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Effects of habitat quality on body size of the litter dwelling scorpion *Tityus pusillus* in fragmented rainforests of Brazil

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Abstract. Understanding how individual body size is affected by habitat quality allows us to assess the consequences of habitat loss and fragmentation on the morphology of arthropods. In this study, we examined the effect of habitat quality (litter depth and dry mass, understory density, canopy openness, and diameter at breast height of trees) on the body size of the litter dwelling scorpion *Tityus pusillus* Pocock, 1893 in fragmented rainforests of Brazil. The study was performed during the dry season in 10 forest fragments, and scorpions were collected with the aid of ultraviolet light lamps. Females, but not males, responded to the environmental attributes measured. Litter dry mass was positively related to individual body size of *T. pusillus*. These results suggest scorpion body size is sensitive to habitat structure. Environmental characteristics determine specific ranges of body size in scorpion populations, wherein smaller individuals inhabit sites that have less litterfall.

Keywords: Atlantic forest, arthropod predator, habitat change, population ecology

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Individual body size is an effective indicator of the life-history, physiological, and ecological traits of organisms and consequently their fitness (Karino et al. 2004; Ferns & Jervis 2016; Rossetti et al. 2017). Highly influenced by food availability, microhabitat preferences, and dispersal ability (Crooks 2002; Rossetti et al. 2017), body size is expected to be under a strong selection pressure across and within species due to habitat loss (Hillaert et al. 2018). Through analysis of individual body size, it is possible to determine the response of species to changes in environmental attributes (Jenkins et al. 2007; Öckinger et al. 2010; Sekar 2012). In the rainforests of North and South America, small and isolated habitat fragments negatively affect body size of dung beetle species (Filgueiras et al. 2011; Salomão et al. 2018). Similarly, the body size of the web-spider *Trichonephila clavata* (L. Koch, 1878), a common species in eastern Japan, is negatively affected by habitat loss (Miyashita et al. 1998). Reduction in food availability has been claimed as the main cause of the decrease in body size of *T. clavata* individuals.

In the Neotropics, the Atlantic forest is a highly fragmented ecosystem, developed over time through environmental transformations induced by agricultural practices and urbanization (Ranta et al. 1998; Enedino et al. 2017). Such landscape transformations have occurred since the 16th century, following the arrival of European settlers in South America (Dean 1995; Cincotta et al. 2000). As a consequence of deforestation within the Atlantic forest, only 11% to 16% of the original forest cover still persists, with more than 80% of the fragments smaller than 50 ha (Ribeiro et al. 2009).

This scenario provides an extreme case for investigating the effects of habitat change on the body size of the tropical biota. Studies analyzing the effect of habitat change in the Atlantic forest have focused on various aspects of diversity (e.g., taxonomic and functional richness), encompassing plants, vertebrates, and invertebrates (e.g., Pardini 2004; Tabarelli et al. 2004; Filgueiras et al. 2011; Lira et al. 2015). However, body size is an important parameter related to fitness and survival of organisms (Garnet 1981; Ameneshewa & Service 1996; LeGrice et al. 2019), and there is preliminary data from the Atlantic forest concerning the body size of beetles that thrive under different environmental attributes in this fragmented landscape (Salomão et al. 2018). The body size of organisms inhabiting disturbed landscapes appears to be related to physiological and body size conditions such as muscle mass, lipid content and body dry mass may influence the persistence of populations facing habitat fragmentation (Sieving & Karr 1997; González-Tokman & Martínez-Garza 2015). Therefore, by understanding how body size of individuals is affected by habitat change, it is possible to obtain clues regarding individual responses to habitat transformation (Penell et al. 2018).

Habitat change caused by fragmentation alters microclimatic conditions and negatively affects the soil arthropod fauna (e.g., Lira et al. 2015; Salomão et al. 2019). For predators, prey supply plays a crucial role in structuring food (Chen & Wise 1999) and has a direct influence on plant communities and ecosystem functions such as production, decomposition, and elemental cycling (Didham 1999; Laurance et al. 2007). Thus, arthropod predators can be particularly sensitive to the effects of habitat fragmentation, which may have effects on individual body size (Miyashita et al. 1998; Ashford et al. 2013). Of the arthropod predators,

scorpions constitute a good indicator group, as they are sensitive to habitat changes (Lira et al. 2019). For example, previous studies have reported that these animals are negatively affected by habitat change caused by humans (e.g., Lira et al. 2016, 2019). However, the ecology of scorpions in the Atlantic forest has only recently been studied (e.g., Dionisio-da-Silva et al. 2018; Lira et al. 2019), and it is unclear how the individual body size of scorpions is affected by habitat alterations.

In addition, environmental effects on individual body size may depend on the sex of the individual. Each scorpion sex possesses different life-history traits; for example, owing to their wide foraging range, males show a higher mortality rate than females (Polis 1990). Therefore, habitat alterations may present sex-specific effects in these arachnids. Thus, understanding how habitat change is related to body size could shed light on the responses of the species to landscape fragmentation. As such, in our study, we aimed to investigate the effect of environmental attributes (density of the understory vegetation, diameter at breast height, canopy openness, litter depth, and litter dry mass) on body size of the scorpion species, *Tityus pusillus* Pocock, 1893. Based on the assumption that changes in environmental attributes affect the food availability of scorpions, we tested the hypothesis that body size of *T. pusillus* species is affected by the environmental structure. Owing to the predatory behavior of this species, we expected that low environmental complexity (i.e., less leaf litter depth and weight) would negatively affect the prey availability and lead to a reduction in *T. pusillus* body size. In addition, due to differences in male and female life histories, we believe there is a differential response between the sexes.

Tityus pusillus is a small (30–35 mm), sedentary, and dimorphic species, with females being larger than males (Lira et al. 2013, 2018a). Approximately 90% of the population of this scorpion in the region occurs in the Atlantic forest of north-eastern Brazil (Lira et al. 2018b). In this habitat, *T. pusillus* is commonly found in leaf litter layers and vegetation (Lira et al. 2018b). The study was conducted in 12 Atlantic forest fragments (for details see Lira et al. 2015); however, two fragments were excluded (fragment 1 – absence of adult individuals; fragment 2 – absence of males and presence of only two females). The vegetation here is classified as dense Ombrophilous forest, and the forest fragments are embedded in a matrix of sugarcane plantations located in the municipal area of Sirinhaém, Pernambuco State, Brazil (8°35′S; 35°06′W). The average annual rainfall of the area is 2,400 mm, with an average temperature of 25 °C (APAC 2013). Scorpions were collected during an active nocturnal search (between 19:00 h and 21:00 h) using UV lamps. We sampled in the dry season (December 2012 to January 2013) because of the greater availability of *T. pusillus* at this time (Dionisio-da-Silva et al. 2018; Lira et al. 2018b). In each forest fragment, six transects of 30 m × 10 m were established. Each scorpion caught was individually stored in a vial containing 70% ethanol. The specimens were identified and sexed according to the methods described by Lira et al. (2018a). Measurements of total body size for each sex were performed in the laboratory, using a digital caliper (0.01 mm precision). We considered the length from the beginning of the prosoma to the end of the metasoma to be the measure of the total body size, according to the method described by Lira et al. (2018a). To avoid any bias towards immature individuals, we only used mature scorpions in the study. Voucher specimens were deposited in the Arachnological Collection of the Universidade Federal de Pernambuco, Brazil. Habitat structure was based on the data of Lira et al. (2015, 2016) which considered five environmental attributes: density of the understory vegetation, diameter at breast height, canopy openness, litter depth, and dry mass of litter. The values of these environmental variables were expressed as the average of measurements obtained in six transects, in each one of the ten fragments studied. Understory vegetation density was estimated as the number of plants that were up to 1.3 m high and touched the transects used for the surveys of *T. pusillus*. Canopy openness was estimated by digital photos taken with a fisheye lens. The photos were taken at the center of each transect, and canopy openness was calculated using Gap Light Analyzer software version 2.0 (Frazer et al. 1999). Diameter at breast height was estimated as the mean diameter obtained from the trees that touched the transects. To estimate the depth of litter, we obtained litter measures with a scale from four corners of 25 cm^2 quadrats placed 10 m apart along each transect. The litter was collected by removing twigs and was dried in an oven at 50 °C for ca. 24 h before weighing. Linear models are sensitive to deviations in data normality and autocorrelation of the independent variables (Zar 1999; Kutner et al. 2005). Therefore, prior to our analyses, the dataset was checked for autocorrelation through a matrix of Pearson correlation coefficient. We considered variables correlated with values $R > 0.7$ (Dormann et al. 2013).

The effect of environmental attributes (independent variable) on body size (dependent variable) of *T. pusillus* males and females was investigated through linear mixed-effect models. Owing to the sexual dimorphism exhibited by *T. pusillus,* with females being larger than males (Lira et al. 2018a), we performed the linear models separately by sex. In addition, collection sites (i.e., forest fragments) were included as a random effect. The models were fitted based on the Akaike Information Criteria (AIC), and the variables that were excluded in the most parsimonious models were considered non-significant. The significance of the dependent variables was tested using a likelihood ratio test between the full and the reduced model, as described in Zuur et al. (2009). The normality of the residuals was visually assessed from normal q–q plots, and the presence of outliers (Cook's Distance > 1) was tested using Cook's distance, although none was found. All analyses were performed in R version 3.2.0, using the nlme library (R Core Team 2015; Pinheiro et al. 2019).

The correlation between the explanatory variables was low (-0.03 to 0.42, Supplementary Table S1, online at https://doi.org/10.1636/JoA-S-19-081.s1). A total of 353 *T. pusillus* specimens were measured; 118 males and 235 females (Table 1). Overall, the size of adult individuals ranged from 27.10 to 37.10 mm, with males ranging from 27.10 to 36.70 mm (mean size 31.38 ± 2.08 mm), and females ranging from 30.20 to 37.10 mm (mean size 32.52 ± 1.88 mm). Except for litter depth and litter dry mass, variations in diameter at breast height, leaf litter depth, and canopy openness had no effect on the individual's body size. The body size of males was best

Table 1.—Body size (mm) of *Tityus pusillus* by sex (mean ± SD) and environmental attributes measured in 10 Brazilian Atlantic forest fragments.

	Body size				Environmental attributes				
Fragment	Male	N	Female	N	Understory density	DBH (cm)	Canopy openness	Litter depth (cm)	Litter dry mass (g/cm^2)
F1	31±2.20	35	32.41±1.40	37	6.66±1.36	11.52±9.58	3.07±0.33	12±5.14	0.41±0.18
F2	30.11±2.20	7	30.63±2.18	14	6.50±3.61	12.11±4.62	3.28±0.35	4.76±5.23	0.18±0.09
F3	32.2±1.41	5	32.09±1.50	24	6.66±1.50	12.71±1.28	3.43±0.31	6.57±3.72	0.18±0.11
F4	31.36±1.53	16	32.18±1.92	28	3.50±1.51	18.84±3.78	4.32±0.49	7.79±3.58	0.25±0.11
F5	31.74±1.98	11	33.25±1.80	46	10±3.16	10.48±11.69	3.05±0.39	4.19±2.78	0.39±0.17
F6	30.48±0.88	5	33.05±1.40	8	5.66±0.81	9.94±2.66	2.93±0.21	4.83±2.64	0.20±0.12
F7	31.88±1.95	6	31.71±1.47	19	3.66±1.86	7.54±6.06	2.63±0.36	3.55±2.25	0.21±0.10
F8	30.11±2.20	7	33.08±2	19	6.66±1.21	11.21±4.62	3.77±0.24	7.88±4.55	0.33±0.20
F9	32.68±1.78	19	33.30±1.99	32	4.66±3.38	11.06±6.62	4.29±0.54	4.71±2.92	0.48±0.17
F10	31.4±2.90	7	31.55±1.63	8	6.66±3.14	19.47±50.53	2.85±0.31	1.73±1.21	0.14±0.03

explained by litter depth and dry mass, but none significantly affected body size (litter depth – $F_{1,7} = 2.35$, $P = 0.16$; dry mass – $F_{1,7} = 5.37$, $P = 0.056$). In relation to females, body size was best explained by litter dry mass, which significantly affected the female body size ($F_{1,8} = 14.64$, $P < 0.01$), showing a positive correlation (Fig. 1).

Our study investigated how environmental attributes influence the body size of *T. pusillus* individuals within a fragmented landscape in the north-eastern Brazilian Atlantic forest. Our results corroborate findings described in Tscharntke et al. (2002), namely, that selective pressure through habitat change acts on specific traits of a species (such as body size), thereby filtering the characteristics that are more favorable to persistence in disturbed conditions. Corroborant with our predictions, we found a sex-based response concerning the effect of environmental attributes on *T. pusillus* body size with females and not males being affected by litter dry mass. The thickness of litter layers may affect arthropod abundance because the thicker layers provide more habitat (Sayer et al. 2010; Sayad et al. 2012; Salomão et al. 2019). In addition, a sparse structure generally contains prey of poor nutritional quality, whereas a dense structure contains abundant, highly nutritional prey (Chen & Wise 1999). According to previous studies on arthropods, the quality and quantity of food during early development affect growth, and ultimately adult body size (e.g., Scriber & Slansky 1981; Tammaru 1998; Filgueiras et al. 2015). Therefore, we believe that sites with low abundance or quality of prey may result in smaller adults of *T. pusillus*. Scorpions show low dispersion rates, living in shelters colonized by other arthropods on which they prey (Brownell & Polis 2001). In addition, litter dry mass is also considered an environmental parameter that reflects habitat structure (Lira et al. 2015). Thus, forest floor in fragments with higher litter dry mass may be considered as more complex habitats than are fragments with lower litter dry mass. In this type of habitat, predation may be more difficult as noted by several authors (e.g., Kalinkat et al. 2013; Günther et al. 2014). Consequently, fragments with higher litter dry mass possibly favor an increase in *T. pusillus* female body size owing to increased resource (food and shelter) availability.

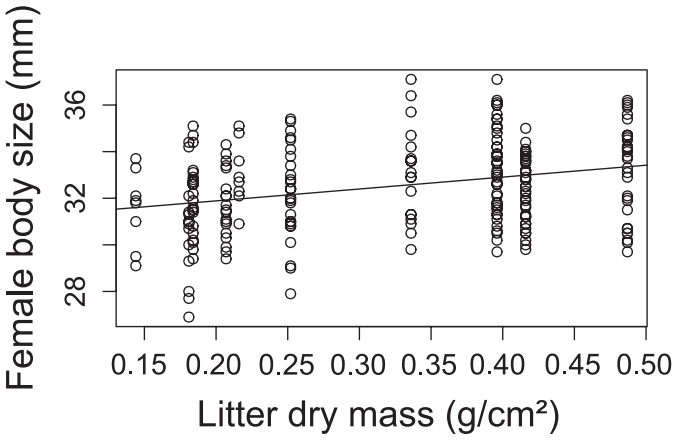

Figure 1.—Relationship between litter dry mass and body size of *Tityus pusillus* females in 10 Brazilian Atlantic forest fragments.

High mortality rates of scorpion individuals are associated with the active behavior of males (Polis 1990). For example, about four times as many females as males are captured in the field even though, in the laboratory, a 1:1 sex ratio has been found for *Tityus pusillus*. Such differences have been attributed to a higher predation risk for males (Albuquerque & Lira 2016). Thus, this specific behavioral trait showed by scorpion males may be negative for both larger and smaller individuals and may explain the absence of significant body size patterns found in this study.

Our findings corroborate previous studies indicating that predators can easily see and capture large scorpions, which would explain the higher frequency of larger specimens in sheltered microhabitats such as dense litter (Polis & McCormick 1987; Lira et al. 2018b). In conclusion, our study showed that variation in microhabitat features regulates the body size of *T. pusillus*. We detected a sex-specific response that may be influenced by the life-history traits of females. Such an effect of habitat change on scorpions may have important consequences for population dynamics and behavioral processes, which are dependent on body size.

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SUPPLEMENTARY FILES

Supplementary Table S1.—Correlation coefficient matrix between environmental attributes measured in 10 Atlantic forest fragments. Online at https://doi.org/10.1636/JoA-S-19-081.s1

LITERATURE CITED

Albuquerque, C.M.R. & A.F.A. Lira. 2016. Insights into reproductive strategies of *Tityus* (*Archaeotityus*) *pusillus* Pocock, 1893 (Scorpiones, Buthidae). Comptes Rendus Biologies 339:179–184.

Ameneshewa, B. & M.W. Service. 1996. The relationship between female body size and survival rate of the malaria vector *Anopheles arabiensis* in Ethiopia. Medical and Veterinary Entomology 10:170–172.

Ashford, O.S., W.A. Foster, B.L. Turner, E.J. Sayer, L. Sutcliffe & E.V. Tanner. 2013. Litter manipulation and the soil arthropod community in a lowland tropical rainforest. Soil Biology and Biochemistry 62:5–12.

APAC. 2013. Agência Pernambucana de Águas e Clima. Online at http://www.apac.pe.gov.br/

Brownell, P. & G.A. Polis 2001. Scorpion Biology and Research. Oxford University Press.

Chen, B. & D.H. Wise 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80:761–772.

Cincotta, R.P., J. Wisnewski & R. Engelman. 2000. Human population in the biodiversity hotspots. Nature 404:990–992.

Crooks, K.R. 2002. Relative sensitivities of mammalian carnivores to habitat fragmentation. Conservation Biology 16:488–502.

Dean, W.B. 1995. With Broadax and Firebrand: the Destruction of the Brazilian Atlantic Forest. University of California Press, Berkeley.

Didham, R. 1999. Altered leaf-litter decomposition rates in tropical forest fragments. Oecologia 116:397–406.

Dionisio-da-Silva, W., A.F.A. Lira & C.M.R. Albuquerque. 2018. Distinct edge effects and reproductive periods of sympatric litter-dwelling scorpions (Arachnida: Scorpiones) in a Brazilian Atlantic forest. Zoology 129:17–24.

Dormann, C.F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, et al. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Enedino, T.R., A. Loures-Ribeiro & B.A. Santos. 2017. Protecting biodiversity in urbanizing regions: The role of urban reserves for the conservation of Brazilian Atlantic Forest birds. Perspectives in Ecology and Conservation 16:17–23.

Ferns, P.N. & M.A. Jervis. 2016. Ordinal species richness in insects—a preliminary study of the influence of morphology, life history, and ecology. Entomologia Experimentalis et Applicata 159:270–284.

Filgueiras, B.K.C., L. Iannuzzi & I.R. Leal. 2011. Habitat fragmentation alters the structure of dung beetle communities in the Atlantic Forest. Biological Conservation 144:362–369.

Filgueiras, B.K.C., M. Tabarelli, I.R. Leal, F.Z. Vaz-de-Mello & L. Iannuzzi. 2015. Dung beetle persistence in human-modified landscapes: combining indicator species with anthropogenic land use and fragmentation-related effects. Ecological Indicators 55:65–73.

Frazer, G.W., C.D. Canham & K.P. Lertzman. 1999. Gap Light Analyzer (GLA), version 2.0: imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, user's manual and program documentation. Simon Fraser University, Burnaby, B.C., Canada, and the Institute of Ecosystem Studies, Millbrook, N.Y. USA.

Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among great tits, *Parus major*. Ibis 123:31–41.

González-Tokman D. & C. Martínez-Garza. 2015. Effect of ecological restoration on body condition of a predator. PLoS One 10:e0133551.

Günther, B., B.C. Rall, O. Ferlian, S. Scheu & B. Eitzinger. 2014. Variations in prey consumption of centipede predators in forest soils as indicated by molecular gut content analysis. Oikos 123:1192–1198.

Hillaert, J., M.L. Vandegehuchte, T. Hovestadt & D. Bonte. 2018. Information use during movement regulates how fragmentation and loss of habitat affect body size. Proceedings of the Royal Society B: Biological Sciences 285:20180953.

Jenkins, D.G., C.R. Brescacin, C.V. Duxbury, J.A. Elliott, J.A. Evans, K.R. Grablow et al. 2007. Does size matter for dispersal distance? Global Ecology and Biogeography 16:415–425.

Kalinkat, G., U. Brose & B.C. Rall. 2013. Habitat structure alters top-down control in litter communities. Oecologia 172:877–887.

Karino, K., N. Seki & M. Chiba. 2004. Larval nutritional environment determines adult size in Japanese horned beetles *Allomyrina dichotoma*. Ecological Research 19:663–668.

Kutner, M.H., C.J. Nachtsheim, J. Neter & W. Li. 2005. Applied Linear Statistical Models. McGraw-Hill, New York.

Laurance W.F., H.E. Nascimento, S.G. Laurance, A. Andrade, J.E. Ribeiro, J.P. Giraldo et al. 2007. Rapid decay of tree-community composition in Amazonian forest fragments. Proceedings of the National Academy of Sciences of the United States of America 103:19010–19014.

LeGrice, R.J., G. Tezanos-Pinto, P. Villemereuil, G.I. Holwell & C.J. Painting. 2019. Directional selection on body size but no apparent survival cost to being large in wild New Zealand giraffe weevils. Evolution 73:1–15.

Lira, A.F.A., V.L.N. Araújo, A.M. DeSouza, F.N.A.A. Rego & C.M.R. Albuquerque. 2016. The effect of habitat fragmentation on the scorpion assemblage of a Brazilian Atlantic Forest. Journal of Insect Conservation 20:457–466.

Lira, A.F.A., A.M. DeSouza & C.M.R. Albuquerque. 2018b. Environmental variation and seasonal changes as determinants of the spatial distribution of scorpions (Arachnida: Scorpiones) in Neotropical forests. Canadian Journal of Zoology 96:963–972.

Lira, A.F.A., A.M. DeSouza, A.A.C. Silva Filho & C.M.R. Albuquerque. 2013. Spatio-temporal microhabitat use by two co-occurring species of scorpions in Atlantic rainforest in Brazil. Zoology 116:182–185.

Lira, A.F.A., L.M. Pordeus, F.N.A.A. Rego, K. Iannuzzi & C.M.R. Albuquerque. 2018a. Sexual dimorphism and reproductive behavior in the Brazilian scorpion *Tityus pusillus* (Scorpiones, Buthidae). Invertebrate Biology 137:221–230.

Lira, A.F.A., L.M. Pordeus, R.P. Salomão, R. Badillo-Montaño & C.M.R. Albuquerque. 2019. Effects of anthropogenic land-use on scorpions (Arachnida: Scorpiones) in Neotropical forests. International Journal of Tropical Insect Science 39:211–218.

Lira, A.F.A., F.N.A.A. Rego & C.M.R. Albuquerque. 2015. How important are environmental factors for the population structure of co-occurring scorpion species in a tropical forest? Canadian Journal of Zoology 93:15–19.

Miyashita, T., A. Shinkai, & T. Chida. 1998. The effects of forest fragmentation on web spider communities in urban areas. Biological Conservation 86:357–364.

Öckinger, E., O. Schweiger, T.O. Crist, D.M. Debinski, J. Krauss, M.

Kuussaari et al. 2010. Life-history traits predict species responses to habitat area and isolation: a cross-continental synthesis. Ecology Letters 13:969–979.
Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. Biodiversity and Conservation 13:2567–2586.
Penell, A., F. Raub & H. Höfer. 2018. Estimating biomass from body size of European spiders based on regression models. Journal of Arachnology 46:413–419.
Pinheiro, J., D. Bates, S. DebRoy, S. Heisterkamp, B.V. Willigen et al. 2019. Linear and nonlinear mixed effects models. https://cran.rproject.org/web/packages/nlme/nlme.pdf Accessed 7 Aug 2019.
Polis, G.A. 1990. The Biology of Scorpions. Stanford University Press, Stanford.
Polis, G.A. & S.J. McCormick. 1987. Intraguild predation and competition among desert scorpions. Ecology 68:332–343.
R Core Team. 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Ranta, P., T. Blom, J. Niemelä, E. Joensuu & M. Siitonen. 1998. The fragmented Atlantic rain forest of Brazil: size, shape and distribution of forest fragments. Biodiversity & Conservation 7:385–403.
Ribeiro, M.C., J.P. Metzger, A.C. Martensen, F.J. Ponzoni & M.M. Hirota. 2009. The Brazilian Atlantic Forest: How much is left, and how is the remaining forest distributed? Implications for conservation. Biological Conservation 142:1141–1153.
Rossetti, M.R., T. Tscharntke, R. Aguilar & P. Batáry. 2017. Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. Ecology Letters 20:264–272.
Salomão, R.P., L.C. Brito, L. Iannuzzi, A.F.A Lira & C.M.R. Albuquerque. 2019. Effects of environmental parameters on beetle assemblage in a fragmented tropical rainforest of South America. Journal of Insect Conservation 23:111–121.
Salomão, R.P., D. Gonzálz-Tokman, W. Dáttilo, J.C. López-Acosta & M.E. Favila. 2018. Landscape structure and composition define the body condition of dung beetles (Coleoptera: Scarabaeinae) in a fragmented tropical rainforest. Ecological Indicators 88:144–151.
Sayad, E., S.M. Hosseini, V. Hosseini & M.H. Salehe-Shooshtari. 2012. Soil macrofauna in relation to soil and leaf litter properties in tree plantations. Journal of Forest Science 58:170–180.
Sayer, E.J., L.M.E. Sutcliffe, R.I.C. Ross & E.V.J. Tanner. 2010. Arthropod abundance and diversity in a lowland tropical forest floor in Panama: The role of habitat space vs. nutrient concentrations. Biotropica 42:194–200.
Scriber, J.M. & F. Slansky Jr. 1981. The nutritional ecology of immature insects. Annual Review of Entomology 26:183–211.
Sekar, S. 2012. A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? Journal of Animal Ecology 81:174–184.
Sieving, K.E. & J.R. Karr. 1997. Avian extinction and persistence mechanisms in lowland Panama. Pp. 156–170. *In* Tropical Forest Fragments: Ecology, Management, and Conservation of Fragmented Communities (W.F. Laurance & R.O. Bierregaard, eds). University of Chicago Press, Chicago.
Tabarelli, M., J.M.C. Silva & C. Gascon. 2004. Forest fragmentation, synergisms and the impoverishment of Neotropical forests. Biodiversity and Conservation 13:1419–1425.
Tammaru, T. 1998. Determination of adult size in a folivorous moth: constraints at instar level? Ecological Entomology 23:80–89.
Tscharntke, T., I. Steffan-Dewenter, A. Kruess & C. Thies. 2002. Characteristics of insect populations on habitat fragments: a mini review. Ecological Research 17:229–239.
Zar, J.H. 1999. Biostatistical Analysis. Prentice Hall, New Jersey.
Zuur, A.F., E.N. Ieno, N.J. Walker, A.A. Saveliev & G.M. Smith. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

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