



# Indirect effects of ecosystem engineering by insects in a tropical liana

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## Abstract

Insects might impact communities and ecosystems through processes that are not trophic, via ecosystem engineering. In this study, we experimentally evaluated the role of the caterpillars *Pandemis* sp. as habitat modifiers in the tropical liana *Trigonía rotundifolia*. Specifically, we examined their effects on the abundance and richness of arthropods that secondarily colonize leaf-rolls (shelters) built by the caterpillars, as well as indirect effects that influence plant herbivory. Two experiments were conducted in the field to evaluate the role of natural and artificial rolls on community structure and plant damage. Plants with artificial leaf-rolls hosted 2.2 times more arthropods than plants without shelters and they had 1.5 times higher richness compared to control plants. Plants with natural shelters exhibited significantly lower arthropod richness than plants with artificial shelters or control plants, but arthropod abundance did not differ among treatments. Although plants with leaf-rolls hosted significantly more arthropods, arthropod species composition did not differ amongst treatments, as Formicidae was the most frequent group in all treatments. Herbivory was almost 3 times higher in plants with leaf-rolls compared to plants with no rolled leaves, indicating that the effect of increased arthropod abundance, and especially herbivore abundance, might influence leaf damage in plants with leaf-rolls. We demonstrate the strong impact of *Pandemis* as a habitat modifier on community structure as well as on community processes through indirect effects.

**Keywords** Community structure · Ecosystem engineers · Herbivory · Leaf-rollers

## Introduction

The role of insects in shaping patterns and processes of terrestrial communities has been long acknowledged, through their impacts on community organization and assembly (Magura and Lövei 2017), species interactions (Del-Claro and Torezan-Silingardi 2009) and species diversity and

composition (Stam et al. 2014). Recent data on their role in ecosystem processes have shown the direct impacts of insects on nutrient cycling (Kozlov et al. 2016), soil dynamic processes (Crutsinger et al. 2008) and flux of energy through ecological networks (Dáttillo and Rico-Gray 2018). Indirectly, insects might impact communities and ecosystems through processes that are not trophic, via ecosystem engineering. Ecosystem engineering can be defined as interactions involving non-trophic relationships amongst species (Jones et al. 1994, 2010). The definition of ecosystem engineering merges with the facilitation theory, in which organisms create or modify physical structures that alter the local environment through habitat modification or amelioration of abiotic stress, with direct and indirect effects on other components of communities and ecosystem properties (Cuddington et al. 2007; Romero et al. 2015).

Through their activity, some organisms physically change the environment in such a way they might increase resource availability to other organisms (Johnson et al. 2016). The role of insects as habitat modifiers has been demonstrated through early observations of secondary occupancy of shelters created and/or used by gall-formers (Fernandes

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et al. 1989), leaf-miners (Askew 1980) and ants (O'Dowd and Wilson 1991) and their effects on community diversity. More recently the use of artificially-created shelters has been more frequent (e.g., Calderón-Cortés et al. 2011, 2016; Vieira and Romero 2013; Novais et al. 2017), as they simulate the effects of the physical structure after insects have left and their use allows the examination of the effects of shelters over time (Lill et al. 2007), seasons (Vieira and Romero 2013) and space (Hastings et al. 2007). Data have accumulated showing that the presence of shelters increases arthropod richness by 128% and arthropod abundance by 135% (Cornelissen et al. 2016), demonstrating the strong effects of shelter use on community organization.

The effects of insect as habitat modifiers, however, can go beyond community structure, as these organisms can initiate cascades of trophic interactions that shape communities in unexpected ways (Wetzel et al. 2016). The increased number of herbivores due to shelter presence in plants might, for example, increase herbivory levels when herbivores are more abundant in shelters compared to unaltered leaves. In an opposite scenario, herbivory levels might be reduced if predatory arthropods—such as spiders—are more abundant in modified plants and control herbivore populations through top-down processes. These alternative scenarios are yet to be explored in tropical plant systems, where plants, herbivores and arthropods are more speciose and plants experience higher levels of leaf damage by herbivory (Dyer and Coley 2002).

This study aimed to evaluate the roles of shelters built by the caterpillar *Pandemis* sp. (Lepidoptera, Tortricidae) on the tropical plant *Trigonía rotundifolia* (Trigoniaceae) answering the following questions: (1) Does the presence of shelters increase the frequency, richness and abundance of arthropods on plants?, (2) Does the type and number of shelters influence secondary colonization and use of shelters?, and (3) How does shelter presence and number influence the herbivory levels experienced by plants? We used two separate experiments to answer these questions, comparing (i) the community of arthropods and level of herbivory in control plants (no shelters) and manipulated plants (shelters added) and (ii) the community of arthropods and level of herbivory on plants without shelters, with natural shelters and with artificial shelters added.

## Methods

### Study site

This study was conducted in a natural fragment of semi-deciduous Atlantic Forest, in a city park of 33.0 ha (19°0'24"S and 49°27'06"W) in the municipality of Ituitaba, Minas Gerais, Brazil. The city park is closed to visitation

and the plant *Trigonía rotundifolia* (Trigoniaceae) is abundant in open areas and trails. Climate is tropical, with dry winter (May–September) and wet summer (October–April).

### Study system

The genus *Trigonía* is composed of 24 species of trees, shrubs and lianas, distributed from Mexico to Paraguay, and common in the south and southeast of Brazil (Lleras 1978). The species *Trigonía rotundifolia* Lleras. is a liana native from Brazil and is very common in areas covered by Atlantic Forest. Leaves are large, hairy and silver-colored on the abaxial surface. In the study site, caterpillars of *Pandemis* sp. (Archipini, Tortricidae) roll entire or parts of the leaves of *Trigonía*, creating leaf-rolls, tying the rolls with silken threads, using the rolls as shelters and abandoning these before pupation. In the study site, plants exhibited between 0 and 5 cylinders naturally, but over 50% of the studied plants exhibited one or two natural leaf-rolls. Both empty and occupied shelters were encountered in the field.

### Data sampling

#### Experiment 1

To evaluate the role of shelters created by *Pandemis* sp. on arthropod community composition, 30 plants were marked in the field and distributed into two groups: (i) control ( $n = 15$ ), composed of plants naturally without shelters and (ii) treatment ( $n = 15$ ), with 2 artificial shelters added per plant. Plants were at least 10 m apart and were marked in the field using metallic tags. To create the artificial shelters, we selected young but fully-expanded leaves with no signs of herbivory. Leaves were manually rolled in the field from the abaxial to the adaxial surface, from the edge to the center of the leaf, to simulate the rolls naturally created by *Pandemis* sp. (Supplementary Material S1). Leaves were kept rolled using antioxidant hair clips and cylinders were about 1.0 cm in diameter. Leaf-rolls naturally created by *Pandemis* averaged about 0.8 cm (0.06 SE,  $n = 30$ ) in diameter.

To evaluate the effects of the presence of shelters on arthropod community, plants in the two groups were monitored for 90 days during the rainy season, which coincides with the peak of activity of *Pandemis* caterpillars and other insects in the studied area. Plants were monitored in 15-day intervals and were visually inspected for 10 min each. All arthropods on leaves and artificial shelters were sampled and rolls were carefully opened, inspected and rolled again to keep shape until the next 15-day evaluation. All specimens sampled were stored, morphotyped, and classified into guilds according to Brescovit et al. (2007), Carrano-Moreira (2015) and consulting specialists.

## Experiment 2

To evaluate differences in arthropod community in plants without shelters, with natural shelters built by *Pandemis* and artificial shelters, another 30 plants at least 2.0 m apart from one another were marked in the field and divided into three groups. Control plants did not exhibit shelters ( $n = 10$  plants), natural plants ( $n = 10$ ) were those with a single shelter built by *Pandemis* but already unoccupied by the caterpillar, and treatment plants ( $n = 10$ ) were those with one artificial shelter added. Artificial shelters were constructed as described before. These plants were monitored for 60 days, at 15-day intervals. All plants were inspected for 10 min each and arthropods were collected from one randomly selected (unrolled) leaf per plant of the control group, inside the natural shelter and inside the artificial roll added. Rolls were carefully opened, inspected and rolled again to keep shape until the next 15-day evaluation. All arthropods collected were stored in alcohol 70% for further identification and classification into guilds.

## Herbivory levels

To evaluate the levels of herbivory on plants with and without shelters, another 30 plants (at least 2 m apart from one another) were divided into three groups: (1) control ( $n = 10$ ), plants without shelters, (2) plants with one shelter ( $n = 10$ ), and (3) plants with two shelters ( $n = 10$ ). In this experiment, we considered only natural, already unoccupied shelters (leaf-rolls) of *Pandemis* sp. Plants were marked in the field at the beginning of the attack season and four intact leaves per plant were selected. Leaves were marked randomly in the control group and for the treatment groups we used the four leaves nearest to the leaf-rollers. All leaves marked were intact, fully-expanded, and of similar size. These leaves were numbered with a permanent pen and left on the plants until the end of the herbivory season, when leaves were collected, digitized and *background herbivory* (*sensu* Kozlov and Zvereva 2017) was measured as the percentage of leaf area lost calculated as  $\text{Herbivory} = (\text{leaf area lost} / \text{total leaf area}) * 100$ . Images were analyzed using ImageTool → after calibrating each picture to 0.01 mm. A total of 40 leaves per group were examined.

## Data analysis

To evaluate the role of shelter on arthropod diversity, we compared mean values of arthropod richness and abundance in plants without shelters and plants with 2 shelters added with an ANCOVA, where factors were treatments and the number of leaves per plant ( $n = 15$  plants per treatment) was used as a co-variate. The number of leaves per plant was added as a co-variate to control for plant size and variation

on leaf availability. The same analysis was used to examine variation in arthropod richness and abundance amongst plants without shelters, with natural shelters and with artificial shelters added. Data normality was checked with Liliefors' test and homoscedasticity of variances was checked through Bartlett's test. To examine arthropod composition and guild composition amongst different treatments, we used One-Way ANOSIM, based on Euclidean distances converted to ranks. The one-tailed significance was computed by permutation of group (control, natural shelters, artificial shelters added) with 9999 permutations. Pair-wise ANOSIMs between all pairs of groups were used as a post-hoc test. To examine differences in herbivory levels in plants without shelters and plants with natural shelters, we averaged herbivory levels using the four leaves per plant as replicates and differences amongst groups were tested using One-Way ANOVA, with 10 replicates per group. All analyses were conducted in R software (R Core Team 2015).

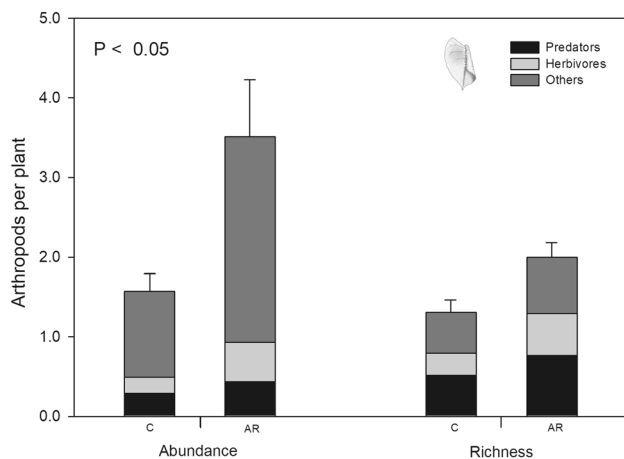
The magnitude of the effects of artificial shelter presence on arthropod richness and abundance was evaluated through a response-ratio analysis (Hedges et al. 1999) using the 15 individuals of each treatment as replicates. The mean and standard deviation of richness and abundance in the control and artificial shelters treatments were calculated using the average of the six samplings (90 days with sampling at 15-day intervals). The natural log of the response-ratio was calculated as  $\ln = \ln(XT/XC)$ , where XT represents the mean of the treatment group (shelters added) and XC represents the mean of the control group (unaltered leaves). Negative proportional numbers indicate a reduction of arthropod richness or abundance compared to that of the control and positive proportional numbers indicate an increase in richness or abundance in the treatment group compared to that of the control. To estimate the cumulative effect (E++) for the 15 replicates per treatment, the effects were combined using weighted averages and a fixed-model analysis (Rosemberg et al. 2000). The cumulative effects were considered significant if the confidence intervals (95%) did not overlap with zero.

## Results

A total of 591 arthropods was sampled from *Trigonía* plants, distributed into 122 morphospecies (Supplementary Material S2).

## Experiment 1

Hymenoptera (Formicidae) were the most common arthropods, representing almost half of all specimens sampled (46.8%), followed by Diptera (17.4%), Araneae (14.2%), Hemiptera (7.4%), Lepidoptera (5.8%), Collembola (5.3%),



**Fig. 1** Arthropod abundance and richness (mean  $\pm$  SE) in control plants (unaltered leaves) and artificially rolled leaves (shelters) of *Trigonía rotundifolia*. C control, AR artificial rolls. Other arthropods include detritivores, omnivores and parasites

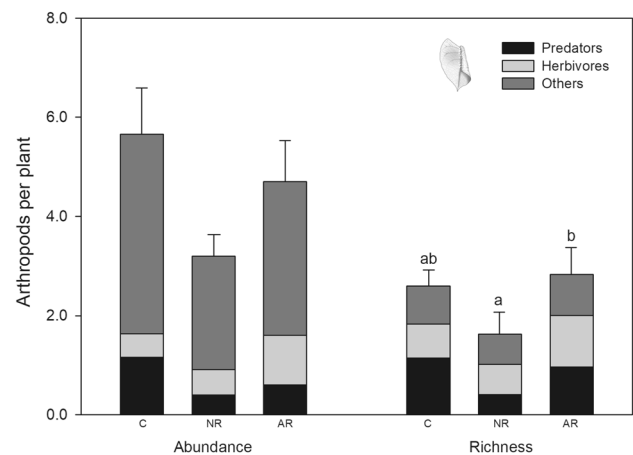
and other orders such as Blattaria, Coleoptera, Mantodea, Odonata, and Orthoptera, representing together less than 4% of all arthropods sampled.

Plants with artificial shelters exhibited 2.2 more arthropods than plants without shelters ( $F_{1,27}=6.84$ ,  $P=0.014$ ). Similarly, plants with shelters added had 1.5 higher richness compared to control plants ( $F_{1,27}=7.92$ ,  $P=0.009$ , Fig. 1). When arthropods were classified into guilds, only the abundance of omnivores was significantly different across treatments ( $F_{1,27}=6.02$ ,  $P=0.021$ ). Predators ( $F_{1,27}=0.90$ ,  $P=0.351$ ), herbivores ( $F_{1,27}=1.71$ ,  $P=0.203$ ), and detritivores ( $F_{1,27}=1.45$ ,  $P=0.238$ ) did not differ in abundance across control and shelter-added plants.

## Experiment 2

Hymenoptera (especially Formicidae) were the most common arthropods, representing 58.1% of all specimens sampled, followed by Araneae (15.21%), Hemiptera (10.47%), Collembola (5.49%), and Diptera (4.74%). Other orders found were Blattaria, Coleoptera, Lepidoptera, Orthoptera, and Thysanoptera, and they made up 6% of all arthropods sampled.

Plants with natural shelters hosted significantly lower arthropod richness than plants with artificial shelters or control plants ( $F_{2,26}=4.73$ ,  $P=0.018$ , Fig. 2). Arthropod abundance, on the other hand, did not differ among treatments ( $F_{2,26}=0.84$ ,  $P=0.439$ ) and ants were the most common insects on control plants. When arthropod guild was taken into account, only the abundance of herbivores was higher in plants with artificial shelters ( $F_{2,26}=3.48$ ,  $P=0.045$ ), but predators, detritivores and omnivores did not differ in occurrence amongst groups.



**Fig. 2** Arthropod abundance and richness (mean  $\pm$  SE) in control plants (unaltered leaves), in plants with natural rolls (leaves rolled by *Pandemis* sp.) and in artificially rolled leaves (shelters) of *Trigonía rotundifolia*. Means followed by the same letters do not differ statistically from each other. C control, NR Natural rolls, AR artificial rolls

## Arthropod composition amongst treatments

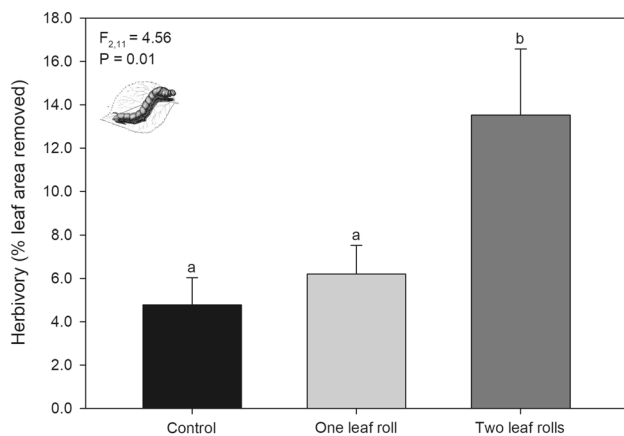
Arthropod fauna composition did not differ across plants without shelters and plants with artificially added shelters (Global  $R=-0.259$ ,  $P=0.082$ ). The same was true for arthropods found on control plants, plants with natural shelters and plants with shelters added (Global  $R=0.102$ ,  $P=0.235$ ).

## Magnitude of the effects of shelters on arthropod community

Artificial shelter addition, altogether, increased arthropod richness by almost 50% ( $E++=0.489$ , CI 0.016–0.96,  $P<0.05$ ) and arthropod abundance by more than 60% ( $E++=0.625$ , CI 0.143–1.106,  $P<0.05$ ), indicating that the effects of treatments were significant on the community of arthropods associated with *Trigonía*.

## Herbivory levels

Herbivory in *Trigonía* varied between zero and 56.7% of leaf area lost to chewers. The highest values of herbivory were found in plants with shelters, and plants with two shelters experienced 2.8 times higher herbivory levels than control plants ( $F_{2,11}=4.56$ ,  $P=0.01$ , Fig. 3). Control plants and plants with one leaf roll did not differ from one another in herbivory levels.



**Fig. 3** Herbivory (percentage of leaf area removed) in leaves of *Trigonía rotundifolia* without rolled leaves (control), with one natural leaf roll and two natural leaf-rolls created by *Pandemis* sp. Control plants and plants with one artificial roll did not differ in levels of herbivory

## Discussion

Ecosystem engineering by insect herbivores occurs as the result of structural modification of plants after manipulation. With our experimental design, we have shown the indirect effects of *Pandemis* on *Trigonía* leaves, as rolled leaves offered shelters to arthropods, which increased in richness and abundance. Additionally, this increase in arthropods and especially in herbivore abundance increased herbivory levels experienced by plants with artificial shelters, indicating the indirect effects of shelter presence. *Trigonía* plants with artificial shelters exhibited much higher levels of leaf area loss—approximately 14% of leaf area removed—than reported in the literature of global herbivory levels (Kozlov et al. 2015), which averages around 7.0%. To the best of our knowledge, this is the first study indicating that facilitation of herbivore colonization due to shelter presence might inflict higher damage on host plants. Although predators such as ants and spiders were common in the shelters (47 and 14% of all arthropods sampled, respectively), their presence was not enough to reduce herbivores and herbivory levels in the plant studied. Predation and its effects on the *Trigonía* insect community is yet to be evaluated, as some authors report that predators sometimes use shelters not as foraging sites, but solely as refuges against climatic adverse conditions (Lill and Marquis 2007).

Through their activity, ecosystem engineers change their physical environment, and in doing so change the availability of resources to other organisms in their vicinity (Johnson et al. 2016). The role of shelters in community structure has been demonstrated previously and in a recent meta-analytical review, Romero et al. (2015) have shown that the overall effect of ecosystem engineering on community

diversity was positive, increasing species richness by about 25% and emphasizing the process of habitat modification and facilitative interactions. They also suggest that effects should be stronger in the tropics, where density-dependent interactions are expected to be stronger. Our results have shown an increase of approximately 50.0% in arthropod richness and 63% in abundance in *Trigonía* plants with artificial rolls, indicating that the presence of such subtle and ephemeral structures in the form of leaf-rollers might be enough to increase colonization of plants and also influence herbivory levels. We suggest that, in the case studied here, rolled leaves by *Pandemis* might represent shelters against abiotic conditions, such as high temperature. Measurements of temperature inside and outside the leaf-rolls created by *Pandemis* indicated a difference of approximately 1.3 °C (unpublished data) and rolled leaves offered cooler habitats than unaltered leaves of *Trigonía rotundifolia*. In a study with leaf-rollers over seasons in another tropical system, Vieira and Romero (2013) have shown that the effects of habitat modification by the caterpillars *Anaea* spp. on *Croton floribundus* (Anacardiaceae) were stronger during the dry season, when leaf-rolls actually offer adequate habitats that protect arthropods against UV-radiation and desiccation. Our study was conducted during the wet, but also hot season, indicating that *Pandemis* shelters might act as shelters against high temperature, wind and precipitation.

Leaf-rolls naturally created by *Pandemis* on *Trigonía* leaves did not influence arthropod abundance and richness (Fig. 2), compared to artificially-created leaf-rolls. Although we did not evaluate differences in species composition amongst leaf-rolls and/or mechanisms responsible for leaf roll selection, we suggest that chemical and visual cues used by arthropods—especially predators—when selecting shelters might be responsible for these results, as empty artificial shelters might be more attractive or acceptable to predators and herbivores than empty natural rolls that had been previously occupied by caterpillars. Our data also show that most arthropods sampled within natural and artificial leaf-rolls were predators, and we believe that this could be explained by the fact that predators stay on the shelters for longer and use it as refuges. Herbivores, on the other hand, do not feed inside the shelters and forage on plant leaves, but might use leaf-rolls as shelters against adverse abiotic conditions. Higher herbivory levels on plants with two leaf-rolls also reinforce the suggestion that the use of shelters by herbivores positively influences leaf damage on *Trigonía rotundifolia* leaves.

Plants and animals modify both the physical and the chemical environment, as well as ecosystem processes (Romero et al. 2015), and our study has shown the effects of leaf-rollers on the organization of a speciose community of arthropods in a tropical liana. They enhanced species richness and abundance, and thus the indirect effects



of increased herbivore abundance on leaf damage. These findings indicate that facilitative interactions such as those created by habitat modifiers can have different effects on different components of communities.

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## References

- Askew RR (1980) The diversity of insect communities in leaf mines and plant galls. *J Anim Ecol* 49:817–829
- Brescovit AD, Rheims CA, Bonaldo AB (2007) Araneomorphae. Identification key to Brazilian spiders. Instituto Butantan
- Calderón-Cortés N, Quesada M, Escalera-Vázquez (2011) Insects as stem engineers: interactions mediated by the twig-girdler *Oncideres albomarginata chamela* enhance arthropod diversity. *PLoS ONE* 6:e19083
- Calderón-Cortés N, Uribe-Mu CA, Martínez-Mendez AK, Escalera-Vázquez LH, Cristobal-Perez EJ, García-Oliva F, Quesada M (2016) Ecosystem engineering and manipulation of host plant tissues by the insect borer *Oncideres albomarginata chamela*. *J Insect Physiol* 84:128–136
- Carrano-Moreira AF (2015) Insects: sampling and identification. Technical Books, Brazil
- Cornelissen T, Cintra F, Santos JC (2016) Shelter-building insects and their role as ecosystem engineers. *Neotrop Entomol* 45:1–12
- Crutsinger GM, Habenicht MN, Classe AT, Sanders NJ (2008) Galling by *Rhopalomyia solidaginis* alters *Solidago altissima* architecture and litter nutrient dynamics in an old-field ecosystem. *Plant Soil* 303:95–103
- Cuddington K, Hastings A (2007) Balancing the engineer-environment equation: the current legacy. In: Cuddington K, Byers JE, Wilson WG, Hastings A (eds) *Ecosystem engineers: plants to protists*. Academic Press, New York, pp 253–274
- Dáttilo W, Rico-Gray V (2018) ecological networks in the tropics. Springer, New York. <https://doi.org/10.1007/978-3-319-68228-0>
- Del-Claro K, Torezan-Silingardi H (2009) Insect-plant interactions: new pathways to a better comprehension of ecological communities in Neotropical savannas. *Neotrop Entomol* 38:159–164
- Dyer L, Coley P (2002) Tri-trophic interactions in tropical versus temperate communities. In: Tschamtk T, Hawkins BA (eds) *Multitrophic level interactions*. Cambridge University press, Cambridge, pp 67–88
- Fernandes GW, Boecklen WJ, Martins RP, Castro AG (1989) Ants associated with a coleopterous leaf-bud gall on *Xylopia aromatica* (Annonaceae). *Proc Entomol Soc Wash* 91:81–87
- Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JA, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. *Ecol Lett* 10:153–164
- Hedges LV, Gurevitch J, Curtis P (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* 80:1150–1156
- Johnson SN, Lopaticki G, Bernett K, Facey SL, Powell JR, Hartley SE (2016) An insect ecosystem engineer alleviates drought stress in plants without increasing plant susceptibility to an above-ground herbivore. *Funct Ecol* 30:894–902
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Jones CG, Gutiérrez JL, Byers JE, Crooks JA, Lambrinos JG, Talley TS (2010) A framework for understanding physical ecosystem engineering by organisms. *Oikos* 119:1862–1869
- Kozlov M, Zvereva E (2017) Background insect herbivory: impacts, patterns and methodology. *Prog Bot*. [https://doi.org/10.1007/124\\_2017\\_4](https://doi.org/10.1007/124_2017_4)
- Kozlov M, Lanta V, Zverev V, Zvereva E (2015) Global patterns in background losses of woody plant foliage to insects. *Glob Ecol Biogeogr* 24:1126–1135
- Kozlov M, Zverev V, Zvereva E (2016) Shelters of leaf-tying herbivores decompose faster than leaves damaged by free-living insects: implications for nutrient turnover in polluted habitats. *Sci Total Environ* 15:946–951
- Lill JT, Marquis RJ (2007) Microhabitat manipulation: ecosystem engineering by shelter-building insects. In: Cuddington K, Byers JE, Hastings A, Wilson WG (eds) *Ecosystem engineers: plants to protists*. Academic Press, New York, pp 107–138
- Lill JT, Marquis RJ, Walker MA, Peterson L (2007) Ecological consequences of shelter-sharing by leaf-tying caterpillars. *Entomol Exper et Applic* 124:45–53
- Lleras E (1978) Trigoniceae. *Flora Neotrop* 19: 1–73
- Magura T, Lövei GL (2017) Environmental filtering is the main assembly rule of ground beetles in the forest and its edge but not in the adjacent grassland. *Insect Sci*. <https://doi.org/10.1111/1744-7917.12504>
- Negrele RRB (2002) The Atlantic forest in the Volta Velha Reserve: a tropical rain forest site outside the tropics. *Biodiver Conserv* 11:887–919
- Novais SMA, DaRocha WD, Caldéron-Cortés N, Quesada M (2017) Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer. *Basic Appl Ecol* 24:53–59
- O'Dowd DJ, Wilson MF (1991) Leaf domatia and mites on Australian plants: ecological and evolutionary implications. *Biol J Linn Soc* 37:191–236
- R Development Core Team (2015) R: a language and environment for statistical computing. R Foundation for Statistical Computing [Internet]. R Foundation for Statistical Computing, Vienna
- Romero GQ, Gonçalves-Souza T, Vieira C, Koricheva J (2015) Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biol Rev* 90:877–890
- Rosemberg MS, Adams D, Gurevitch J (2000) MetaWin: Statistical software for meta-analysis
- Stam JM, Kroes A, Li Y, Gols R, vanLoon JA, Poelman EH, Dicks M (2014) Plant interactions with multiple insect herbivores: from community to genes. *Annu Rev Plant Biol* 65:689–713
- Vieira C, Romero GQ (2013) Ecosystem engineers on plants: indirect facilitation of arthropod communities by leaf-rollers at different scales. *Ecology* 94:1510–1518
- Wetzel WC, Screen RM, Li I, McKenzie J, Philips KA, Cruz M, Zhang W, Greene A, Lee E, Singh N, Tran C, Yang LH (2016) Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. *Ecology* 97:427–438