Assessing habitat quality when forest attributes have opposing effects on abundance and detectability: a case study on Darwin's frogs

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Abstract

Forest management can be used to increase the local abundance of species of conservation concern. To achieve this goal, managers must be sure that the relationships between the targeted forest attributes and the focal species abundance are based on robust data and inference. This is a critical issue as the same forest attributes could have opposing effects on species abundance and the detectability of individuals, impairing our ability to detect useful habitat quality surrogates and to provide correct forest management recommendations. Using spatially stratified capture-recapture models (a.k.a. multinomial *N*-mixture models), we evaluated the effects of stand-level forest attributes on detection probability and local abundance for the endangered Southern Darwin's frog (*Rhinoderma darwinii*), a forest-specialist and fully terrestrial amphibian endemic to the South American temperate forest. Our results show that an increase of stand basal area and a decrease of daily microclimatic fluctuation (i.e. an increase in structural complexity) were positively associated with the local abundance of *R. darwinii*. These stand-level forest attributes also explained the among-population variation in detection probability, although the relationships were opposite to those for abundance. Consequently, an analysis of raw frog counts (i.e. not adjusted for imperfect detection) did not reveal all the factors associated with local abundance. Our results provide further support to previous claims that raw counts of individuals should not be used, generally, as a proxy of abundance in species inhabiting forest ecosystems and elsewhere. More importantly, the opposite effect of forest attributes on abundance and detectability observed in our study highlights the need to use methods that quantify species-habitat relationships in a robust way and which take habitat-specific imperfect detection into account.

Keywords: amphibian; conservation; habitat degradation; multinomial *N*-mixture model; unmarked

1. Introduction

Anthropogenic land use change is one of the main threats to terrestrial biodiversity (Newbold et al., 2015). Understanding species-habitat relationships is vital to inform the protection and management of imperilled species and their habitats (Martin et al., 2017). Habitat is a species-specific concept referring to the resources and conditions present in an area that allow occupancy, survival and reproduction of individuals (Hall et al., 1997). Yet, from a practical perspective, it is neither possible nor efficient to measure all the resources and conditions that comprise the habitat of a given species. Furthermore, the concept of habitat is not restricted to a binary classification of the environment into habitat and non-habitat but considers a gradient of habitat quality (Fischer and Lindenmayer, 2007). Consequently, conservation biologists interested in managing habitat to increase the local abundance of species of conservation concern, have traditionally focused on habitat quality surrogates (e.g. vegetation types, cover of herbaceous understory, etc.) that may exhibit strong correlations with local abundance or vital rates (e.g., survival and recruitment) of focal species (Franklin et al., 2000; Oldham et al., 2000; Indermaur and Schmidt, 2011; Romano et al., 2017; Unglaub et al., 2018). In forested ecosystems, structural attributes of forest stands seem to be particularly good habitat quality surrogates for forest-specialist animals (Ross et al., 2000; Payer and Harrison, 2003; Watson et al., 2004; Berg et al., 2012; Ibarra et al., 2014; Romano et al. 2017).

In the context of habitat protection and management, it is vital that the relationships between the proxies for habitat quality and the focal species abundance are based on robust data and inference (Kroll et al., 2009; Welsh et al., 2009; Otto et al., 2013; Romano et al., 2017). For instance, the inadequacy of relative abundance (i.e., simple counts) as a proxy of true abundance has been largely acknowledged: due to imperfect detection, true abundance can be underestimated to an unknown degree following this approach (Preston, 1979; Anderson, 2001; Schmidt, 2004; Kéry and Schmidt, 2008). Indeed, the probability of counting an individual that is present and exposed to sampling (i.e. detection probability) often shows a spatial and/or temporal variation associated with observational and environmental covariates (MacKenzie and Kendall, 2002; Pollock et al., 2002; Kéry, 2008;

Tanadini and Schmidt, 2011). Worryingly, if covariation between detection probability and habitat quality exists, the confounding effect of imperfect detection could hamper our capability to detect any association between habitat attributes and true abundance (Bailey et al., 2004; Kéry, 2008).

By taking advantage of recently developed spatially stratified capture-recapture (CR) models, a special class of so-called *N*-mixture models (Royle et al., 2007; Kéry and Royle, 2010, 2016), we evaluated the parallel effects of forest stand attributes on local abundance and detection probability in the endangered Southern Darwin's frog (*Rhinoderma darwinii*). This forest-specialist and fully terrestrial amphibian is endemic to the South American temperate forest (Valenzuela-Sánchez et al. 2015). This ecosystem, with its high levels of species endemism and threats, comprises one of the 35 global biodiversity hotspots (Mittermeier et al., 2011). Despite its uniqueness and ecological importance, around half of the South American temperate forest has been lost due to anthropogenic activity (Tecklin et al., 2010). The major threats to *R. darwinii* are habitat loss and the fungal disease, chytridiomycosis (Soto-Azat et al., 2013a, 2013b; Valenzuela-Sánchez et al., 2017). Additionally, based on evidence from other forest-specialist animals, where a positive correlation between stand structural complexity and species abundance has been often found (e.g. Ross et al., 2000; Payer and Harrison, 2003; Watson et al., 2004; Berg et al., 2012; Ibarra et al., 2014), we hypothesise that a reduction of forest structural complexity could lead to habitat degradation for this frog. Habitat degradation could reduce individual vital rates and population abundance and viability. For instance, a reduction of structural complexity could increase microclimatic variability (Spies & Franklin, 1988; Chen et al., 1999), which can negatively affect several organismal processes in amphibians (Raffel et al., 2012; Nowakowski et al. 2018). In particular, we expect to find a positive correlation between *R. darwinii* local abundance and stand-level forest structural attributes such as stand basal area. We test this prediction by using CR data from 10 local populations inhabiting forest stands of differing structural complexity. Additionally, we provide empirical evidence showing that commonly measured forest attributes can have opposing effects on local abundance and detection probability; a possibility that is not always recognized by conservation scientists and managers. Failure to recognize and account for this can impair both the ability to detect useful habitat quality surrogates and to provide correct forest management recommendations.

2. Materials and methods

2.1 Study area

We conducted our field study during January 2013 near Neltume, in the Reserva Biológica Huilo Huilo, southern Chile (39°49’48”S, 72°03’14”W). In this part of the South American temperate forest, the vegetation types vary according to altitude (Caviedes and Ibarra, 2017). We selected 10 forest stands with known presence of *R. darwinii*, all located at a similar altitude (range = 444 – 623 m a.s.l) in the transition zone between the Valdivian forest and the *Nothofagus dombeyi* forest types (sensu Teillier et al., 2013). The dominant tree species in these stands are: *Eucryphia cordifolia*, *Aextoxicon punctatum*, *Weinmannia trichosperma*, *Saxegothaea conspicua*, *Laureliopsis philippiana*, *Nothofagus dombeyi*, *N. obliqua* and *N. aplina*. Intensive selective logging of commercially valuable tree species (e.g. *N. aplina*), which had taken place until the second half of the 20th century, was common in our study area, but at present these forests are used only for tourism, low-intensive selective logging and occasional cattle grazing (Teillier et al., 2013; A. Valenzuela-Sánchez, pers. obs.).

Within each native forest stand we defined a rectangular plot of different size (hereafter ‘study sites’; Table 2) to demarcate each local population of *R. darwinii* and in which to conduct our CR study. At these plots we also measured several stand-level forest attributes (Table 1; see ‘covariates’ below). Distances between plots ranged from 200 to 4,500m, which is longer than the longest annual displacement estimated for this species (~150m; Valenzuela-Sánchez, 2017). Median daily displacement of *R. darwinii* individuals is <1m (Valenzuela-Sánchez, 2017), therefore, at the spatial and temporal scales considered here, we assume *R. darwinii* populations are closed, i.e. both temporary emigration and permanent emigration/immigration occur at negligible rates.

2.2 Capture-recapture of frogs

On each day for five consecutive days, the same two persons (AV-S and CP) surveyed each study site for 1 hr per day, always during daylight hours (09:00–19:00). *Rhinoderma darwinii* individuals are normally found active during day at the ground level within vegetation, leaf litter and woody debris, so during each capture occasion we performed a visual survey in a manner that each researcher covered the entire plot with an equal search effort throughout the site. We captured frogs by hand, wearing a new pair of nitrile gloves, and held them in individual, disposable plastic bags until processing, which consisted of taking photographs of the ventral colouration patterns of each frog to enable individual recognition (Valenzuela-Sánchez et al., 2017). All juveniles and adults captured were visually identified by CP; all identifications were confirmed by AV-S. Recently metamorphosed frogs (<11mm of snout-to-vent length) have not completely developed their individual ventral markings and, therefore, we did not include them in our CR analyses.

2.3 Covariates

We considered six site-level covariates for the modelling of *R. darwinii* detectability and abundance (Table 1 and 2). At each site, we randomly selected 30 sub-plots of 1 m^2, in which we measured the: density of saplings (SAP), tree diversity (*H*), stand basal area (SBA), richness of ferns, flowering plants and other epiphytes (RFE), and fine and coarse woody debris coverage (WD). The procedure used to summarize these measurements at the study site-level is detailed in Table 1. Additionally, using one data logger per site (RHT10, Extech Instruments Corporation, Waltham, MA, USA), we calculated the daily microclimatic fluctuation (DMF), which is a composite of the daily fluctuations of air temperature and air relative humidity measured at the ground level (the procedure used to derive this variable from raw microclimatic data is presented in Appendix A). Correlations between all paired combinations of site-level covariates were low (i.e. Pearson's r < 0.7). Finally, we also considered two observation-level covariates on detection probability: mean air temperature of each day when searches were conducted (TEMP), and an integer representing the day of January when each capture occasion was performed (DAY). To account for the variability in the size of each study site, we used the area of each plot (AREA).

2.4 Modelling detectability and abundance

We used the multinomial *N*-mixture model to estimate local abundance (*N*) while accounting for detection probability (*p*; Royle et al., 2007; Kéry and Royle, 2010, 2016). We applied the *N*-mixture within the context of CR protocols and, therefore, this can be regarded as an extension of classical closed CR models used to estimate local abundance (a.k.a. 'population size'), but which integrates, within a single hierarchical model, data from multiple sites (Royle et al., 2007). Therefore, the multinomial *N*-mixture model allows evaluation of the effect of different covariates on *N* and *p* within the same model (Royle et al. 2007; Kéry and Royle, 2016).

We did not evaluate all possible combinations of model structures for detectability and abundance, because this approach would result in a very large set of alternative models, increasing the chances of finding spurious results (Burnham and Anderson 2002). Instead, we followed a two-stage ad hoc strategy (Doherty et al. 2012). First, we evaluated different models for *p* ('detection models') while keeping *N* constant across study sites (Kéry and Royle 2016). Subsequently, we selected the AIC-best detection model and used this model structure as a basis for expanding the multinomial *N*-mixture model to include the effect of covariates on *N* ('abundance models'). Using a general (i.e. highly parameterized) structure for *N* when evaluating the detection models, as has been previously considered (e.g. Doherty et al. 2012), led to similar results, including the same detection model as best ranked (results not shown).

We modelled frog detectability in two steps. In the first step, we considered only the effect of site-level covariates that are associated with stand structural complexity (i.e. SAP, SBA, WD and DMF), because we expected that a higher forest structural complexity could decrease the chances of detecting frogs due to reduced visibility. Our set of models for detectability included models with only one of the four variables and all pairwise combinations of the four variables, considering only linear relationships and additive effects. We additionally fitted detection models considering the additive effect of a third site-level covariate, with SAP being always present, because this covariate was consistently retained among the top-ranked two-covariate detection models (Appendix A, Table A1). In the second step, we added two observation-level variables (i.e, variables that vary both among sites and capture occasions). To do so, we kept the structure of the AIC-best detection model and added the effect of one of the two observation-level covariates. TEMP was used to account for variation in detectability due to behavioural changes in frogs related to thermoregulation. DAY was used to account for the possibility that researchers could get exhausted or could improve their searching skills throughout the month. We also evaluated a model with p being constant across sites and capture occasions (M_0). This yielded a set of 16 alternative detection models (Appendix A, Table A1).

For the abundance models, we considered site-level covariates associated with compositional (H and RFE) and structural forest stand attributes. Our set of models for local abundance included models with only one of the six variables and all pairwise combinations of the six variables, considering only linear relationships and additive effects. This yielded a set of 22 alternative abundance models (Appendix A, Table A2).

To fit the models to the data we used the gmultmix function in the R package unmarked (Fiske and Chandler, 2011), which allow us to fit Poisson and negative binomial abundance models (Kéry and Royle, 2016). The gmultmix function has an ‘availability parameter’ (the complement of temporary emigration); we set this parameter at 1 because we are dealing with ordinary closed CR models and, therefore, it is assumed that temporary emigration did not occur during our short study periods (five consecutive days). Based on the AIC-best abundance model, a negative binomial abundance model performed slightly better than a Poisson model (ΔAIC = 1.92), and, therefore, we only report results from negative binomial models. Because study sites varied in area, we included this variable in the models. The inclusion of AREA to the AIC top ranked model did not improve the detection model (ΔAIC without/with AREA = 1.35) nor the abundance model (ΔAIC = 1.55). To assess model fit we performed bootstrap goodness-of-fit (GoF) testing using the parboot function of unmarked. To this end, we used three fit statistics (sum-of-squared errors, Chi-square and Freeman-Tukey) which are used to assess the adequacy of the tested model for predicting *N* (Kéry and Royle, 2016).

3. Results

We made a total of 351 captures of 179 different frogs (Table 2). Of these, 98 (54.7%) were recaptured at least once across capture occasions.

Most of the detection models with *p* being modelled as a function of one or more covariates exhibited a higher support than the M_0 model (Appendix A, Table A1). The ΔAIC between the M_0 model and the AIC best detection model was 34.32. The top ranked model, which was retained as a basis for the modelling of *N*, included the additive effect of three site-level covariates: *p*(SAP+SBA+DMF) (Fig. 1 and Table 3). The models that included TEMP and DAY had only a slightly lower support than the best ranked detection model, but the confidence intervals of the regression coefficients of these observation-level covariates included zero (Table 3).

In the best supported abundance model, *N* was modelled as a function of two site-level covariates: *N*(SBA+DMF) (Fig. 1 and Table 4). This model had an AIC weight of 0.57 and predicted the local abundance well (GoF testing *P* values, sum-of-squared errors = 0.28, Chi-square = 0.28 and Freeman-Tukey = 0.20; c-hat = 1.13; number of simulations = 10,000). As depicted in Fig. 1, the directions of the relationships of DMF and SBA with abundance and detection probability were opposite. As daily microclimatic fluctuation increases, *N* decreases and *p* increases. On the other hand, as stand basal area increases, *N* increases and *p* decreases.

Considering measured covariates values (Table 2), the best abundance model predicted a *p* of 0.78 (95% C.I. = 0.64–0.88) at sites with a high SAP, high DMF and low SBA, and of 0.11 (95% C.I. = 0.06–0.19) at sites with a low SAP, low DMF and high SBA. Estimated *p* at sites with average SAP, DMF and SBA was 0.39 (95% C.I. = 0.35–0.44). For local abundance, this model predicted a value of three frogs (95% C.I. = 1–7) at site with a high DMF and low SBA, and of 99 frogs (95%

C.I. = 45–220) at sites with a low DMF and high SBA. Estimated *N* at sites with an average DMF and SBA is 18 frogs (95% C.I. = 14–22).

4. Discussion

Our results support the hypothesis that forest structural attributes are an important component of the habitat of this forest-specialist frog. Namely, an increase of stand basal area and a decrease of daily microclimatic fluctuation (i.e. an increase in structural complexity; see below) were positively associated with the local abundance of *R. darwinii* (Fig. 1).

In the forests inhabited by *R. darwinii*, stand structural complexity is determined by forest successional stage and the level of natural and anthropogenic disturbances (Gutiérrez et al., 2009; Caviedes and Ibarra, 2017). In these forests, stand basal area (a measure of stand biomass) correlates positively with stand age, as it differentiates old-growth forests (i.e. stands containing trees >200 years old) from earlier successional stages (Gutiérrez et al., 2009; Caviedes and Ibarra, 2017; Ponce et al., 2017). A lesser daily microclimatic fluctuation is also expected to occur in older, structurally-complex forest stands (Spies and Franklin, 1988; Chen et al., 1999). An association between the density of saplings (a variable retained in the best and second best detection and abundance models, respectively) and the forest successional stage in our study stands is less clear to us, but it is noteworthy that the three sites with the highest density of saplings (i.e. > 700 sapling x ha^{-1}) have an unusually high proportion of saplings belonging to species in the Myrtaceae family (Appendix A, Fig. A1), a group abundant in early successional stages in our study area (Teillier et al., 2013). Altogether, this evidence indicates that local abundance of *R. darwinii* in our study area is higher (and frog detectability is lower) in old-growth, more structurally-complex forest stands in comparison to earlier successional stages. Although we did not identify stand age, based on information from other forest stands of similar composition located near to our study area, 40% of our study sites have a stand basal area value corresponding to an old-growth forest (i.e. >80 m^2 x ha^{-1}; Caviedes and Ibarra, 2017; Ponce et al., 2017), and these held some of the highest local abundances of *R. darwinii* (Fig. 1 and Table 2).

The mechanisms behind the species-habitat relationship found in this study might be complex. For example, a lower structural complexity could increase microclimatic variation (Spies & Franklin, 1988; Chen et al., 1999). Reduced microclimatic variation may decrease *R. darwinii* survival rates due to acute or chronic thermal stress, reduced activity, or by altering host response to infectious diseases such as chytridiomycosis, possibly resulting in population declines and a reduced local abundance (Raffel et al., 2012; Nowakowski et al. 2018). Indeed, some thermal traits of amphibians, such as heat tolerance and evaporative water loss, are important predictors of species responses to habitat modification (Nowakowski et al. 2018). An evaluation of the relationship between forest structural complexity and other individual (e.g. body condition) and population (e.g. vital rates, population growth rates) state variables might provide a better understanding about the mechanisms driving the spatial variation of *R. darwinii* local abundance (Franklin et al., 2000; Janin et al., 2011; Unglaub et al., 2018).

Anthropogenic disturbance, either occurring at large or small spatial scales, is considered to be one of the main threats to forests and their associated biodiversity (Pan et al., 2013). As observed in other ecosystems, anthropogenic disturbance in forests can lead to a combination of habitat loss, fragmentation and degradation (Fischer and Lindenmayer, 2007). While habitat loss and fragmentation usually co-occur, and might be easily perceived by people, habitat degradation (i.e., the gradual deterioration of habitat quality) can result from unapparent or small-scale environmental changes taking place even in non-fragmented forest landscapes (Mortelliti et al., 2010; Ware et al., 2015). Habitat loss appears to be the main threat to *R. darwinii* (Soto-Azat et al., 2013a), but our study provides evidence that habitat degradation, due to a reduction of forest structural complexity, might be an important additional threat to this species. This is particularly concerning considering that most of the remaining South American temperate forest has been degraded by anthropogenic disturbance and old-growth forests are very scarce, especially at low-elevation (Tecklin et al., 2010;

Caviedes and Ibarra, 2017; Ponce et al., 2017). In this context, our study provides support to the idea that forest management of the more common mid-successional forests, to promote old-growth characteristics and enhance structural complexity (Caviedes and Ibarra, 2017; Ponce et al., 2017), will be an important conservation action to improve the local abundance of *R. darwinii* and, most likely, of other forest-specialist animals inhabiting this important ecosystem (e.g. rufous-legged owls; Ibarra et al., 2014). Additionally, our findings can be used to inform the selection of sites for the reintroduction of captive bred *R. darwinii* individuals, as two *ex-situ* conservation breeding programs for this imperilled species are currently underway in Chile (IUCN 2018, http://www.iucnredlist.org/details/19513/0).

Critically, the analysis of forest attributes that determine frog abundance depended on the use of statistical models which accounted for imperfect detection. Empirical evidence shows that the detection probability of wild animals and plants is almost always lower than 1 and that it exhibits considerable temporal and spatial variation (Kéry and Schmidt, 2008; Kellner and Swihart, 2014). Covariates, such as time, species and sampling methodology, have been commonly used to account for spatial and temporal heterogeneity in detection probability, while habitat characteristics are less frequently considered (Kellner and Swihart, 2014). We show that the detectability of *R. darwinii* individuals is related to habitat covariates. Because habitat characteristics have the potential to strongly affect detectability (Bailey et al., 2004; Gu and Swihart, 2004; Kéry, 2004), we suggest that they should be more commonly taken into account in studies dealing with species-habitat relationships.

Our results show that habitat characteristics may affect both detectability and abundance. There is a risk, therefore, that one might conclude that a habitat characteristic affects abundance when in fact it affects detectability. Thus, the use of statistical models which can disentangle the effects of habitat characteristics on abundance and detectability seems important (Kéry, 2008). Additionally, not properly accounting for complex relationships between detectability and abundance may cancel out important effects of habitat covariates on abundance (Kéry and Royle, 2016). For instance, in our study, the same forest attributes affected both abundance and detection probability of *R. darwinii* individuals, but in opposite ways. If raw counts are used in this specific case, abundance will tend to be underestimated to a larger degree in sites with good habitat quality than in those with poorer habitat quality, hampering the detection of appropriate habitat quality surrogates. In fact, if we regress the counts of *R. darwinii* individuals obtained in this study against the two forest attributes that were retained in the best supported abundance model, only a significant relationship (i.e. P-value < 0.05) is found for daily microclimatic fluctuation, but not for stand basal area (Appendix A, Fig. A2). Consequently, an analysis of simple frog counts that were not adjusted for imperfect detection, would not have revealed all factors associated with local abundance. It was only through the use of models which explicitly model the observation process, and through the use of habitat characteristics as covariates for detectability, that we could unravel the factors that truly matter. Previous authors (e.g. Kroll et al. 2009) have argued that only reliable metrics of distribution and abundance should be used to inform forest management. The results of our study suggest that multinomial *N*-mixture models, and similar modelling frameworks, are a useful tool for the reliable evaluation of species-habitat relationships and for determining the appropriateness and effectiveness of different habitat management options.

5. Conclusions

Our results provide further support to previous claims that raw counts of individuals should not be used, generally, as a proxy of abundance in species inhabiting forest (Kroll et al., 2009; Otto et al., 2013) and other ecosystems (Anderson, 2001; Kellner and Swihart, 2014). More importantly, the opposite effect of forest attributes on abundance and detectability observed in our study highlights the need to use methods that quantify species-habitat relationships in a robust way and which take habitat-specific imperfect detection into account.

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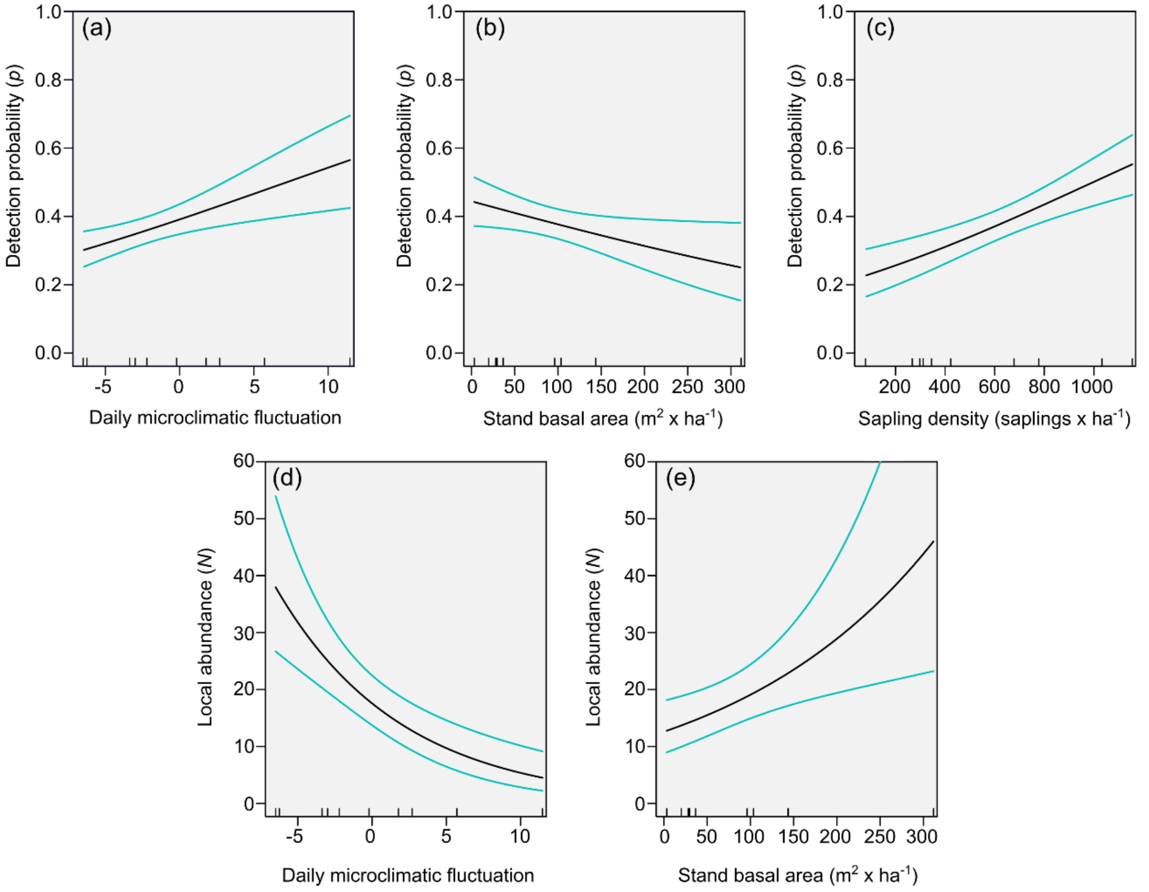

Figure 1 Relationships between forest stand attributes and frog detection probability (a,b,c) and local abundance (d,e) of Southern Darwin's frogs (*Rhinoderma darwinii*) from Neltume, Reserva Biológica Huilo Huilo, southern Chile. Lines were drawn using estimates from the best supported multinomial N-mixture model (i.e. p(SAP+SBA+DMF), N(SBA+DMF)). The relationship between either p or N and each covariate is predicted while using, for the corresponding component of the model, an average value for the remaining covariates. Pale blue lines stand for 95% confidence intervals. Hash marks in the x-axis represent measured values of the forest attributes.

Table 1 Site- and observational-level covariates used to model detectability and local abundance of Southern Darwin's frogs (*Rhinoderma darwinii*) from Neltume, Reserva Biológica Huilo Huilo, Southern Chile.

Variable	**Abbreviation**	**Description**	**Model component**
Site-level covariates			
Density of saplings (saplings x ha $^{-1}$**)**	**SAP**	Derived from the total number of trees and bushes between 0.5 – 2 m tall that were detected across the 30 sub-plots	detection, abundance
Diversity of trees (*H*)	***H***	Shannon diversity index; calculated from all the trees and bushes (>2 m tall) species detected across the 30 sub-plots	abundance
Stand basal area (m^{2} **x ha**$^{-1}$**)**	**SBA**	Derived from the sum of the cross-sectional area at the breast height (1.4m) of all trees (>2 m tall) detected across the 30 sub-plots	detection, abundance
Richness of ferns, flowering plants and other epiphytes	**RFE**	Number of species identified across the 30 sub-plots	abundance
Fine and coarse woody debris coverage (%)	**WD**	Percentage of this coverage averaged from the 30 sub-plots	detection, abundance
Daily microclimatic fluctuation	**DMF**	PCA solution containing 'air temperature daily fluctuation' and 'air relative humidity daily fluctuation' at each site	detection, abundance
Observation-level covariates			
Air temperature (°C)	**TEMP**	Mean air temperature of each searching day (capture occasion) obtained from the Lago Verde weather	detection

		station which is located at ~60 km south-west from our study sites (Agromet, Red Metereológica de INIA, Chile)	
Day	**DAY**	An integer representing the day of January 2013 when the capture occasion was performed	detection

Table 2 Size of the study sites, total counts (number of captures), number of individuals captured, and values of site-level covariates used to study species-habitat relationships in populations of the Southern Darwin's frog (*Rhinoderma darwinii*) from Neltume, Reserva Biológica Huilo Huilo, Southern Chile. Covariates names are detailed in Table 1.

Site	Area (m^2)	No. captures	No. individuals	SAP (saplings x ha^{-1})	SBA (m^2 x ha^{-1})	RFE	*H*	DMF	WD (%)
BOT	563	49	26	678	96	19	1.5	-2.22	27
CAS	1304	51	29	422	28	18	1.0	-6.27	63
CEN	791	27	15	344	143	20	1.9	5.70	57
ESP1	396	52	19	1033	30	19	1.5	-3.39	67
ESP2	514	13	3	1156	4	23	1.4	11.47	26
HOT	569	62	40	297	104	19	1.1	-6.52	50
PUD1	775	19	6	778	20	17	1.8	-0.22	60
PUD2	874	21	8	311	30	21	1.7	-3.01	43
PUD3	531	24	14	78	37	15	1.3	2.69	45
PUM	1052	33	19	267	311	20	0.5	1.77	55

Table 3 Five top-ranked detection models from multinomial *N*-mixture models of Southern Darwin’s frogs (*Rhinoderma darwinii*) captured in Southern Chile. Models are ranked from the best to the worst based on AIC values and only covariates retained among these top-ranked detection models, and their regression coefficients (and standard errors), are shown. In these models, abundance was kept constant across study sites. w_i =Akaike weights. AIC of the best model was 420.53. Covariates names are detailed in Table 1.

Model for p	Coefficients (SE)[a]						Model selection	
	SAP	SBA	WD	DMF	TEMP	DAY	ΔAIC	w_i
SAP + SBA + DMF	0.48	-0.22	—	0.32	—	—	0.00	0.36
	(0.11)	(0.12)		(0.12)				
SAP + DMF	0.57	—	—	0.24	—	—	1.49	0.17
	(0.10)			(0.11)				
SAP + SBA + DMF + TEMP	0.47	-0.22	—	0.32	0.02	—	1.49	0.17
	(0.11)	(0.12)		(0.12)	(0.02)			
SAP + SBA + DMF + DAY	0.48	-0.19	—	0.30	—	0.01	1.86	0.14
	(0.11)	(0.13)		(0.13)		(0.01)		
SAP + WD + DMF	0.57	—	0.06	0.26	—	—	3.02	0.08
	(0.10)		(0.09)	(0.11)				

[a] all covariates were scaled and centered for analyses.

Table 4 Five top-ranked abundance models from multinomial *N*-mixture models of Southern Darwin's frogs (*Rhinoderma darwinii*) captured in Southern Chile. Models are ranked from the best to the worst based on AIC values and only covariates retained among these top-ranked abundance models, and their regression coefficients (and standard errors), are shown. In these models, detection probability was modelled as *p*(SAP+SBA+DMF). w_i =Akaike weights. AIC of the best model was 411.27. Covariates names are detailed in Table 1.

Model for *N*	Coefficients (SE)[a]					Model selection	
	SAP	*H*	SBA	RFE	DMF	ΔAIC	w_i
SBA + DMF			0.39		-0.66	0.00	0.57
	—	—	(0.14)	—	(0.15)		
SAP + DMF	-0.31				-0.55	3.07	0.12
	(0.17)	—	—	—	(0.17)		
H + DMF		-0.27			-0.51	3.41	0.10
	—	(0.15)	—	—	(0.16)		
DMF					-0.58	4.14	0.07
	—	—	—	—	(0.18)		
RFE + DMF				-0.06	-0.57	6.06	0.03
	—	—	—	(0.21)	(0.19)		

[a] all covariates were scaled and centered for analyses.