

Lower density of arthropod biomass in small high-Andes *Polylepis* fragments affects habitat use in insectivorous birds

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Abstract. *Polylepis* forests are endemic to the high-Andes, with trees characterized by multi-layered, exfoliating bark-providing protection against harsh, high-elevation conditions, both for individual trees and the wide array of organisms dependent on them. However, *Polylepis* habitat has suffered severe human-induced land conversion and currently mainly occurs as fragmented remnants only. Here, we studied the effects of fragment size on local ambient temperature and on biomass of bark and its bark-dwelling arthropods. We did so by comparing multiple samples at the edge and interior of both large and small fragments, while also accounting for branch size, tree width, and tree structure. Because arthropod biomass is likely to impact higher trophic levels, we also studied abundance and foraging behavior of two bird species specialized on *Polylepis* forest. We show that arthropod biomass was relatively higher in wider, larger trees, which were preferred for foraging by both bird species. Moreover, we show that small forest fragments are not only environmentally less buffered but are also characterized by lower amounts of bark and lower densities of bark-dwelling arthropods than larger fragments. Our study highlights the conservation value of large trees. Also, we advise it is now timely to test to what degree restoration efforts to increase fragment size could mitigate the negative effects of reduced arthropod biomass for higher trophic levels of endemic specialist insectivores.

Key words: bark-dwelling arthropods; biodiversity hotspot; *Conirostrum binghami*; edge effects; habitat fragmentation; *Polylepis besseri*; restoration ecology; *Sylvioorthorhynchus yanacensis*; trophic cascades.

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INTRODUCTION

Human-induced habitat loss and fragmentation are key drivers of the global biodiversity crisis (Fischer and Lindenmayer 2007, Haddad et al. 2015). The loss of native vegetation due to land-use change forces many species to survive with less habitat and more fragmented habitat,

which typically implies smaller habitat patches and relatively more habitat edge (Haddad et al. 2015, Fahrig 2017). Smaller fragments are under greater pressure from edge effects, such as microclimatic fluctuations, reducing habitat quality, and hence individual abundance and species richness (Davies et al. 2000, Laurance 2008). Species most vulnerable to these edge effects are

interior habitat specialists, as has been shown for several arthropod communities in forest fragments (Didham et al. 1998, Merckx et al. 2012, Slade et al. 2013).

Forests in the tropical high-Andes, which formed naturally patchy woodlots prior to human occupation, have become hyper-fragmented over the last millennium (Valencia et al. 2018). As a result, these forests are now considered one of the most threatened Neotropical vegetation types (Cierjacks et al. 2007, Toivonen et al. 2011). In Bolivia, for instance, only 10% of the original extent remains, mostly as fragments of only a few hectares (Fjelds  et al. 1996, Jameson and Ramsay 2007, Valencia et al. 2018). Considered among the world's highest elevation forest ecosystems, they are made up exclusively of *Polylepis* trees, whose bark consists of multi-layered, exfoliating sheets that provide efficient protection against the harsh, high-elevation (3000–5200 m asl) climatic conditions (i.e., extreme daily and seasonal variations in temperature and water availability: Rada et al. 1996, Garc a-N  n ez et al. 2004). This protection applies not only to the individual trees but also to the wide array of endemic arthropod species living inside these loose layers of bark (Fjelds  1993, Gareca et al. 2010, Sevillano-R os and Rodewald 2017). Specifically, *Polylepis* trees have been pointed out as important refuges for insects and arachnids (Fjelds  et al. 1996), and this most probably so for thermoregulatory reasons in this high-elevation ecosystem. As such, these forests are essential resources for a large diversity of species in otherwise often treeless landscapes, providing them with sheltered and richly structured habitats (Zutta and Rundel 2017).

Here, we quantified the impact of fragment size and edge effects on local ambient temperature profiles and the biomass of bark and bark-dwelling arthropods. We compared multiple samples at the edge and interior parts of both large and small fragments of *Polylepis besseri*, taking also into account branch size, tree size, and plot-level characteristics of tree structure. As we predict that the amount of arthropod biomass within *Polylepis* bark impacts higher trophic levels, we also studied abundance and foraging behavior of two habitat specialist bird species of *Polylepis* forest. Giant Conebill *Conirostrum binghami* and Tawny Tit-Spinetail *Sylviorhynchus yanacensis* are labeled

as near threatened and suspected to be in decline owing to the ongoing destruction and degradation of their habitat throughout their range (Bird-Life International 2016). Both insectivorous species forage primarily on bark-dwelling arthropods from *Polylepis* trees; *C. binghami* selects mature trees and forages primarily on tree trunks by prying in the bark, whereas *S. yanacensis* forages on twigs and small branches (Lloyd 2008a, Matthysen et al. 2008). Previous studies have shown that their abundance is lower in smaller fragments and near fragment edges, like in other *Polylepis* bird specialists too (Cahill and Matthysen 2007, Lloyd 2008b, Sevillano-R os and Rodewald 2017). However, it is unclear if and to what extent this is related to habitat quality (i.e., lower abundance of food resources) or fragment size. Here, we test whether patterns of resource use correspond to the relative abundance levels of arthropods. We expect lower relative abundance of arthropods in small fragments and in fragment edges, in line with microclimatic impacts of edge effects. As such, we determine whether and to what extent fragment size and edge effects affect foraging behavior of both specialist birds.

METHODS

Study area

Sampling occurred in *Polylepis* fragments near the villages of Sacha Loma (17 44'22.85" S, 65 34'3.99" W) and Cuturi (17 43'6.55" S, 65 33'23.72" W), a study area of ~30 km² in the Cochabamba region of Bolivia (Fig. 1). This area is in the supra-tropical bioclimatic region, which is characterized by dry and rainy seasons (April–August and September–February, respectively) during which daily temperature fluctuations are much larger than any seasonal fluctuations (Navarro et al. 2005). Fragments were spread across mountain slopes above 3000 m asl, embedded in a highly contrasting matrix of high-Andean puna grassland (5–20 cm height). Within the fragments, *P. besseri* (Rosacea; 6 m maximum height) is admixed with *Berberis*, *Ribes*, *Gynoxis*, *Bacharis*, and *Brachiotum* shrubs (Herzog et al. 2002).

We selected two large (A: 34 ha; B: 32 ha) and two small (H: 2 ha; I: 3 ha) fragments (surface areas exclude boulder areas devoid of vegetation; Fig. 1). Fragment A and B are located 500 m apart, whereas fragment H and I are 200 m

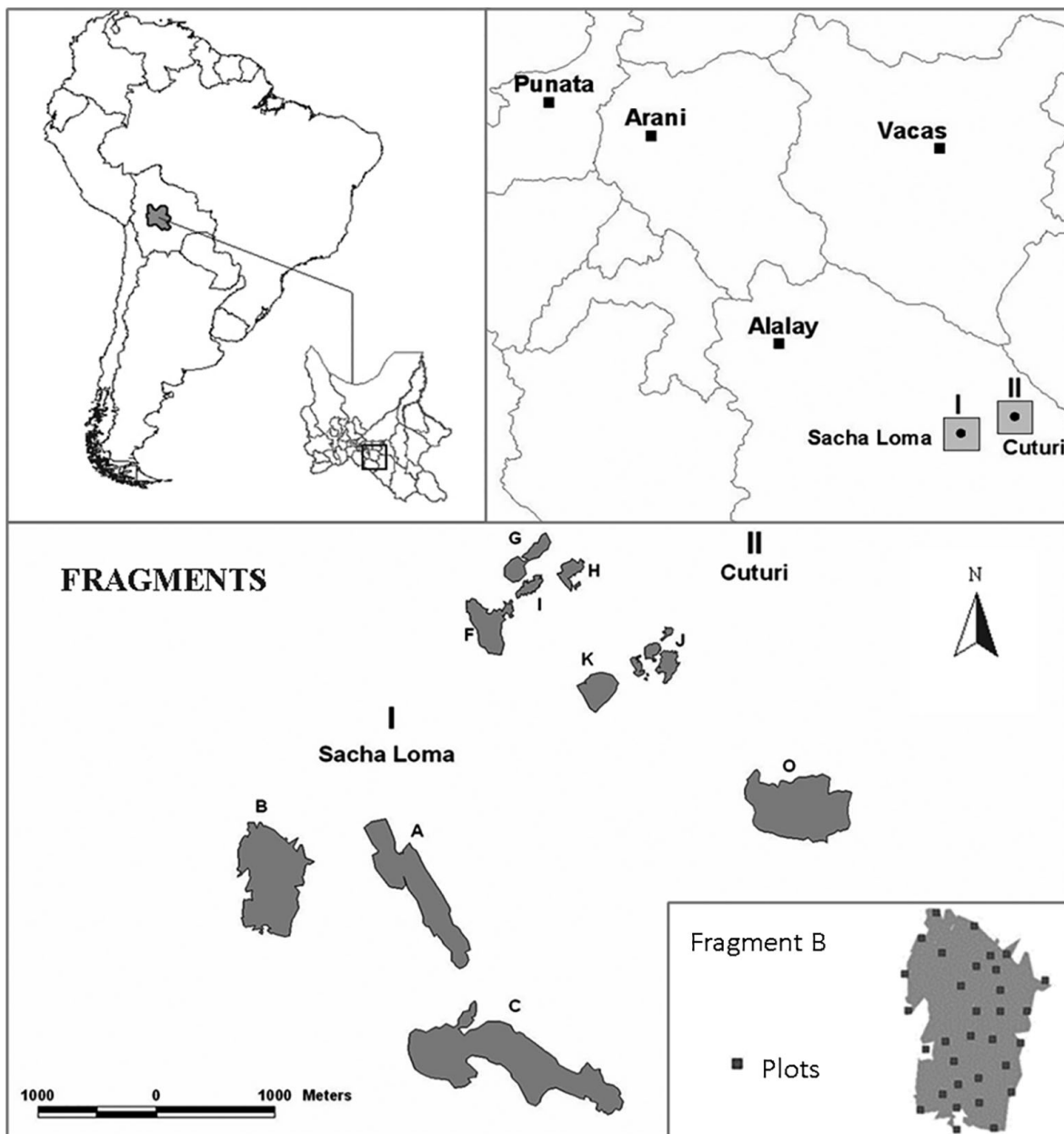


Fig. 1. Map of the study sites, indicating the location of the two large (A/B) and two small (H/I) sampled fragments within the configuration of *Polylepis* patches at the landscape scale. For one of the large fragments (B), the location of the various sampling plots is indicated.

apart, with both sites 2.3 km apart. Fragment sizes are representative for large vs. small fragments within the *Polylepis* remnants in Bolivia (Fjeldsø et al. 1996). The number of fragments and their size changed little in recent decades, although moderate human disturbance was

evident from small clearings and wood cutting, particularly in the smaller fragments.

Sampling plots

In order to assess ambient temperature profiles, vegetation structure and biomass of bark,

and bark-dwelling arthropods, we established across the four fragments a total of 103 sampling plots (20×20 m each), positioned systematically at approximately equidistant positions (38.0 ± 3.7 m, mean $\pm$ standard error [SE]), except where access was impossible due to the terrain either being too steep or being covered with huge stone boulders (Fig. 1). Consequently, we ended up with a sampling cover of 1.0–1.6 plots/ha for the large fragments and 2.6–4.0 plots/ha for the small fragments (i.e., 4.0–6.4% and 10.4–16.0% cover, respectively). As edge effects on vegetation composition are known to penetrate over 50 m (Kessler 1995, Fjeldså et al. 1996), we arbitrarily established an edge area of 50 m. Plots located within 50 m from the forest's edge were labeled as edge plots, as opposed to all other interior plots (N_{edge} and N_{interior} respectively: A, 27 and 28; B, 16 and 16; H, 4 and 4; I, 4 and 4).

Temperature

Ambient temperature was measured half-hourly using data loggers (HOBO Pro Series H08-032-08, Onset, MA, USA) positioned at 1 m height on tree trunks or plastic rods in the matrix. For both large fragments and the surrounding matrix, a total of 24 loggers recorded simultaneously and during three complete days (22 September, 28 October, and 22 November 2007). In each fragment, three data loggers were placed at approximately 12 m from the edge and three at 37 m from the edge, to cover the outer (0–25 m) and inner (25–50 m) edge zones, and this separated by a distance of at least 130 m from each other. Three data loggers were placed in the core area of the fragment (50–80 m from the edge) and another three loggers in the matrix (5–8 m from the edge). Matrix data loggers were placed close to the edges in order to avoid sheep and goat trails found further into the matrix. Similarly, for the small fragments, temperatures were simultaneously recorded during three complete days using 21 data loggers (24 September, 30 October, and 24 November 2007): Five data loggers were positioned at 12 m and three at 37 m from the edge of each fragment, while five loggers were placed in the matrix (at 5–8 m) surrounding fragments H and I (three and two loggers, respectively).

Trees

Within each plot, we counted all trees and recorded tree density (N/ha). For each individual tree (diameter >2 cm), we recorded height, diameter at breast height (DBH), and foliage height (in cm from the lowest branch with leaves to the treetop). For foliage density, we considered foliage divided into three horizontal quadrants—lower-level, mid-level, and upper-level—for each tree. With the use of a vegetation profile board placed behind each tree, foliage density (in %) was estimated as the amount of obscured area by plant parts, and this separately for each of the horizontal quadrants (Hays et al. 1981), thus obtaining mid- and upper-level foliage density. Lower-level foliage was not considered for further analysis, as it was not a reliable estimation of foliage due to the inclusion of many branches. All individual tree data were averaged per plot.

Bark and arthropods

During September 2006, we selected in each plot a large, medium, and small tree (i.e., 4–6, 3–4, and 2–3 m height; 21–34, 14–21, 8–14 DBH, respectively), separated at least 5 m from each other ($N_{\text{total}} = 309$). On each selected tree, we drew a sampling quadrant with a marker, and we sampled bark and bark-dwelling arthropods removing them from the tree trunk, from the thickest primary branch and from three small quadrants of a secondary thin branch chosen at random. Sampled areas comprised 15×15 cm quadrants for tree trunks (at 1 m height) and primary branches (30–60 cm away from the branch collar), whereas for thin branches (20–40 cm away from the primary branch) we collected instead from three 5×15 cm quadrants (separated by 15–20 cm along the thin branch). Bark was manually scraped from each quadrant into a plastic bag. Next, each bag was sprayed with insecticide (Baygon, SC Johnson, effective for most arthropods) and sealed. In the laboratory, samples were oven-dried for 24 h (30°C). Next, arthropods were carefully separated from the bark. Finally, and for each sample, the dry mass of bark and total dry mass of arthropods were measured (Mettler Toledo [Worthington, OH, USA]; precision: 0.1 mg).

Birds

Foraging behavior of Giant Conebill *C. binghami* and Tawny Tit-Spinetail *S. yanacensis* was

studied from June to September 2004, from February to April 2005 (i.e., non-breeding period, see also Cahill et al. 2008) and from September 2005 to February 2006. Birds were observed for five to six hours a day (06:30–10:30 and 16:00–18:00) during monthly five-day periods, excluding days with non-suitable weather (e.g., rain, strong wind, low temperature, hail). During slow random walks in all four fragments, we visually located and observed individual birds (most of which were color-ringed). We determined whether the observed bird was either foraging alone or as part of a flock. Individual birds were assigned to flocks when other birds (of the same or different species) were foraging within 10 m (Lee et al. 2005, Matthysen et al. 2008). We also recorded time of day and total time of individual foraging in the same tree, within a time period of maximum 10 min (the observer timed the activity period by using a stopwatch; Morrison et al. 1987, Matthysen et al. 2008). Multiple foraging records of the same individual were only retained if the time between records exceeded one hour. Behavioral records included (1) total foraging time per tree, (2) tree size (i.e., small, medium, or large, based on tree height and diameter by visual estimation; Remsen and Robinson 1990), (3) foraging singly or in mixed flock (Matthysen et al. 2008), and (4) foraging substrate, recorded as trunk (TT), thick branch (TB), or small branch (SB; Alatalo 1982, Matthysen et al. 2008).

Statistical analyses

Based on the half-hourly temperature data, we calculated for each location and day: (1) the temperature range (i.e., $T_{\max} - T_{\min}$), (i + iii) the mean diurnal (10:30–17:00) and nocturnal (17:30–10:00) temperature, and (iv + v) the standard deviation of diurnal and nocturnal temperature. Next, we performed linear mixed regression analyses (SAS Institute, Cary, NC, USA) with this set of five variables as dependent variables. Position (four classes: matrix, edge12, edge37, and interior) was the fixed effect in a first set of analyses. Using fragment size (two classes: large and small) as fixed effect, we performed a second and third set of analyses on the subsets of edge12 and edge37 data. Date (six classes) and fragment ID (four classes) were included consistently as random effects.

At plot level, tree and vegetation characteristic variables were converted using two principal component analyses (PCA), as some of these variables are highly correlated (i.e., tree height and DBH, $r = 0.87$; see also Cahill and Matthysen 2007). A first PCA dealt only with variables on tree structure (i.e., height, DBH and foliage height). Applying the Kaiser criterion (Kaiser 1960), we chose the first principal component only (eigenvalue 2.74) and retained this for further analysis (Appendix S1: Table S1). This principal component showed positive factor loadings for height, foliage height, and DBH (+0.59, +0.57, +0.56, respectively), which means that tree height, foliage height, and tree diameter are positively correlated with the component. As such, we interpret this principal component as a composite variable indicative of mature trees (MTPC). A second PCA dealt with upper-level foliage density, mid-level foliage density, and tree density variables at plot level. We chose the first principal component only (eigenvalue: 1.75), again applying the Kaiser criterion (Appendix S1: Table S2). It showed highly positive factor loadings for upper-level foliage density and mid-level foliage density and negative factor loadings for tree density (+0.55, +0.63, –0.54, respectively), which means that foliage density was negatively correlated with tree density. As such, we interpret this principal component to be indicative of trees with dense foliage in more open areas (DFPC). Both the MTPC and DFPC principal components were then used in further analyses to relate them to the biomass of bark and arthropods at plot level (total of 103 calculated variables for both MTPC and DFPC).

Bark and arthropod biomass were log-transformed in order to obtain normally distributed residuals, and we examined the correlation between both variables. Next, we tested for differences in bark biomass, arthropod biomass, and adjusted arthropod biomass (i.e., arthropod biomass/bark biomass) between edge and interior locations, and between small and large fragments. We did so by using nested linear mixed models (Littell et al. 1996)—with the restricted maximum likelihood (REML) method to estimate covariance matrices—and by using a full model and testing separately for each response variable. The full model was reduced through backward selection of factors using the Akaike information

criterion (AIC). The full model included fixed effects, fragment size, plot location, MTPC and DFPC at plot level, DBH (of trees from which bark and arthropods were collected), and tree part (i.e., trunk, thick or small branch from where bark and arthropods were collected) and the two-way interactions of the proposed fixed effects. The model also included random effects: (1) Plot identity (i.e., plot from where bark and arthropods were collected) nested within the interaction of fragment identity by plot location, and (2) tree identity (i.e., tree from which bark and arthropods were collected) nested within the interaction of plot identity by plot location by fragment identity, and the error.

Regarding bird foraging behavior, we used chi-squared tests to assess whether and to which degree birds used differently sized trees and different foraging substrates (1) in small vs. large fragments, and (2) in mixed flocks vs. when foraging alone. Both species were analyzed separately because of their different habitat use, whereby Giant Conebills mainly probe into thick bark layers and Tawny Tit-Spinetails glean insects from small branches and twigs. Next, and separately per species too, a nested linear mixed model (REML) was used to test for the effect of tree size (i.e., small, medium, or large) and social environment (i.e., singly or flock) as fixed effects on individual total foraging time per tree. The model included bird identity, fragment size (nested within fragment group), and fragment group as random effects. The factor bird identity refers to individual bird identity for color-ringed individuals (i.e., ~90% of the birds) and to observation identity for the non-ringed individuals. Using AIC, we reduced the full model through backward selection of factors.

RESULTS

Temperature

Minimum and maximum temperatures (°C) were recorded for each fragment and the surrounding matrix (Table 1). While distance from the edge inside forest had no effect, mean temperature was higher (>4°C) in the matrix than inside the forest during the day ($F_{3,118.4} = 56.5$; $P < 0.0001$), but not at night ($F_{3,118.4} = 0.6$; $P = 0.62$). Standard deviations were also larger in the matrix than inside forest both during the

day ($F_{3,119.5} = 25.3$; $P < 0.0001$) and at night ($F_{3,118.7} = 34.5$; $P < 0.0001$), while distance from the edge inside forest had no effect. In the matrix, the temperature range was twice the range inside forest ($F_{3,118.9} = 38.3$; $P < 0.0001$), with no differences among forest sites at varying distance from the edge (Fig. 2a). At 12 and 37 m inside the forest, there was no effect of fragment size on diurnal and nocturnal mean temperatures and standard deviations ($P > 0.20$). However, there was a ~50% larger temperature range in small compared to large fragments, although the effect was not statistically significant (12 m, $F_{1,4.5} = 2.9$, $P = 0.16$; 37 m, $F_{1,4.0} = 3.1$, $P = 0.15$; Fig. 2b, c).

Bark and arthropods

Overall, arthropod biomass was positively correlated with bark biomass ($r = 0.48$; $N = 927$). Bark biomass was highest for samples of trunks, intermediate for thick branches, and lowest for small branches (mean $\pm$ SE [g]: 67.6 ± 1.0 , 56.2 ± 1.0 , 26.3 ± 1.0 , respectively; $F_{2,590} = 315.2$; $P < 0.0001$; Table 2). Also, bark biomass was higher in large than in small fragments ($F_{2,96.9} = 24.8$; $P < 0.0001$; Table 2), and this was especially the case for trunks and thick branches, rather than for small branches (Fig. 3a). Bark biomass increased with abundance of mature trees in the plots ($F_{1,122} = 11.9$; $P = 0.0008$; Table 2). Bark biomass also increased with tree width, and this especially so at fragment interiors rather than at fragment edges ($F_{1,291} = 8.2$; $P = 0.004$; Table 2; Appendix S1: Fig. S3).

Sampled arthropods belonged to the following taxa: Acarina, Araneae, Chelonethida, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Polidesmida, and some other taxa that were not identified (particularly larvae). Further

Table 1. Minimum and maximum temperatures (mean $\pm$ standard error) inside fragments (large, A and B; small, H and I) and in the surrounding matrix of each fragment.

Fragment	Fragment T (°C)		Matrix T (°C)	
	Min	Max	Min	Max
A	5.1 $\pm$ 0.3	13.5 $\pm$ 1.4	3.7 $\pm$ 0.5	21.5 $\pm$ 3.2
B	5.1 $\pm$ 0.4	13.7 $\pm$ 1.2	3.7 $\pm$ 0.7	17.4 $\pm$ 1.9
H	3.9 $\pm$ 0.4	16.0 $\pm$ 0.4	4.1 $\pm$ 0.5	23.7 $\pm$ 2.2
I	4.1 $\pm$ 0.5	16.9 $\pm$ 1.2	3.7 $\pm$ 0.4	28.2 $\pm$ 4.1

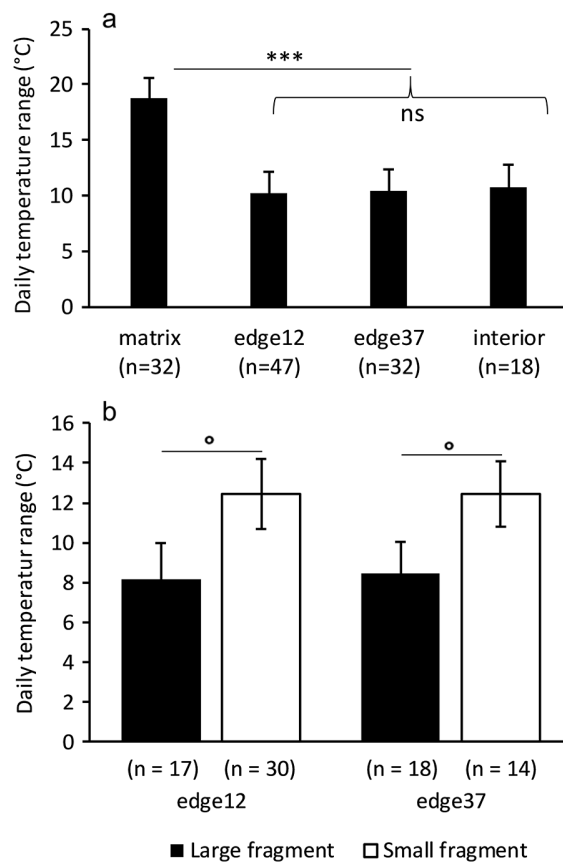


Fig. 2. Modeled daily mean temperature range at the puna grassland matrix vs. *Polylepis* forest sites at varying distance from the edge (a), and at positions inside forest at 12 and 37 m from the edge, contrasting large vs. small fragment size (b). Error bars depict standard errors. ^{ns} $P > 0.2$; [°] $P < 0.2$; *** $P < 0.001$.

taxonomic description was not possible due to many incomplete bodies and lack of species descriptions. We found highly significant differences of bark-dwelling arthropod biomass ($F_{2,592} = 256.3$; $P < 0.0001$; Table 2) and adjusted arthropod biomass ($F_{2,590} = 73.5$; $P < 0.0001$; Table 2) between the different tree areas: Biomass was highest for trunks, intermediate for thick branches, and lowest for small branches (arthropod biomass mean $\pm$ SE [mg]: 83.0 ± 10.7 ; 53.1 ± 10.7 ; 26.6 ± 10.7 , respectively). Moreover, absolute and adjusted biomass of arthropods was higher in large than in small fragments (arthropod biomass: $F_{1,97} = 6.5$; $P = 0.01$; Table 2), with this effect being particularly pronounced for adjusted biomass at small branches ($F_{2,590} = 5.0$; $P = 0.005$; Table 2; Fig. 3b). Arthropod biomass was twice as high in large than in small fragments (mean $\pm$ SE [mg]: 54.8 ± 10.9 vs. 26.7 ± 10.0 , respectively). Both absolute and adjusted arthropod biomass increased with tree width (Table 2; Fig. 4a), while arthropod biomass also increased with the number of mature trees in the immediate surroundings (Table 2; Fig. 4b).

Birds

Giant Conebills were most often observed foraging in large trees compared to medium and small trees, and this was more strongly expressed in large fragments (59% vs. 22% and 19%, respectively) than in small fragments (40% vs. 31% and 29%; $\chi^2 = 14.56$; degrees of freedom [df] = 2; $P = 0.0007$). Moreover, the extent of foraging

Table 2. Output of the best linear mixed regression models explaining variation in biomass of (1) bark, (2) arthropods, and (3) arthropods adjusted to bark biomass, in relation to fragment size (large vs. small), plot location (interior vs. edge), sample location (trunks, thick branches or small branches), tree width (DBH), and the principal component indicative of mature trees (MTPC).

Characteristic	Bark biomass			Arthropod biomass			Arthropods/bark biomass (adjusted)		
	df	F	P	df	F	P	df	F	P
Fragment size	1	24.8	<0.0001	1	6.5	0.01	1	5.0	0.02
Plot location	1	3.1	ns						
Sample location	2	315.2	<0.0001	2	256.3	<0.0001	2	73.5	<0.0001
Tree width	1	3.9	0.04	1	13.0	0.0004	1	15.4	<0.0001
Mature trees	1	11.9	0.0008	1	4.1	0.04			
Fragment size $\times$ sample location	2	10.2	<0.0001				2	5.0	0.005
Plot location $\times$ tree width	1	8.2	0.004						

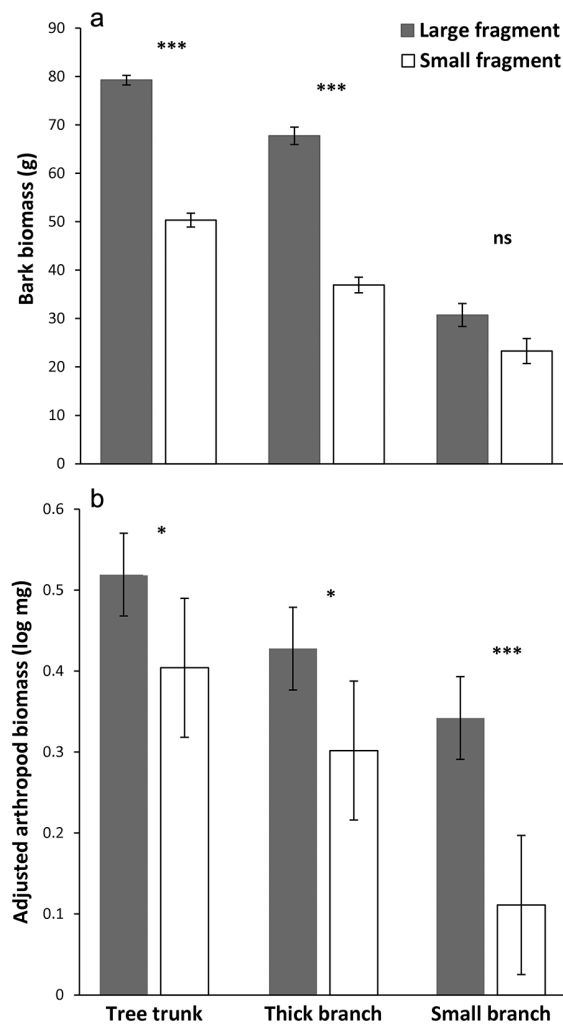


Fig. 3. Bark biomass (g; a) and arthropod biomass (log mg; proportional to the available biomass of bark; b) per 225 cm² bark sample, contrasting tree trunks, thick, and small branches of *Polylepis bessi* in large vs. small forest fragments. Error bars depict standard errors. ^{ns} $P > 0.05$; * $P < 0.05$; *** $P < 0.001$.

activity in differently sized trees showed Giant Conebills to forage for longer periods in large than in medium and small trees (mean $\pm$ SE [s]: 25.6 $\pm$ 1.9, 18.4 $\pm$ 1.0, 14.4 $\pm$ 0.8, respectively; $F_{2,376} = 10.89$; $P < 0.0001$) regardless of fragment size or of foraging alone vs. in mixed flocks. Nevertheless, while single Giant Conebills foraged more often on thick branches as foraging substrates (TB 53%, TT 25%, SB 22%), tree trunks were selected more often by Giant Conebills foraging in mixed

flocks (TT 50%, TB 40%, SB 10%; $\chi^2 = 27.85$; $df = 2$; $P < 0.0001$). Foraging substrate use by Giant Conebills did not differ between large and small fragments ($\chi^2 = 0.89$; $df = 2$; $P = 0.64$).

Tawny Tit-Spinetails showed no difference in foraging time between large and small fragments ($F_{5,283} = 0.44$; $P = 0.82$) nor between foraging alone or in mixed flocks ($F_{1,283} = 0.17$; $P = 0.68$). Their use of foraging substrates was also unrelated to fragment size ($\chi^2 = 1.17$; $P = 0.56$) or if foraging alone vs. in mixed flocks ($\chi^2 = 0.18$; $P = 0.91$). However, when Tawny Tit-Spinetails were foraging in mixed flocks, large trees were used more often (large trees 58%, medium trees 26%, and small trees 16%), while both large and medium-sized trees were preferred by single foraging Tawny Tit-Spinetails (large trees 43%, medium trees 46% and small trees 11%; $\chi^2 = 12.20$; $P = 0.002$).

DISCUSSION

We demonstrate that there is less bark biomass in trunks and thick branches (approximately –40% and –50%, respectively) of *Polylepis* trees of small compared to large forest fragments as well as an increasingly higher amount of bark biomass for wider trees in the interior of fragments compared to the edges. The difference related to fragment size applies to all parts of the trees, but particularly for trunks and thick branches, that are the most important bark-providing structures. The prevailing strong wind of the high-Andes (Kessler et al. 2007, Hertel and Wesche 2008) could explain this result, as wind disturbance is a potent ecological force in much of the tropics (Laurance and Curran 2008). As *Polylepis* fragments are surrounded by a puna matrix of only a few centimeters tall, wind collision is strong at the forest edge and at low tree density, since trees are wind barriers (Hale et al. 2011). Thus, we assume that bark removal is more prevalent for trees at edges and in small fragments compared to similar trees in large fragments. We also found that wider trees had more bark, which probably indicates that bark thickness increases with age, as in other trees (Arco Molina et al. 2016). A reduced amount of bark is likely to cause adverse effects both for the trees and forest ecosystem (Rada et al. 1996, García-Núñez et al. 2004) since the typically

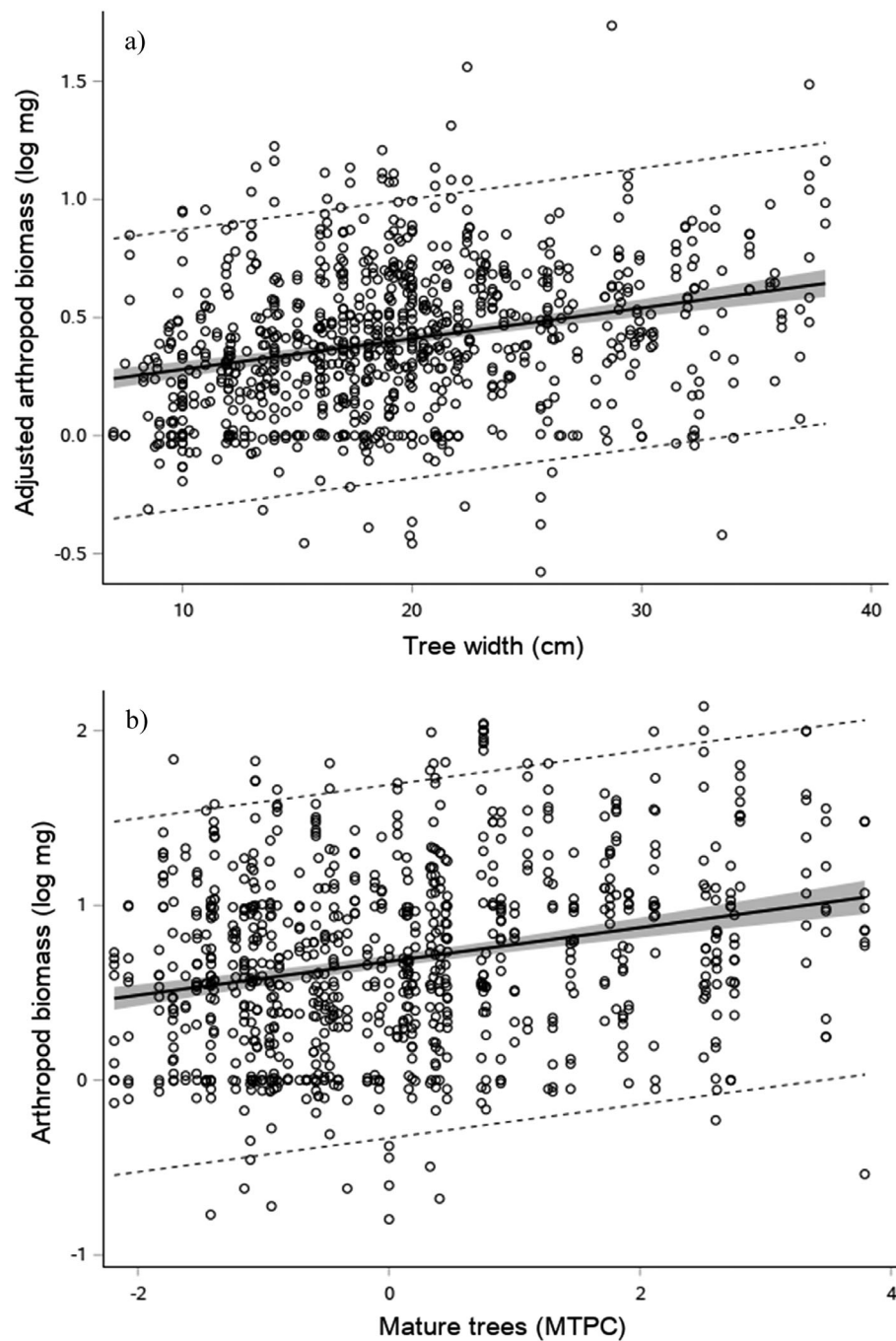


Fig. 4. Arthropod biomass (log mg) per 225 cm² bark sample (adjusted) in relation to tree width (DBH; a) and arthropod biomass (log mg) in relation to the principal component indicative of mature trees within sampling plots (MTPC; b). Dashed lines indicate 95% prediction intervals and blue shading indicates 95% confidence intervals.

multi-layered bark provides insulating protection against extreme temperatures and fire and favors detachment of epiphytic parasites (Fjeldså et al. 1996, Purcell et al. 2004).

We also observed a positive correlation between bark and bark-dwelling arthropod biomass, indicating that arthropods accommodate themselves more abundantly in (parts of) trees with a higher amount of bark. This suggests that bark functions as a fundamental resource within these *Polylepis* forest systems, providing a habitat in otherwise harsh and exposed conditions for these arthropods (Domic and Capriles 2009), which in turn are important host and food resources for other trophic levels, such as parasitic insects and insectivorous birds. Compared to ambient conditions, bark layers provide indeed milder environmental conditions for bark-dwelling arthropods, such as springtails, barklice, woodlice, mites, and spiders, that are known to track subtle microclimatic differences (Prinzing 2003). Moreover, as *P. besseri* is the only tree species in native forests at this elevation and geographic area, bark-dwelling arthropods are entirely dependent on this tree species for their survival. Especially bark from trunks of wide, large trees appears to fulfill this role, as we observed a higher amount of both bark and arthropod biomass for samples from trunks and large trees, compared to samples from thick and small branches and from smaller trees. Corrected for bark biomass, trunks and wide trees still provided the highest arthropod biomass per gram of bark. It is known from other forest ecosystems too that larger trees—owing to their deeper bark furrows—can support a higher biomass of bark-dwelling arthropods (Nicolai 1986, Morrison et al. 1987, Majer and Delabie 1999).

Our results fit the general observation that decreasing size of habitat fragments leads to a lower abundance of arthropods (Didham et al. 1996, Connor et al. 2000, Debinski and Holt 2000, Haddad et al. 2015, Rossetti et al. 2017). This effect of fragment size has indeed also been attributed to altered microclimatic conditions in small fragments, more specifically in terms of increased wind speed, higher temperature variability, decreased humidity, and increased luminosity (Turner and Corlett 1996, Harrison and Bruna 1999, Grimbacher et al. 2006, Broadbent et al. 2008, Laurance 2008, Haddad et al. 2015).

Here too, the marked differences in daily temperature profiles between the matrix and *Polylepis* fragments show the buffering capacity of the latter. Buffered environments are especially important for ectothermic organisms (Grimbacher et al. 2006, Merckx et al. 2008, Savilaakso et al. 2009), such as bark-dwelling arthropods, as they are highly dependent on ambient conditions for activity (Nicolai 1986, 1989). The immature stages of these arthropods are probably even more susceptible to environmental fluctuations and extreme conditions than adults. For instance, it has been shown that arthropod body size acts as a buffer against dehydration caused by convective cooling in exposed and isolated trees (Ozanne et al. 2000).

For insectivorous birds, arthropod biomass is an essential resource, which can become critically low in small fragments (Canaday 1997, Burke and Nol 1998, Zanette et al. 2000, Kilgo 2005). Here, we show this is also the case for two insectivorous bird specialists of *Polylepis* forests. Besides showing direct responses to fragment size in their abundances (Lloyd 2008b), both species respond to habitat and tree quality, with positive impacts of larger trees as these contain relatively more arthropods as a food resource. Giant Conebill was previously known to be more abundant, and to have smaller home ranges, at sites with a high density of large, mature trees (Cahill and Matthysen 2007, Lloyd 2008b, De Coster et al. 2009, Sevillano-Ríos and Rodewald 2017, Astudillo et al. 2020), but we now show that the bird indeed preferentially forages on larger trees, and this more often so in large fragments, in response to higher arthropod density. Some other insectivorous birds have also been shown to select trees based on arthropod density for increased foraging efficiency. For instance, in the southern USA, foraging Red-cockaded Woodpeckers select the pine species with highest arthropod biomass (Horn and Hanula 2002), and Hooded Warblers exert higher foraging activity as a function of arthropod abundance (Kilgo 2005). On the other hand, Tawny Tit-Spinetail did not show differences in foraging, which could mean that the observed differences in arthropod biomass are not impacting this bird's foraging efficiency. Previous studies also showed that this species' abundance is less dependent on habitat structure (Cahill and Matthysen 2007) or

habitat quality (measured via vegetation characteristics; Lloyd 2008c).

As foraging substrates, Giant Conebills use trunks and thick branches more often than small branches, while Tawny Tit-Spinetails use thin branches and twigs, which has been reported earlier from our own study sites as well as from Peru (Herzog et al. 2002, Lloyd 2008a, Matthysen et al. 2008). Also, Giant Conebills foraged more often on thick branches when alone, whereas when in mixed flocks they foraged more often on tree trunks, regardless of fragment size, confirming previous observations in the same area (Matthysen et al. 2008). The latter is most likely a behavioral response to competition. Giant Conebills foraged for longer periods in larger trees than in medium and small trees, again irrespective of fragment size. However, they appeared to be less selective in smaller fragments, which would help them to somehow buffer the lower quality conditions.

The only other study that addressed foraging behavior and habitat selection of birds in relation to *Polylepis* forest fragment size was done in Peru by Lloyd (2008a) and included our two study species. Although results are not fully comparable because of the use of different variables to characterize foraging behavior, there are interesting parallels between the two studies. Lloyd (2008a) found both species to be tolerant to small fragment size. As an explanation, the author provided flexibility in foraging behavior, using fewer substrates and fewer prey attack maneuvers in smaller fragments. A tentative but untested interpretation, which integrates both findings, is that the birds may compensate for the lower availability of large food-rich trees by focusing on the most productive substrates and foraging techniques.

Our finding may well be applicable to the whole guild specialized on bark-dwelling arthropods in fragmented *Polylepis* forests (Gareca et al. 2010) as it is unlikely that the bottom-up effect of bark-dwelling arthropod abundance in small fragments, fragment edges, and fragments with predominance of medium and small trees would be restricted to these two bird species. This bottom-up effect may also explain the previously observed reduced abundances of Giant Conebills and other insectivorous forest specialists (e.g., *Cinclodes aricomae*, *Anairetes alpinus*, *Conirostrum*

ferrugineiventre, *Leptasthenura xenothorax*, and *Xenodacnis parina*) in small *Polylepis* fragments of relatively low habitat quality (Lloyd 2008b, Astudillo et al. 2020).

In order to counter such negative effects of reduced arthropod abundance on higher trophic levels in this specialized and threatened ecosystem, we advise to protect large and medium-sized trees of *P. bessi* and indeed of other *Polylepis* species that are similarly characterized by large amounts of bark. Negative anthropogenic activities, such as fires to increase green grass shoots in the matrix and branch extraction from large trees for charcoal production (Fjeldsø et al. 1996), should be avoided completely or carefully regulated and controlled. Moreover, as we here have shown a positive correlation between fragment size and relative arthropod biomass, it is now timely to test whether and to what degree restoration efforts to increase fragment size could mitigate the negative effects of reduced arthropod biomass for higher trophic levels.

CONCLUSIONS

Our study contrasted multiple edge and interior locations of both small and large *Polylepis* forest fragments, while accounting for branch size, tree width, and tree structure. We found that small forest fragments are environmentally less buffered and characterized by lower amounts of bark and lower densities of bark-dwelling arthropods than larger fragments. We also show that bark-dwelling arthropod biomass was relatively higher in wider, larger trees, and that these trees were preferred for foraging by two *Polylepis* specialist bird species. Our study, hence, highlights the conservation value of larger trees. However, it also points out that it is now timely to quantify the capacity of fragment edges to buffer against harsh prevailing environmental conditions and to quantify the biotic response to such microclimatic buffering in terms of bark biomass growth. This knowledge will be essential to better design and predict the effectiveness of restoration actions focused on increasing fragment size and regenerating edges. Evidence-based restoration projects are now critically needed to mitigate negative effects of reduced arthropod biomass for higher trophic levels, notably threatened and endemic specialist insectivores.

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