

Research Article

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Ecological release in lizard endoparasites from the Atlantic Forest, northeast of the Neotropical Region

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Abstract

We compared lizard endoparasite assemblages between the Atlantic Forest and naturally isolated forest enclaves to test the ecological release hypothesis, which predicts that host specificity should be lower (large niche breadth) and parasite abundance should be greater for parasites from isolated forest enclaves (poor assemblages) than for parasites from the coastal Atlantic Forest (rich assemblages). Parasite richness per specimen showed no difference between the isolated and non-isolated areas. Parasite abundance did not differ between the isolated and non-isolated areas but showed a positive relationship with parasite richness considering all areas (isolated and non-isolated). Furthermore, host specificity was positively related to parasite richness. Considering that host specificity is inversely proportional to the host range infected by a parasite, our results indicate that in assemblages with greater parasite richness, parasites tend to infect a smaller range of hosts than do those in simple assemblages. In summary, our study partially supports the ecological release hypothesis: in assemblages with greater parasite richness, lizard parasites from Atlantic Forest are able to increase their parasite abundance (per host), possibly through facilitated infection; however, the amplitude of infected hosts only expands in poor assemblages (lower parasite richness).

Introduction

Islands, hereafter isolated areas, are any isolated system surrounded by a different habitat matrix. They usually harbour less species when compared to mainland areas due to isolation (MacArthur and Wilson, 1967). The smaller richness in such assemblages could lead to a fewer potential competitors, and consequently, lower interspecific competition (Ehrlich and Raven, 1964). Here, we define potential competitors as parasitic species that co-occur and compete for resources from a host (Poulin, 2007). Under this scenario of reduced competition, species could respond with higher abundance and/or niche breadth (Yoder *et al.*, 2010). This phenomenon was first described for bird assemblages inhabiting oceanic islands and was initially called density compensation (Crowell, 1962), since species respond to lack of competition by increasing their abundance. In addition, the absence of potential competitors in poorer assemblages may promote the reduction of specialization (Losos, 1994), which may be reflected in an increase of niche breadth, with species occupying portions of the niche that in richer assemblages are usually occupied by other species; phenomenon described as niche expansion (Crowell, 1962; MacArthur *et al.*, 1972; Pianka, 1994; Ricklefs and Miller, 1999). Together, density compensation and niche expansion are often referred to as ecological release (Pianka, 1994; Ricklefs and Miller, 1999). Besides that, the density compensation phenomenon may also help explain other models, such as the island syndrome hypothesis, in which it predicts that species populations on islands, besides presenting a higher population density, manifest changes in the reproduction pattern, presenting smaller number of offspring, but with larger body size (Smith and Fretwell, 1974; Blondel, 2000; Pafilis *et al.*, 2011; Novosolov *et al.*, 2013).

According to Faeth (1984), although competition theory is the main proposition to explain the ecological variations of species on islands, factors such as climate tend to be more moderate on islands and may affect population size directly, by increasing the survival of individuals or indirectly (according to Competition Theory) by increasing or decreasing amounts of seasonal resource fluctuations (Case, 1975). On the other hand, restrictions on gene fluctuations between island populations and continents may result in increased levels of island species adaptation to local conditions and thus increase population density (Emlen, 1978; Emlen, 1979). In addition, the 'Edge' effect may also explain the increase in island population density (MacArthur *et al.*, 1972; Emlen, 1979), probably originating from isolation barriers that block the emigration of individuals who could occupy marginal habitats on the continent.

Historically, among the vertebrate group, lizards have been the main model used to test the ecological release hypothesis (Yoder *et al.*, 2010). On one hand, Losos and Queiroz (1997) and Eaton *et al.* (2002) failed to detect ecological release for Caribbean *Anolis* lizards; on the other, Mesquita *et al.* (2007) found evidence of ecological release when verifying that *Trupidurus* lizards presented niche expansion in depleted assemblages, just as Des Roches *et al.* (2011) observed that populations of lizards recently introduced in White Sands-New Mexico were under ecological release. Additionally, there are a few research studies on the effect of insularity on the abundance (Dobson *et al.*, 1992) and niche breadth of vertebrate parasites (Belloq *et al.*, 2002). In the first case, Dobson and Pacala (1992) studied helminths that infect Caribbean *Anolis* lizards but they did not find relationships between parasite abundance and island size and no differences between island and mainland areas. More recently, Belloq *et al.* (2002) realized that host specificity (inverse of niche breadth) decreased in islands when studying helminth parasites from small mammals in Western Palearctic.

Parasites live inside or on the surface of another species (host) and present pre-adaptations for survival, feeding and reproduction on the host (Price, 1977). Generally, these pre-adaptations are host specific (Adamson and Caira, 1994) and reflect a small niche breadth (Poulin and Mouillot, 2003); parasites tend to inhabit phylogenetically related hosts, thereby avoiding the costs of by-passing the immune systems of less related hosts (Poulin, 2007). In addition to host specificity, interspecific interactions between parasites can affect their niche breadth (Holmes, 1973; Holmes and Price, 1986). The effect of these interactions may be positive when a parasite species expands its niche breadth in the presence or absence of a potential competitor (Holmes, 1973; Bush and Holmes, 1986; Holmes and Price, 1986; Adamson and Noble, 1992; Poulin, 2007) or negative when the presence of parasites affects the abundance, distribution or reproduction of others (Adamson and Caira, 1994; Poulin, 2007). Therefore, when a parasite colonizes a new host, it must 'cross' barriers to adapt to a set of new conditions; the strength of these barriers tends to correspond closely to the phylogenetic distance between the original and new host (Poulin and Mouillot, 2004).

Because of host specificity and the fact that infection patterns are often related to host richness (Hechinger and Lafferty, 2005), parasitic assemblages associated with host populations on islands (i.e. isolated habitats, having fewer possible host species) should present lower parasite richness and increased niche breadth than do those in non-isolated habitats (Belloq *et al.*, 2002). In this study, we aimed to test whether endoparasites associated with lizards in the Pernambuco Center of Endemism (PCE), northeast of the Neotropical Region, are experiencing ecological release. The PCE, besides encompassing remnants of the coastal Atlantic Forest (non-isolated areas), presents various phytosociologies that distinguish it from other areas of the Brazilian Atlantic Forest (Muylaert *et al.*, 2018). It also includes naturally isolated forest enclaves, locally called 'Brejos de Altitude', the origins of which are associated with the expansion of Atlantic Forest during the Pleistocene (the last 2 million to 10 000 years) into areas dominated by Caatinga (Andrade-Lima, 1982). This expansion resulted in isolated regions with favourable microclimate (Andrade-Lima, 1960) providing an opportunity to test the ecological release hypothesis. The hypothesis predicts that parasite niche breadth should be larger (i.e. lower host specificity) and that parasite abundance should be higher in isolated forest enclaves than in the non-isolated coastal Atlantic Forest. Alternatively, if the parasite assemblages in the PCE are not undergoing ecological release, we expect host specificity and parasite abundance in these assemblages to be similar to those of non-isolated areas.

Materials and methods

Study sites

Currently, the Atlantic Forest mostly occur on east coast, south-east and south of Brazil, east of Paraguay and Misiones province in Argentina (Santos *et al.*, 2007). However, because of its large latitudinal variation, three centres of endemism can be identified in Brazil: Pernambuco Center, Bahia-Espírito Santo Center and Rio de Janeiro-São Paulo Center (Prance, 1987; Cavalcanti and Tabarelli, 2004; Tabarelli and Santos, 2004; Santos *et al.*, 2007). All forest areas located north of San Francisco River, including coastal forests and naturally isolated forest enclaves, within the semiarid Caatinga (Veloso *et al.*, 1991) are part of the Pernambuco Center of Endemism (Andrade-Lima, 1982). These isolated forest enclaves, locally called 'Brejos de Altitude', are composed of disjunctions of semideciduous montane seasonal forests. Their origin is hypothesized to be associated with climatic variations during the Pleistocene (in the last 2 million to 10 000 years) (Andrade-Lima, 1982). After interglacial periods, islands of the Atlantic Forest with favourable microclimate (Andrade-Lima, 1982) remained on mountains, plateaus and plains of 500–1100 m in elevation, generally located near the coast, receiving precipitation levels above 1200 mm year⁻¹ through orographic rainfall (Andrade-Lima, 1960; Araújo *et al.*, 2007).

Lizards were collected in three naturally isolated forest enclaves (correspond to isolated areas): (A) ARIE Mata de Goiamunduba – ARIEMG (06°45'03.78"S, 35°38'00.06"W), located in the Bananeiras municipality, in October 2016; and in (B) PE Mata do Pau Ferro – PEMPF (06°48'13.9"S, 35°05'07.3"W) and (C) Sítio Socorro – SS (06°59'37.6"S, 35°40'15"W), both located in the Areia municipality, between September and October 2017. In contrast, lizards were collected in three remnants of the coastal Atlantic rainforest (correspond to non-isolated areas): (D) REBIO Guaribas – SEMA III (06°48'14.9"S, 35°05'13.9"W) in the Rio Tinto municipality in December 2017; (E) RPPN Engenho Gargaú – RPPNEG (06°59'52"S, 34°57'30"W) in the Santa Rita municipality in September 2016 and (F) Benjamim Maranhão Botanical Garden – BMBG (07°08'08"S, 34°51'37"W), in the João Pessoa municipality in November 2016. All of the study sites are in Paraíba State, Brazil (Fig. 1). The average annual rainfall of the areas is 1490 mm, and the average annual temperature of 24.6°C.

The isolation in the 'Brejos de Altitude' is natural (Tabarelli and Santos, 2004). Therefore, the isolation caused by anthropic fragmentation in the coastal areas were not considered; areas affected by this fragmentation are recent relative to the naturally isolated enclaves (Carnaval and Bates, 2007).

Lizard collection and parasite identification

All specimens were captured manually or using pitfall traps (25 traps per study site). The traps were constructed with four buckets (20 L) arranged in a 'Y' formation, with 100 buckets per area (Oliveira *et al.*, 2017). Lizards were collected during the same period of the year (dry season) to ensure that our data were not influenced by seasonality. The dry period was defined between September and December, based on historical rainfall data provided by AESA (Agência Executiva de Gestão das Águas do Estado da Paraíba).

Each study site was sampled for 20 days. The active search was standardized, being performed every day during each sampling period. The team consisted of three researchers, and search was conducted from 8:00 a.m. to 4:00 p.m., when it becomes dark in the forest. To test for significant differences in lizard richness between isolated and non-isolated areas, we performed a Student's *t*-test.

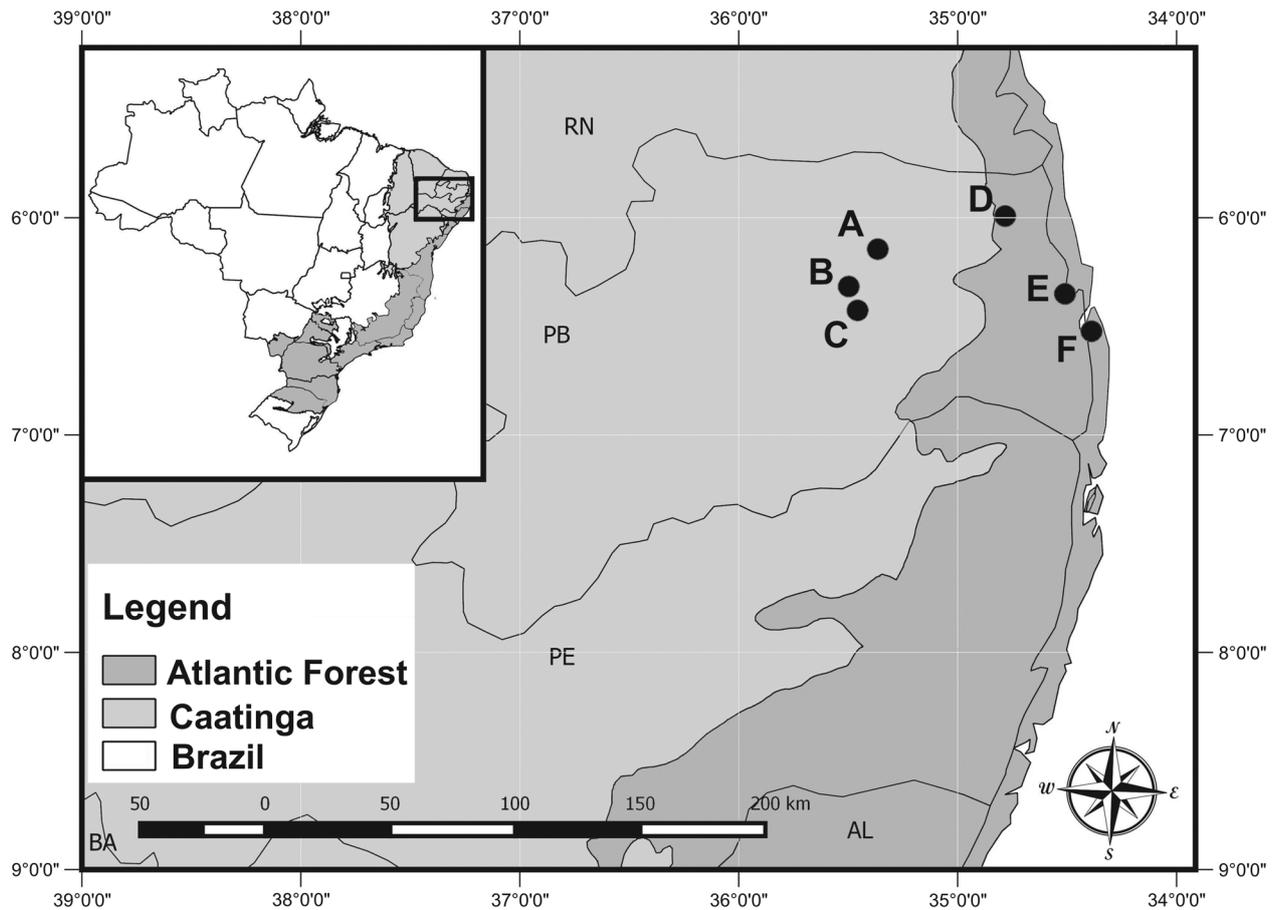


Fig. 1. Study sites. Three naturally isolated forest enclaves (A, B and C) and three remnants of the coastal Atlantic rainforest (D, E and F). (Final artwork created in QGIS 2.14.0 Software).

All lizards were sacrificed following all applicable international, national and/or institutional guidelines for the care and use of animals. The lizards were killed with lethal doses of 2% lidocaine, fixed with 10% formaldehyde, preserved in 70% alcohol and housed in the Coleção Herpetológica da Universidade Federal da Paraíba – CHUFPB. We dissected all lizards under a stereomicroscope and identified the sexes by inspecting their gonads. We inspected the respiratory and gastrointestinal tracts for endoparasites. When present, we counted the parasites, mounted them on slides with lactophenol, analysed them under a microscope and identified according to the following identification keys (Silva *et al.*, 2007; Anderson *et al.*, 2009).

Parasite richness and abundance

We recorded the parasite richness (total number of parasite species per host specimen) and parasite abundance (total number of parasite, regardless of species, in a single infected host) according to Bush *et al.* (1997). If ecological release is occurring, the abundance of parasites in each sampling site should be higher in assemblages with lower parasite richness.

Index of host specificity (S_{TD}^*)

The index of host specificity S_{TD}^* was calculated as the taxonomic distance measured for all possible pairs of host species weighted by the product of the parasite prevalence in each pair of host species. The weighting factor varies from one (1) (maximum weight), when the prevalence is 100% in both host species, to zero (0), when the prevalence in host species is very low. We considered the five taxonomic classification levels above species, as follows (i.e. genus, family, order, class and phylum). The maximum value attainable by a parasite species is five, i.e. when it infects

hosts belonging to more than one of all taxonomic classes, and the minimum value is one, i.e. when it infects hosts belonging to only one genus (Poulin and Mouillot, 2005).

In addition, because the type of parasite life cycle can influence the parasite's host range (Adamson and Caira, 1994), we calculated the index of host specificity S_{TD}^* separately for parasites with monoxenous (without the use of intermediate hosts) and heteroxenous life cycles (with at least one intermediate host) to determine whether life cycle can alter the amplitude of hosts used in isolated and non-isolated areas. We obtained S_{TD}^* values using the software TaxoBiodiv2 (Poulin and Mouillot, 2005).

Statistical analysis

To determine whether ecological release is occurring in parasite species from isolated forest enclaves, we used generalized linear mixed models (GLMMs). GLMMs were used because mixed models allow the insertion of random variables to correct the degrees of freedom and avoid the effects of pseudoreplication (Bates *et al.*, 2014). In the first model, parasite abundance was tested with a Poisson distribution and log link function (Wilson and Grenfell, 1997), with study site (nested within area) and lizard species (this category allowed us to remove the ontogenetic effect of each lizard species, as well as the effect of lizard abundance) included as random effects, as well as parasite richness and area (isolated and non-isolated) included as fixed effects. Next, parasite richness was analysed with a Poisson distribution and log link function (Wilson and Grenfell, 1997), with study site (nested within area) and lizard species included as random effects and area (isolated and non-isolated) included as a fixed effect. Finally, the index of host specificity S_{TD}^* was modelled with a

Table 1. Lizards collected at the sampling sites – non-isolated: RPPN-EG, BMBG, SEMA-III and isolated: ARIE-MG, PE-MPF, SS

	RPPN-EG		BMBG		SEMA-III		ARIE-MG		PE-MPF		SS	
	N	SVL ± SD	N	SVL ± SD	N	SVL ± SD	N	SVL ± SD	N	SVL ± SD	N	SVL ± SD
Family Anguidae												
<i>Diploglossus lessonae</i>	–	–	–	–	–	–	2	131	–	–	–	–
Family Dactyloidae												
<i>Dactyloa punctata</i>	3	85 ± 22.2	3	34.8 ± 13.2	33	72.4 ± 22.4	–	–	–	–	–	–
<i>Norops fuscoauratus</i>	2	45	5	36.2 ± 14	–	–	–	–	–	–	–	–
<i>Norops ortonii</i>	–	–	–	–	–	–	6	41.6 ± 30.2	–	–	–	–
Family Gymnophthalmidae												
<i>Dryadosaura nordestina</i>	6	46.4 ± 20.3	27	39.3 ± 14.3	14	37.4 ± 20	23	31.8 ± 26.3	2	45	25	39.8 ± 23.4
<i>Cercosaura ocellata</i>	–	–	–	–	2	43	–	–	–	–	–	–
<i>Micrablepharus maximiliani</i>	2	37	–	–	–	–	–	–	–	–	–	–
Family Leiosauridae												
<i>Enyalius bibronii</i>	–	–	–	–	–	–	–	–	1	95.3	–	–
<i>Enyalius catenatus</i>	–	–	–	–	–	–	5	85 ± 30.7	–	–	–	–
Family Mabuyidae												
<i>Copeoglossum nigropunctatum</i>	1	94.62	2	71.5	1	90.27	–	–	–	–	3	97.3 ± 27.9
<i>Psychosaura agmosticha</i>	–	–	–	–	–	–	–	–	1	61.6	–	–
<i>Psychosaura macrorhyncha</i>	2	64.6	3	54.5 ± 15.1	8	67.8 ± 20.9	–	–	–	–	–	–
Family Phyllodactylidae												
<i>Gymnodactylus darwini</i>	–	–	14	42.2 ± 14.6	–	–	–	–	–	–	–	–
Family Sphaerodactylidae												
<i>Coleodactylus meridionalis</i>	16	23.1 ± 20.6	6	21.6 ± 15	21	22 ± 22.4	16	24.5 ± 26.3	25	23.8 ± 22.2	3	25.4 ± 20.7
Family Teiidae												
<i>Ameiva ameiva</i>	3	52.8 ± 21.3	2	75.3	4	61.6 ± 20	1	46.84	3	97.2 ± 25	3	72.3 ± 21.1
<i>Ameivula ocellifera</i>	3	52 ± 20.4	–	–	–	–	–	–	–	–	–	–
<i>Kentropyx calcarata</i>	47	56.5 ± 20.6	57	51 ± 14.7	29	58.5 ± 20.6	–	–	–	–	2	98.5
Family Tropiduridae												
<i>Strobilurus torquatus</i>	12	57 ± 21.1	8	60.6 ± 15	–	–	–	–	–	–	–	–
<i>Tropidurus hispidus</i>	1	–	4	46.2 ± 14	2	73.6	–	–	3	79 ± 2	1	62.5

SVL mean snout-vent length; s.d., standard deviation.

Table 2. Composition of helminths from remnants of coastal Atlantic rainforest and infected hosts, prevalence (%); mean intensity of infection (I); index of host specificity (Std*); infection sites (SI): stomach (S), small intestine (SI), large intestine (LI), lungs (L), celomatic cavity (CC)

Parasite	Host	%	I	Std*	IS
<i>RPPN Gargaú</i>					
NEMATODA					
Family Cosmocercidae					
<i>Aplectana</i> sp.	<i>Dryadosaura nordestina</i>	83.33	17.8 ± 5.66	3	S, SI, LI
	<i>Norops fuscoauratus</i>	50	2		L
<i>Cosmocerca</i> sp.	<i>Dryadosaura nordestina</i>	16.66	1	1	LI
Family Heterakidae					
<i>Strongyluris oscar</i>	<i>Dactyloa punctata</i>	33.33	7	2.29	S, LI
	<i>Norops fuscoauratus</i>	50	9		S, SI
	<i>Strobilurus torquatus</i>	8.3	17		LI
Family Pharyngodonidae					
<i>Spauligodon lobo</i>	<i>Strobilurus torquatus</i>	41.66	13 ± 11.87	1	SI, LI
Family Physalopteridae					
<i>Physaloptera lutzi</i>	<i>Strobilurus torquatus</i>	75	11.66 ± 8.39	3	S
	<i>Dactyloa punctata</i>	33.33	4		L
Family Seuratoidae					
<i>Skrjabinellazia intermedia</i>	<i>Norops fuscoauratus</i>	50	5	1	S
TREMATODA					
Family Plagiorchiidae					
<i>Haplometroides odhneri</i>	<i>Dryadosaura nordestina</i>	33.33	3–11	1	S, SI, LI
<i>JB Benjamim Maranhão</i>					
CESTODA					
Family Anoplocephalidae					
<i>Oochoristica</i> sp.	<i>Tropidurus hispidus</i>	25	1	1	LI
NEMATODA					
Family Cosmocercidae					
<i>Aplectana</i> sp.	<i>Dryadosaura nordestina</i>	70.37	6.94 ± 5.01	3	S, SI, LI
	<i>Gymnodactylus darwinii</i>	21.42	3		SI, LI
Family Pharyngodonidae					
<i>Parapharyngodon alvarengai</i>	<i>Tropidurus hispidus</i>	25	4	1	SI
Family Physalopteridae					
<i>Physaloptera lutzi</i>	<i>Strobilurus torquatus</i>	75	9 ± 7.64	1	S, SI
TREMATODA					
Family Plagiorchiidae					
<i>Haplometroides odhneri</i>	<i>Dryadosaura nordestina</i>	14.81	4 ± 2.3	3	SI
	<i>Tropidurus hispidus</i>	25	1		LI
<i>REBIO Guaribas SEMA III</i>					
CESTODA					
Non identified	<i>Kentroptyx calcarata</i>	10.71	11.66 ± 11.01	1	S, SI, LI
NEMATODA					
Family Cosmocercidae					
<i>Aplectana</i> sp.	<i>Dryadosaura nordestina</i>	42.85	16.16 ± 15.99	1	LI
<i>Cosmocerca</i> sp.	<i>Dryadosaura nordestina</i>	7.14	1	1	LI
Family Physalopteridae					
<i>Physaloptera retusa</i>	<i>Tropidurus hispidus</i>	100	(2–13)	1	S, SI

(Continued)

Table 2. (Continued.)

Parasite	Host	%	I	Std*	IS
Family Heterakidae					
<i>Strongyluris oscari</i>	<i>Tropidurus hispidus</i>	50	3	1	S, SI
Family Seuratoidae					
<i>Skrjabinellazia intermedia</i>	<i>Dactyloa punctata</i>	6.25	1	1	SI
TREMATODA					
Family Plagiorchiidae					
<i>Haplometroides odhneri</i>	<i>Coleodactylus meridionalis</i>	4.76	1	3	S
	<i>Dactyloa punctata</i>	3.12	3		SI
	<i>Dryadosaura nordestina</i>	14.28	(2-5)		S
	<i>Psychosaura agmosticha</i>	12.5	3		S

Gamma distribution and inverse link function (Bolker *et al.*, 2009), with study site (nested within area) and parasite species being included as random effects and host specificity and area (isolated and non-isolated) being included as fixed effects. GLMMs were performed using the 'lme4' package (Bates *et al.*, 2014) of R software.

Results

We collected 467 lizards representing 19 species and nine families (Table 1). In the coastal Atlantic rainforest, 13 lizard species from seven families were collected, whereas in the naturally isolated forest enclaves we found 11 lizard species from eight families. The remnants of the coastal Atlantic rainforest presented larger lizard richness (mean lizard richness in non-isolated areas = 10.6; range: 9–12) than did naturally isolated forest enclaves (six lizard species across all areas), (t -value = 5.2915; P value = 0.03).

After dissecting the hosts, we found 1,338 endoparasites, 15 species corresponding to 11 species of nematodes (seven families and ten genera), one species of trematode (one family and one genus), two species of cestodes (one family and one genus) and one species of acanthocephalans (one family and one genus) (Tables 2 and 3). The parasite richness per specimen showed no difference between isolated (1.39 ± 0.55) and non-isolated (1.33 ± 0.53) areas, ($R^2 = 0.0008$; Z -value = 0.287; P value = 0.77).

Parasite abundance did not differ between isolated and non-isolated areas ($R^2 = 0.4549$; Z -value = 0.316; P value = 0.75). However, parasite abundance showed a positive relationship with parasite richness ($R^2 = 0.4549$; Z -value = 4.633; P value < 0.0001) across all areas (isolated and non-isolated), the opposite of predicted by the hypothesis of density compensation.

The mean Std^* value of the non-isolated areas was 1.6; on the other hand, the mean Std^* value of the isolated areas was 1.8. The same was verified when we analysed separately monoxenous (mean Std^* of non-isolated areas = 1.6 versus isolated areas = 1.7) and heteroxenous parasites (mean Std^* of non-isolated areas = 1.5, against 1.9 of isolated areas). Host specificity was positively related to parasite richness ($R^2 = 0.946$; t value = 417; P value < 0.0001) across all areas (isolated and non-isolated), and this pattern was maintained when we analysed monoxenous ($R^2 = 0.9446$; t -value = 401; P value < 0.0001) and heteroxenous ($R^2 = 0.0319$; t -value = 2314; P value < 0.0001) parasites separately. Considering that host specificity is inversely proportional to the range of hosts infected by a parasite, our results indicate that in assemblages with greater parasite richness (more competitors), parasites tend to infect a smaller range of hosts than they do in simple assemblages (fewer competitors).

The values of prevalence, mean intensity of infection and index Std^* for each parasite identified can be viewed in the Tables 2 and 3. The isolated area 'SS' presented the highest average prevalence value (46.26) among all the studied areas, whereas the non-isolated area 'SEMA III' had the lowest average prevalence value (25.16).

Discussion

Our results indicated that non-isolated coastal Atlantic rainforest areas presented higher lizard richness than did naturally isolated forest enclaves. However, there was no difference between areas regarding parasite richness. Furthermore, parasite abundance showed a positive relationship with parasite richness considering all areas (isolated and non-isolated). In addition, host specificity increases with parasite richness. This pattern was also observed when we considered monoxenous and heteroxenous parasites separately.

The isolated areas present a poorer richness of lizard fauna than did the non-isolated areas, similar to results presented in studies with fish communities in Australian desert springs (Kodric-Brown and Brown, 1993), bat assemblages of tropical caves in central Mexico (Brunet and Medellin, 2001), Caribbean *Anolis* lizards (Losos and Queiroz, 1997), lizard assemblages of Neotropical savannas (Mesquita *et al.*, 2007) and vascular plants in the Stockholm Archipelago, Sweden (Löfgren and Jerling, 2002). According to MacArthur and Wilson (1967), islands should have fewer species than comparable continental areas due to their small size and reduced heterogeneity (which are associated with fewer microhabitat types, microclimates and refuges against predators). Analogously, when dealing with parasite assemblages, spatial heterogeneity corresponds to the sum of all potential hosts present in the same space/at the same time (Hechinger and Lafferty, 2005; Kuris *et al.*, 1980), since these hosts represent 'habitats', providing places to live, forage and reproduce (Krasnov *et al.*, 2002). In addition to possessing lower host richness than non-isolated areas, islands can also present lower parasite richness (Wootten, 1973; Kennedy, 1990). In this way, naturally isolated forest enclaves are suitable for testing whether parasitic assemblages associated with lizard populations are under ecological release in contrast to comparable areas from remnants of the coastal Atlantic rainforest.

Parasite richness did not differ significantly between isolated and non-isolated areas. Previous studies on the structure and composition of parasitic fauna in mainland regions and islands have obtained inconsistent results. Kennedy (1978) found no correlation between the parasite richness associated with the fish

Table 3. Composition of helminths from naturally isolated forest enclaves and infected hosts, prevalence (%); mean intensity of infection (I); index of host specificity (Std*); infection sites (SI): stomach (S), small intestine (SI), large intestine (LI), lungs (L), celomatic cavity (CC)

Parasite	Host	%	I	Std*	IS
<i>ARIE Goiamunduba</i>					
ACHANTHOCEPHALA					
Family Oligacanthorhynchidae					
<i>Oligacanthorhynchus</i> sp.	<i>Coleodactylus meridionalis</i>	6.25	1	1	S
NEMATODA					
Family Cosmocercidae					
<i>Aplectana</i> sp.	<i>Diploglossus lessonae</i>	50	1	3	LI
	<i>Dryadosaura nordestina</i>	56.52	5.15 ± 3.69		S, SI, LI
	<i>Enyalius catenatus</i>	20	1		LI
Family Physalopteridae					
<i>Physaloptera lutzi</i>	<i>Coleodactylus meridionalis</i>	75	12.5 ± 12.95	3	S, SI
	<i>Dryadosaura nordestina</i>	26.1	12 ± 4.81		S
	<i>Norops ortonii</i>	16.66	1		S
Family Rabdiasidae					
<i>Rabdias</i> sp.	<i>Enyalius catenatus</i>	20	5	3	L
	<i>Norops ortonii</i>	16.66	1		L
TREMATODA					
Family Plagiorchiidae					
<i>Haplometroides odhneri</i>	<i>Coleodactylus meridionalis</i>	6.25	2	3	S
	<i>Dryadosaura nordestina</i>	14.8	4 ± 2.3		S
	<i>Norops ortonii</i>	16.66	16		S
<i>PE Mata Pau-Ferro</i>					
ACHANTHOCEPHALA					
Family Oligacanthorhynchidae					
<i>Oligacanthorhynchus</i> sp.	<i>Ameiva ameiva</i>	33.33	1	3	LI
	<i>Coleodactylus meridionalis</i>	8	1-2		CC
CESTODA					
Family Anoplocephalidae					
<i>Oochoristica</i> sp.	<i>Ameiva ameiva</i>	33.3	2	1	LI
NEMATODA					
Family Cosmocercidae					
<i>Aplectana</i> sp.	<i>Dryadosaura nordestina</i>	50	18	1	LI
Family Pharyngodonidae					
<i>Parapharyngodon alvarengai</i>	<i>Tropidurus hispidus</i>	33.33	5	1	LI
<i>Pharyngodon</i> sp.	<i>Ameiva ameiva</i>	33.33	26-33	1	LI
Family Physalopteridae					
<i>Physaloptera retusa</i>	<i>Enyalius bibronii</i>	100	3	3	S
	<i>Tropidurus hispidus</i>	33.33	1		S
<i>Mata Sítio Socorro</i>					
ACHANTHOCEPHALA					
Family Oligacanthorhynchidae					
<i>Oligacanthorhynchus</i> sp.	<i>Coleodactylus meridionalis</i>	33.33	1	1	CC
CESTODA					
Não identificado	<i>Kentropyx calcarata</i>	50	42	1	S, LI
NEMATODA					

(Continued)

Table 3. (Continued.)

Parasite	Host	%	I	Std*	IS
Family Cosmocercidae					
<i>Aplectana</i> sp.	<i>Dryadosaura nordestina</i>	24	6.83 ± 4.21	1	SI, LI
<i>Cosmocerca</i> sp.	<i>Dryadosaura nordestina</i>	28	12.71 ± 6.6	1	SI, LI
Family Pharyngodonidae					
<i>Pharyngodon</i> sp.	<i>Kentropyx calcarata</i>	50	9	1	S
<i>Parapharyngodon alvarengai</i>	<i>Tropidurus hispidus</i>	100	1	1	SI
Family Physalopteridae					
<i>Physaloptera retusa</i>	<i>Copeoglossum nigropunctatum</i>	33.33	1	3	S
	<i>Kentropyx calcarata</i>	50	5		S
Family Onchocercidae					
<i>Piratuba</i> sp.	<i>Kentropyx calcarata</i>	50	1	1	LI
TREMATODA					
Family Plagiorchiidae					
<i>Haplometroides odhneri</i>	<i>Dryadosaura nordestina</i>	44	3.36 ± 2.41	1	S, LI

Salvelinus valpinus and island size or distance from the continent. In contrast, the number of parasites was higher in small and distant islands from the Arctic compared to the mainland. Nearly a decade later, Kennedy *et al.* (1986) found that parasite richness was much lower in freshwater fish from the Channel Islands than in those from comparable adjacent areas on the European continent. Subsequently, Dobson *et al.* (1992) and Dobson and Pacala (1992) studied helminths that infect *Anolis* lizards in the Antilles and found that the parasite fauna assemblages of the small islands were depleted relative to those of the greater Caribbean islands and the mainland. Furthermore, Fromont *et al.* (2001) found a greater parasite richness in feral cats from Lyon/France than in corresponding hosts from Kerguelen Islands. In addition, Rocha and Vrcibradic (2003) studied the helminth parasite fauna of *Mabuya* lizards on islands along the eastern coast of Brazil found no variation in helminth richness with island size or distance to the mainland and no difference between isolated and mainland areas. According to Dobson and Pacala (1992) and Apanius *et al.* (2000), the way the parasite richness is manifested in islands may perhaps be justified by the influences of colonization and extinction processes, which could alter infra-community composition in host populations.

Similarly, our results did not identify differences in parasite abundance between isolated and non-isolated areas, probably because parasite richness did not differ between these areas and because shifts in the presence/absence of competing species is necessary for density compensation to occur (Crowell, 1962; MacArthur *et al.*, 1972; Faeth, 1984; Fromont *et al.*, 2001). Apparently, the smaller host availability in the isolated areas, does not act as a limiting resource for parasites. The theory of density compensation is based on the premise that in simpler assemblages, resources tend to be more abundant than in continental areas due to the lower number of competitors, which promotes population size increases (Crowell, 1962; MacArthur *et al.*, 1972; Faeth, 1984). This hypothesis has been corroborated by studies of helminth parasites of feral cats from Kerguelen Islands in France (Fromont *et al.*, 2001) and King Islands in Australia (Gregory and Munday, 1976) and those of small mammals from Skomer Island in Wales (Lewis, 1968a, 1968b). In these studies, low helminth richness reduced interspecific competition, contributing to a higher intensity of infection among island hosts. On the other hand, studies of parasitic helminths from lizards

found no relationships among parasite density, parasite abundance, infection rate and island size and no differences between island and mainland areas (Dobson *et al.*, 1992; Rocha and Vrcibradic, 2003), similar to our results. An alternative explanation of the increased abundance of island parasites relative to that of mainland parasites has been widely described. According to Bellocq *et al.* (2002), hosts inhabiting islands are subject to low parasitic pressure (low parasite diversity), which may lead to a lower allocation of resources to the development of the immune system than is exhibited by mainland, who experience higher parasitic pressure.

Our results revealed a significant positive relationship between parasite abundance and parasite richness; which is, as the number of parasites (competitors) increased in the studied areas (regardless of whether isolated or not), the number of parasites per individual host increased, apparently uninfluenced by competition (Holmes, 1973; Bush and Holmes, 1986; Holmes and Price, 1986; Adamson and Noble, 1992), leading us to believe that the resources are not limiting factors in the structuring of the parasitic assemblages studied here (Poulin, 1997, 2007). These results can be explained by the facilitation process among parasite species, in which the occurrence of a particular parasite species enables the presence of others through the creation of conditions adequate for their survival (Hart and Marshall, 2013).

The niche expansion hypothesis was corroborated in our study, even when we evaluated parasites separately according to life cycle (monoxenous and heteroxenous). We found that host specificity decreased in sites with lower parasite richness. This result is consistent with Bellocq *et al.* (2002)'s study of helminth parasites from small mammals in Western Palearctic but is in contrast to Kennedy *et al.* (1986), who found no variation in host fish specificity from Channel Islands, even in the absence of potential competing parasites.

Niche expansion is a phenomenon that when coupled with density compensation composes the ecological release process (Pianka, 1994; Ricklefs and Miller, 1999). According to Kennedy *et al.* (1986), in insular assemblages, non-realized niches (hosts) are likely to exist such that parasite species can expand their niche breadth by infecting hosts that would probably be unavailable in comparable mainland areas. In this case, even parasites having co-evolved with their hosts (host specificity), it is possible for island parasites to expand their niche using the new

resources (hosts) available in these locations (Adamson and Caira, 1994). However, with the increasing phylogenetic distance between historically infected hosts and new colonized hosts, most profitable should be these new infections (Poulin and Mouillot, 2004).

Non-isolated areas have higher lizard richness than isolated areas. However, this pattern was not observed when we analysed the parasite richness. In addition, the values of parasite abundance were positively related to those of parasite richness (competitors). This finding is in conflict with the predictions of the density compensation hypothesis and indicates a possible facilitation of infection in the presence of possible competitors. Moreover, our findings support the niche expansion hypothesis: in simpler assemblages, parasites tend to decrease their specificity (expand niche breadth) to infect hosts that are likely unavailable in areas with more parasite competitors, indicating that the absence of competition is one of the models that corroborates this hypothesis. In summary, our study partially supports the ecological release hypothesis: in assemblages with greater parasite richness, lizard parasites from Atlantic Forest present a greater parasite abundance (per host), possibly through facilitated infection; however, the amplitude of infected hosts only expands in poor assemblages (lower parasite richness). In addition, although 'brejos' have a natural isolation, eventual migrations of lizards/parasites from the surrounding semiarid matrix may occur. Thus, this influence may have led to the absence of some expected effects, such as higher parasite richness in non-isolated areas.

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