

# Evolution of ecological structure of anole communities in tropical rain forests from north-western South America

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The coexistence of several anoles in the same place is attributed to differential partitioning of resources. Although several mainland and island communities show a similar structure, differences in life-history traits, absence of niche complementarity, higher food supply and higher numbers of predators in mainland environments support the idea that predation, rather than competition, is a more important structuring force in mainland than in island anole communities. To analyse the pattern of ecological structure in mainland anole communities, we studied communities in three tropical rain forests of north-western South America to obtain data about the use of resources on three niche axes [spatial, thermal and morphological (as a proxy of diet)] for 17 species of anoles. We analysed the patterns of niche overlap for each axis and found that overlap on the dietary axis was less than the overlap on the other axes, indicating that species using similar spatial or thermal resources diverge strongly in their diet. In addition, we identified a niche complementarity among niche axes, suggesting that intraspecific competition is also an important process in those communities. Finally, this study revealed a similar ecological structure in different communities of mainland rain-forest anoles, which share seven ecomorphs, suggesting ecological adaptation and convergence in mainland anoles.

ADDITIONAL KEYWORDS: adaptive radiation – anoles – Colombia – convergent evolution – coexistence – niche theory.

## INTRODUCTION

Adaptive radiation is a type of evolutionary radiation whereby a phylogenetic lineage produces an exceptional amount of phenotypic disparity among its taxa, which can be interpreted as a variety of adaptive forms that have evolved to use different ecological resources (Losos & Mahler, 2010; Mahler *et al.*, 2010). Adaptive radiation has often been responsible for the existence of highly diverse and phenotypically disparate communities, where species from the same lineage coexist through ecological differentiation promoted by ecological opportunity (e.g. new resources or new traits representing key innovations) and accompanied by the diversification of ecologically relevant phenotypic traits among newly evolving forms, driven mainly by mechanisms of competition (Schluter, 2000; Mahler *et al.*, 2010).

An iconic and well-studied example of adaptive radiation is *Anolis*, a species-rich genus of lizards, whose diversification was facilitated by the emergence and diversification of toepads among newly evolving species. The emergence of toepads represented a key innovation that allowed anoles to fill arboreal niches in new ways not available to lizards without toepads. The partitioning of local habitat resources through ecological differentiation, mediated mainly by mechanisms of competition, therefore allows more species to occupy the same space than would otherwise be possible (Rand, 1964; Rummel & Roughgarden, 1985; Losos, 2009). Although morphological innovation has often been considered to have allowed species to use, and then adapt to, a wide variety of different niches (Losos, 2009; Mahler *et al.*, 2010), Anderson & Poe (2018) did not find evidence to support the idea that ecological opportunity (owing to the island effect and morphological innovation) was the trigger for morphological diversity in anoles.

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Independent of the cause of morphological diversity in anoles, their communities are typically composed of between two and 15 species (Losos, 2009) that are assembled according to their differential use of habitat resources (Rand, 1964; Schoener, 1968; Duellman, 1978; Castro-Herrera, 1988; Pounds, 1988; Losos, 1990a; Vitt *et al.*, 1999; D'Cruze & Stafford, 2006). In a similar manner to other lizards that coexist sympatrically, anoles partition resources principally along three main axes: (1) structural habitat; (2) thermal microhabitat; and (3) prey size and type (Pianka, 1974; Williams, 1983). Groups of anole species that share similar microhabitat, behavioural and morphological attributes, without necessarily being phylogenetically close, are termed ecomorphs (Williams, 1972). Currently, six anole ecomorphs have been recognized and named according to the predominant microhabitat they use (e.g. grasses, open ground, different parts of trees): 'crown giant', 'trunk-crown', 'trunk', 'twig', 'trunk-ground' and 'grass-bush'. Originally described on the basis of island studies of anole communities, these ecomorphs seem to be exclusive to Greater Antillean island anole radiations, with evidence suggesting few similarities to mainland anole species (Irschick *et al.*, 1997; Velasco & Herrel, 2007; Pinto *et al.*, 2008; Schaad & Poe, 2010).

The numbers and types of ecomorphs present within a given locality give rise to distinct anole communities, with similar habitats giving rise to similar anole communities. Two hypotheses have been proposed to explain ecomorphological evolution in both Greater and Lesser Antillean anole communities (Losos, 1992, 2009): (1) the character displacement hypothesis; and (2) the niche compression hypothesis. The character displacement hypothesis (Brown & Wilson, 2006) suggests that structuring in the early stages of diversification is driven mainly by divergence in body size among species that share the same microhabitat, followed by subsequent divergence owing to differences in microhabitat and food (Losos, 1992). In contrast, the niche compression hypothesis (MacArthur & Wilson, 1967) suggests that structuring in the early stages is driven mainly by divergence in microhabitat among species of similar body size, followed by subsequent divergence owing to body size and food (Losos, 1992). Ecological and phylogenetic analyses have confirmed that niche compression has played an important role in the faunal assembly of anole communities from the southern Lesser and Greater Antilles, through sequential microhabitat partitioning (Losos, 1992, 2009). Furthermore, it has been demonstrated that analogous anole communities from the Greater Antilles are the result of convergent evolution driven by one-to-one convergent evolution at the species level, through the channelling of both global and local optimization

to several adaptive peaks (Losos, 2009; Sanger *et al.*, 2011; Mahler *et al.*, 2013).

Differences in ecological structure between Caribbean island and South American mainland anole communities are attributed to differences in food resource availability and predator density between island and mainland habitats (Andrews, 1979; Losos, 2009), with fewer food resources and fewer predators on islands resulting in greater predation and reduced interspecific competition in mainland communities than in island communities. These differences, in turn, affect the life-history characters of species (Andrews, 1979). However, despite these differences, some studies (Rand & Humphrey, 1968; Duellman, 1978; Castro-Herrera, 1988) have shown similarities in ecological structure between mainland and island anole communities.

The Andes are a continental mountain range that extends along the western edge of South America. In north-western South America, the Andes split into three mountain chains, producing several tropical forest habitats in inter-Andean valleys, in addition to separating the lowlands of Chocó west of the Andes and the Amazon basin to the south-east. These have followed relatively independent biogeographical histories for  $\geq 33$  Myr (Hoorn *et al.*, 2010). In these forests, *Anolis* are also highly diverse and morphologically disparate (particularly in Colombia), and represent the dominant fauna in communities of arboreal lizards (Moreno-Arias *et al.*, 2008).

Despite the importance of anoles in arboreal lizard communities in South America, the natural history of many species is poorly known, with the ecology of only a few species having been studied (Losos *et al.*, 1991; Vitt & Zani, 1996; Vitt *et al.*, 2001, 2003a, b; Miyata, 2013). Few studies have focused on ecological structure and of those that have, most are restricted to anole communities either in the Amazon region (Rand & Humphrey, 1968; Duellman, 1978; Vitt *et al.*, 1999) or in the Chocó region along the north-western Pacific coast of Colombia (Castro-Herrera, 1988). To date, no studies have examined anole communities from inter-Andean forests, thus the importance of inter-Andean forests in north-western South America as a reservoir of anole diversity is unknown.

Recently, Moreno-Arias & Calderón-Espinosa (2016) showed how the morphological diversification of continental anole lizards from north-western South America fitted better to models describing non-random evolutionary processes than to other models and described the close similarity in morphological structure found between mainland anole communities. These patterns could be consistent with the convergent evolution hypothesis used to explain similarity among community assemblages in Greater Antillean

anoles, where similar sets of habitat specialists have evolved independently on each island (Williams, 1983; Losos *et al.*, 1998; Jackman *et al.*, 1999; Nicholson *et al.*, 2005). As predicted by adaptive radiation models (Schluter, 2000), anole lizards partition local habitat resources through ecological differentiation, therefore allowing more species to occupy the same space than would otherwise be possible (Rand, 1964; Rummel & Roughgarden, 1985). Furthermore, local habitat partitioning has been shown to have evolved independently on separate Caribbean islands (Losos *et al.*, 1998). This contrasts with the idea of historical contingency (Gould, 1989), whereby phenotypic expression is contingent on past evolutionary history or prior mutations in that population, meaning that species, despite evolving in similar conditions, will present more differences than similarities (Wiens, 1989).

We hypothesize that ecological differentiation through habitat partitioning among mainland anole species should be reflected in the morphology of the species (Losos, 1990b, c), that the structure of mainland anole communities evolved mainly by microhabitat partitioning, in a similar manner to the island counterparts (Losos, 1992), and that there is an ecological convergence, as evidenced by previous studies (Moreno-Arias & Calderón-Espinosa, 2016; Poe & Anderson, 2019).

Under this hypothesis, our first prediction is that anole species coexisting in the same community partition local habitat along at least one of the three axes recognized by Williams (1983; microhabitat structure, thermal or dietary) and that these differences follow a trajectory independent of the phylogenetic history. Our second prediction is that mainland tropical rain-forest anole communities evolving in similar environmental conditions will exhibit a similar ecological structure composed of the same groups of species, each associated with a particular use of habitat resources.

To test these predictions, we examined the ecological diversity of anoles in three biogeographically independent mainland rain-forest regions in Colombia: the Amazon biogeographical region, the Chocó biogeographical region and the Inter-Andean region (the Magdalena Valley). The main objectives of the present study were as follows: (1) to describe the pattern of partitioning of spatial, thermal and dietary resources and the morphology of anole communities from tropical rain forests in the three different biogeographical regions; (2) to identify groups of species with similar use of resources and similar morphology across tropical rain forests; (3) to describe scenarios of the evolution of habitat use by anole communities from north-western South America; and (4) to examine the importance of inter-Andean forests in north-western South America as a reservoir of anole diversity.

## MATERIAL AND METHODS

### FIELDWORK

We conducted fieldwork at three sites in Colombia dominated by tropical rain-forest vegetation. These localities were chosen because they represent three geographically independent communities of anoles owing to the formation of the Andes, allowing comparison between the effects of evolutionary history (such as vicariance, where past historical events have influenced population differentiation) and ecology (adaptation by natural selection for current ecological conditions) on community structure and niche differentiation in mainland anole lizards. The first site, referred to as 'Chocó', corresponds to the Biological Station El Amargal in the village of Arusí, in the municipality of Nuquí, department of Chocó (5°35'14.91"N, 77°29'30.58"W; WGS 84; 41 m a.s.l.). The second site, referred to as 'Magdalena', corresponds to Haciendas Javas and Pampas in the municipality of Yondó, department of Antioquia (6°42'48.4"N, 74°20'44.1"W; WGS 84; 109 m a.s.l.). The third site, referred to as 'Amazonas', corresponds to the Tanimboca Nature Reserve in the municipality of Leticia, department of Amazonas (4°7'37.8"S, 69°57'12.8"W; WGS 84; 95 m a.s.l.).

The forest type at all sites is multistratified, with: (1) a dense leaf-litter stratum; (2) an herbaceous stratum dominated by young palms and trees shorter than 1.5 m; (3) an understorey (reaching 20 m tall), with small trees, shrubs, palms, vines and epiphytes; and (4) a canopy stratum that includes trees reaching 40 m tall, with vines and epiphytes.

Reported annual mean precipitation and temperature for each site are as follows: Chocó, 7245 mm and 26.0 °C (Galeano, 2001); Magdalena, 2399 mm and 28.4 °C; and Amazonas, 3250 mm and 26.4 °C (Domínguez, 1999).

At each site, we recorded habitat structure and attributes of the microclimate for each male individual observed. The following habitat structure attributes were recorded: (1) habitat type [forest edge, defined as an ecotone of 20 m from the physical edge of the forest (Urbina-Cardona *et al.*, 2006), open areas/pastures or clearings inside the forest]; (2) stratum (canopy, comprising trees or vines with an estimated height > 20 m; understorey, comprising trees, bushes or vines between 1.5 and < 20 m in height; herbaceous: trees, bushes or herbs < 1.5 m in height; and terrestrial, comprising ground, grass or leaf litter); and (3) perch type [ground (including bare ground, leaf litter and fallen logs), grass, herbs, vines, branches and twigs, trunks and leaves]. The following microhabitat attributes were also recorded: (1) perch exposure, i.e. sun, if there was no vegetation cover above the perch, or shade, if there was vegetation above the

perch; (2) perch height; (3) perch diameter; (4) nearest perch; (5) perch temperature; and (6) environmental temperature.

Observations were made in January and July 2013 and in January and February 2014, using visual encounter surveys (Crump & Scott, 1994). Measurements were performed during daytime surveys between 08:00 and 16:00 h, to maintain temperature and light intensity distributions that allowed for adequate microclimate partitioning. Sampling effort ranged from 192 to 576 person-hours per site. A Rand census was implemented (Rand, 1964) to characterize microhabitat use by species.

To analyse the morphology of species, we measured individuals captured in this study. We used as variables the mean of snout–vent length (SVL) and the residuals of mean hindleg length (HLL), head width (HW), head height (HH), head length (HL) and the number of lamellae in the third and fourth phalanges of the fourth toe (LN) against SVL. We used these variables as a proxy of feeding behaviour and prey size. The relationship of body size and head dimensions to prey size has been well documented (e.g. Duellman, 1978; Castro-Herrera, 1988; Vitt *et al.*, 1999, 2001, 2002, 2003a, b), whereas hindlimb length and number of lamellae are correlated with locomotor performance related to feeding and predator avoidance in the Caribbean (Losos, 1990a, b; Irschick & Losos, 1996; Losos & Irschick, 1996) and in mainland anoles (Moreno-Arias, 2014).

#### DATA ANALYSIS

Competition theory predicts that community or assemblage structure in anole lizards should be shaped by differences in resource partitioning between co-occurring species. As such, quantifying the differences in the degree of resource partitioning (i.e. microhabitat/niche overlap) is a key part of studies examining community structure. We used two resource axes and an axis of morphology to quantify the niche and morphological space, respectively. The use of each resource was defined by the frequency of use per species for each category of discrete variable and the mean value of each continuous variable.

Variables were grouped into one of three axes, each representing one of three distinct niche axes: spatial, thermal and morphological. The spatial axis was composed of the following variables related to the nature and position of perches or structural habitat (Rand, 1964): stratum; perch type; perch height and diameter; and nearest perch. The thermal axis was composed by habitat type, perch exposure and perch and air temperatures, which describe the intensity of solar radiation in the microhabitat and therefore

represent a thermoregulation resource. Finally, we describe the morphological variation of communities by means of a principal components analysis with the previously mentioned variables that are closely related to feeding behaviour and prey size.

To detect the existence of differences in resource use between species across niche axes, we performed a unified analysis of niche overlap (UANO; Geange *et al.*, 2011) on each anole community. This method estimates the distribution of probabilities for each data type (e.g. categorical, binary, continuous), calculates niche overlap statistics between two species as the overlapping area between distributions, and creates a composite statistic of niche overlap for all types of data. This method uses null models to determine whether differences between niche overlap resource axes (i.e. thermal, spatial and morphology) and overall overlap (niche axes combined) are attributable to sampling variation (Gotelli, 2000). UANO performs permutation tests to produce a null distribution, calculating pseudo-values of niche overlap from pseudo-communities, and tests the distribution of niche overlap values from the observed community against the null distribution for a given *P*-value (Geange *et al.*, 2011). To describe the patterns of resource use among species across the communities studied, we performed an additional UANO with all species pooled.

Given that niche overlap values between species are a measure of ecological similarity, we used the niche overlap matrix to perform non-metric multidimensional scaling (nMDS) to visualize the overall ecological similarity among species. Non-metric multidimensional scaling allows the identification of structure in a complicated dataset by reducing the spatial representation of relationships to a few dimensions (Cox & Cox, 2001). In this case, nMDS was used to summarize or depict general ecologically similar groups, in such a way that most similar species (as determined by niche overlap values) would be close together, and most dissimilar species would be separated. In addition, the nMDS calculates a 'stress' value that is a measure of the degree of fit between the distances in reduced dimensions and the predicted distance values from the regression; stress values  $\leq 0.01$  indicate a good fit. The UANO and nMDS analyses were performed in R software (R Core Team, 2013), with source code provided by Geange *et al.*, (2011) and the R package *vegan* (Oksanen *et al.*, 2013).

We defined an ecomorph as a group of ecologically equivalent species exhibiting non-significant values of niche overlap, indicating use of the same niche. However, we emphasize that we do not provide behavioural data, which permit linking form and function to any formal definition of ecomorph (Losos, 1990a, b, c).



**Table 1.** Percentage of observed individuals according to habitat, stratum, perch type and perch exposure for the 17 species of anoles observed in the three tropical rain-forest localities of north-western South America

Sites	<i>Anolis</i> species	N	Habitat			Stratum				Perch type					
			FE	F	OV	I	II	III	IV	G	Gb	Tr	B-T	V	L
Chocó	<i>A. anchicayae</i>	13	–	100.0	–	–	–	38.5	61.5	–	–	92.3	7.7	–	–
	<i>A. chloris</i>	9	100.0	–	–	–	–	–	100.0	–	–	55.6	44.4	–	–
	<i>A. granuliceps</i>	16	6.3	93.8	–	50.0	37.5	12.5	–	46.7	–	26.7	–	–	26.7
	<i>A. latifrons</i>	5	–	100.0	–	–	–	40.0	60.0	–	–	80.0	20.0	–	–
	<i>A. maculiventris</i>	19	15.8	73.7	10.5	15.8	31.6	31.6	21.1	15.8	5.3	36.8	15.8	10.5	15.8
	<i>A. triumphalis</i>	1	100.0	–	–	–	–	–	100.0	–	–	–	100	–	–
	<i>A. vittigerus</i>	2	–	100.0	–	–	–	50.0	50.0	–	–	50.0	–	50.0	–
Magdalena	<i>A. auratus</i>	28	75.0	–	25.0	14.3	71.4	7.1	7.1	21.4	57.1	10.7	10.7	–	–
	<i>A. frenatus</i>	8	–	100.0	–	–	–	25.0	75.0	–	–	100.0	–	–	–
	<i>A. sp.</i>	5	20.0	80.0	–	–	40.0	60.0	–	–	–	60.0	40.0	–	–
	<i>A. sulcifrons</i>	12	100.0	–	–	–	–	–	100.0	–	–	91.7	8.3	–	–
	<i>A. tropidogaster</i>	11	27.3	72.7	–	9.1	18.2	72.7	–	9.1	9.1	27.3	–	54.5	–
	<i>A. vittigerus</i>	2	–	100.0	–	50.0	–	50.0	–	50.0	–	50.0	–	–	–
	<i>A. trachyderma</i>	1	–	100.0	–	–	–	–	–	–	–	–	–	–	–
Amazonas	<i>A. fuscoauratus</i>	19	52.6	36.8	10.5	10.5	21.1	63.2	5.3	11.8	–	29.4	35.3	5.9	17.6
	<i>A. ortonii</i>	9	–	100.0	–	–	–	–	100.0	–	–	22.2	66.7	11.1	–
	<i>A. punctatus</i>	4	25.0	75.0	–	–	–	–	100.0	–	–	50.0	50.0	–	–
	<i>A. trachyderma</i>	14	7.1	92.9	–	35.7	50.0	14.3	–	35.7	28.6	14.3	–	7.1	14.3
	<i>A. transversalis</i>	6	–	100.0	–	–	–	–	66.7	33.3	–	–	33.3	66.7	–

Habitat: F, forest; FE, forest edge; OV, open vegetation. Perch type: B-T, branches and twigs; G, ground; Gb, grass and bushes; L, leaves; Tr, trunks; V, vines. Stratum: I, terrestrial; II, herbaceous; III, understorey; IV, canopy.

species in Chocó, four vs. one in Magdalena and three vs. two in Amazonas. There were no significant differences in species abundance across localities ( $\chi^2 = 1.3$ ,  $P \leq 0.5$ ), perch exposure ( $\chi^2 = 1.0$ ,  $P \leq 0.6$ ), stratum ( $\chi^2 = 0.5$ ,  $P \leq 0.8$ ), perch type ( $\chi^2 = 2.2$ ,  $P \leq 0.3$ ) or body size ( $\chi^2 = 2.7$ ,  $P \leq 0.3$ ).

#### SPECIES AND MICROHABITAT USE IN EACH ANOLE COMMUNITY

The most diverse habitat was the 'forest', where 14 species (five in Chocó, five in Amazonas and four in Magdalena) and 109 individuals were found (49, 22 and 38 in Chocó, Magdalena and Amazonas, respectively), followed by 'forest edge' (11 species and 63 individuals) and 'open vegetation', where we recorded only three species and 11 individuals (Table 1). The highest anole abundance was recorded in the 'canopy' stratum in Chocó (28 individuals) and Magdalena (21 individuals), whereas the 'understorey' in Amazonas was the stratum that harboured the highest abundance of lizards (Table 1). Also, in Chocó and Magdalena, anoles used trunks more frequently than branches or twigs, whereas in Amazonas the branches or twigs were the most frequently used perches rather than the trunks (Table 1).

Anoles were observed on perches of different sizes from ground level to > 30 m high. *Anolis chloris*

Boulenger, 1898 in Chocó, *Anolis sulcifrons* Cope, 1899 in Magdalena and *Anolis ortonii* Cope, 1868 in Amazonas used the highest perches (Table 2). The lowest perches were used by *Anolis granuliceps* in Chocó, *A. auratus* in Magdalena and *Anolis trachyderma* Cope, 1875 in Amazonas (Table 2). The widest perches were used by *Anolis latifrons* Berthold, 1846, *Anolis sulcifrons* and *Anolis ortonii* in Chocó, Magdalena and Amazonas, respectively (Table 2). The narrowest perches were used by *A. triumphalis* in Chocó, *Anolis sp.* in Magdalena and *A. trachyderma* in Amazonas (Table 2).

Regarding the Chocó, Magdalena and Amazonas communities, the microhabitats surrounded by dense vegetation were preferred by *A. granuliceps*, *A. vittigerus* and *A. trachyderma*, whereas less densely vegetated microhabitats were preferred by *A. chloris*, *A. auratus* and *A. punctatus*, respectively. With regard to the microhabitat exposure, most of the anole species preferred shaded microhabitats, with the exception of *A. chloris* and *Anolis maculiventris* Boulenger, 1898 in Chocó, *A. sulcifrons* and *A. auratus* in Magdalena, and *A. ortonii* and *A. punctatus* in Amazonas, which were more common in sunny microhabitats (Table 2).

The morphology of anoles was described in a different manner in each community. In Chocó, it was described mainly by HH and HW (first principal component, with 26.1% of variance), FLL and HLL (second principal

**Table 2.** Mean (SD) microhabitat features and frequency of perch exposure of 17 species of anoles from three tropical rain forests of north-western South America

Site	<i>Anolis</i> species	Perch height (cm)	Perch diameter (cm)	Nearest perch (cm)	Perch exposure		Temperature (°C)	
					Sun	Shade	Perch	Air
Chocó	<i>A. anchicayae</i>	182.3 (20.6)	32.7 (7.3)	48.2 (12.2)	30.8	69.2	26.7 (0.1)	26.4 (1.2)
	<i>A. chloris</i>	765.8 (140.4)	17.0 (5.6)	62.2 (15.1)	100.0	0.0	28.3 (1.5)	29.0 (0.8)
	<i>A. granuliceps</i>	30.5 (8.19)	25.4 (12.9)	30.2 (9.2)	0.0	100.0	26.0 (1.1)	25.9 (1.2)
	<i>A. latifrons</i>	332.6 (41.9)	33.6 (19.1)	50.3 (21.1)	25.0	75.0	26.4 (1.7)	25.7 (1.1)
	<i>A. maculiventris</i>	221.6 (43.9)	9.8 (4.0)	46.3 (8.5)	53.3	46.7	26.6 (1.5)	26.4 (1.5)
	<i>A. triumphalis</i>	–	0.5 (0.0)	–	100.0	0.0	27.7 (0.0)	28.4 (0.0)
	<i>A. vittigerus</i>	97.5 (50.5)	9.5 (0.0)	19.5 (14.5)	50.0	50.0	28.0 (0.0)	28.5 (0.0)
Magdalena	<i>A. auratus</i>	32.5 (8.0)	13.3 (11.4)	265.8 (16.6)	92.6	7.4	28.0 (2.0)	28.5 (0.9)
	<i>A. frenatus</i>	172.6(25.8)	11.2 (2.9)	68.4 (15.1)	0.0	100.0	27.6 (0.0)	27.5 (1.7)
	<i>A. sp.</i>	46.4 (14.6)	5.6 (3.3)	22.4 (4.4)	0.0	100.0	27.7 (0.0)	28.8 (0.0)
	<i>A. sulcifrons</i>	326.8 (48.2)	54.6 (11.2)	77.3 (35.9)	66.7	33.3	28.2 (0.6)	29.1 (0.3)
	<i>A. tropidogaster</i>	100.0 (19.9)	20.1 (17.4)	42.7 (6.9)	20.0	80.0	28.5 (0.0)	27.9 (1.4)
	<i>A. vittigerus</i>	100.0 (50.0)	12.5 (2.5)	32.5 (7.5)	0.0	100.0	27.5 (0.0)	29.0 (0.0)
Amazonas	<i>A. fuscoauratus</i>	205.8 (35.3)	4.3 (2.6)	29.5 (7.1)	58.8	41.2	29.6 (0.6)	28.0 (0.9)
	<i>A. ortonii</i>	3633.3 (89.7)	33.3 (6.6)	58.9 (12.7)	88.9	11.1	27.5 (0.4)	27.8 (0.0)
	<i>A. punctatus</i>	1909.2 (947.5)	22.7 (4.5)	79.0 (22.85)	75.0	25.0	28.4 (0.5)	28.6 (0.5)
	<i>A. trachyderma</i>	56.41 (17.34)	1.2 (0.8)	13.0 (4.3)	23.1	76.9	27.0 (1.4)	27.4 (0.9)
	<i>A. transversalis</i>	407.5 (143.86)	2.7 (0.6)	14.0 (1.0)	16.7	83.3	27.4 (0.2)	26.5 (0)

**Table 3.** Univariate values of mean niche overlap for Chocó, Magdalena and Amazonas communities and [pseudocommunities] of anoles

Site	Overall	Thermal	Spatial	Morphology
Chocó	0.40 [0.56]	0.48 [0.67]	0.48 [0.63]	0.28 [0.43]
Magdalena	0.38 [0.58]	0.36 [0.63]	0.36 [0.64]	0.41 [0.50]
Amazonas	0.33 [0.55]	0.37 [0.58]	0.35 [0.60]	0.30 [0.48]

For all pseudocommunities, the mean values for niche overlap were significantly different from the mean niche overlap recorded.

component, with 18.8% of variance) and SVL and HL (third principal component, with 17.7% of variance). In Magdalena, it was described by HH and HW (first principal component, with 25.7% of variance), NL (second principal component, with 21.1% of variance) and FLL and HLL (third principal component, with 16.2% of variance). In Amazonas, it was described by FLL and HLL (first principal component, with 34.1% of variance), SVL and LN (second principal component, with 23.1% of variance) and HW and HH (third principal component, with 12.6% of variance).

The observed values of niche overlap were lower than the values of niche overlap estimated by the null models in all communities (Table 3). The mean value of niche overlap did not differ among axes in Magdalena ( $H = 1.45, P = 0.48$ ) and Amazonas ( $H = 0.96, P = 0.62$ ), but it did in Chocó ( $H = 11.29, P = 0.003$ ). The overlap in thermal and spatial axes were greater than that in

the morphological axis in the Chocó and Amazonas communities, but in Magdalena the overlap of these axes was lower than that in the morphological axis (Table 3). In each community, all pairs of species were differentiated along at least one axis, except for the species pairs *A. vittigerus* and *A. latifrons* in Chocó, *Anolis* sp. and *A. tropidogaster* Hallowell, 1856 in Magdalena and *A. ortonii* and *A. punctatus* in Amazonas (Supporting Information, Appendix S2, Table S1).

NICHE OVERLAP AND HABITAT USE ACROSS ANOLE COMMUNITIES

The extent of niche overlap showed the same pattern across Chocó and Amazonas communities, with the greatest niche overlap being observed in the thermal axis (0.42), followed in order by the spatial (0.41) and

morphological (0.37) axes, with the last axis being different from the other two ( $H = 25.3$ ,  $P = 0.000003$ ). There were no significant correlations between values of niche overlap along axes, but there was a general negative trend between morphological and spatial overlap values, suggesting niche complementarity among these axes (thermal vs. morphological,  $r = 0.13$ ,  $P = 0.15$ ; spatial vs. morphological,  $r = 0.10$ ,  $P = 0.35$ ; and thermal vs. spatial,  $r = 0.14$ ,  $P = 0.11$ ).

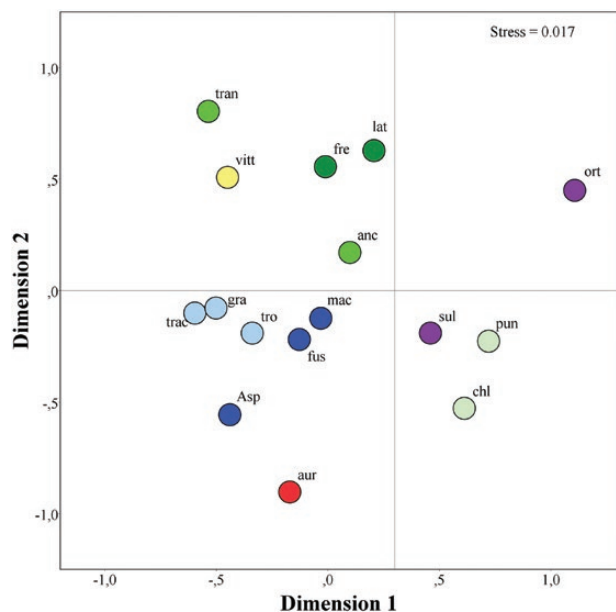
Based on similarities in resource use and the significant differences in niche overlap across axes (Fig. 1; Supporting Information, Appendix S2, Table S2), we recognized the following eight groups of ecologically equivalent species or ecomorphs.

#### *Leaf-litter anole*

This category included small forest species found mostly in leaf litter and on secondary perches < 0.25 m in diameter located on herbaceous plants and trees of understorey strata. Perches were not exposed to direct sun and were typically < 1.0 m off the ground.

#### *Trunk-ground anole*

This category included medium-sized forest species that mostly used trunks and secondarily leaf litter. They were



**Figure 1.** Ordination of 16 species of anoles of tropical rain forests of north-western South America, according to their overall niche similarity. Colours indicate ecomorphs, as follows: red, grass-bush; yellow, trunk-ground; light blue, leaf litter; dark blue, bush-forest; purple, trunk; light green, edge-trunk-crown; medium green, forest-trunk-crown; dark green, crown giant.

characterized by their tendency to perch on branches < 0.12 m in diameter located on trees of understorey and canopy strata. Perches were usually not exposed to the sun and typically < 1.5 m off the ground. We did not record species of this ecomorph in Amazonas.

#### *Bush-forest anole*

This category included small species found in forest and forest edge habitat. They used trunks, branches and twigs of trees of the understorey stratum. Perches were typically < 0.10 m in diameter and occurred < 2.5 m off the ground.

#### *Grass-bush anole*

This category included small species found in forest edge habitat and open vegetation. They used exposed trunks, branches and twigs of bushes, grass and herbs from ground to understorey strata. Perches were < 0.13 m in diameter and < 0.4 m off the ground. We recorded species of this ecomorph only in Magdalena.

#### *Trunk anole*

This category included small species found in canopy forest and forest edge habitat. They were characterized by a tendency to use wide, exposed trunks and branches of trees of understorey and canopy strata. Perches were > 0.3 m in diameter and occurred ~3–35 m off the ground.

#### *Edge-trunk-crown anole*

This category included medium-sized species found mostly in forest edge habitat on exposed trunks and branches of trees of understorey and canopy strata. Perches were < 0.3 m diameter and occurred ~7–35 m off the ground. We did not record species of this ecomorph in Magdalena.

#### *Forest-trunk-crown anole*

This category included medium-sized species found in forest habitat on trunks of trees of understorey and canopy strata. Perches might be narrow or wide, were typically not exposed and were found ~2 m off the ground. We did not record species of this ecomorph in Magdalena.

#### *Crown giant anole*

This category included the largest species, inhabiting forest habitat on trunks and branches of trees of the understorey and canopy strata. Perches were > 0.10 m in diameter and were typically not exposed and found > 2 m off the ground. We did not record species of this ecomorph in Amazonas.

EVOLUTION OF HABITAT USE BY ANOLES FOUND IN  
 TROPICAL RAIN FORESTS IN NORTH-WESTERN SOUTH  
 AMERICA

Estimates of the magnitude and significance of the phylogenetic signal between phylogenies were similar for all traits, with the exception of hindlimb length and perch type (Table 4), for which the phylogenetic signal values significantly exceeded one in the study by Poe *et al.* (2017). In addition, both phylogenies performed with similar power (Table 4; Supporting Information Appendix 3, Fig. S3). Our phylogeny could estimate the phylogenetic pattern for nine traits, whereas the phylogeny of Poe *et al.* (2017) was able to estimate the phylogenetic pattern for eight traits (Table 4). The Blomberg's *K* statistic was significantly less than one for most traits, indicating greater trait variation within clades than would be expected by Brownian motion and an evolutionary pattern of dependence across the phylogeny (Table 4). For the remaining traits, the evolutionary pattern fitted a model expected by Brownian motion, but the statistical power of both phylogenies to estimate this evolutionary pattern was poor (10–45%; Table 4).

The fitting of different models of evolution to the combined ecological data supported an explanation of ecological differentiation via non-random processes as the most likely cause of ecomorph diversification (Fig. 2; Supporting Information Appendix 3, Fig.

S4). The Ecomorph-Bwd model provided the best fit to explain the evolution of ecological traits. All the remaining models provided a poor explanation of ecological trait evolution for the studied species. The Ecomorph-Bwd model was able to identify eight adaptive regimen shifts across the phylogeny in four distinct adaptive peaks: two non-convergent adaptive peaks corresponding to the crown giant and grass-bush ecomorphs, and two convergent adaptive peaks corresponding to ecomorphs inhabiting the highest strata with high solar radiation (trunk and edge-trunk-crown) and ecomorphs exclusively inhabiting the forest at intermediate to lower forest strata (leaf litter, bush-forest, trunk-ground and forest-trunk-crown; Fig. 2).

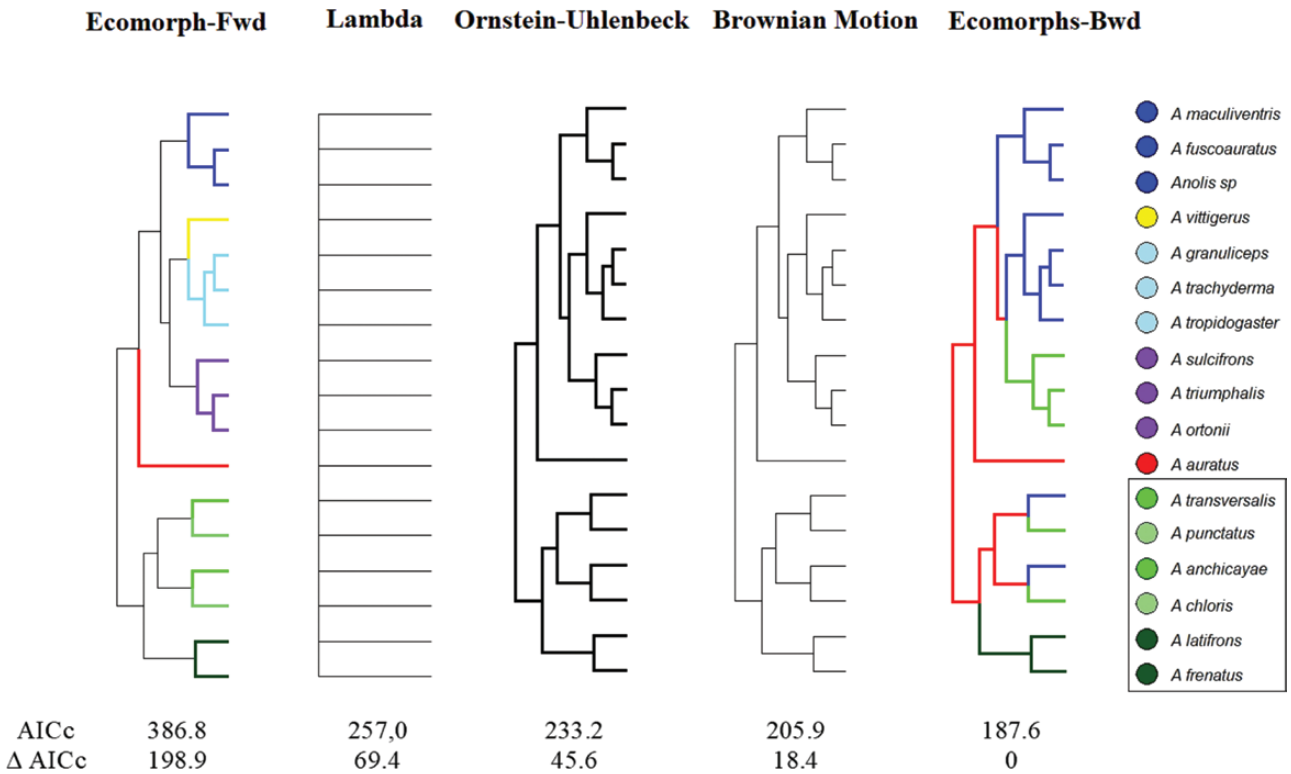
## DISCUSSION

The 17 species of *Anolis* recorded in the present study exhibit ecological diversity that can be summarized into eight different ecomorphs, with most ecomorphs being present in each of the three anole communities studied (Choco, Magdalena and Amazonas). Species exhibit local habitat partitioning along spatial, thermal and dietary niche axes, both within and across anole communities. Inferences regarding feeding characteristics (using attributes of the morphological

**Table 4.** Blomberg's *K* values (probability of being different from one) [probability of being in the Blomberg's *K* null distribution calculated in 100 random trees]

Trait	Phylogeny from this study	Phylogeny from Poe <i>et al.</i> (2017)
Snout-vent length	<b>1.318 (0.001) [0.02]*</b>	<b>1.828 (0.001) [0.02]*</b>
Hindlimb length	<b>0.703 (0.006) [0.05]*</b>	<b>1.474 (0.001) [0.01]*</b>
Head width	<b>0.750 (0.006) [0.05]*</b>	<b>0.746 (0.136) [0.05]*</b>
Head height	0.420 (0.212) [0.41]	0.531 (0.549) [0.18]
Head length	0.262 (0.735) [0.79]	0.401 (0.899) [0.45]
Number of lamellae	<b>0.703 (0.013) [0.05]*</b>	<b>0.983 (0.014) [0.02]*</b>
Perch height	0.417 (0.243) [0.35]	0.542 (0.500) [0.17]
Perch diameter	<b>0.580 (0.040) [0.05]*</b>	0.604 (0.352) [0.06]
Nearest perch	<b>1.104 (0.002) [0.03]*</b>	<b>1.039 (0.009) [0.03]*</b>
Stratum d1	<b>1.045 (0.001) [0.01]*</b>	<b>1.276 (0.004) [0.01]*</b>
Stratum d2	0.377 (0.252) [0.56]	0.568 (0.423) [0.20]
Perch type d1	<b>0.761 (0.015) [0.03]*</b>	<b>1.574 (0.001) [0.01]*</b>
Perch type d2	0.423 (0.150) [0.32]	0.651 (0.229) [0.10]
Habitat type d1	0.331 (0.420) [0.54]	0.559 (0.402) [0.17]
Habitat type d2	0.407 (0.226) [0.44]	0.763 (0.083) [0.04]
Perch exposure d1	<b>0.643 (0.020) [0.05]*</b>	<b>0.891 (0.050) [0.02]*</b>
Perch exposure d2	0.372 (0.289) [0.45]	0.457 (0.727) [0.31]
Perch temperature	0.342 (0.440) [0.54]	0.468 (0.715) [0.29]
Air temperature	0.360 (0.353) [0.53]	0.575 (0.380) [0.12]

Values in bold are significantly different from one. d1 and d2 indicates values of species in the first and second axes from NMDS analyses.  
 \*Values significantly different from the null distribution calculated in 100 random trees with probability  $\leq 0.95$ .



**Figure 2.** Models of ecological evolution of *Anolis* species from tropical rain forests of north-western South America. Colours indicate ecomorphs, as follows: red, grass–bush; yellow, trunk–ground; light blue, leaf litter; dark blue, bush–forest; purple, trunk; light green, edge–trunk–crown; medium green, forest–trunk–crown; dark green, crown giant. Branches not shown in bold indicate no regimen. Species of the *Dactyloa* clade are inside the box. Abbreviations: A, Amazonas; C, Chocó; M, Magdalena.

axis as a proxy) are restricted to partitioning on prey size and foraging behaviour rather than prey composition (e.g. Duellman, 1978; Castro-Herrera, 1988; Vitt *et al.*, 2003a). Furthermore, morphological overlap values are likely to underestimate the degree of partitioning in food resources, especially if species differ greatly in the type of prey they eat. Therefore, we assume that our niche overlap in morphology represents the extreme scenario of species eating the same types of prey items.

Niche partitioning is similar across two communities, Chocó and Amazonas, where species share more attributes along the spatial and thermal axes than along the morphological axis. In contrast, in the Magdalena community, species are more similar along the morphological axis than along the spatial or thermal axes. Despite the difference in niche overlap values, these results permit us to interpret two aspects of the relationship between anole species. Firstly, the lower than expected values from null models in all communities indicate that at present the resources are highly partitioned as result of a past competition, i.e. ‘the ghost of past competition’ *sensu* Connell (1980).

Secondly, the higher values of overlap in spatial and thermal resources than in morphology suggests that the present similarity among species for spatial and thermal resources is most likely to be a consequence of food being more scarce than microhabitat and habitat resources. The inverse trend found in the Magdalena community is likely to be related to an evident reduction in spatial and thermal resources owing to the high degree of habitat loss and fragmentation that has occurred at this site compared with the much more conserved sites of the Amazonas and Chocó. In this sense, future research on niche overlap trends across gradients from non-disturbed to anthropogenically disturbed habitats could be useful to assess the conservation status of anole communities and species.

The importance of food for niche partitioning in mainland anoles has been demonstrated previously, with species exhibiting differences in prey types (Vitt *et al.*, 2003b) or, more commonly, in prey size when anoles occupy the same forest stratum (Vitt *et al.*, 2001, 2002, 2003a). This pattern has also been reported for Caribbean anole communities, where species partition more by food than by other resources



structure are similar among mainland and island anole communities, but also indicate the presence of ecomorphs exclusive to mainland communities. Both mainland and island anole radiations include closely related species in terms of structural and thermal habitat features, with species occurring from the ground to the canopy and using different types of perches across shaded or sunny microhabitats, and the present study is no exception.

All the sites studied here offer similar ecological opportunities for anole communities, but also the same ecological constraints. All the sites have the same climatic regimens and therefore similar vegetation structure and physiognomy, i.e. stratified forests with abundant epiphytic plants and heights of 35–40 m (Rangel-Ch *et al.*, 1997; Galeano, 2001; Cantillo & Rangel, 2008), with a more anthropogenically disturbed habitat in Magdalena. Across sites, not only is vegetation structure similar, but also the potential lizard predation pressures. Snakes from the lowlands of South America are made up of the same historical lineages (Cadle, 1985), and omnivorous and raptorial bird guilds show similar abundance and biomass across Neotropical rain forests (Anderson & Naka, 2011). In addition, potential competitors for food are also comparable among the different rain-forest sites. The abundance of insectivorous birds inhabiting the understorey is similar across Neotropical rain forests (Anderson & Naka, 2011), and other lizard groups competing with anoles for food or spatial resources are similar across all rain-forest sites; for example, species of *Basiliscus* and *Corytophanes* in Chocó and Magdalena, *Plica* and *Uracentron* in Amazonas, and *Enyalioides* and *Gonatodes* across all rain forests.

Similar features in vegetation structure and in the predation and competition regimens across rain forests are linked to maintain the ecological structure pattern of the communities reported here. This indicates that ecological interactions among species, interplaying with the evolutionary history of the main clades, play an important role in the non-random structuring of the rain-forest *Anolis* communities of north-western South America. These results are in agreement with the previous adaptive pattern of evolution in morphology (Moreno-Arias & Calderón-Espinosa, 2016) and support the well-known phenomenon that ecology and morphology are strongly correlated in anoles (Losos, 1990a, b, c).

Eight analysed traits (four of morphology, three of spatial habitat and one of thermal habitat) show high statistical support in comparative analyses, and they are sufficient to reveal several evolutionary patterns that could also be confirmed for the traits with low support when more species and communities are added in future research. These patterns include the following: (1) congruence of adaptive regimens and a

non-random pattern of evolution for most of ecological traits, which indicates selective forces acting on ecological diversification; (2) the anole clades compose rain-forest communities that have diversified in different ways, with *Dactyloa* species exhibiting more arboreal ecomorphs and *Draconura* species exhibiting semi-arboreal or terrestrial ecomorphs, and these differences could suggest a possible niche conservatism of each clade that should be evaluated in a future study; (3) in addition to the history of the clade, the changes in the early stages of their ecological diversification are more strongly related to changes in the microhabitat of species with similar body size than to changes in the body size of species sharing the same microhabitats, suggesting that structuring within individual anole communities follows a niche compression path instead of a character displacement path.

The ecological diversity of the anole communities studied is composed of eight ecomorphs that represent four optimal adaptive peaks, with two convergent peaks. According to the dated diversification of anoles (Poe *et al.*, 2017), this diversity originated ~34.5 Mya when at least an arboreal *Dactyloa* and a semi-arboreal or terrestrial *Draconura* ancestor already coexisted in north-western South American rain forests. During the Miocene (23.0–5.3 Mya), rain forests suffered fragmentation owing to uplift of the Andes and formation of the Pebas wetland system (Hoorn *et al.*, 2010), which most probably resulted in the splitting of a widespread anole ancestor into trans-Andean and cis-Andean assemblages of early anole communities, in addition to the greatest ecomorphological diversification, with at least all ecomorphs already being present at this time, including ancestors of the studied species from the oldest to the most recent *sensu* Poe *et al.* (2017; *A. auratus* ~28 Mya; *A. ortonii*, *A. sulcifrons* and *A. triumphalis* ~27 Mya; *A. anchicayae* Poe *et al.*, 2009 and *A. chloris* ~23 Mya; *A. vittigerus* ~16 Mya; *A. frenatus* Cope, 1877 and *A. latifrons* ~14 Mya; *A. tropidogaster*, *A. granuliceps* and *A. trachyderma* ~13 Mya, *A. transversalis* Duméril, 1851 and *A. punctatus* ~12 Mya; and *A. fuscoauratus*, *A. maculiventris* and *Anolis* sp. ~11 Mya), and showing *Draconura* species diversifying to arboreality and *Dactyloa* species diversifying to crown giants (only in trans-Andean forests). Later, towards the Late Miocene (11.6–5.3 Mya) and with all ecomorphs already coexisting, the formation of the main basins (Magdalena and Chocó), owing to the uplift of the most northern Andes (Hoorn *et al.*, 2010), could have promoted diversification inside each ecomorph (e.g. leaf litter, bush–forest), to produce the present ecological composition of these three rain-forest anole communities.

Obtaining large datasets for mainland anole communities is a challenge because of their low

population densities (Andrews, 1979; Losos, 2009). Despite this challenge, the abundance values reported here were higher than those reported in other studies of mainland anole communities when we consider sampling effort (e.g. Rengifo M *et al.*, 2015). Although our dataset permitted us to describe the ecological structure of each anole community, it did not perform well when describing the ecology of rare species (with fewer than five individuals recorded). Therefore, ecological inferences made here for rare anole species are weakly supported. However, given that the rare species do not belong to a unique morphological group (Moreno-Arias & Calderón-Espinosa, 2016) nor do they belong to any single anole community, their inclusion or exclusion from the analyses would not have a significant impact on the patterns of ecological evolution across the anole communities studied here.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Appendix S1.** Laboratory procedures, and phylogenetic trees used in comparative analyses.

**Appendix S1, Figure S1.** Maximum clade credibility tree showing phylogenetic relationships among *Anolis* species from three Northwestern South America tropical rain forests. Numbers in nodes are posterior probabilities. Scale indicate number of nucleotide substitutions per 100 sites.

**Appendix S1, Figure S2.** Poe *et al.* (2017)'s phylogeny, pruned to include 15 of the 17 species of *Anolis* studied. anch: *A. anchicayae*, aura: *A. auratus*, chlr: *A. chloris*, fren: *A. frenatus*, fusc: *A. fuscoauratus*, gran: *A. granuliceps*, lati: *A. latifrons*, macv: *A. maculiventris*, orto: *A. ortonii*, punc: *A. punctatus*, sulc: *A. sulcifrons*, trac: *A. trachyderma*, tran: *A. transversalis*, trgs: *A. tropidogaster*, vitt: *A. vittigerus*.

**Appendix S2.** Pairwise comparison of overall niche overlap among species.

**Appendix S2, Table S1.** Pairwise comparison of niche overlap in thermal, spatial and morphological axes for anoles from three tropical rain forests of north-western South America. The standard deviation is given in parentheses. Values shown in bold indicate different niches at  $P \leq 0.05$ .

**Appendix S2, Table S2.** Pairwise comparison of overall niche overlap and thermal, spatial and morphology axes of 16 species of anoles from tropical rain forests of north-western South America. The standard deviation is given in parentheses. Values shown in bold indicate different niche overlap at  $P \leq 0.01$ . Abbreviations: anc, *Anolis anchicayae*; Asp, *Anolis* sp.; aur, *Anolis auratus*; chl, *A. chloris*; fre, *Anolis frenatus*; fus, *Anolis fuscoauratus*; gra, *Anolis granuliceps*; lat, *Anolis latifrons*; mac, *Anolis maculiventris*; ort, *Anolis ortonii*; pun, *Anolis punctatus*; sul, *Anolis sulcifrons*; trac, *Anolis trachyderma*; tran, *Anolis transversalis*; tro, *Anolis tropidogaster*; vit, *Anolis vittigerus*.

**Appendix S3.** Statistical power of the phylogenetic comparative methods used.

**Appendix S3, Figure S2.** Blomberg's  $K$  values of traits obtained with our phylogeny vs. the null distributions of Blomberg's  $K$  values of traits obtained from 100 randomly generated trees.

**Appendix S3, Figure S3.** Phylogeny from the study by Poe *et al.* (2017), pruned to include 15 of the 17 species of *Anolis* studied. Abbreviations: anch, *Anolis anchicayae*; aura, *Anolis auratus*; chlr, *Anolis chloris*; fren, *Anolis frenatus*; fusc, *Anolis fuscoauratus*; gran, *Anolis granuliceps*; lati, *Anolis latifrons*; macv, *Anolis maculiventris*; orto, *Anolis ortonii*; punc, *Anolis punctatus*; sulc, *Anolis sulcifrons*; trac, *Anolis trachyderma*; tran, *Anolis transversalis*; trgs, *Anolis tropidogaster*; vitt, *Anolis vittigerus*.

**Appendix S3, Figure S4.** Number of regimen shifts ( $k$ ), number of distinct regimens ( $k$  prime) and reduction in complexity of the adaptive landscape when accounting for convergence (delta  $k$ ) observed in the best SURFACE model vs. the null distributions obtained from 100 randomly generated trait datasets.