Habitat use in three-dimensional environments: A camera-trap assessment of vertical profile use by wildlife in the temperate forests of Chile

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ABSTRACT

Habitat use is how animals use the physical and biological components of the environment. Studies relating habitat and wildlife in forest ecosystems have typically been conducted from the ground, even though most wildlife use the three-dimensional space. The objective of our study was to understand how wildlife uses the whole vertical profile of the forest and to analyze possible associations between different species and vertical forest strata, using camera traps and occupancy models. We defined four strata (forest floor, understory, lower canopy, and upper canopy) that range from 0 to 32 m from the ground. We installed 16 camera-traps per stratum (n = 64), and we analyzed the use of each stratum by seven taxa using occupancy models. We detected 24 wildlife taxa, including 17 birds, six mammalian taxa and one reptile. Occupancy models showed that rodents and two bird species were associated either to the forest floor or to the lower strata (understory and ground), whereas one furnariid bird and one marsupial used the vertical profile more frequent than the forest floor. Finally, the lizard and a furnariid bird preferentially used the lower and upper canopy. For all but one of the species, activity patterns were similar between the upper and lower strata of the forest. Our study shows that wildlife species differ in the use of the vertical profile of the forest and suggests that occupancy of species that select the canopy can be largely underestimated from ground-based surveys affecting management decisions.

1. Introduction

Habitat use is defined as the way animal use the physical and biological components of the environment (Morrison and Mathewson, 2015), defined from the perspective of the species involved (Hall et al., 1997). Commonly, studies that link wildlife and habitat in forest ecosystems are conducted from the ground and tend to consider only bidimensional variables, such as land cover, tree composition and structure (e.g., Bull and Holthausen, 1993; García-Marmolejo et al., 2015; Wang et al., 2019). However, forests are three dimensional ecosystems, with strong vertical heterogeneity that could lead to differences in the use of space by different animals (Parker and Brown, 2000; Renner et al., 2018; Shaw, 2004; Thiel et al., 2021). For example, the availability of foliage, branches, cavities, epiphytes and physical conditions such as solar radiation, moisture and temperature vary at different heights from the ground (Hallé et al., 2012; Jung et al., 2012; Shaw, 2004). Therefore, wildlife sampling conducted from the ground could lead to strong biases in the estimations of abundance, occupancy, home-range size and activity patterns of species that use the vertical profile of the forests (Azcarraga et al., 2020; Bowler et al., 2017; Hongo et al., 2020; Moore et al., 2020; Rader and Krockenberger, 2006). Despite the recognition of the importance of habitat structure (Ferreira de Camargo et al., 2018; Oliveira and Scheffers, 2018; Pearson, 1975; Seidl et al., 2020), the vertical structuring in the use of space by wildlife has been less addressed, especially in temperate ecosystems. Despite major advances, the current understanding of how fauna uses vertically complex ecosystems is incipient, with only a few studies comparing species occupancy between canopy and forest floor (Moore et al., 2021).

Understanding how wildlife use the vertical profile of the forest can provide important insights for forest wildlife conservation, monitoring, and management (Walther, 2003).

One of the state variables frequently used in animal surveys that could be affected by ground-level sampling is occupancy: the proportion of a given area occupied by a species of interest (MacKenzie et al., 2002). In forest ecosystems, most occupancy studies have been conducted from the ground (e.g., Guzy et al., 2019; Morante-Filho et al., 2021; Thornton et al., 2011), despite the important proportion of animals that use the canopy. A recent review of surveys with arboreal camera traps (Moore et al., 2021) found only three studies (see Bowler et al., 2017; Moore et al., 2020; Whitworth et al., 2019) that addressed occupancy of arboreal species, all of them focused on mammals. Authors attributed the scarcity of studies to the logistic difficulties of obtaining an appropriate sample size in the forest canopies. Among these studies, only one compared between ground and canopy, finding that probability of detection was higher at ground for some and at canopy for other primate species (Moore et al., 2020). Then, for species that preferentially use the upper forest canopy, it is possible to expect larger biases from ground-based occupancy estimation. Occupancy models could help to reduce these biases by measuring the uncertainty in the probability of detection (MacKenzie et al., 2017; MacKenzie et al., 2002). However, if the upper forest strata are not sampled, inferences from the ground will only be valid for the forest species that: i) select the lower strata of the forest (e. g., ground and/or understory); ii) use in similar way the whole vertical profile; and iii) those species whose detectability is high from the ground (e.g., highly vocal birds).

The main goal of this study was to compare the use of different strata within the vertical profile of the forest by vertebrates. Specifically, we compared occupancy and activity patterns among four different strata: forest floor, understory, lower canopy, and upper canopy, while accounting for imperfect detection. To address our goals, we set a study in the temperate forests of southern Chile, a system characterized by naturally low animal species richness and high levels of endemism (Armesto et al., 1998, 1995). Previous explorations in the canopy showed that the vertical profile of these forests are used by one marsupial, five rodents, at least one carnivore, two frogs, one reptile and many birds (Díaz et al., 2010; Godoy-Güinao et al., 2018; Godoy-Güinao and Díaz, 2018; Moreira-Arce et al., 2021; Rabanal et al., 2021; Tejo and

Fontúrbel, 2019). Nevertheless, little is known on wildlife use of different strata within the vertical profile. The few exceptions correspond to comparisons between ground level and low height (c. 2-m), mostly focused on small mammals (e.g., Fontúrbel and Jiménez, 2009). Our surveys were based on fauna detection by camera traps located across the entire vertical profile, —from the ground to the canopy—and occupancy modelling and activity patterns. Based on our results, we discuss about possible bias, similarities and differences between ground-based surveys and our tri-dimensional approach to study forest fauna occupancy.

2. Methods

2.1. Study area

We conducted our study in Bosque Pehuén, an 880-ha private protected area owned by Mar Adentro foundation. This area is in the Andean range (860–1350 m.a.s.l.) of the South American Temperate Forests ecoregion, southern Chile (39°25′ S, 71°45′ W, Mellado-Mansilla et al., 2018, Fig. 1). The area is dominated by large areas of secondary forests, with a belt of old-growth forests in the center of the area and anthropogenic pastures located at both extremes of the park (Díaz et al., 2019). The weather is temperate, with cold winters and mild summers (di Castri and Hajek, 1976). The nearest climatic station showed a mean annual temperature of 10.3° C and annual precipitation of 2680 mm (Instituto de Innovación Agraria, 2019). The forest is dominated by *Nothofagus dombeyi*, *Nothofagus alpina* (both Nothofagaceae) and *Saxegothaea conspicua* (Podocarpaceae) trees, with individuals over 350 years old, with trunks over 2 m diameter that can reach 30 m height (Mellado-Mansilla et al., 2017). The understory is dominated by *Chusquea culeou* and *Drimys andina*, and can reach 4-m height (Godoy-Güinao and Díaz, 2018; Mellado-Mansilla et al., 2018).

2.2. Study design

We used Quantum GIS 3.20.0 (QGIS Development Team, 2022) to generate a grid composed by squared cells of 4 ha (200 × 200 m, Fig. 1). The area of the cells was determined considering the home range and territory size of the main species to be included in the study (Bowler
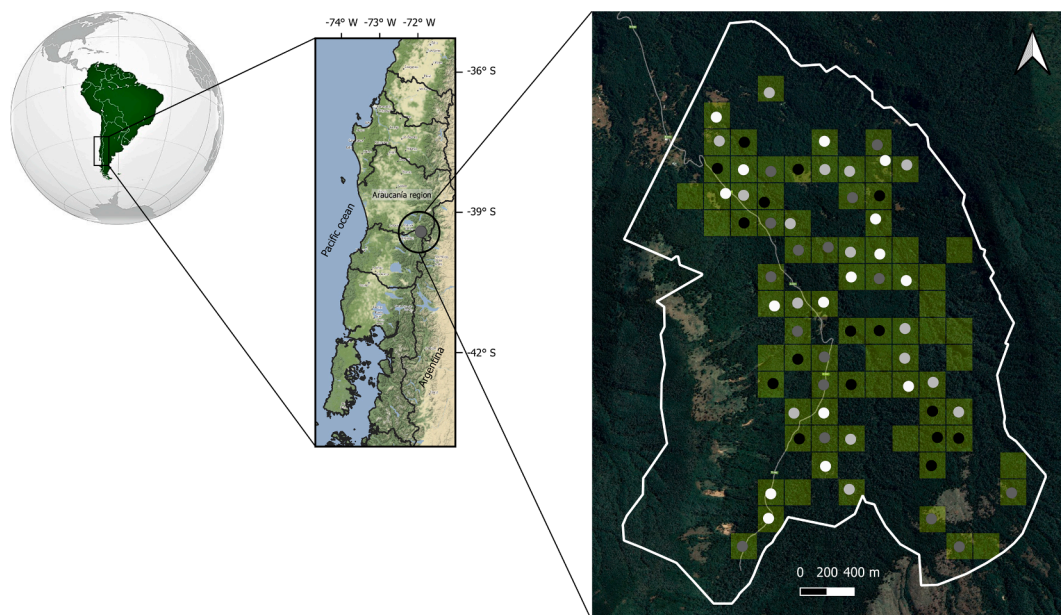

Fig. 1. Study area in Bosque Pehuén park, Araucanía region, southern Chile. The cells available for sampling are shown in green. Selected cells include dots that indicate the location of camera traps, and the color of dots represents the different strata sampled: forest floor (black), understory (dark gray), lower canopy (light gray) and upper canopy (white).

et al., 2017; MacKenzie et al., 2017). For example, the marsupial *Dromiciops gliroides* has a home range of 1.6 ha (Fontúrbel et al., 2010), whereas endemic Rhinocryptidae understory birds have territories of 1 to 4-ha (Castellón and Sieving, 2007). To secure feasibility and safety protocols, we excluded all cells located in areas with steep slopes. Within the remaining area, we randomly selected 80 cells, and sixty-four of them were included in the study. The number of cells selected aimed at securing both feasibility and a sample size large enough as to allow occupancy modelling (Kays et al., 2020; Rovero et al., 2013).

The determination of the different vertical strata of the forest followed Scheffers et al. (2017), with modifications based on the field experience of the research team in the temperate forests of Chile, its canopy and its potential use by forest wildlife (Díaz et al., 2005, 2010, 2012, 2020; Godoy-Güinao et al., 2018; Godoy-Güinao and Díaz, 2018). We considered four different vertical strata: (i) forest floor, (ii) understory, (iii) lower canopy, and (iv) upper canopy. The ground was defined as the forest floor. Understory was defined as the stratum located above ground level, between 0.5-m and up to 4-m, depending on the height of the bamboo cover, the dominant understory species in the study area (Godoy-Güinao and Díaz, 2018). The lower canopy was defined as the space between the understory (3 to 4-m) and up to the height where the first branches of the canopy emerge (up to 12-m). The upper canopy considered the area of the crown of the tree from 13 to 32 m. In each selected cells we sampled only one of the four strata available, which was randomly determined. Therefore, we assigned 16 cells to each vertical stratum.

2.3. Camera trap setting

Camera traps (Bushnell Trophy Cam, Bushnell Corporation, Overland Park, Kansas, models: Trophy Camera Brown 119736 and E2 119836) were set as closest as possible to the center of each cell, considering accessibility, logistics and tree characteristics. In the ground stratum, camera traps were installed at 20 ± 5 cm (mean $\pm$ SD) from the ground, following standard protocols (e.g., Rovero et al., 2010, Silva-Rodríguez et al. 2018). The understory stratum was installed on trees at 1.5 m $\pm$ 0.4 m (mean $\pm$ SD, range: 1.1 – 2.3 m) from the ground, pointing towards a horizontal branch that was manually installed between the dense bamboo thickest that surrounded the main tree. To access the canopy strata we used single and double rope arborist techniques (Díaz et al., 2012; Perry, 1978). Camera traps were installed on camera holders (HME Trail Camera Holder, HME Products, Irving, Texas). In the lower canopy camera traps were installed on the main trunk before the first canopy branches, pointing towards the ground at a mean height of 8.2 $\pm$ 2.4 m (mean $\pm$ SD, range: 3.8 – 11.7 m) above ground level. Finally, upper canopy cameras were installed at 18.4 $\pm$ 4.3 m (mean $\pm$ SD, range: 13.5 – 32.0 m) from the ground, pointing towards horizontal branches. For both canopy levels and understory, camera traps were installed at 1–2 m from the target branch, to secure both an adequate detection area and the identifiability of photographed animals (Suzuki and Ando, 2018). The specific height and location of the cameras on the vertical strata was decided based on tree accessibility to climbers, foliage, and branch features. We tried to avoid the branches and trunks with abundant foliage, to prevent excessive triggering of the camera-traps (Gregory et al., 2014). In summary, we installed cameras in the whole vertical profile of the forest ranging from 0.2 to 32 m from the ground. Camera traps were active 24 h a day and were set with automatic PIR and to capture two pictures per trigger, with a delay of 3 s between triggers. During camera installation we recorded (1) the stratum where it was installed, (2) its distance to the ground (measured with a measuring tape), and (3) the direction where the camera was aimed (preferentially south). We did not use lures.

Camera traps were active between January and April 2019: The first 32 points were sampled between January and March (55–59 days active per camera) and the remaining 32 between March and April (42–46 days active per camera). During each sampling period we installed eight traps

per stratum. One camera from the upper canopy was discarded due to malfunction, leaving such stratum with 15 cells and a total effort of 63 camera-sites.

2.4. Data analysis

Pictures were analyzed using the protocols developed by Sanderson and Harris (2013), https://smallcats.org/resources/#camerasweet). Records were classified to species, with the exception of rodents that were grouped because it was difficult to classify them to species (Meek and Vernes, 2016) and lizards. Although all the lizards (*Liolaemus* sp.) that could be identified to species corresponded to *L. pictus*, there were pictures of lizards that could not be identified. Therefore, although it is likely that all lizards detected correspond to *L. pictus*, we cautiously classified all lizard images as *Liolaemus* sp.

We only included in further analyses those species that were detected in a minimum of 18 cameras (29%). These species included four birds: *Aphrastura spinicauda*, *Pygarrhichas albogularis* (both Furnariidae), *Scelorchilus rubecula* and *Pteroptochos tarnii* (both Rhinocryptidae), small mammals such as the marsupial *Dromiciops gliroides* (Microbiotheriidae) and rodents (as a group), and reptiles (lizard, *Liolaemus* sp., Liolaemidae).

Model structure. We used single season single species occupancy models to determine the use of the different strata (MacKenzie et al., 2002). We considered two covariates to explain uncertainty in probability of detection. First, we considered the detection area (Area) of the cameras as a covariate. A priori we considered that cameras located on the forest floor and lower canopy (trunk surface) had a larger detection area than cameras located in the understory and upper canopy, because the latter pointed towards single or multiple branches that cover lower area than forest floor and lower canopy traps, potentially affecting the probability of detecting wildlife (Suzuki and Ando, 2018). Sampling period (Season) was also included as a covariate. The first sampling period was conducted during the austral summer, whereas the second period also included fall (April). This could influence uncertainty in detection due to differences in the activity patterns of the species involved (e.g., Rodríguez-Gómez and Fontúrbel, 2020).

To model the probability of occupancy, we used the vertical strata and the height at which cameras were installed. Based on these variables we generated six candidate models to explain the use of the vertical profile by wildlife: (1) *Strata*, under the assumption that wildlife will use differentially the four strata previously defined (forest floor, understory, lower canopy, and upper canopy); (2) lower strata versus upper strata (*Lower-Upper* from here on), based on the assumption that animals use either the lower strata (forest floor and understory) or the upper strata (lower canopy and upper canopy) of the forest; (3) *Forest floor* versus *height*, if certain species are exclusively ground users and others are generalist vertical profile users (understory, lower canopy and upper canopy as a whole); (4) *Substrata,* if wildlife use differentially the forest floor, understory, and canopy as a whole (lower and upper canopy together); (5) *Null,* under the assumption of no differences between strata; and (6) *Height,* if the use of the vertical profile is influenced by the height (i.e., meters above the ground, Moore et al. 2020) rather than the structure of the strata.

Model fit. The history of detection was built considering periods of 7 days each, up to a maximum of eight survey occasions. The effective number varied according to the operation period of each camera. Model selection was conducted in two stages (see Gálvez et al., 2021; Silva-Rodríguez and Sieving, 2012). First, we used the most general use model (Strata) to determine the best detection model using the small sample-corrected Akaike Information Criterion (AICc, Burnham and Anderson, 2002). Then, using the best detection model, we determined the best occupancy model, also using AICc. We considered as plausible all models whose delta AICc (Δ) was < 2 units (Burnham and Anderson, 2002). Model fit was evaluated on the most general model through the MacKenzie and Bailey (2004) method (10,000 bootstrap iterations).

When models did not fit (p < 0.05) and showed evidence of moderate overdispersion (c-hat < 2 in all cases), we used QAICc (MacKenzie and Bailey, 2004; Mazerolle, 2020) and corrected the standard errors according to the square-root of the c-hat of the most general model (Kéry and Royle, 2016). Analyses were conducted in R-Studio version 1.4.1106 (RStudio Team, 2020), using packages *unmarked* (Fiske and Chandler, 2011) and *AICcmodavg* (Mazerolle, 2020).

2.5. Activity patterns

We compared overlap in activity patterns between strata at species level. For this purpose, we fitted kernel density functions for each species (Ridout and Linkie, 2009). Activity patterns were fitted only for species that obtained a minimum of 25 independent records for each strata compared (Ridout and Linkie, 2009). We considered records obtained in a given device to be independent when they were separated by at least 60 min (Rovero and Marshall, 2009). We evaluated activity overlap between strata—using the best occupancy models selected for each species—to determine if activity patterns differed between strata that were used differentially. In two cases, we did not use the best model for comparison due to scarcity of records in the less used stratum. In these cases, we used the models that ranked second (*S. rubecula*) and third (*A. spinicauda*), according to model selection. Considering that sampling included four months (January to April, but all cameras installed during summer time, UTC-3) that differed in day length, activity patterns were adjusted by sunrise and sunset (Nouvellet et al., 2012), using the function *sunTime* in package *Overlap* (Meredith and Ridout, 2021). This function transform clocktime to suntime, adjusting the data according to the date and location of the records (Meredith and Ridout, 2021). In most cases, we used the Dhat1 (Δ_1) overlap estimator coefficient, because it provides a better fit for samples lower than 50 independent records (Meredith and Ridout, 2021). The only exception was rodents (that had higher detection rates), where we used the Dhat4 (Δ_4) estimator (Meredith and Ridout, 2021). Confidence interval (95%) were calculated using the basic0 estimator and a non-parametric bootstrapping involving 10,000 iterations (Meredith and Ridout, 2021). We considered overlap to be high if > 0.8; medium if = 0.5 – 0.79; and low if < 0.5 (Allen et al., 2018; Lynam et al., 2013). In the case of birds, we also compared general (across strata) activity patterns between species, to evaluate potential differences in activity patterns. To evaluate overlap between birds we used the Dhat4 (Δ_4) estimator and calculated basic0 confidence intervals as explained above (Meredith and Ridout, 2021).
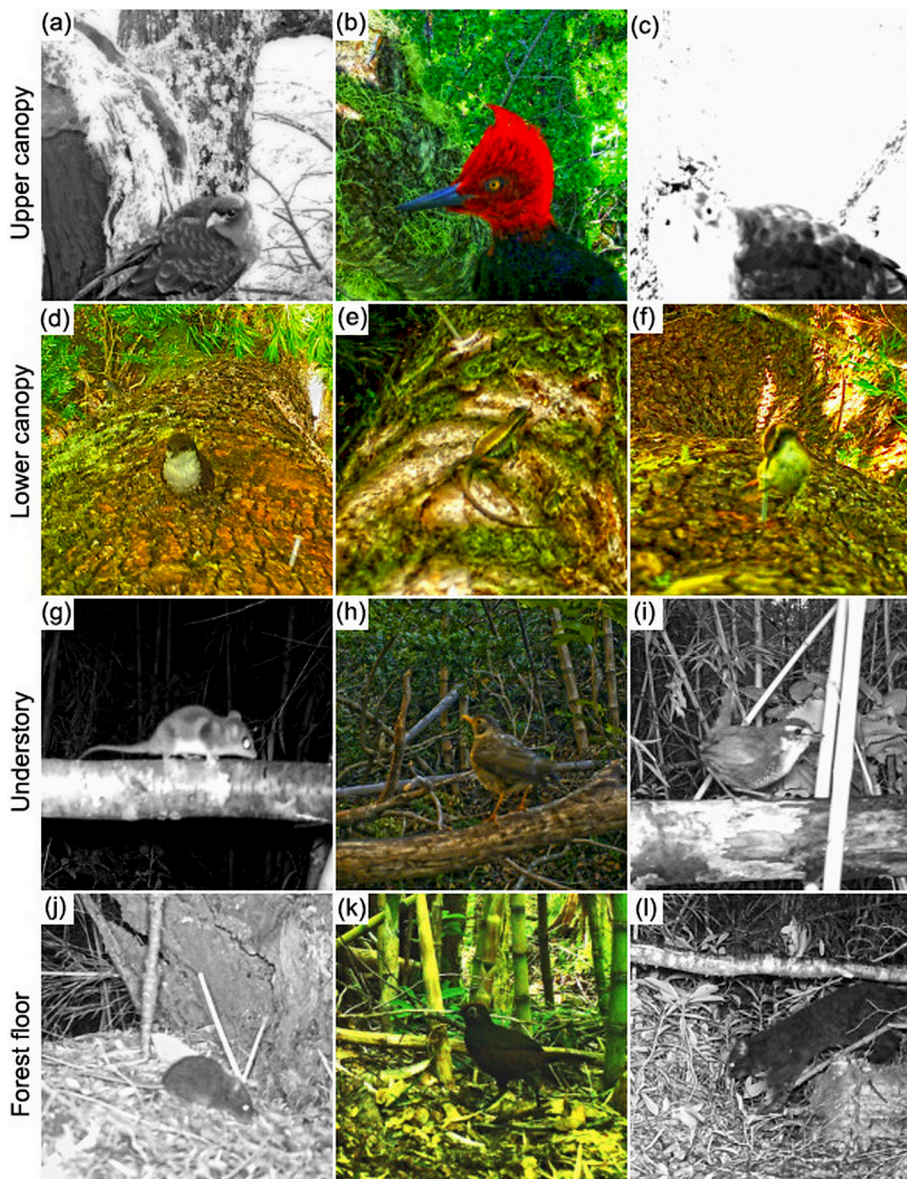

Fig. 2. Photographic records of wildlife along the vertical strata of the forest. **Upper canopy**: (a) *Phalcoboenus chimango* (Falconidae); (b) *Campephilus magellanicus* (Picidae); (c) *Accipiter bicolor* (Accipitridae). **Lower canopy**: (d) *P. albogularis* (Furnariidae); (e) *Liolaemus* sp. (Liolamidae); (f) *A. spinicauda* (Furnariidae). **Understory**: (g) *D. gliroides* (Microbiotheriidae); (h) *Turdus falcklandii* (Turdidae); (i) *S. rubecula* (Rhinocryptidae). **Forest floor**: (j) rodents; (k) *P. tarnii* (Rhinocryptidae); (l) *Leopardus guigna* (Felidae).

Activity patterns and overlap were analyzed in package *Overlap* (Meredith and Ridout, 2021) in R-Studio version 1.4.1106 (RStudio Team, 2020).

3. Results

We recorded 24 wildlife taxa belonging to 18 families: 17 bird species, five mammalian species, one mammalian order (rodents) and a reptile genus (*Liolaemus* sp.) (Fig. 2, Supp. Material 1). The highest number of species were recorded in the understory and upper canopy, with 15 taxa respectively, followed by the forest floor and lower canopy with 12 and 8 taxa respectively (Supp. Material 1). The marsupial *D. gliroides* was detected in 71% of the sites, followed by the *A. spinicauda* (59%) and rodents (48%) (Supp. Material 1). Some species were detected across the whole vertical profile (e.g., *D. gliroides, A. spinicauda*, and rodents), whereas others were detected in one or few strata (Supp. Material 1). For example, larger mammals such as *Leopardus guigna* (Felidae), *Conepatus chinga* (Mephitidae), and the invasive *Lepus europaeus* (Leporidae) and *Sus scrofa* (Suidae) were only detected on the forest floor. Further analyzes were conducted for seven taxa that were detected in at least 18 camera traps: the furnarids *Aphrastura spinicauda* and *Pygarrichas albogularis,* the rhinocryptids *Scelorchilus rubecula* and *Pteroptochos tarnii*, the marsupial *Dromiciops gliroides*, rodents and the lizards *Liolaemus* sp.

3.1. Occupancy modelling

Aphrastura spinicauda. The detection model that better predicted its occupancy was the null model ($\omega = 0.42$) (Supp. Material 3). Two plausible models explained the use of the vertical profile by this bird, being the Forest floor versus height the one with better performance ($\omega = 0.63$; Table 1). The use of the vertical profile by *A. spinicauda* was negatively associated to the forest floor and positively associated to the vertical profile, without differences between understory, lower canopy, and upper canopy (Fig. 3).

Scelorchilus rubecula. The detection model that better explained uncertainty in detection included Area and Season as covariate ($\omega = 0.52$; Supp. Material 3). Three plausible models were able to explain use of the vertical profile by *S. rubecula* (Table 1). Among them, the Substrata model was the one that better explained this bird occupancy ($\omega = 0.40$; Table 1). The best model shows that the use of space by *S. rubecula* is higher on the forest floor, intermediate in the understory and lower on the canopy (Fig. 3). This is also supported by the second models, that suggests a higher use of floor than the vertical profile (Table 1).

Pygarrichas albogularis. The null detection model had the highest support among candidate models ($\omega = 0.53$; Supp. Material 3). In terms of use, two models were plausible. The best model (Lower–Upper, $\omega = 0.49$, Table 1) shows that this bird strongly selects for the upper and lower canopy of the forest (Fig. 3).

Pteroptochos tarnii. The model that better explained uncertainty in detection included Area as a covariate ($\omega = 0.54$; Supp. Material 3). The model that better explained its use of space was the Lower-Upper model ($\omega = 0.56$, Table 1). This model shows that this bird species is positively associated to the forest floor and understory (Fig. 3), without differences between these strata.

Dromiciops gliroides. The best detection model included Area as a covariate ($\omega = 0.46$; Supp. Material 3). The best occupancy model was the Forest floor versus height ($\omega = 0.54$; Table 1). *D. gliroides* preferred the vertical strata over the forest floor (Fig. 3), without differences between understory, lower canopy, and upper canopy.

Rodents. The best detection model ($\omega = 0.63$) included Area and Season as covariates (Supp. Material 3). Three occupancy models were considered as plausible (Table 1). The best occupancy model was the Lower-Upper model ($\omega = 0.33$; Table 1), that showed a preference for the lower strata of the forest (Fig. 3). All plausible models show that lower strata, the forest floor and the understory, have a higher

Table 1

Selection of candidate models to explain occupancy (ψ) of wildlife taxa along the vertical profile of the forest. Plausible models (ΔAICc/QAICc < 2 units) are presented in bold. We report the number of parameters (k), Akaike Information Criteria with small samples size correction (AICc) or Quasi-Akaike Information Criteria with small sample size correction, delta AICc or QAICc (Δ), and weights (ω).

Species	Models	k	AICc	QAICc	Δ	ω
A. spinicauda	p(.),Ψ(Forest floor)	4	–	353.86	**0.00**	0.63
	p(.),Ψ(Substrata)	5	–	355.59	**1.73**	0.26
	p(.),Ψ(Strata)	6	–	357.53	3.67	0.10
	p(.),Ψ(Lower_Upper)	4	–	364.57	10.72	0.00
	p(.),Ψ(Height)	4	–	365.00	11.15	0.00
	p(.),Ψ(.)	3	–	371.89	18.04	0.00
S. rubecula	p(Area + Season),Ψ(Substrata)	6	265.70		**0.00**	0.40
	p(Area + Season),Ψ(Forest floor)	5	267.09		**1.38**	0.20
	p(Area + Season),Ψ(Lower_Upper)	5	267.24		**1.54**	0.18
	p(Area + Season),Ψ(Strata)	7	268.22		2.52	0.11
	p(Area + Season),Ψ(Height)	5	268.37		2.67	0.10
	p(Area + Season),Ψ(.)	4	279.09		13.39	0.00
P. albogularis	p(.),Ψ(Lower_Upper)	4	–	133.58	**0.00**	0.49
	p(.),Ψ(Substrata)	5	–	134.48	**0.90**	0.31
	p(.),Ψ(Strata)	6	–	136.91	3.34	0.09
	p(.),Ψ(Forest floor)	4	–	137.91	4.34	0.06
	p(.),Ψ(Height)	4	–	138.36	4.79	0.04
	p(.),Ψ(.)	3	–	143.51	9.93	0.00
P. tarnii	p(Area),Ψ(Lower_Upper)	4	204.74	–	**0.00**	0.56
	p(Area),Ψ(Substrata)	5	206.99	–	2.24	0.18
	p(Area),Ψ(Strata)	6	207.32	–	2.58	0.15
	p(Area),Ψ(Height)	4	208.21	–	3.47	0.10
	p(Area),Ψ(Forest floor)	4	216.01	–	11.27	0.00
	p(Area),Ψ(.)	3	226.01	–	21.27	0.00
D. gliroides	p(Area),Ψ(Forest floor)	5	–	348.24	**0.00**	0.54
	p(Area),Ψ(Substrata)	6	–	350.68	2.44	0.16
	p(Area),Ψ(.)	4	–	350.91	2.67	0.14
	p(Area),Ψ(Lower_Upper)	5	–	351.43	3.19	0.11
	p(Area),Ψ(Strata)	7	–	352.92	4.68	0.05
	p(Area),Ψ(Height)	5	–	357.28	9.04	0.01
Rodents	p(Area + Season),Ψ(Lower_Upper)	5	338.15	–	**0.00**	0.33
	p(Area + Season),Ψ(Substrata)	6	338.23	–	**0.07**	0.32
	p(Area + Season),Ψ(Forest floor)	5	339.10	–	**0.95**	0.21
	p(Area + Season),Ψ(Strata)	7	340.62	–	2.46	0.10
	p(Area + Season),Ψ(Height)	5	342.19	–	4.03	0.04
	p(Area + Season),Ψ(.)	4	349.35	–	11.20	0.00
Liolaemus sp.	p(Season),Ψ(Lower_Upper)	5	–	214.19	**0.00**	0.53
	p(Season),Ψ(Substrata)	6	–	215.18	**0.99**	0.32
	p(Season),Ψ(Strata)	7	–	217.70	3.51	0.09
	p(Season),Ψ(Height)	5	–	218.53	4.34	0.06
	p(Season),Ψ(.)	4	–	225.52	11.33	0.00
	p(Season),Ψ(Forest floor)	5	–	225.98	11.78	0.00

probability of being used by rodents ($\omega = 0.86$; Table 1). Furthermore, candidate models show a preference for the understory over the canopy, without clear preferences between the forest floor and the understory.

Liolaemus sp. The best detection model ($\omega = 0.40$) included Season as a covariate (Supp. Material 3). Two models appeared as plausible to explain lizard occupancy (Table 1). The best occupancy model was the Lower-Upper model ($\omega = 0.53$; Table 1) and showed a preference of
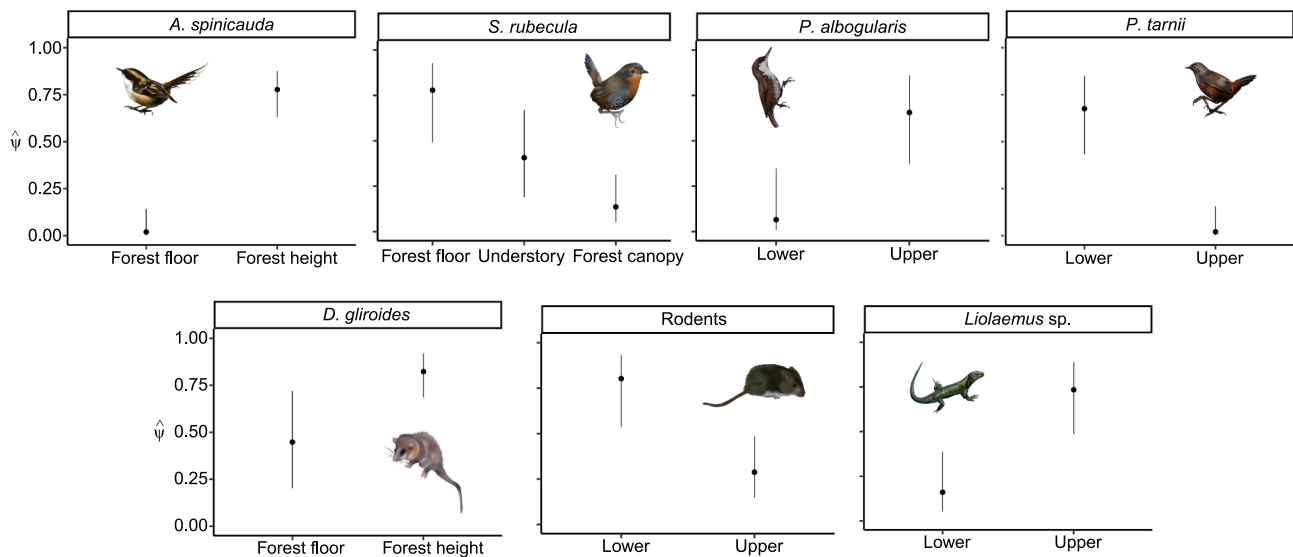
Fig. 3. Predicted occupancy for the seven taxa analyzed in the vertical profile of the forest, based on the best model selected. Error bars correspond to 95% confidence intervals.

lizards for the upper strata (lower and upper canopy, Fig. 3). The second candidate was the substrata model (Table 1), with similar results, although suggesting differences between the forest floor and the understory.

3.2. Activity patterns

The four species of birds and the lizard showed diurnal activity patterns, while *D. gliroides* and the rodents were nocturnal (Fig. 4). For most species, we found high activity overlap when using different strata ($\Delta = 0.86$ to 0.92, Fig. 5). The exception was the lizard (Fig. 5e), that showed little overlap ($\Delta_1 = 0.35$) between activity in the lower and upper strata of the forest (Fig. 5e). The activity of the lizard in the lower strata was highly concentrated at noon, while in the upper strata of the forest it was active most of the day (Fig. 5e).

In the case of birds, activity patterns were similar when comparing species within a family, and different between species of different families (Fig. 6). The rhinocryptids (*S. rubecula* and *P. tarnii*) had very similar activity patterns ($\Delta_4 = 0.84$), with activity peaks in the first hours of the day, and a second—but lower—peak close to sunset

(Fig. 6a). Similarly, the furnarids (*A. spinicauda* and *P. albogularis*) presented a high overlap in their activity patterns ($\Delta_4 = 0.91$), and with highest activity concentrated around noon (Fig. 6f). Comparisons between species of different families (*S. rubecula* vs *P. albogularis*, *S. rubecula* vs *A. spinicauda*, *P. tarnii* vs *P. albogularis* and *P. tarnii* vs *A. spinicauda*) showed an intermediate overlap, with Δ_4 values of 0.69, 0.69, 0.61 and 0.59, evidencing differences in activity patterns depending on the bird families (Fig. 5).

4. Discussion

Our study is among the first systematic efforts (see Moore et al., 2021)—and the first in Chile—to compare wildlife occupancy across the vertical forest profile. The studied animals differed in their use of the vertical profile of the forest (Fig. 3). Some species preferentially used the strata linked to the canopy, others the whole vertical profile—except for the forest floor—and others the lower strata of the forest (forest floor and understory). Therefore, our study, together with others that have addressed variation in diversity and relative abundance (Chmel et al., 2021; Ferreira de Camargo et al., 2018; Jayson and Mathew, 2003;
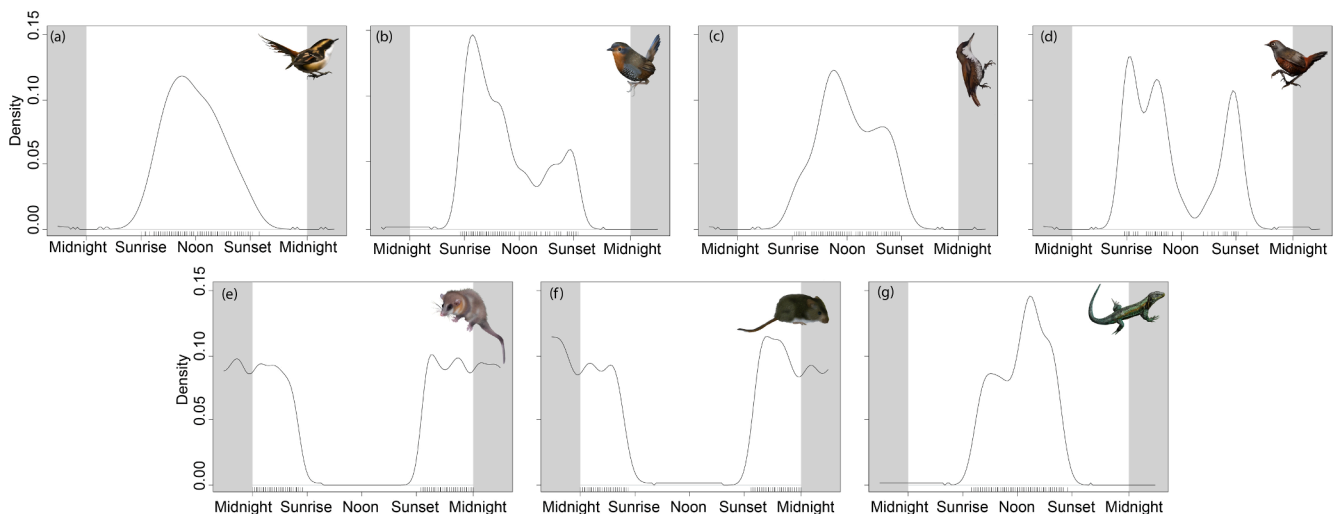

Fig. 4. Activity patterns of (a) *A. spinicauda*; (b) *S. rubecula*; (c) *P. albogularis*; (d) *P. tarnii*; (e) *D. gliroides*; (f) rodents and (g) *Liolaemus* sp., in Bosque Pehuén Park, Chile.
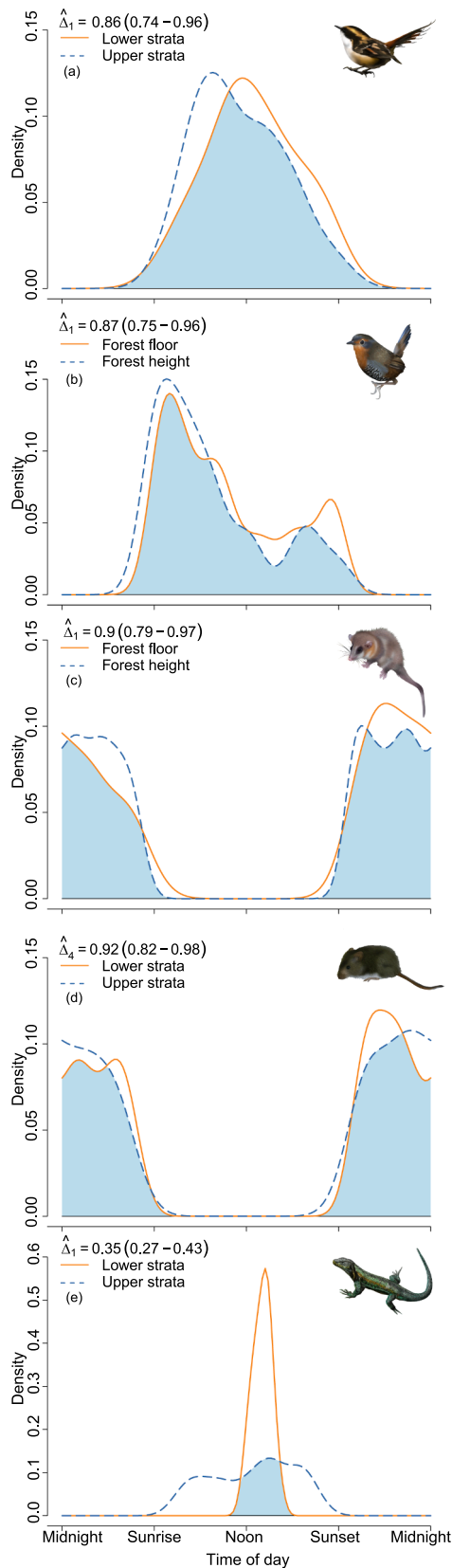
Fig. 5. Comparison of activity patterns between different forest strata for five different species: (a) *A. spinicauda*; (b) *S. rubecula*; (c) *D. gliroides*; (d) rodents and (e) *Liolaemus* sp. Overlap estimates ($\hat{\Delta}_1$ or $\hat{\Delta}_4$) and confidence intervals are also shown.

Pearson, 1971; Thiel et al., 2021), strongly suggests that vertical heterogeneity and forest stratification play an important role in how wildlife is distributed in forest ecosystems.

In this study we compared six different models to characterize the use of the vertical forest profile by wildlife. Three of these models were consistently better at explaining the use of space by the seven taxa analyzed. The first of these models is the Forest floor versus height strata. This model provided the better fit for two species (*A. spinicauda* and *D. gliroides*), both associated to the vertical profile, without distinction between understory, lower canopy, and upper canopy (Table 1, Fig. 3). The second corresponds to the Lower-Upper model that provided better fit for four taxa. Two of them (rodents and *P. tarnii*) were associated to the lower strata (forest floor and understory), and the other two (*P. albogularis* and lizards) were associated to the upper strata (lower and upper canopy, Table 1, Fig. 3). Finally, the use of the vertical profile by one bird (*S. rubecula*) was better explained by the Substrata model. In this case, *S. rubecula* used preferentially, the forest floor followed by the understory. The Height from the ground model was not supported for any of the analyzed taxa. The lack of association between height and occupancy reported here and in previous work (Moore et al., 2020), is likely explained by the fact that forest species respond to structural elements of the habitat, rather than height itself (see also Altamirano et al., 2017; Díaz et al., 2005; Reid et al., 2004). The differences between strata found in our work clearly illustrate that estimates from the ground and/or lower strata severely underestimate the area occupied by the species that inhabit the canopy of the forest. For example, the area occupied by the *P. albogularis* was high in the upper strata (66%) and low in lower strata (7%, Fig. 3). Based on traditional bird counts, it has often been reported that this species occurs at low abundances (<0.2 ind/ha; e.g., Díaz et al., 2005, 2019; Fontúrbel et al., 2016; Jiménez, 2000) and detected in relatively small proportion of the sampling sites (<20%, e.g., Drake et al., 2021; Jiménez, 2000). However, our results suggest that these studies largely underestimate true abundance and occupancy. Similarly, the presence of *Liolaemus* sp. lizards was associated with the upper strata of the forest (Fig. 3). The current understanding of the biology of these species (e.g., *Liolaemus pictus*, the most common species in the forests of this area) indicates that they preferentially use the ecotones and not the interior of the forest—except for clearings—(Abdala et al., 2016; Pincheira-Donoso and Núñez, 2005). On the contrary, our data reveal a strong use of the interior of the forest, but that this use occurs in the upper strata of the canopy (Fig. 3). In both cases, ground surveys would lead to significant underestimation of the area occupied by canopy species, inducing biases in the understanding of patterns of habitat use and selection.

In general, our analyses show that there are no important intra-taxa differences in activity patterns between forest strata (Fig. 5). The only exception is the lizard, which was active most of the day in the canopy, whereas activity in the lower strata was restricted to the noon (Fig. 5e). These differences may be explained by thermoregulation. The activity patterns of *Liolaemus* lizards are limited by thermal constrains and concentrate at hours when solar radiation is higher (Marquet et al., 1989). Solar radiation in the lower strata of the forest is very limited in contrast with the high canopy. Then, differences both in activity patterns and use of different strata likely correspond to behavioral strategies to cope with the thermal challenges that prevail in the area (see Artacho et al., 2017). The remaining species, behave predictably showing strictly nocturnal (small mammals) or diurnal (birds) activity patterns (Fig. 4). However, it is interesting that the activity patterns of two of the four birds analyzed peaked close to noon and not at sunrise and sunset (Fig. 6), as usually assumed in the design of ornithological studies (Bibby et al., 2000; Ralph et al., 1996). These findings must be taken into account for the design of ornithological studies (e.g., Ellis and Taylor, 2018), especially when the focus is to carry out community analyses.

Three-dimensionality is a key component in the use of forested environments by wildlife (Chmel et al., 2021; Harel et al., 2022; Thiel
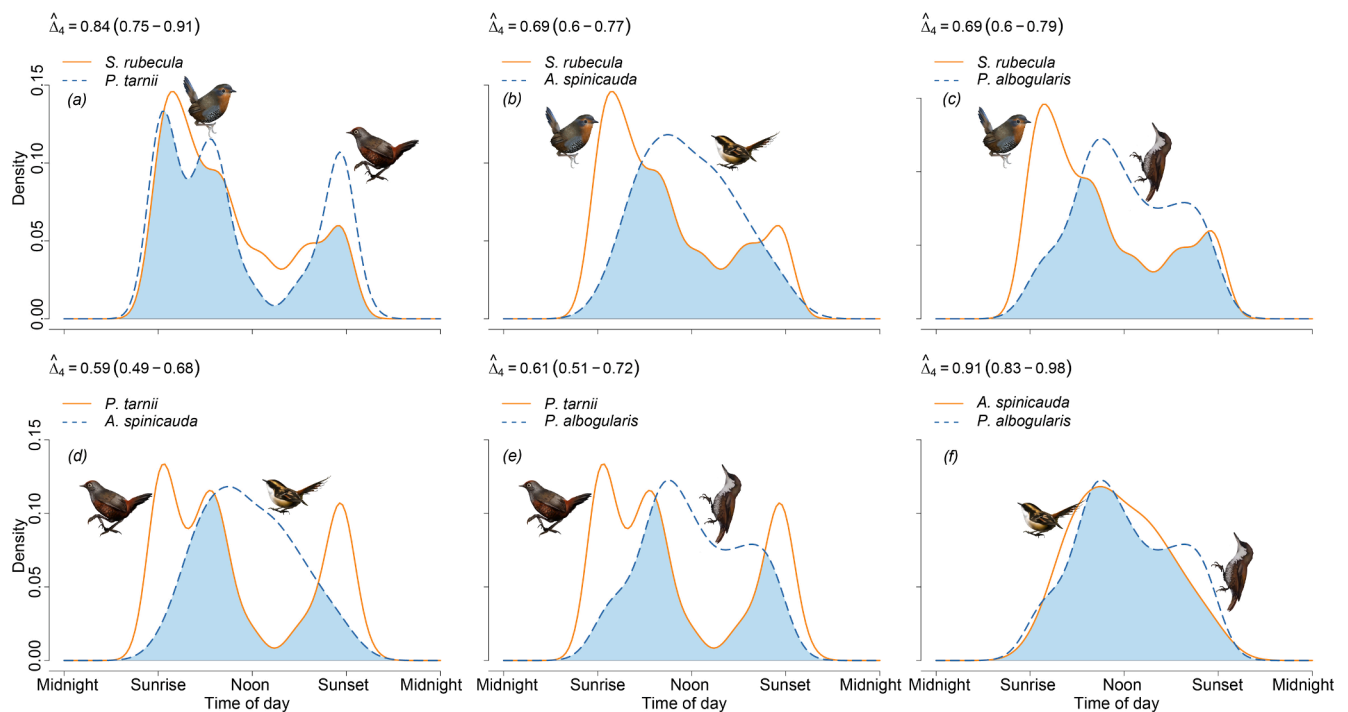
Fig. 6. Comparison of activity patterns between four different bird species. Overlap estimates ($\hat{\Delta}_4$) and confidence intervals are also shown.

et al., 2021; Whitworth et al., 2019). However, much of the work that evaluates patterns of occupancy or abundance of taxa that use the vertical profile of the forest—such as birds and small mammals—have been conducted from the ground, both in the South American temperate forests and in forest ecosystems elsewhere (e.g., Acharya and Vijayan, 2017; Albanese et al., 2011; Díaz et al., 2005; Melo et al., 2013; Rajaonarivelo et al., 2020). Our results showed that two-dimensional sampling designs for species that occupy the upper strata of the vertical profile could induce strong biases in occupancy estimation, underestimating the area occupied by species that use preferentially the canopy (Whitworth et al., 2019). This could be partially addressed using occupancy models, but this solution is only adequate for species that are highly detectable from the ground. The severity of these biases is probably even greater in abundance and, by extension, relative abundance estimation. It is likely that the estimated abundance of species that are highly detectable from the ground will appear as higher than that of cryptic species that preferentially use the canopy (Walther, 2003), even if there are no differences in abundance, also affecting community indexes (e.g., Shannon's index). Based on the above, we emphasize the need to model uncertainty in detection when estimating abundance and occupancy (e.g., Dias et al., 2019; Rich et al., 2016; Wang et al., 2015). Some species—especially highly vocal birds—are detectable from the ground (for example, by acoustic monitoring), and it is feasible to estimate occupancy with ground surveys (as traditionally done). However, in this case it is necessary to ensure an adequate design for each species involved. This implies an adequate number of sites and sampling occasions to model detection uncertainty (Guillera-Arroita et al., 2010; Guillera-Arroita and Lahoz-Monfort, 2012; Kays et al., 2020), and considering the biology of target species (e.g., activity patterns) when designing survey protocols. However, in the case of cryptic species that select the canopy, proper assessment of occupancy and abundance requires sampling the canopy (e.g., Bowler et al., 2017; Moore et al., 2020; Whitworth et al., 2019).

Our study provides novel insights onto wildlife use of the vertical forest profile, but it is not exempt from limitations. First, the approach used to sample the canopy is better suited for species that preferentially use the tree-trunks. However, some of the most abundant birds in

Chilean forests such as the flycatcher *Elaenia albiceps* (Tyrannidae) and the hummingbird *Sephanoides sephaniodes* (Trochilidae) (e.g., Díaz et al., 2005; Jiménez, 2000) were barely recorded, probably because these species use the foliage, a different substratum that we did not survey for safety and logistical reasons. A combination of different technologies, including automated recorders (e.g., Acevedo et al., 2009; Furnas and Callas, 2015) and camera traps, could help to fulfill this gap in the future. Second, our study was designed to compare the use of different strata by species that are relatively frequent. For example, we were unable to model occupancy by the *Campephilus magellanicus* (Picidae), because sample size was insufficient. However, the species was clearly associated to the upper strata (detected between 20 and 25% of upper and 0% of lower cameras, Supp. Material 1). We recommend that future studies that aim at modelling less frequent species—such as *C. magellanicus*—consider larger sample sizes and/or focus exclusively on the strata that are used by target species. In both scenarios sampling design should consider expected probabilities of detection and occupancy (see recommendations in Gálvez et al., 2016; MacKenzie et al., 2017), but also the logistical difficulties and challenges of arboreal surveys (e.g. time, costs, access to treetops, risk, etc., Moore et al., 2021). Despite these limitations, camera traps have proven useful to study many different canopy species, including birds and even reptiles (this study, Bowler et al., 2017; Gregory et al., 2014; Moore et al., 2021).

Habitat use by vertebrates in three-dimensional ecosystems is important for forest management and conservation. Our study showed that wildlife species differ in the use of the vertical profile of the forest, and this should be considered in forests biodiversity assessments (Belant et al., 2012; Cunha and Vieira, 2004; Harel et al., 2022; Moore et al., 2020). This implies that general surveys from the ground needs to be complemented with canopy surveys. Furthermore, our study opens further questions. For example, many studies have already showed the importance of large old trees (e.g., Lindenmayer and Laurance, 2016) and standing dead trees (Moreira-Arce et al., 2021) for conservation. We suspect that the use of the vertical profile might differ between young and old trees, and between forests under different types of management. The formal acknowledgement of the role of the forest canopy as wildlife habitat is therefore, an important first step towards the conservation of

forest ecosystems.

CRediT authorship contribution statement

Javier Godoy-Güinao: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Eduardo A. Silva-Rodríguez:** Conceptualization, Funding acquisition, Methodology, Formal analysis, Writing – review & editing. **Brayan Zambrano:** Investigation, Writing – review & editing. **Iván A. Díaz:** Conceptualization, Funding acquisition, Project administration, Methodology, Investigation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120668.

References

Abdala, S., Avila, L., Sallabery, N., Ortiz, J.., Victoriano, P., Nunez, J., Garin, J., Marambio, C., Nunez, H., Vidal, M., Avilés, R., 2016. *Liolaemus pictus*, Painted Tree Iguana. IUCN Red List Threat. Species e.T56085628A56085843.

Acevedo, M.A., Corrada-Bravo, C.J., Corrada-Bravo, H., Villanueva-Rivera, L.J., Aide, T. M., 2009. Automated classification of bird and amphibian calls using machine learning: a comparison of methods. Ecol. Inform. 4, 206–214. https://doi.org/10.1016/j.ecoinf.2009.06.005.

Acharya, B.K., Vijayan, L., 2017. Vertical stratification of birds in different vegetation types along an elevation gradient in the Eastern Himalaya, India. Ornithol. Sci. 16, 131–140.

Albanese, S., Rodríguez, D., Ojeda, R.A., 2011. Differential use of vertical space by small mammals in the Monte Desert, Argentina. J. Mammal. 92, 1270–1277. https://doi.org/10.1644/10-MAMM-A-353.1.

Allen, M.L., Peterson, B., Krofel, M., 2018. No respect for apex carnivores: distribution and activity patterns of honey badgers in the Serengeti. Mamm. Biol. 89, 90–94. https://doi.org/10.1016/j.mambio.2018.01.001.

Altamirano, T.A., Ibarra, J.T., Martin, K., Bonacic, C., 2017. The conservation value of tree decay processes as a key driver structuring tree cavity nest webs in South American temperate rainforests. Biodivers. Conserv. 26, 2453–2472. https://doi.org/10.1007/s10531-017-1369-x.

Armesto, J.J., Villagrán, C., Arroyo, M.K., 1995. Ecología de los Bosques Nativos de Chile, 1st ed. Editorial Universitaria, S.A., Santiago, Chile.

Armesto, J.J., Rozzi, R., Smith-Ramírez, C., Arroyo, M.T., 1998. Conservation targets in South American temperate forests. Science 282, 1271–1272.

Artacho, P., Saravia, J., Perret, S., Bartheld, J.L., Le Galliard, J.-F., 2017. Geographic variation and acclimation effects on thermoregulation behavior in the widespread lizard *Liolaemus pictus*. J. Therm. Biol. 63, 78–87. https://doi.org/10.1016/j.jtherbio.2016.11.001.

Azcarraga, A.A., Tessaro, S.G., Delfin-Alfonso, C.A., 2020. Activity patterns of arboreal mammals in a tropical rain forest in México. Therya 11, 225–231. https://doi.org/10.12933/therya-20-779.

Belant, J.L., Millspaugh, J.J., Martin, J.A., Gitzen, R.A., 2012. Multi-dimensional space use: the final frontier. Front. Ecol. Environ. 10, 11–12. https://doi.org/10.1890/12.WB.003.

Bibby, C., Burgess, N., Hill, D., Mustoe, S., 2000. Bird Census Techniques, second ed. Academic Press, London, UK.

Bowler, M.T., Tobler, M.W., Endress, B.A., Gilmore, M.P., Anderson, M.J., 2017. Estimating mammalian species richness and occupancy in tropical forest canopies with arboreal camera traps. Remote Sens. Ecol. Conserv. 3, 146–157. https://doi.org/10.1002/rse2.35.

Bull, E.L., Holthausen, R.S., 1993. Habitat use and management of pileated woodpeckers in Northeastern Oregon. J. Wildl. Manage. 57, 335–345.

Burnham, K.P., Anderson, D.R., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed. Springer-Verlag, New York.

Castellón, T.D., Sieving, K.E., 2007. Patch network criteria for dispersal-limited endemic birds. Ecol. Appl. 17, 2152–2163.

Chmel, K., Kamga, S.M., Awa II, T., Ewome, F.L., Uceda-Gómez, G., Horák, D., Mlíkovosky, J., Molua, L.L., Riegert, J., Janecek, S., 2021. Vertical stratification and seasonal changes of the avian community in Mount Cameroon lowland rainforest. Afr. J. Ecol. 1–12 https://doi.org/10.1111/aje.12877.

Cunha, A.A., Vieira, M.V., 2004. Two bodies cannot occupy the same place at the same time, or the importance of space in the ecological niche. Bull. Ecol. Soc. Am. 116, 25–26.

di Castri, F., Hajek, E.R., 1976. Bioclimatología de Chile. Ediciones Universidad Católica de Chile, Santiago, Chile.

Dias, D.D.M., Lima Massara, R., Bueno De Campos, C., Guimarães Rodrigues, F.H., 2019. Human activities influence the occupancy probability of mammalian carnivores in the Brazilian Caatinga. Biotropica 1–13. https://doi.org/10.1111/btp.12628.

Díaz, I., Armesto, J., Reid, S., Sieving, K., Willson, M., 2005. Linking forest structure and composition: avian diversity in successional forests of Chiloé Island. Chile. Biol. Conserv. 123, 91–101. https://doi.org/10.1016/j.biocon.2004.10.011.

Díaz, I.A., Correa, C., Pena-Foxon, M.E., Mendez, M.A., Charrier, A., 2010a. First record on an amphibian in the canopy of temperate rainforests of southern South America: *Eupsophus calcaratus* (Cycloramphidae). Bosque 31, 165–168. https://doi.org/10.4067/S0717-92002010000200010.

Díaz, I.A., Sieving, K.E., Peña-Foxon, M.E., Larraín, J., Armesto, J.J., 2010b. Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: a neglected functional component. For. Ecol. Manage. 259, 1490–1501. https://doi.org/10.1016/j.foreco.2010.01.025.

Díaz, I.A., Sieving, K.E., Peña-Foxon, M., Armesto, J.J., 2012. A field experiment links forest structure and biodiversity: epiphytes enhance canopy invertebrates in Chilean forests. Ecosphere 3, 1–17.

Díaz, I.A., Godoy-Güinao, J., Sidler, H., Mellado-Mansilla, D., Ortega, G., 2019. Bird communities along a post-disturbance succesional gradient in Andean Forest of Bosque Pehuén park, Araucanía region, Southern Chile. Ornitol. Neotrop. 30, 113–122.

Díaz, I.A., Godoy-Güinao, J., Mellado-Mansilla, D., Moreno-González, R., Cuq, E., Ortega-Solís, G., Armesto, J.J., 2020. Advanced canopy regeneration: an unrecognized mechanism of forest dynamics. Ecology 102, 2019–2022. https://doi.org/10.1002/ecy.3222.

Drake, A., Zwaan, D.R. De, Altamirano, T.A., Wilson, S., Hick, K., Bravo, C., Tomás, J., Martin, K., 2021. Combining point counts and autonomous recording units improves avian survey efficacy across elevational gradients on two continents 1–29. doi: 10.1002/ece3.7678.

Ellis, M.V., Taylor, J.E., 2018. Effects of weather, time of day, and survey effort on estimates of species richness in temperate woodlands. Emu - Austral Ornithol. 118, 183–192. https://doi.org/10.1080/01584197.2017.1396188.

Ferreira de Camargo, N., Sano, N.Y., Vieira, E.M., 2018. Forest vertical complexity affects alpha and beta diversity of small mammals. J. Mammal. 99, 1444–1454. https://doi.org/10.1093/jmammal/gyy136.

Fiske, I., Chandler, R., 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. J. Statical Softw. 43, 1–23.

Fontúrbel, F.E., Jiménez, J.E., 2009. Underestimation of abundance of the monito del monte (*Dromiciops gliroides*) due to a sampling artifact. J. Mammal. 90, 1357–1362.

Fontúrbel, F.E., Silva-Rodríguez, E.A., Cárdenas, N.H., Jiménez, J.E., 2010. Spatial ecology of monito del monte (*Dromiciops gliroides*) in a fragmented landscape of southern Chile. Mamm. Biol. 75, 1–9. https://doi.org/10.1016/j.mambio.2009.08.004.

Fontúrbel, F.E., Candia, A.B., Castaño-Villa, G.J., 2016. ¿Son las plantaciones abandonadas de eucalipto amigables con la avifauna? Un estudio de caso del bosque lluvioso valdiviano. Rev. Mex. Biodivers. 87, 1402–1406. https://doi.org/10.1016/j.rmb.2016.09.011.

Furnas, B.J., Callas, R.L., 2015. Using automated recorders and occupancy models to monitor common forest birds across a large geographic region. J. Wildl. Manage. 79, 325–337. https://doi.org/10.1002/jwmg.821.

Gálvez, N., Guillera-Arroita, G., Morgan, B.J.T., Davies, Z.G., 2016. Cost-efficient effort allocation for camera-trap occupancy surveys of mammals. Biol. Conserv. 204, 350–359. https://doi.org/10.1016/j.biocon.2016.10.019.

Gálvez, N., Meniconi, P., Infante, J., Bonacic, C., 2021. Response of mesocarnivores to anthropogenic landscape intensification: activity patterns and guild temporal interactions. J. Mammal. 1–16 https://doi.org/10.1093/jmammal/gyab074.

García-Marmolejo, G., Chapa-Vargas, L., Weber, M., Huber-Sanwald, E., 2015. Landscape composition influences abundance patterns and habitat use of three ungulate species in fragmented secondary deciduous tropical forests. Mexico. Glob. Ecol. Conserv. 3, 744–755. https://doi.org/10.1016/j.gecco.2015.03.009.

Godoy-Güinao, J., Díaz, I.A., Celis-Diez, J.L., 2018. Confirmation of arboreal habits in *Dromiciops gliroides*: a key role in Chilean Temperate Rainforests. Ecosphere 9, 1–6. https://doi.org/10.1002/ecs2.2424.

Godoy-Güinao, J., Díaz, I.A., 2018. First records of Rhynocriptid understory birds in the Canopy of Chilean Temperate Rainforest. Ornitol. Neotrop. 29, 297–300.

Gregory, T., Carrasco Rueda, F., Deichmann, J., Kolowski, J., Alonso, A., 2014. Arboreal camera trapping: taking a proven method to new heights. Methods Ecol. Evol. 5, 443–451. https://doi.org/10.1111/2041-210X.12177.

Guillera-Arroita, G., Lahoz-Monfort, J.J., 2012. Designing studies to detect differences in species occupancy: power analysis under imperfect detection. Methods Ecol. Evol. 3, 860–869. https://doi.org/10.1111/j.2041-210X.2012.00225.x.

Guillera-Arroita, G., Ridout, M.S., Morgan, B.J.T., 2010. Design of occupancy studies with imperfect detection. Methods Ecol. Evol. 1, 131–139. https://doi.org/10.1111/j.2041-210X.2010.00017.x.

Guzy, J.C., Halloran, K.M., Homyack, J.A., Thornton-Frost, J.E., Willson, J.D., 2019. Differential responses of amphibian and reptile assemblages to size of riparian buffers within managed forests. Ecol. Appl. 29, e01995.

Hall, L.S., Krausman, P.R., Morrison, M.L., 1997. The habitat concept and a plea for standard terminology. Wildl. Soc. Bull. 25, 173–182.

Hallé, F., Oldeman, R., Tomlinson, P., 2012. Tropical Trees and Forests: An Architectural Analysis. Springer-Verlag, Berlin.

Harel, R., Alavi, S., Ashbury, A.M., Aurisano, J., Berger-Wolf, T., Davis, G.H., Hirsch, B. T., Kalbitzer, U., Kays, R., Mclean, K., Núñez, C.L., Vining, A., Walton, Z., Worsoe Havmoller, R., Crofoot, M.C., 2022. Life in 2.5D: animal movement in the trees. Front. Ecol. Evol. 10, 801850 https://doi.org/10.3389/fevo.2022.801850.

Hongo, S., Dzefack, Z., Vernyuy, L., Minami, S., Nakashima, Y., Djiéto-Lordon, C., Yasuoka, H., 2020. Use of multi-layer camera trapping to inventory mammals in rainforests in Southeast Cameroon. Afr. Study Monogr. 60, 21–37.

Instituto de Innovación Agraria, I., 2019. Red agrometeorológica de INIA. Available from: <https://agrometeorologia.cl/> (accessed 8.3.20).

Jayson, E.A., Mathew, D.N., 2003. Vertical stratification and its relation to foliage in tropical forest birds in Western Ghats (India). Acta Ornithol. 38, 111–116.

Jiménez, J., 2000. Effect of sample size, plot size, and counting time on estimates of avian diversity and abundance in a Chilean rainforest. J. F. Ornithol. 71, 66–87. https://doi.org/10.1648/0273-8570-71.1.66.

Jung, K., Kaiser, S., Böhm, S., Nieschulze, J., Kalko, E.K.V., 2012. Moving in three dimensions: effects of structural complexity on occurrence and activity of insectivorous bats in managed forest stands. J. Appl. Ecol. 49, 523–531. https://doi.org/10.1111/j.1365-2664.2012.02116.x.

Kays, R., Arbogast, B.S., Baker-Whatton, M., Beirne, C., Boone, H.M., Bowler, M., Burneo, S.F., Cove, M.V., Ding, P., Espinosa, S., Gonçalves, A.L.S., Hansen, C.P., Jansen, P.A., Kolowski, J.M., Knowles, T.W., Lima, M.G.M., Millspaugh, J., McShea, W.J., Pacifici, K., Parsons, A.W., Pease, B.S., Rovero, F., Santos, F., Schuttler, S.G., Sheil, D., Si, X., Snider, M., Spironello, W.R., 2020. An empirical evaluation of camera trap study design: How many, how long and when? Methods Ecol. Evol. 11, 700–713. https://doi.org/10.1111/2041-210X.13370.

Kéry, M., Royle, J.A., 2016. Modeling static occurrence and species distributions using site-occupancy models. Appl. Hierarchical Modeling Ecol. 551–629. https://doi.org/10.1016/b978-0-12-801378-6.00010-2.

Lindenmayer, D.B., Laurance, W.F., 2016. The ecology, distribution, conservation and management of large old trees. Biol. Rev. https://doi.org/10.1111/brv.12290.

Lynam, A.J., Jenks, K.E., Tantipisanuh, N., Chuting, W., Ngoprasert, D., Gale, G.A., Steinmetz, R., Sukmasuang, R., Bhumpakphan, N., Grassman Jr., L.I., Cutter, P., Kitamura, S., Reed, D.H., Baker, M.C., McShea, W., Songsasen, N., Leimgruber, P., 2013. Terrestrial activity patterns of wild cats from camera-trapping. raffles Bull. Zool. 61, 407–415.

MacKenzie, D.I., Bailey, L.L., 2004. Assessing the fit of site-occupancy models. J. Agric. Biol. Environ. Stat. 9, 300–318. https://doi.org/10.1198/108571104X3361.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2017. Occupancy Estimation and Modeling: Inferring Patterns aSnd Dynamics of Species Occurence, second ed. Elsevier Academic Press, London, UK.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Royle, A., Langtimm, C.A., 2002. Estimating site occupancy rates when detection probabilities are less than one. Ecology 83, 2248–2255. https://doi.org/10.1111/j.1365-3040.1991.tb00950.x.

Marquet, P.A., Ortiz, J., Bozinovic, F., Jaksic, F.M., 1989. Ecological aspects of thermoregulation at high altitudes: the case of Andean *Liolaemus* lizards in northern Chile. Oecologia 81, 16–20.

Mazerolle, M.J., 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.3-0. https://cran.r-project.org/package=AICcmodavg.

Meek, P.D., Vernes, K., 2016. Can camera trapping be used to accurately survey and monitor the Hastings River mouse (*Pseudomys oralis*)? Aust. Mammal. 38, 44–51.

Mellado-Mansilla, D., León, C.A., Ortega-Solís, G., Godoy-Güinao, J., Moreno, R., Díaz, I. A., 2017. Vertical patterns of epiphytic bryophyte diversity in a montane *Nothofagus* forest in the Chilean Andes. New Zeal. J. Bot. 55, 514–529. https://doi.org/10.1080/0028825X.2017.1364273.

Mellado-Mansilla, D., Díaz, I.A., Godoy-Güinao, J., Ortega-Solís, G., Moreno-Gonzalez, R., 2018. Bosque Pehuén park's flora: A contribution to the knowledge of the Andean Montane Forests in the Araucanía Region. Chile. Nat. Areas J. 38, 298–311. https://doi.org/10.3375/043.038.0410.

Melo, G.L., Miotto, B., Peres, B., Cáceres, N.C., 2013. Microhabitat of small mammals at ground and understorey levels in a deciduous, Southern Atlantic Forest 85, 727–736.

Meredith, M., Ridout, M., 2021. Package "overlap." Available from: <https://cran.r-project.org/web/packages/overlap/overlap.pdf>. Accesed 15 June 2022.

Moore, J.F., Pine, W.E., Mulindahabi, F., Niyigaba, P., Gatorano, G., Masozera, M.K., Beaudrot, L., 2020. Comparison of species richness and detection between line transects, ground camera traps, and arboreal camera traps. Anim. Conserv. https://doi.org/10.1111/acv.12569.

Moore, J.F., Soanes, K., Balbuena, D., Beirne, C., Bowler, M., Carrasco-Rueda, F., Cheyne, S.M., Coutant, O., Forget, P., Haysom, J.K., Houlihan, P.R., Olson, E.R., Lindshield, S., Martin, J., Tobler, M., Whitworth, A., Gregory, T., 2021. The potential and practice of arboreal camera trapping. Methods Ecol. Evol. 2021, 1–12. https://doi.org/10.1111/2041-210x.13666.

Morante-Filho, J.C., Benchimol, M., Faria, D., 2021. Landscape composition is the strongest determinant of bird occupancy patterns in tropical forest patches. Landsc. Ecol. 36, 105–117. https://doi.org/10.1007/s10980-020-01121-6.

Moreira-Arce, D., Vergara, P.M., Fierro, A., Pincheira, E., Crespin, S.J., Alaniz, A., Carvajal, M.A., 2021. Standing dead trees as indicators of vertebrate diversity: bringing continuity to the ecological role of senescent trees in austral temperate forests. Ecol. Indic. 129, 107878 https://doi.org/10.1016/j.ecolind.2021.107878.

Morrison, M.L., Mathewson, H.A., 2015. Wildlife Habitat Conservation: Concepts, Challenges and Solutions. JHU Press, Baltimore, Maryland.

Nouvellet, P., Rasmussen, G.S.A., MacDonald, D.W., Courchamp, F., 2012. Noisy clocks and silent sunrises: measurement methods of daily activity pattern. J. Zool. 286, 179–184. https://doi.org/10.1111/j.1469-7998.2011.00864.x.

Oliveira, B.F., Scheffers, B.R., 2018. Vertical stratification influences global patterns of biodiversity. Ecography (Cop.) 41, 1–10. https://doi.org/10.1111/ecog.03636.

Parker, G.G., Brown, M.J., 2000. Forest canopy stratification — Is it useful? Am. Nat. 155, 473–484.

Pearson, D.L., 1971. Vertical stratification of birds in a tropical dry forest. Condor 73, 46–55.

Pearson, D.L., 1975. The relation of foliage complexity to ecological diversity of three amazonian bird communities. Condor 77, 453–466.

Perry, D.R., 1978. A method of access into the crowns of emergent and canopy trees. Biotropica 10, 155–157. https://doi.org/10.1017/CBO9781107415324.004.

Pincheira-Donoso, D., Núñez, H., 2005. Las especies chilenas del género *Liolaemus wiegmann*, 1834 (Iguania: Tropiduridae: Liolaeminae). Taxonomía, sistemática y evolución. Santiago, Chile.

QGIS Develop Team. 2022. QGIS Geographic Information System. Open Source Geospatial Found. Available from: <http://qgis.osgeo.org>.

Rabanal, F.E., Úbeda, C., Tejo, C.F., Lavilla, E.O., 2021. Tree-holes as alternative reproductive sites of *Batrachyla antartandica* Barrio, 1967 (Anura: Batrachylidae). South Am. J. Herpetol. 20, 24–32.

Rader, R., Krockenberger, A., 2006. Three-dimensional use of space by a tropical rainforest rodent, *Melomys cervinipes*, and its implications for foraging and home-range size. Wildl. Res. 33, 577–582.

Rajaonarivelo, J.A., Andrianarimisa, A., Raherilalao, M.J., Goodman, S.M., 2020. Vertical distribution and daily patterns of birds in the dry deciduous forests of central western Madagascar. Trop. Zool. 33, 36–52. https://doi.org/10.4081/tz.2020.66.

Ralph, J.C., Geupel, G.R., Pyle, P., Martin, T.E., Desante, D.F., Milá, B., 1996. Manual de métodos de campo para el monitoreo de aves terrestres. Pacific Southwest Research Station, Forest Service, Albany, CA.

Reid, S., Díaz, I.A., Armesto, J.J., Willson, M.F., 2004. Importance of native bamboo for understory birds in Chilean temperate forests. Auk 121, 515–525. https://doi.org/10.2307/4090415.

Renner, S.C., Suarez-Rubio, M., Kaiser, S., Nieschulze, J., Kalko, E.K.V., Tschapka, M., Jung, K., 2018. Divergent response to forest structure of two mobile vertebrate groups. For. Ecol. Manage. 415–416, 129–138. https://doi.org/10.1016/j.foreco.2018.02.028.

Rich, L.N., Miller, D.A.W., Robinson, H.S., Mcnutt, J.W., Kelly, M.J., 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. J. Appl. Ecol. 53, 1225–1235. https://doi.org/10.1111/1365-2664.12650.

Ridout, M.S., Linkie, M., 2009. Estimating overlap of daily activity patterns from camera trap data. J. Agric. Biol. Environ. Stat. 14, 322–337. https://doi.org/10.1198/jabes.2009.08038.

Rodríguez-Gómez, G.B., Fontúrbel, F.E., 2020. Regional-scale variation on *Dromiciops gliroides* occurrence, abundance, and activity patterns along a habitat disturbance gradient. J. Mammal. 101, 733–741. https://doi.org/10.1093/jmammal/gyaa022.

Rovero, F., Tobler, M., Sanderson, J., 2010. Camera trapping for inventorying terrestrial vertebrates. In: Manual on Field Recording Techniques and Protocols for All Taxa Biodiversity Inventories and Monitoring. The Belgian National Focal Point to the Global Taxonomy Initiative. pp. 100–128.

Rovero, F., Marshall, A.R., 2009. Camera trapping photographic rate as an index of density in forest ungulates. J. Appl. Ecol. 46, 1011–1017. https://doi.org/10.1111/j.1365-2664.2009.01705.x.

Rovero, F., Zimmermann, F., Berzi, D., Meek, P., 2013. "Which camera trap type and how many do I need?" A review of camera features and study designs for a range of wildlife research applications. Hystrix 24, 148–156. https://doi.org/10.4404/hystrix-24.2-6316.

RStudio Team, 2020. RStudio: Integrated Development for R. RStudio, PBC, Boston, MA. Available from: <https://www.rstudio.com/>.

Sanderson, J., Harris, G., 2013. Automatic data organization, storage and analysis of camera trap pictures. J. Indones. Nat. Hist. 1, 11–19. https://doi.org/10.1890/0012-9623-91.3.352.

Scheffers, B.R., Shoo, L., Phillips, B., Macdonald, S.L., Anderson, A., VanDerWal, J., Storlie, C., Gourret, A., Williams, S.E., 2017. Vertical (arboreality) and horizontal

(dispersal) movement increase the resilience of vertebrates to climatic instability. Glob. Ecol. Biogeogr. 26, 787–798. https://doi.org/10.1111/geb.12585.

Seidl, C.M., Basham, E.W., Andriamahohatra, L.R., Scheffers, B.R., 2020. Bird's nest fern epiphytes facilitate herpetofaunal arboreality and climate refuge in two paleotropic canopies. Oecologia 192, 297–309. https://doi.org/10.1007/s00442-019-04570-2.

Shaw, D.C., 2004. Vertical Organization of Canopy Biota. In: Lowman, M.D., Rinker, B.H. (Eds.), Forest Canopies. Elsevier Inc., San Diego, California, p. 543.

Silva-Rodríguez, E.A., Sieving, K.E., 2012. Domestic dogs shape the landscape-scale distribution of a threatened forest ungulate. Biol. Conserv. 150, 103–110. https://doi.org/10.1016/j.biocon.2012.03.008.

Silva-Rodríguez, E.A., Ovando, E., González, D., Zambrano, B., Sepúlveda, M.A., Svensson, G.L., Cárdenas, R., Contreras, P., Farías, A.A., 2018. Large-scale assessment of the presence of Darwin's fox across its newly discovered range. Mamm. Biol. 92, 45–53. https://doi.org/10.1016/j.mambio.2018.04.003.

Suzuki, K.K., Ando, M., 2018. Early and efficient detection of an endangered flying squirrel by arboreal camera trapping. Mammalia 83, 372–378.

Tejo, C.F., Fontúrbel, F.E., 2019. A vertical forest within the forest: millenary trees from the Valdivian rainforest as biodiversity hubs. Ecology 100, 1–4. https://doi.org/10.1002/ecy.2584.

Thiel, S., Tschapka, M., Heymann, E.W., Heer, K., 2021. Vertical stratification of seed dispersing vertebrate communities and their interactions with plants in tropical forest. Biol. Rev. 96, 454–469. https://doi.org/10.1111/brv.12664.

Thornton, D.H., Branch, L.C., Sunquist, M.E., 2011. The relative influence of habitat loss and fragmentation: Do tropical mammals meet the temperate paradigm? Ecol. Appl. 21, 2324–2333.

Walther, B.A., 2003. Why canopy access is essential to understand canopy birds: Four examples from the Surumoni Crane Project. Ornitol. Neotrop. 15, 41–52.

Wang, Y., Allen, M.L., Wilmers, C.C., 2015. Mesopredator spatial and temporal responses to large predators and human development in the Santa Cruz Mountains of California. Biol. Conserv. 190, 23–33. https://doi.org/10.1016/j.biocon.2015.05.007.

Wang, B., Rocha, D.G., Abrahams, M.I., Antunes, A.P., Costa, H.C.M., Sousa Gonçalves, A.L., Spironello, W.R., de Paula, M.J., Peres, C.A., Pezzuti, J., Ramalho, E., Lima Reis, M., Carvalho Jr, E., Rohe, F., Macdonald, D.W., Wei Tan, C. K., 2019. Habitat use of the ocelot (*Leopardus pardalis*) in Brazilian Amazon. Ecol. Evol. 9, 5049–5062. https://doi.org/10.1002/ece3.5005.

Whitworth, A., Beirne, C., Huarcaya, R.P., Whittaker, L., Rojas, S.J.S., Tobler, M.W., Macleod, R., 2019. Human disturbance impacts on rainforest mammals are most notable in the canopy, especially for larger-bodied species. Divers. Distrib. 25, 1166–1178. https://doi.org/10.1111/ddi.12930.