being heavier than males.

Habitat structure and occurrence

Relating *D. gliroides* occurrence to structural features, moss abundance was the only significant variable explaining occurrence patterns between habitats ($\chi^2 = 6.853, df = 2, P = 0.033$; goodness-of-fit test, Hosmer–Lemeshow = 6.863, $P = 0.551$). Analyzing native and transformed habitat separately, there was no significant explanatory variable for *D. gliroides* occurrence in the transformed habitat (goodness-of-fit test, Hosmer–Lemeshow = 13.217, $P = 0.105$), whereas moss ($\chi^2 = 12.187, df = 2, P = 0.002$) and fern abundance ($\chi^2 = 7.851, df = 2, P = 0.019$), bamboo cover ($\chi^2 = 7.335, df = 1, P = 0.007$), stem density ($\chi^2 = 5.413, df = 1, P = 0.019$), the number of cavities ($\chi^2 = 6.469, df = 1, P = 0.011$) and luminosity ($\chi^2 = 8.393, df = 1, P = 0.004$) explained *D. gliroides* occurrence in the native habitat (goodness-of-fit test, Hosmer–Lemeshow = 7.738, $P = 0.459$).

Spatial ecology and habitat selection

Home ranges (FK 90%) at the native habitat were 0.71 ± 0.26 ha and at the transformed habitat were 0.76 ± 0.31 ha. Core areas (FK 50%) were 0.19 ± 0.08 ha at the native habitat, and 0.20 ± 0.09 ha at the transformed

habitat (Table 1), there were no significant differences for core areas (Mann–Whitney test, $U = 9.00, P = 0.55$) and home ranges ($U = 9.00, P = 0.55$) between habitats. Regarding inter-individual overlapping (Fig. 2), home range overlapping at the native habitat ranged between 8% and 97% ($46.20\% \pm 7.58\%$, mean \pm SE), whereas at the transformed habitat ranged from 11 to 100% ($52.48\% \pm 7.02\%$). Core area overlapping at the native habitat ranged between 0 and 91% ($30.64\% \pm 7.42\%$), whereas at the transformed habitat ranged from 0 to 100% ($29.42\% \pm 6.82\%$). Detailed overlapping results are available in Table S3.

Regarding *D. gliroides* movement behavior, tracked individuals fitted a random walk model, except for 1 individual at the native habitat and 2 others at the transformed habitat that showed a directional displacement (Table 2). When examining whether travel distances depended on the time elapsed between locations, no significant relationships between time and distance travelled were found at both habitats (Fig. 3). Finally, our data on habitat use and selection patterns at the transformed habitat showed that tracked individuals tend to use native vegetation more than the vegetation associated with the abandoned *Eucalyptus* plantation, but the differences between them are not significant and, therefore, they may correspond to the availability of each vegetation

Table 1 Locations, core area and home range estimations for tracked individuals at native (N) and transformed (T) habitats

Individual	Locations	Core area (FK 50%)	Home range (FK 90%)
N1	45	0.09	0.50
N2	55	0.15	0.46
N3	67	0.06	0.21
N4	40	0.37	1.34
N5	37	0.04	0.27
T1	72	0.05	0.20
T2	43	0.14	0.60
T3	65	0.10	0.32
T4	71	0.32	1.43
T5	65	0.55	1.80

Individuals N1, N4 and N5 were males whereas individuals N2 and N3 and the 5 individuals in the transformed habitat were females. FK, fixed kernel estimator.

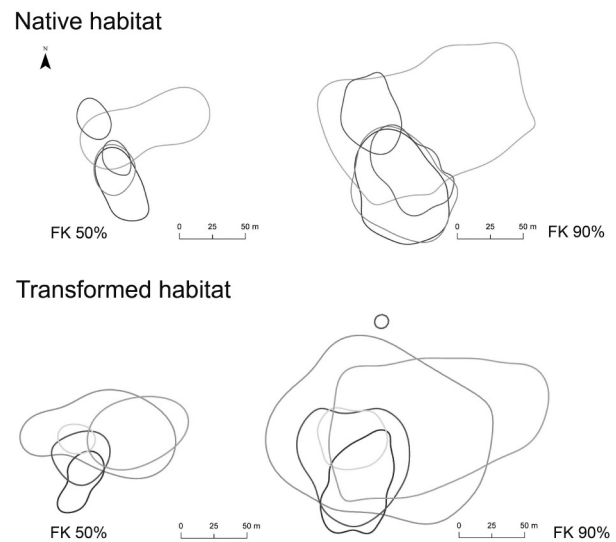
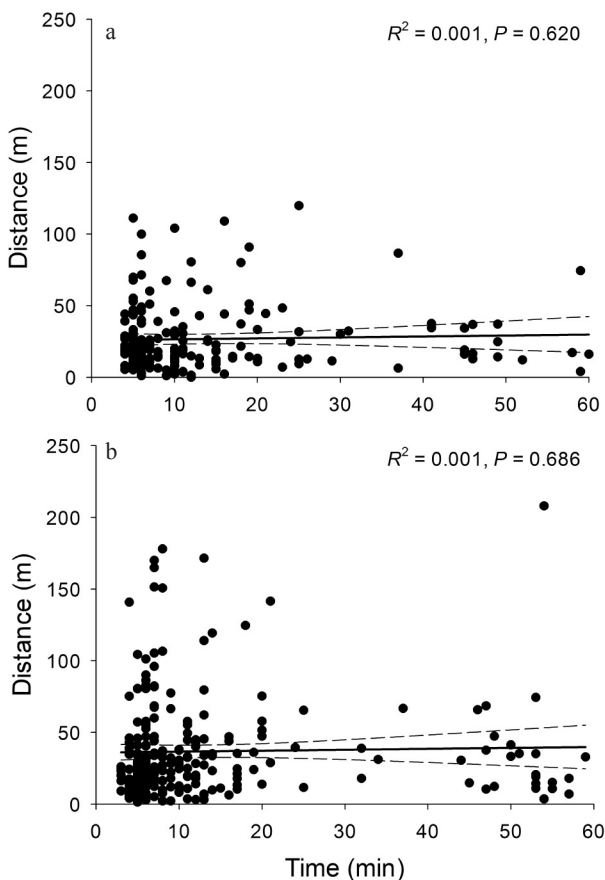


Figure 2 Core areas (FK 50%) and home ranges (FK 90%) of the tracked individuals in native and transformed habitats.

Table 2 Movement behavior assessed for the tracked individuals at native (N) and transformed (T) habitats

Individual	Rao <i>U</i> -statistic	<i>P</i> -value
N1	136.91	0.34
N2	131.24	0.50
N3	129.13	0.57
N4	150.02	0.09
N5	161.48	0.01
T1	134.47	0.40
T2	137.22	0.34
T3	159.23	0.03
T4	154.97	0.01
T5	139.77	0.25

Random walk model was evaluated using the Rao test (significant *P*-values indicates directional movement).

**Figure 3** Time versus distance travelled in (a) native habitat and (b) transformed habitat, based on telemetry data.

type within the landscape (preference for native vegetation over *Eucalyptus*-associated vegetation was 0.23 ± 0.22 [mean \pm SE], estimated using compositional analysis). However, diurnal locations (we obtained 15 diurnal locations from 3 individuals at the transformed habitat) were always in the neighboring native vegetation.

DISCUSSION

Native and transformed habitat differed in most structural features, as was expected considering that the original canopy composed of a variety emerging species (e.g. *Nothofagus dombeyi*, *Eucryphia cordifolia* and *Fitzroya cupressoides*) was replaced by a single *Eucalyptus* species in the transformed habitat, resulting in a less complex canopy structure. Conversely, transformed habitats presented a more complex understory composed by several early-successional and shade-intolerant shrubs (e.g. *Rhaphithamnus spinosus*, *Aristotelia chilensis* and *Ugni molinae*) and thick clumps of the native bamboo *Chusquea quila*. However, this situation is not commonplace for *Eucalyptus* plantations because this species usually prevents other vegetation from growing by causing water shortages (Engels *et al.* 2005). This may not be a limiting factor here because this area receives approximately 2500 mm of annual rainfall (Delgado 2010).

Dromiciops gliroides occurrence at habitats dominated by exotic tree species was recently reported (Fontúrbel *et al.* 2014). A recent review (Fontúrbel *et al.* 2012) showed that this marsupial can thrive in Myrtaceae-dominated secondary-growth forests as long as they have a certain amount of structural complexity. This may be also the case for exotic tree-dominated habitats, in which *D. gliroides* occurrence could be determined by a dense understory presenting 5 Myrtaceae species (*Ugni molinae*, *Luma apiculata*, *Amomyrtus luma*, *Amomyrtus meli* and *Myrceugenia planipes*), and *C. quila* bamboo that is used as nesting material and has been reported to be an important factor influencing its occurrence at the landscape level (Rodríguez-Cabal & Branch 2011). A similar pattern has been described for some tropical marsupials (Stallings 1990). Based on these results, *D. gliroides* seems to be acting as a forest-generalist species.

The structural features measured poorly explained *D. gliroides*' occurrence between habitats, with moss cover being the only significant explanatory variable. This may emerge from the great structural inter-habitat variation, which also might be leading to behavioral responses.

es by *D. gliroides*, because this species is responding to a set of environmental features at the native habitat that are coherent with previous reports on this species (Kelt 2000). However, it is not responding to any of the measured variables in the transformed habitat. This suggests that, in the transformed habitat, *D. gliroides* may be responding to environmental variables other than those measured in this study. Considering that all diurnal locations were found in native vegetation, *D. gliroides* might be using *Eucalyptus* plantations only for feeding purposes, as they present greater food resource availability, but nesting sites are probably restricted to the native forest remnants. In any case, the compositional analysis performed revealed that both native and *Eucalyptus*-associated vegetation are used according to their availability in the landscape. Because both vegetation types are neighboring and occur within *D. gliroides* maximum dispersal distance (up to 500 m; Fontúrbel *et al.* 2012), without any physical barrier in between, it is possible for *D. gliroides* to move between these 2 vegetation types. Nonetheless, these results should be interpreted with caution as we were able to track only 5 individuals per vegetation type, which may limit the generality of our conclusions.

Despite the strong differences in habitat structure, *D. gliroides* used the space in a similar way in native and transformed habitats, as there were no differences in core area and home range extents or in displacement behavior (i.e. most individuals fitted a random walk model). Moreover, core area and home range values found in this study are similar to those previously reported for *D. gliroides* in other locations of Argentina and Chile (Fontúrbel *et al.* 2012); weight, size and body condition values are also similar among populations. These findings suggest that *D. gliroides* has a well-defined suite of life history traits that remain mostly constant across its distribution range (comprising approximately 800 km from north to south, and approximately 300 km from east to west) despite strong habitat structural differences, even within habitats dominated by exotic tree species. Considering that *D. gliroides* is an important seed disperser for at least 16 native plant species at the South American temperate rainforests (Amico *et al.* 2009; Mora & Soto-Gamboa 2011), its presence in abandoned forestry plantations may constitute an opportunity for the natural recovery of degraded lands.

Our results showed that the occurrence of *D. gliroides* in the transformed habitat was poorly explained by habitat structure, but it may be determined by an increased

landscape heterogeneity resulting from neighboring native and transformed forest stands. Our telemetry data show that *D. gliroides* forages in both vegetation types but nesting sites are likely to be restricted to native vegetation; therefore, the occurrence of *D. gliroides* at the abandoned *Eucalyptus* plantations may depend on the contiguous native forest remnants and the presence of reproductive individuals. It is likely that *D. gliroides* establish nests in the native vegetation remnants but use the *Eucalyptus*-associated vegetation for feeding due to the large fleshy fruit on offer (Fontúrbel *et al.* 2015b). This situation is consistent with the “intermediate landscape complexity hypothesis” (Tscharntke *et al.* 2012), which argues that structurally simple habitats (such as agricultural fields) can offer more food resources whereas complex habitats (such as a native forest) can offer shelter and nesting sites, and, therefore, intermediate situations may provide a combination of both and, hence, enhance biodiversity. Nevertheless, having captured only adult females in the transformed habitat may be related to 2 non-mutually exclusive explanations: (i) only reproductive females can afford to leave the native vegetation and explore the *Eucalyptus*-associated vegetation to ensure their food supply (even when this may represent being more exposed to predators) and to gather enough energetic reserves for wintertime; and (ii) it is known that marsupials respond to stress by biasing their offspring sex ratio towards one gender (Myers 1978; Moore *et al.* 2015), in this case to females. Regardless of whether one or both explanations are true, the potential effects of habitat transformation on *D. gliroides* reproductive biology are yet to be assessed.

Landscape heterogeneity resulting from neighboring native and *Eucalyptus*-associated vegetation types appears to be more important than habitat structural features in explaining *D. gliroides* occurrence, which may also explain why this marsupial does not alter its movement behavior between habitats. In addition, *D. gliroides* may act as an umbrella species (Fontúrbel & Jiménez 2011) because a habitat that meets its requirements may be also able to hold many dispersal-restricted bird species (e.g. Rhynocryptids; Castellón & Sieving 2007). Based on our results, we recommend maintaining the connectivity between native forest remnants and productive lands (whether operational or abandoned) to increase habitat heterogeneity for *D. gliroides*, which may help to recover degraded areas through seed dispersal.

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SUPPLEMENTARY MATERIALS

Additional supporting information may be found in the online version of this article.

Table S1 Comparison of structural features between native (N) and transformed (T) habitats. Moss and fern abundances are categorical variables measured in 3 discrete levels: absent (0% cover), scant (<50%) and abundant (≥50%)

Table S2 Descriptive data (sex, age, weight and longitude) of the captured *Dromiciops gliroides* individuals in native and transformed habitats

Table S3 Pairwise home range and core area overlap for the tracked individuals in native (N) and transformed (T) habitats

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