Journal of Tropical Ecology

www.cambridge.org/tro

Local environmental context determines the colonisation of leaf shelters by arthropods: an experimental study

Samuel Novais[1], Vicente Hernández-Ortiz[1], Karla Rodríguez-Hernández[2], Mauricio Quesada[3,4], G. Wilson Fernandes[5], Carolina Bañol-Pérez[6], Edgar A. Sánchez-García[2], Fabian A. Aldaba-Núñez[2], Luis J. Méndez-Vázquez[2], Manuel Ochoa[2], Marisol A. Zurita-Solís[2] and Armando Aguirre-Jaimes[1]

[1]Instituto de Ecología A.C., Red de Interacciones Multitróficas, Carretera Antigua a Coatepec 351, El Haya, Xalapa, Veracruz 91070, Mexico; [2]Posgrado del Instituto de Ecología A.C., Carretera Antigua a Coatepec 351, El Haya, Xalapa, Veracruz 91070, Mexico; [3]Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores Unidad Morelia, Universidad Nacional Autónoma de México, Morelia, Michoacán 58190, Mexico; [4]Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Morelia, Michoacán 58190, Mexico; [5]Laboratório de Ecologia Evolutiva e Biodiversidade, Departamento de Genética, Ecologia e Evolução, Universidade Federal de Minas Gerais, Belo Horizonte, MG 30270-971, Brasil and [6]Programa de Biología, Facultad de Ciencias de la Vida, Universidad Estatal Amazónica, Km. 2. 1/2 vía Puyo a Tena (Paso Lateral), Ecuador

Research Article

Cite this article: Novais S, Hernández-Ortiz V, Rodríguez-Hernández K, Quesada M, Fernandes GW, Bañol-Pérez C, Sánchez-García EA, Aldaba-Núñez FA, Méndez-Vázquez LJ, Ochoa M, Zurita-Solís MA, and Aguirre-Jaimes A (2022) Local environmental context determines the colonisation of leaf shelters by arthropods: an experimental study. *Journal of Tropical Ecology* **38**, 118–126. https://doi.org/10.1017/S0266467421000523

Received: 23 April 2021
Revised: 23 October 2021
Accepted: 7 November 2021
First published online: 14 January 2022

Keywords:
Arthropod diversity; ecosystem engineering; indirect interactions; leaf shelter; limiting resources; microclimatic refuges

Author for correspondence:
Armando Aguirre-Jaimes,
Email: armando.aguirre@inecol.mx

Abstract

The magnitude of facilitation by shelter-building engineers on community structure is expected to be greater when they increase limited resources in the environment. We evaluated the influence of local environmental context on the colonisation of leaf shelters by arthropods in a Mexican evergreen tropical rainforest. We compared the species richness and abundance of arthropods (total and for different guilds) colonising artificially rolled leaves in habitats differing in understory heterogeneity (forest edge > old-growth forests > living fences). Arthropod abundance of the most representative arthropod taxa (i.e., Araneae, Blattodea, Collembola and Psocoptera) colonising the rolled leaves was greater at forest edge, a trend also observed for average arthropod abundance, and for detritivore and predator guilds. In addition, fewer arthropod species and individuals colonised the rolled leaves in the living fence habitat, a trend also observed for most arthropod guilds. As forest edge is expected to have a greater arthropod diversity and stronger density-dependent interactions, a greater limitation of refuges from competitors or predators may have determined the higher colonisation of the rolled leaves in this habitat. Our results demonstrate that local environment context is an important factor that affects the colonisation of arthropods in leaf shelters.

Introduction

Several invertebrates build refuges for themselves through rolling, folding, or tying leaves together with silk, creating a better microclimate, protection from natural enemies, and/or improving the quality of food resources (Fukui 2001, Danks 2002, Lill & Marquis 2007, Cornelissen *et al.* 2016, Novais *et al.* 2020a, Pereira *et al.* 2021). After abandonment, these structures might persist on plants and provide microhabitats for other arthropods, thus influencing species diversity through a facilitative interaction process (Henriques *et al.* 2019, Lill & Marquis 2007, Martinsen *et al.* 2000, Novais *et al.* 2017). As such, invertebrates that build leaf shelters are acting as physical ecosystem engineers, organisms that create or modify habitats which, in turn, affect directly or indirectly the availability of resources for other species (Jones *et al.* 2010).

A large number of studies have demonstrated the role of arthropods (e.g., caterpillars, gall-inducers, mites and wood-boring beetles) acting as ecosystem engineers (Cornelissen *et al.* 2016, Novais *et al.* 2017, 2018, 2020a, 2021, Vieira & Romero 2013, Wetzel *et al.* 2016). However, few studies have shown when and where the facilitation by them will have large or small impacts on associated arthropod communities (but see Novais *et al.* 2018, Vieira & Romero 2013). These physical engineers will have a greater positive effect on the structure of arthropod communities when they increase limited resources that enable the establishment of species that otherwise would be unable to persist in the environment (Crain & Bertness 2006). These limiting resources are strongly associated with community-structuring processes (e.g., predation, competition and abiotic stress) which may differ among environments or habitats and, therefore, the positive impact of facilitators on the community structure depends on the capacities of the facilitators for alleviating these driving factors (Bruno *et al.* 2003; Crain & Bertness 2006).

© The Author(s), 2022. Published by Cambridge University Press

CAMBRIDGE UNIVERSITY PRESS

In stressful environments (e.g., deserts), where the harsh conditions often limit the ability for organisms to inhabit them, physical engineers are likely to have a greater positive impact on the community structure by promoting microclimatic refuges (Crain & Bertness 2006, Romero *et al.* 2015). On the other hand, in benign environments such as tropical rainforests, where density-dependent interactions (competition and predation) are major forces structuring natural communities, engineers who create new habitats that alleviate competition and predation pressures, or change the availability of limiting competitive resources, are expected to have major community impacts (Crain & Bertness 2006, Romero *et al.* 2015). These hypotheses were supported by a global scale meta-analysis that compared the magnitude of the facilitation by animals (including insects) among geographic regions (Romero *et al.* 2015). This study reported a stronger facilitation effect in deserts compared to other ecosystems (i.e., forests, grasslands and savannas) and at the tropics compared with temperate biomes at higher latitudes. In this sense, as variations in the physical structure within an ecosystem, especially those resulting from anthropogenic activities, significantly affect arthropod diversity and interactions (Grass *et al.* 2018, Floren & Linsenmair 2001, Tylianakis *et al.* 2007), it is also expected that the magnitude of the facilitation by shelter-building engineers varies depending on the local environmental context.

Alterations of tropical rainforests are mainly determined by land use change such as deforestation, agricultural and urban expansion (Gatti *et al.* 2015, Parrotta *et al.* 2002, Urquiza-Haas *et al.* 2007, Sales *et al.* 2020). In southeast Mexico, the region of Los Tuxtlas represents the northernmost limit of tropical rainforests in the Americas which has suffered extensive habitat loss over the last decades (Dirzo & Garcia 1992, Von Thaden *et al.* 2018). Most remaining old-growth forests of Los Tuxtlas are isolated fragments lying within a pasture matrix (Dirzo & Garcia 1992, Guevara *et al.* 2004). Overall, forest structure in fragments is greatly affected by altered abiotic conditions at the edges, including higher temperature levels and greater light incidence compared to the interior, which allow an increased diversity and abundance of saplings, herbs and shrubs in the understory of forest edges (Harper *et al.* 2005). These edge characteristics, in turn, generally result in more diverse and/or abundant vegetation-dwelling arthropod communities when compared to those in the nearby anthropogenic matrices and forest interior (De Araújo and Espírito-Santo Filho 2012, Barbosa *et al.* 2005, De Carvalho Guimarães *et al.* 2014, Jokimäki *et al.* 1998). Another important component of the Los Tuxtlas landscape is the presence of living fences that delimit areas used by cattle, where few tree species are planted very close together and connect some forest fragments (Guevara *et al.* 2004). Despite the simple structure, these living fences generate particular environmental conditions that allow some vertebrate (e.g., bats and birds) and invertebrate (e.g., dung beetles) species to move through them among forest fragments (Díaz *et al.* 2010, Estrada *et al.* 2000, Estrada & Coates-Estrada 2001).

The goal of our study was to evaluate the influence of local environmental context on the colonisation of leaf shelters by arthropod communities. We conducted an experimental study in a Mexican evergreen tropical rainforest comparing the species richness and abundance of arthropods colonising artificially rolled leaves in habitats differing in understory heterogeneity (i.e., forest edge > old-growth forests > living fences). We also verified the consistency of our results evaluating the response of different arthropod guilds (i.e., detritivores, omnivores, predators and herbivores) among these habitats. We hypothesised that habitats with increased habitat heterogeneity favour an increase in arthropod diversity and density-dependent interactions (competition and predation), resulting in a greater occupation of new shelters. We predict that species richness and abundance of arthropods colonising rolled leaves will be greater in forest edges, followed by old-growth forests, and smaller in living fences.

Methods

Study area

This study was carried out in the Los Tuxtlas Biosphere Reserve (LTBR; 18°05′–18°43′N, 94°35′–95°25′W), inside to the Los Tuxtlas Biological Station-UNAM (LTBS) located in southeastern Veracruz, Mexico, which range from 150 to 750 m a.s.l. The vegetation within the reserve consists primarily of evergreen tropical rainforest with a mean annual temperature of 26°C, and a mean annual rainfall of 4,700 mm, with a relatively dry season from March to May (Gutiérrez-García & Ricker 2011).

Sampling design

During June 2019, we randomly selected 20 plants of non-specific species at least 20 m apart from each other in a transect (up to 500 m) in the understory of 3 distinct habitats: living fences (18° 35'21.5"N, 95°04'20.9"W), forest edge (18°35'05.4"N, 95° 04'12.2"W) and old-growth forests (18°35'04.4"N, 95°04'34.6"W). In the study area, living fences are generally made with *Bursera simaruba* (Sapindales: Burseraceae), *Erythrina folkersii* (Fabales: Fabaceae), or *Gliricidia sepium* (Fabales: Fabaceae) trees planted very close together, with a width of one to a few metres depending on the tree canopies (Díaz *et al.* 2010). Due to the great diversity of vascular plants in the tropical forest studied (2548 species; Villaseñor *et al.* 2018) and the natural variation in the occurrence of these species locally, we decided not to use specific plant species in our experiment. Thus, for each habitat, following our experimental design, the first plant individual that met our selection criteria (see below) was selected regardless of the species. In addition, although plant species identity can have a major effect on colonisation of artificial shelters (Wang *et al.* 2014), not controlling by plant species is advantageous when evaluating this colonisation for the entire plant community on a habitat scale. We only used plant species that did not bear any apparent type of indirect defence (e.g., domatia, extra-floral nectaries), flowers or fruits. For each plant, we selected five young, expanded leaves without apparent damage, ranging from 0.5 to 1.5 m height (N total = 100 leaves per habitat). Prior to the experiment, the leaves were gently cleaned with a soft brush to exclude all arthropods. The leaves were manually completely rolled from the adaxial to the abaxial surface in a manner similar to some engineering by a caterpillar (Figure 1). The leaves were kept rolled with stainless hairpins and stayed in the field during five consecutive days to allow colonisation and establishment of arthropod communities. Artificially rolled leaves from each plant were placed in separate Ziploc® bags (26.8 cm × 27.3 cm) and transported to the laboratory, where they were frozen in order to incapacitate any inhabitants and then carefully unrolled for arthropod collection. Leaf width did not differ among habitats ($F = 2.45$, $P = 0.1$). All sampled arthropods were transferred to vials with 70% ethanol for further identification at order level and according to their feeding guilds. Individuals belonging to the orders Coleoptera and Hemiptera were identified at family level and classified in a given guild depending on the predominant feeding habit of their respective family. Species richness (number of morphospecies) and abundance (number of individuals)

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press



Figure 1. Artificially rolled leaves simulating the engineering by arthropods. Photo credit: Karla Rodríguez-Hernández.

per plant for all arthropods and for each guild were determined. The sampled arthropods were deposited in the entomological collection of the Laboratory of Evolutionary Ecology and Conservation of Tropical Forests of the National Autonomous University of Mexico.

Data analysis

Generalised linear models were used to test whether richness and abundance of arthropods differed among habitats. Species richness and abundance of all arthropods and per guild were used as response variables, while habitat type (living fences, forest edge and old-growth forests) and average leaf width were used as explanatory variables. We applied a Poisson distribution of errors to the models; overdispersion was adjusted with a negative binomial distribution of errors, while underdispersion was adjusted with a 'Quasi-Poisson' when needed. The minimum adequate model was obtained by extracting non-significant terms ($P > 0.05$) from the full model (Crawley 2013). The package *emmeans* using Tukey's method was used for posteriori comparisons (Lenth *et al.* 2021). The explained variance (R^2) of significant regressions was calculated using the following formula: Explained deviance = deviance H1/deviance H0. All statistical analyses were conducted with the R software (R Core Team 2020).

Results

In total, 450 arthropods from 125 morphospecies were sampled inside the artificially rolled leaves (Table 1; Supplementary material 1). On average, 7.5 arthropods were found per plant, with 7 arthropods per plant being the most frequent number (8 times), followed by 2 and 3 arthropods (7 times each; Supplementary material 2). Springtails (Collembola) were the most common arthropods found in our studied system (46.2%), followed by Araneae (14%), Blattodea (10.2%), Psocoptera (9.3%), Hymenoptera (5.1%), Thysanoptera (4.2%), Orthoptera (3.6%), Acari (2.2%), Coleoptera (2.2%) and Hemiptera (1.8%). Other orders such as Lepidoptera, Geophilomorpha, Diptera and Thysanura represented less than 1% of all sampled arthropods each. The greater number of morphospecies and individuals were collected at the forest edge habitat (58 morphospecies and 210 individuals), followed by forest interior (53 and 142), and living fences (45 and 98; Table 1). The taxa Collembola, Araneae, Blattodea and Psocoptera together represented 80% of all arthropods sampled and had a greater number of individuals in the rolled leaves at the forest edge, followed by forest interior, and were less abundant in living fences (Table 1).

Arthropod species richness did not differ between forest edge and interior habitats, which showed approximately 1.5 times higher species richness compared with the living fence habitat (Table 2; Figure 2A). Detritivores and omnivores showed greater species richness in the forest interior compared to living fences (1.77 and 2.33 times greater, respectively), and there was no difference between edge and interior habitats, neither between edge and living fence habitats (Table 2; Figure 2A). Predators and herbivores did not differ in species richness among habitats ($P > 0.05$; Table 2; Figure 2A). Predator species richness was positively affected by average leaf width ($P = 0.007$; Table 2; Figure 3A). Arthropod abundance was 2.16 times greater in forest edge habitat compared to living fence habitat, and there was no difference between edge and interior habitats, neither between interior and living fence habitats (Table 2; Figure 2B). Detritivores and predators showed the same trend (2.6 and 2.21 times greater, respectively), while the abundance of omnivores did not differ between forest edge and interior habitats, which showed approximately 2.9 times higher abundance compared with the living fence habitat (Table 2; Figure 2B). Herbivores did not differ in abundance among habitats ($P > 0.05$; Table 2; Figure 2B). Predator abundance was positively affected by average leaf width (Table 2; Figure 3B).

Discussion

Our results demonstrated that local environment context is an important factor that affects the colonisation of arthropods in leaf shelters. In general, the present data support the hypothesis that the colonisation of shelters by arthropod communities in tropical rainforests is stronger in more heterogeneous habitats. The number of individuals of the most representative arthropod taxa (i.e., Collembola, Araneae, Blattodea and Psocoptera) colonising the artificially rolled leaves was greater at the forest edge; a trend that was also observed for average arthropod abundance, and for detritivore and predator guilds. In addition, fewer arthropod species and individuals colonised the artificially rolled leaves in the simplest habitat, the living fences, and this trend was also observed for most arthropod guilds (i.e., detritivores, omnivores and predators).

Although no direct measurements of the arthropod communities in the studied habitats have been carried out, negative effects of simplification of natural ecosystems by anthropogenic activities on arthropod diversity have been reported extensively in the literature (e.g., Beng *et al.* 2016, Floren & Linsenmair 2001, Lichtenberg *et al.* 2017, Novais *et al.* 2016, Schulze *et al.* 2004). A study

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press

Table 1. Richness (Rich.) and abundance (Abund.) of arthropod morphospecies sampled in artificially rolled leaves among habitats differing in vegetation structure in Los Tuxtlas tropical rainforest, Veracruz, Mexico. Guilds: F = Fungivores, D = Detritivores, H = Herbivores, Om = Omnivores, P = Predators, Un = Undetermined

			Living fences		Edge		Forest		Total		
Taxon			Rich.	Abund.	Rich.	Abund.	Rich.	Abund.	Rich.	Abund.	Guild
Arachnida	Acari		2	2	3	5	3	3	6	10	Un
	Araneae		12	13	23	31	13	19	40	63	P
Chilopoda	Geophilomorpha		–	–	–	–	1	1	1	1	P
Entognatha	Collembola		4	46	7	101	5	61	8	208	D
Insecta	Blattodea		3	4	3	27	6	15	8	46	D
	Coleoptera	Chrysomelidae	1	2	–	–	1	1	2	3	H
		Curculionidae	1	1	–	–	–	–	1	1	H
		Eucnemidae	1	1	–	–	1	1	2	2	Un
		Erotylidae	–	–	–	–	1	1	1	1	F
		Nitidulidae	–	–	–	–	1	1	1	1	Om
		Melolonthidae	1	1	–	–	–	–	1	1	H
		Staphylinidae	–	–	–	–	1	1	1	1	P
	Diptera	Drosophilidae	1	1	–	–	–	–	1	1	H
	Hemiptera	Aleyrodidae	–	–	1	1	–	–	1	1	H
		Cicadelidae	1	3	1	1	–	–	2	4	H
		Cixiidae	1	1	–	–	–	–	1	1	H
		Lygaeidae	1	1	–	–	1	1	2	2	H
	Hymenoptera	Formicidae	4	5	6	9	4	8	13	22	Om
	Hymenoptera	Pompilidae	1	1	–	–	–	–	1	1	P
	Lepidoptera		2	2	–	–	–	–	2	2	H
	Orthoptera	Gryllidae	1	4	3	3	7	9	11	16	Om
	Psocoptera		3	3	6	24	4	15	9	42	Om
	Thysanoptera		5	7	5	8	3	4	9	19	H
	Thysanura		–	–	–	–	1	1	1	1	Om
Total			45	98	58	210	53	142	125	450	

conducted in the same study area for dung and carrion beetles found that forest fragments and forest–pasture edges had the highest number of individuals and species compared to living fences (Díaz *et al.* 2010). For arboreal arthropods, the key factors driving this pattern have been associated with more harsh conditions, decreased food resources and suitable microhabitats caused by the reduction in canopy cover, plant abundance and diversity in altered habitats (Floren & Linsenmair 2001, Lichtenberg *et al.* 2017, Novais *et al.* 2016). Although harsh conditions have been suggested as a possible factor that could increase the magnitude of the ecosystem engineering by insects in seasonal tropical forests (Novais *et al.* 2018, Vieira & Romero 2013), the variations in abiotic conditions among habitats in the evergreen tropical rainforest studied are expected to be considerably smaller compared to those between seasons in seasonal forests. In the case studied here, we suggest that the reduced vegetation structure of living fences may have determined a general decrease in arthropod diversity, and consequently, decreasing the probability of a shelter being encountered by a wandering arthropod. In addition, a reduced arthropod diversity in living fences may had led to decreased competition/predation pressures, therefore reducing the importance of the artificially rolled leaves as shelter sites in this habitat.

An opposite mechanism must be determining the highest abundance of arthropods occupying the rolled leaves in the forest edge, which have the most heterogeneous understory vegetation compared with the other habitats. In a study conducted in the Amazon rainforest, Fowler *et al.* (1993) found significantly more individuals of flying insects at the forest edge than in the forest understory, and this pattern was consistent for the majority of insect orders throughout a year. Positive edge effects have also been reported for different arthropod groups belonging to different guilds, such as detritivores (Bogyó *et al.* 2015, De Smedt *et al.* 2016), herbivores (De Araújo & Espírito-Santo Filho 2012, Barbosa *et al.* 2005, De Carvalho Guimarães *et al.* 2014, Wirth *et al.* 2008) and predators (De Smedt *et al.* 2019). Previous studies have also demonstrated a greater predation pressure by both vertebrate and invertebrate predators in forest edges than in forest understory (Barbaro *et al.* 2012, Drozdová *et al.* 2013). Following these patterns, a study conducted by Richards & Coley (2007) in the lowland moist forest of Barro Colorado

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press

Table 2. Results of generalised linear models showing the differences in species richness and abundance of arthropods sampled in artificially rolled leaves among habitats differing in vegetation structure (living fences, forest edge and interior) in Los Tuxtlas tropical rainforest, Veracruz, Mexico. The average width of the leaves per plant was used as a covariate

Response variable		Explanatory variable	Errordistribution	Deviance	Df	*P*
All arthropods	Species richness	Habitats	Poisson	8.91	2	0.011*
		Covariate		0.67	1	0.414
Detritivores		Habitats	Quasi-Poisson	5.22	2	0.018*
		Covariate		1.2	1	0.173
Omnivores		Habitats	Poisson	6.71	2	0.035*
		Covariate		0.67	1	0.41
Predators		Habitats	Poisson	5.35	2	0.069
		Covariate		7.39	1	0.007*
Herbivores		Habitats	Poisson	3.24	2	0.198
		Covariate		3.13	1	0.08
All arthropods	Abundance	Habitats	Negative binomial	13.45	2	0.001*
		Covariate		0.04	1	0.838
Detritivores		Habitats	Negative binomial	9.79	2	0.007*
		Covariate		1.03	1	0.31
Omnivores		Habitats	Negative binomial	9.1	2	0.011*
		Covariate		0.002	1	0.963
Predators		Habitats	Poisson	6.65	2	0.036*
		Covariate		5.56	1	0.018*
Herbivores		Habitats	Negative binomial	5.8	2	0.055
		Covariate		2.6	1	0.11

*Significant differences.

Island in Panama demonstrated that the densities of understory plants, young leaves, arthropod herbivores and predators were significantly more abundant in forest gaps than in interior. These authors also evaluated the predation rates on artificial caterpillars and found a higher predation pressure in forest gaps. In our study, as forest edge was also expected to have a greater arthropod diversity, leaf shelters in this habitat should be quickly occupied by an arthropod. Furthermore, as stronger density-dependent interactions are also expected at forest edges compared to the other habitats, a greater limitation of refuges from competitors or predators may have determined the higher colonisation of the artificially rolled leaves in this habitat.

Other studies have reported differences in the magnitude of the facilitation by shelter-building insects within forest ecosystems in time and space (Novais *et al.* 2018, Novais *et al.* 2020b, Vieira & Romero 2013). Regarding temporal variations, Vieira & Romero (2013) found that vegetation-dwelling arthropods colonising rolled leaves were more abundant in the dry season than in the rainy season in the seasonal Brazilian Atlantic Rainforest. These authors suggested that adverse climatic conditions may have led to an increase in the magnitude of the engineering effect in the dry season. Similarly, Novais *et al.* (2018) found a greater arthropod colonisation in abandoned branch cavities left by wood-boring beetles during the dry season in the understory of a Mexican topical dry forest compared to branches exposed in the rainy season. These authors suggested that this pattern was also influenced by a dramatic reduction in the availability of other shelters in the arboreal vegetation, since most trees shed their leaves as a drought-resistant mechanism in this ecosystem. Unlike our study, which was carried out in an evergreen tropical rainforest and showed a lower colonisation of shelters in the structurally simpler habitat and with harsher conditions (i.e., living fences), the great fluctuation of abiotic factors in seasonal ecosystems (e.g., tropical dry forests) seems to represent a major mechanism in determining variations in the magnitude of facilitation effect by shelter-building engineers. Regarding spatial variations, differences in the magnitude of the facilitation by shelter-building insects have been reported between forest strata. For example, as ant nesting sites represent a limited resource in the arboreal stratum, the importance of the facilitation by wood-boring beetles that create ant nesting cavities is increased in this stratum compared to the ground stratum (Novais *et al.* 2018, 2020b).

The guild of predator arthropods, represented almost exclusively by spiders, was the only arthropod guild that responded significantly to the average leaf width, increasing in species richness and abundance in plants with wider leaves. In general, more complex habitats tend to have higher species richness and abundance of spiders (Diehl *et al.* 2013, Jiménez-Valverde & Lobo 2007, Langellotto & Denno 2004), although the response may differ depending on the spatial scale and foraging strategies (Gonçalves-Souza *et al.* 2011, Halaj *et al.* 2000). At a small spatial scale, density and species number of hunting spiders (those species lacking webs such as jumping spiders, ambushers and runners) decrease with the simplification of branch structure (Halaj *et al.* 2000). A similar result was found for hunting spiders associated with bromeliads, which were more abundant in bromeliad species

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press

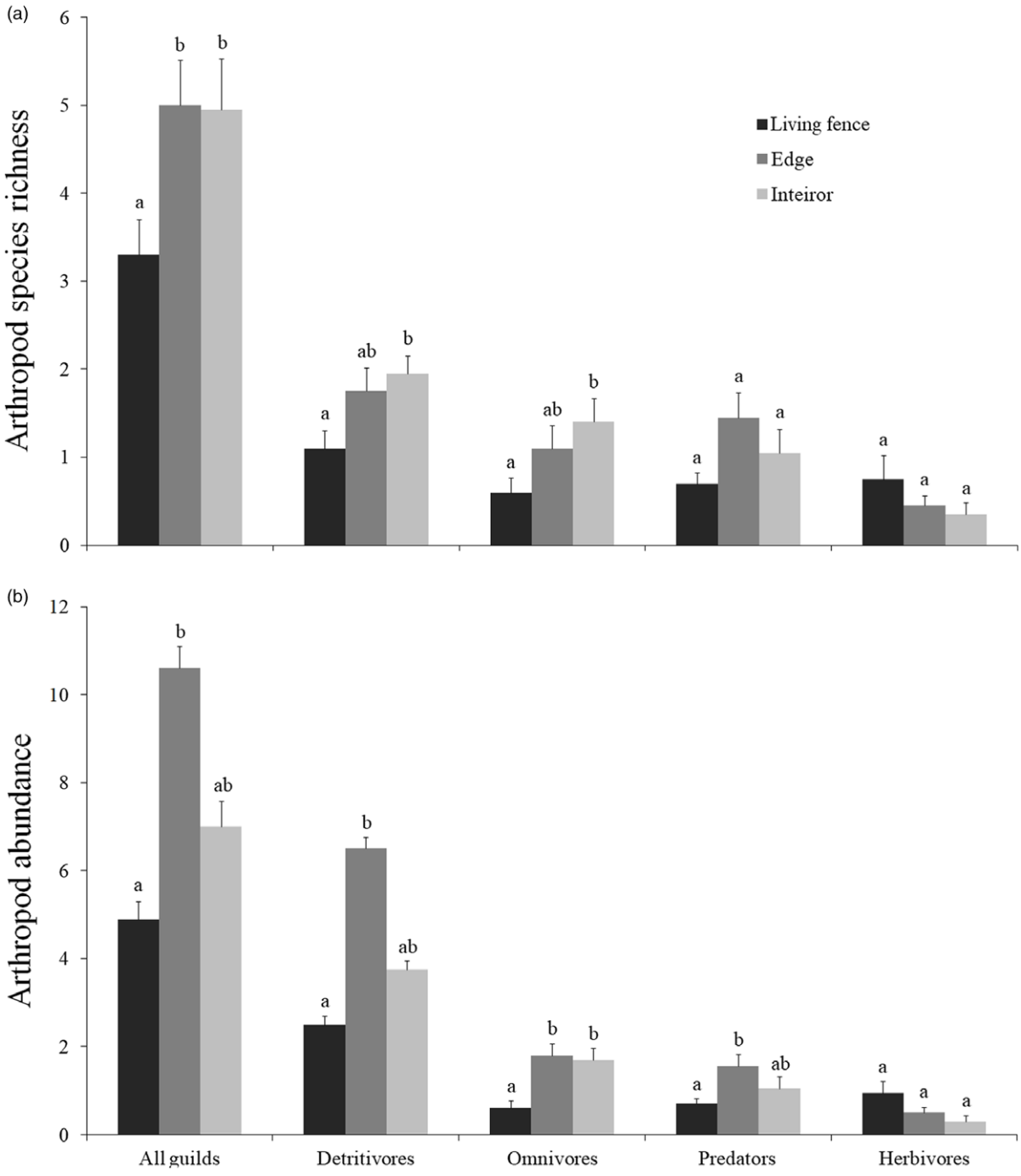


Figure 2. Species richness (a) and abundance of arthropods (b) (mean ± SE) per plant for different guilds sampled in artificially rolled leaves between habitats differing in vegetation structure in Los Tuxtlas tropical rainforest, Veracruz, Mexico. Means followed by the same letters do not differ statistically from each other ($P > 0.05$).

with more leaves (Gonçalves-Souza *et al.* 2011). In our study, spiders may prefer plants with wider leaf shelters because they can favour a more stable microclimate and increased space availability for protection, molting or egg-laying. In addition, as many spiders also curl leaves to build shelters, they may save time and energy occupying preexisting structures (Fukui 2001; Pereira *et al.* 2020).

Conclusion

This experimental study demonstrated that local environmental context is an important factor affecting the colonisation of leaf shelters by arthropod communities. Our results showed that the colonisation of the shelters was stronger at the forest edge, likely because the new habitats provided through the artificially rolled leaves may have helped to minimise the greater potential of competition and predation pressures on resident arthropod species. Our study also showed a lower colonisation of the shelters in the structurally simplest habitat with harsher conditions, differing from those studies that found a greater magnitude of the facilitation by shelter-building insects in the dry seasons of seasonal forests, when the arboreal stratum is structurally simpler and conditions are very harsh. This difference suggests a greater

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press

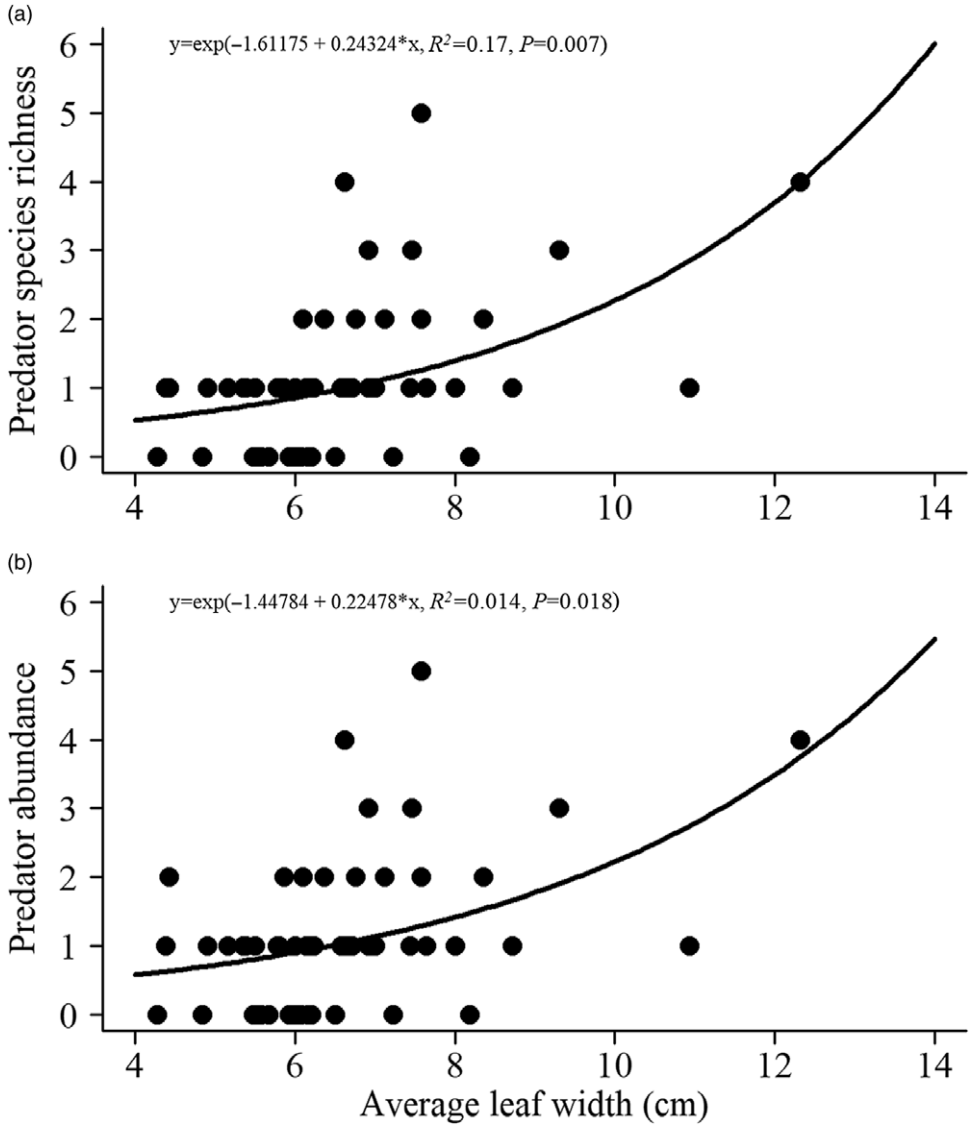


Figure 3. Relationship between average leaf width and species richness (a) and abundance (b) of predatory arthropods per plant sampled colonising artificially rolled leaves in Los Tuxtlas tropical rainforest, Veracruz, Mexico.

importance of environmental conditions in determining the magnitude of the facilitation effect in seasonal forest ecosystems than in evergreen rainforests, where density-dependent interactions appear to play a more important role.

Supplementary material. To view supplementary material for this article, please visit https://doi.org/10.1017/S0266467421000523

Acknowledgements. We are grateful to Rosamond Ione Coates, head of the Biological Station Los Tuxtlas-UNAM for her support and provision of facilities to conduct this research. SN thanks CAPES for grant support while GWF thanks CNPq and Fapemig. Noemí Matías Ferrer (INECOL) helped with reviews of previous drafts.

This study was supported by grants from Universidad Nacional Autónoma de México (MQ, PAPIIT # IN212714-3); CONACyT (MQ, # 2009-131008 and # 155016); CONACYT-UNAM-UAGro to LANASE (MQ, 2015-LN250996, 2016-LN271449, 2017-LN280505); and Programa Ibero Americano de Ciencia y Tecnología para el Desarrollo RED CYTED SEPODI (MQ, 417RT0527).

Conflicts of interest. The authors declare that they have no conflict of interest.

Ethical statement. Not applicable.

References

Barbaro L, Brockerhoff EG, Giffard B and van Halder I (2012) Edge and area effects on avian assemblages and insectivory in fragmented native forests. *Landscape Ecology* **27**, 1451–1463.

Barbosa VS, Leal IR, Iannuzzi L and Almeida-Cortez J (2005) Distribution pattern of herbivorous insects in a remnant of Brazilian Atlantic Forest. *Neotropical Entomology* **34**, 701–711.

Beng KC, Tomlinson KW, Shen XH, Surget-Groba Y, Hughes AC, Corlett RT and Slik JF (2016) The utility of DNA metabarcoding for studying the response of arthropod diversity and composition to land-use change in the tropics. *Scientific Reports* **6**, 24965.

Bogyó D, Magura T, Nagy DD and Tóthmérész B (2015) Distribution of millipedes (Myriapoda, Diplopoda) along a forest interior – forest edge – grassland habitat complex. *ZooKeys* **510**, 181–195.

Bruno JF, Stachowicz JJ and Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* **18**, 119–125.

Cornelissen T, Cintra F and Santos JC (2016) Shelter-building insects and their role as ecosystem engineers. *Neotropical Entomology* **45**, 1–12.

Crain CM and Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. *BioScience* **56**, 211–218.

Crawley MJ (2013) *The R Book*. Chichester: John Wiley and Sons.

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press

Danks HV (2002) Modification of adverse conditions by insects. *Oikos* **99**, 10–24.

De Araújo WS and do Espírito-Santo Filho K (2012) Edge effect benefits galling insects in the Brazilian Amazon. *Biodiversity and Conservation* **21**, 2991–2997.

De Carvalho Guimarães CD, Viana JPR and Cornelissen T (2014) A meta-analysis of the effects of fragmentation on herbivorous insects. *Environmental Entomology* **43**, 537–545.

De Smedt P, Baeten L, Proesmans W, Van de Poel S, Van Keer J, Giffard B, Martin L, Vanhulle R, Brunet J, Cousins SA and Decocq G (2019) Strength of forest edge effects on litter-dwelling macro-arthropods across Europe is influenced by forest age and edge properties. *Diversity and Distributions* **25**, 963–974.

De Smedt P, Wuyts K, Baeten L, De Schrijver A, Proesmans W, De Frenne P, Ampoorter E, Remy E, Gijbels M, Hermy M and Bonte D (2016) Complementary distribution patterns of arthropod detritivores (woodlice and millipedes) along forest edge-to-interior gradients. *Insect Conservation and Diversity* **9**, 456–469.

Díaz A, Galante E and Favila ME (2010) The effect of the landscape matrix on the distribution of dung and carrion beetles in a fragmented tropical rain forest. *Journal of Insect Science* **10**, 81.

Diehl E, Mader VL, Wolters V and Birkhofer K (2013) Management intensity and vegetation complexity affect web-building spiders and their prey. *Oecologia* **173**, 579–589.

Dirzo R and Garcia MC (1992) Rates of deforestation in Los Tuxtlas, a neotropical area in southeast Mexico. *Conservation Biology* **6**, 84–90.

Drozdová M, Sipos J and Drozd P (2013) Key factors affecting the predation risk on insects on leaves in temperate floodplain forest. *European Journal of Entomology* **110**, 469–476.

Estrada A, Cammarano P and Coates-Estrada R (2000) Bird species richness in vegetation fences and in strips of residual rain forest vegetation at Los Tuxtlas, Mexico. *Biodiversity and Conservation* **9**, 1399–1416.

Estrada A and Coates-Estrada R (2001) Bat species richness in live fences and in corridors of residual rain forest vegetation at Los Tuxtlas, Mexico. *Ecography* **24**, 94–102.

Floren A and Linsenmair KE (2001) The influence of anthropogenic disturbances on the structure of arboreal arthropod communities. *Plant Ecology* **153**, 153–167.

Fowler HG, Silva CA and Venticinque E (1993) Size, taxonomic and biomass distributions of flying insects in Central Amazonia: Forest edge versus understory. *Revista de Biología Tropical* **41**, 755–760.

Fukui A (2001) Indirect interactions mediated by leaf shelters in animal–plant communities. *Population Ecology* **43**, 31–40.

Gatti RC, Castaldi S, Lindsell JA, Coomes DA, Marchetti M, Maesano M, Di Paola A, Paparella F and Valentini R (2015) The impact of selective logging and clearcutting on forest structure, tree diversity and above-ground biomass of African tropical forests. *Ecological Research* **30**, 119–132.

Gonçalves-Souza T, Almeida-Neto M and Romero GQ (2011) Bromeliad architectural complexity and vertical distribution predict spider abundance and richness. *Austral Ecology* **36**, 476–484.

Grass I, Jauker B, Steffan-Dewenter I, Tscharntke T and Jauker F (2018) Past and potential future effects of habitat fragmentation on structure and stability of plant–pollinator and host–parasitoid networks. *Nature Ecology and Evolution* **2**, 1408–1417.

Guevara S, Laborde J and Sánchez-Ríos G (2004) *La deforestación*. In Guevara S, Laborde J and Sánchez-Ríos G (eds.), *Los Tuxtlas. El paisaje de la sierra*. Xalapa: Instituto de Ecología A.C. and European Union. pp. 85–108.

Gutiérrez-García G and Ricker M (2011) Climate and climate change in the region of Los Tuxtlas (Veracruz, Mexico): a statistical analysis. *Atmósfera* **24**, 347–373.

Halaj J, Ross DW and Moldenke AR (2000) Importance of habitat structure to the arthropod food-web in Douglas-fir canopies *Oikos* **90**, 139–152.

Harper KA, Macdonald SE, Burton PJ, Chen J, Brosofske KD, Saunders SC, Euskirchen ES, Roberts DA, Jaiteh MS and Esseen PA (2005) Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* **19**, 768–782.

Henriques NR, Cintra F, Pereira CC and Cornelissen T (2019) Indirect effects of ecosystem engineering by insects in a tropical liana. *Arthropod-Plant Interactions* **13**, 499–504.

Jiménez-Valverde A and Lobo JM (2007) Determinants of local spider (Araneidae and Thomisidae) species richness on a regional scale: climate and altitude vs. habitat structure. *Ecological Entomology* **32**, 113–122.

Jokimäki J, Huhta E, Itämies J and Rahko P (1998) Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Canadian Journal of Forest Research* **28**, 1068–1072.

Jones CG, Gutiérrez JL, Byers JE, Crooks JA, Lambrinos JG and Talley TS (2010) A framework for understanding physical ecosystem engineering by organisms *Oikos* **119**, 1862–1869.

Langellotto GA and Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. *Oecologia* **139**, 1–10.

Lichtenberg EM, Kennedy CM, Kremen C, Batary P, Berendse F, Bommarco R, Bosque-Pérez NA, Carvalheiro LG, Snyder WE, Williams NM and Winfree R (2017) A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology* **23**, 4946–4957.

Lill JT and Marquis RJ (2007) *Microhabitat manipulation: ecosystem engineering by shelter-building insects*. In Cuddington KMD, Byers JE, Hastings A, Wilson WG (eds.), *Ecosystem Engineers: Concepts, Theory, and Applications in Ecology*. San Diego: Elsevier Press. pp. 107–138.

Lenth RV, Buerkner P, Herve M, Love J, Riebl H and Singmann H (2021) Package 'emmeans'. https://cran.r-project.org/web/packages/emmeans/emmeans.pdf

Martinsen GD, Floate KD, Waltz AM, Wimp GM and Whitham TG (2000) Positive interactions between leafrollers and other arthropods enhance biodiversity on hybrid cottonwoods. *Oecologia* **123**, 82–89.

Novais S, Aguirre-Jaimes A, Quesada M and Hernández-Ortiz V (2020a) Ecosystem engineering by leaf-rolling mites enhances arthropod diversity. *The Science of Nature* **107**, 45.

Novais S, Calderón-Cortés N, Sánchez-Montoya G and Quesada M (2018) Arthropod facilitation by wood-boring beetles: Spatio-temporal distribution mediated by a twig-girdler ecosystem engineer. *Journal of Insect Science* **18**, 14.

Novais S, Cristóbal-Perez EJ, Aguirre-Jaimes A and Quesada M (2021) Arthropod facilitation mediated by abandoned dead domatia. *Ecosphere* **12**, e03323.

Novais S, DaRocha WD, Calderón-Cortés N and Quesada M (2017) Wood-boring beetles promote ant nest cavities: extended effects of a twig-girdler ecosystem engineer. *Basic and Applied Ecology* **24**, 53–59.

Novais S, Hernández-Ortiz V, Rodríguez-Hernández K, Quesada M, Valenzuela J, Fernandes GW and Aguirre-Jaimes A (2020b) Ants nesting in dry fallen petioles of *Cecropia obtusifolia* Bertol (Urticaceae): vertical stratification and nest site limitation. *Insectes Sociaux* **67**, 273–279.

Novais S, Macedo-Reis LE, DaRocha WD and Neves FS (2016) Effects of habitat management on different feeding guilds of herbivorous insects in cacao agroforestry systems. *Revista de Biologia Tropical* **64**, 763–777.

Parrotta JA, Francis JK and Knowles OH (2002) Harvesting intensity affects forest structure and composition in an upland Amazonian forest. *Forest Ecology and Management* **169**, 243–255.

Pereira CC, Sperandei VDF, Henriques, NR, Silva ÁAN, Fernandes GW and Cornelissen T (2021). Gallers as leaf rollers: Ecosystem engineering in a tropical system and its effects on arthropod biodiversity. *Ecological Entomology* **46**, 470–481.

R Core Team (2020) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.Rproject.org/

Richards LA and Coley PD (2007) Seasonal and habitat differences affect the impact of food and predation on herbivores: a comparison between gaps and understory of a tropical forest. *Oikos* **116**, 31–40.

Romero GQ, Gonçalves-Souza T, Vieira C and Koricheva J (2015) Ecosystem engineering effects on species diversity across ecosystems: a meta-analysis. *Biological Reviews* **90**, 877–890.

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press

Sales LP, Galetti M and Pires MM (2020) Climate and land-use change will lead to a faunal "savannization" on tropical rainforests. *Global Change Biology* **26**, 7036–7044.

Schulze CH, Waltert M, Kessler PJA, Pitopang R, Veddeler D, Mühlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I and Tscharntke T (2004) Biodiversity indicator groups of tropical land-use systems: Comparing plants, birds, and insects. *Ecological Applications* **14**, 1321–1333.

Tylianakis JM, Tscharntke T and Lewis OT (2007) Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* **445**, 202–205.

Urquiza-Haas T, Dolman PM and Peres CA (2007) Regional scale variation in forest structure and biomass in the Yucatan Peninsula, Mexico: effects of forest disturbance. *Forest Ecology and Management* **247**, 80–90.

Vieira C and Romero GQ (2013) Ecosystem engineers on plants: Indirect facilitation of arthropod communities by leaf-rollers at different scales. *Ecology* **94** 1510–1518.

Villaseñor J L, Ortiz E and Campos-Villanueva A (2018) High richness of vascular plants in the Tropical Los Tuxtlas region, Mexico. *Tropical Conservation Science* **11**, 1–12.

Von Thaden JJ, Laborde J, Guevara S and Venegas-Barrera CS (2018) Forest cover change in the Los Tuxtlas Biosphere Reserve and its future: the contribution of the 1998 protected natural area decree. *Land Use Policy* **72**, 443–450.

Wang HG, Marquis RJ and Baer C (2012) Both host plant and ecosystem engineer identity influence leaf-tie impacts on the arthropod community of *Quercus*. *Ecology* **93** 2186–2197.

Wetzel WC, Screen RM, Li I, McKenzie J, Phillips KA, Cruz M, Zhang W, Greene A, Lee E, Singh N and Tran C (2016) Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. *Ecology* **97**, 427–438.

Wirth R, Meyer ST, Leal IR and Tabarelli M (2008) *Plant herbivore interactions at the forest edge*. In Lüttge U, Beyschlag W and Murata J (eds.), *Progress in Botany*. Berlin, Heidelberg: Springer. pp. 423–448.

https://doi.org/10.1017/S0266467421000523 Published online by Cambridge University Press