



Animal Ecosystem Engineering Using Plants

Background

Interactions between organisms determine the distribution and abundance of species in a community

Direct trophic interactions have been extensively studied

Only fairly recently has the effects of environmental modifications on community interactions been explored

Organisms as ecosystem engineers

Clive G. Jones, John H. Lawton and Moshe Shachak

OIKOS 69: 373-386. Copenhagen 1994

Table 1. Examples of organisms acting as ecosystem engineers. Classification according to Fig. 1. Additional examples are discussed in the text.

Organism	Habitat	Activity	Impact	Refs.
Case 2 (allogenic)				
American alligators, <i>Alligator mississippiensis</i>	Everglades National Park	create wallows	retain water in droughts; provide refuges for fish, fish-eating birds, etc.	Finlayson & Moser (1991)
Rabbit, <i>Oryctolagus cuniculus</i> , badgers, <i>Meles meles</i>	Europe	dig extensive burrows (rabbit warrens, badger setts)	burrows occupied by other species, e.g. fox, <i>Vulpes vulpes</i> , and by many invertebrates	Southern (1964); Neal & Roper (1991)
Case 3 (autogenic)				
Marine phytoplankton	Gulf of Maine	blooms of phytoplankton particles scatter and absorb light in upper layers of water column	enhance warming of surface waters that may initiate development of thermocline	Townsend et al. (1992)
Microalgae in sea ice	Antarctica	scatter and absorb light within ice and underlying seawater; reduce strength of ice	enhance melting and break up of ice	Boydinsky (1986); Arigo et al. (1991)
Freshwater phytoplankton	Lake St. George, Ontario	intercept light in upper water column; small algal spp. more effective than large spp.	light interception leads to shallower mixing depth, lower metalimnetic temperatures and lower heat content of water column	Mazumder et al. (1990)
Cyanobacteria and other nonvascular plants	desert and semi-desert soils	exude mucilaginous organic compounds	glue the organisms, organic matter and soil particles together to form a microphytic crust; change infiltration, percolation, retention and evaporation of water; reduce soil erosion; affect seedling emergence	West (1990)
Bog moss, <i>Sphagnum</i> spp.	Northern and western Britain	build 'blanket' and 'raised' bogs via accumulated peat	major changes in hydrology, pH, and topography	Tansley (1949)
Submerged macrophytes	freshwater lakes, ponds and rivers	grow to create weed beds	attenuate light; steepen vertical temperature gradient; retard flow; enhance sedimentation; oxygenate rhizosphere	Carpenter & Lodge (1986)
Forest trees (broad-leaved and conifers)	Hubbard Brook Experimental Forest, New Hampshire	shed branches and trunks into streams	create debris dams; alter morphology and stability of stream channels, storage and transport of dissolved organic matter and sediments; different tree species may create dams which differ in persistence	Likess & Bilby (1982); Hedin et al. (1988)
Higher plants	ubiquitous	dead leaves etc. accumulate as litter	alter microenvironment of soil; change surface structure, affecting drainage, and transfer of heat and gases; act as physical barrier for seeds and seedlings; numerous impacts on structure and composition of plant communities	Facelli & Pickett (1991)
Terrestrial plants in 29 families, with >1,500 species	ubiquitous	grow structures (modified leaves, leaf axils etc.) that impound water	create small aquatic habitats, supporting a highly specialised insect fauna	Fish (1983)
Case 4 (allogenic)				
Marine invertebrates (protozoa and representatives of many invertebrate phyla)	ubiquitous	biodeposition, bioturbation, porewater circulation, and faecal pellet production	change physical, chemical and biological properties of sediments; change direction and magnitude of nutrient fluxes; increase oxygenation of sediments	Reichelt (1991)
Marine burrowing macrofauna	ubiquitous	burrow into and redistribute sediments; bioturbation, burrow ventilation	create dynamic sediment mosaics; actively transport solutes into burrows; increase oxygenation of sediments; stimulate microflora; increase decomposition rates	Anderson & Kristensen (1991); de Wilde (1991); Meadows & Meadows (1991b) (cont.)

OIKOS 69:3 (1994)

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Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Marine zooplankton	ubiquitous	filter living, dead organic and inorganic (e.g. clay) particles, and concentrate into faecal pellets	sinking faecal pellets important in vertical transport and exchange of elements and organic compounds in oceans	Dunbar & Berger (1981); Wallace et al. (1981); Fowler & Knauer (1986)
Fiddler crab, <i>Uca pugnax</i>	New England salt marsh	dig burrows	increase soil drainage and oxidation-reduction potential; increase decomposition rates; increase primary production at intermediate tidal heights	Bertness (1985)
European periwinkle, <i>Littorina littorea</i>	New England rocky beach	bulldoze sediments from hard substrates	prevent sediment accumulation and hence growth and establishment of algal canopy; algae are case 3 engineers and further increase sedimentation rates; faunal composition markedly different with and without snails	Bertness (1984a)
Snails, <i>Euchondrus</i> spp.	Negev desert	eat endolithic lichens and the rock they grow in	increase rate of nitrogen cycling, soil formation and rock erosion	Shachak et al. (1987); Jones & Shachak (1990)
Bagworm caterpillars, <i>Ptenostolosa</i> sp.	Golden Gate Highlands, South Africa	eat endolithic lichens and construct larval shelters ('bags') from quartz crystals	small increase in erosion rate, nutrient cycling and soil formation	Wessels & Wessels (1991)
Mound-building termites, Isoptera	widespread in tropics and subtropics	mound and subterranean gallery construction; redistribution of soil particles	change mineral and organic composition of soils; alter hydrology and drainage	Wood & Sands (1978); Lal (1991)
Ants, Formicidae	ubiquitous	nest and subterranean gallery construction; redistribution of soil particles	change local structure and composition of soils; alter 'above nest' vegetation; produce microsite enrichment	Elmes (1991)
Earthworms, Lumbricidae, Megascolocidae	ubiquitous	burrowing, mixing and casting	change mineral and organic composition of soils; affect nutrient cycling; alter hydrology and drainage; affect plant population dynamics and community composition	Lal (1991); Thompson et al. (1993)
Bhind mole rats, <i>Sipolar ehenbergi</i>	Israel	digging and tunnelling	move large quantities of soil; increase aeration; create distinctive ecosystem	Heth (1991)
Mole rats, Bathyergidae (several genera)	South African lowland fynbos	digging and tunnelling	create impressive, cratered landscapes, with effects on soil formation, plant productivity and species composition	Richardson et al. (in press)
Prairie dogs, <i>Cynomys</i> spp.	North American short and mixed grass prairie	continual intense disruption by burrowing, creating soil mounds	change physical and chemical properties of soil persisting for 100-1000s of years	Whicker & Detling (1988)
Pocket gophers, <i>Geomys bursarius</i>	North American grasslands and arid shrublands	construct tunnels and move soil to surface mounds	alter patterns and rates of soil development, nutrient availability and microtopography; change plant demography, diversity and primary productivity; affect behaviour and abundance of other herbivores	Huntly & Inoué (1988); Moloney et al. (1992)
Indian crested porcupine, <i>Hystrix indica</i>	Negev desert	digging for food	dig up to 2-3 holes m ⁻² ; diggings accumulate organic matter, runoff water, create favourable sites for seed germination	Yair & Rabin (1981); Guterman (1982)
Elephants, <i>Loxodonta africana</i>	East African woodland and savannah	physical disturbance and destruction of trees and shrubs	widespread vegetation changes; alteration of fire regime; effects on food supply and population dynamics of other animals; ultimately changes in soil formation, riparian zones, and biogeochemical cycling	Naiman (1988)

(cont.)

OIKOS 69:3 (1994)

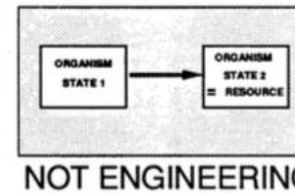
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Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Case 5 (autogenic) and case 6 (allogenic) (examples combining elements of both)				
Crustose coralline algae, <i>Porellidium</i> , <i>Lithothamnium</i>	coral reefs	overgrow and cement together detritus on outer algal ridge of barrier reef	break force of water and protect corals against major wave action; effect via own bodies (case 5) and secretion of 'cement' (case 6)	Anderson (1992)
Ribbed mussels, <i>Groenlandia demissa</i>	Rhede Island Sparina salt marsh	secrete byssal threads, and form dense mussel beds	on marsh edge, dense beds of mussels (case 5) and byssal threads (case 6) bind and protect sediments and prevent physical erosion and disturbance, e.g. by storms	Bertness (1984b)

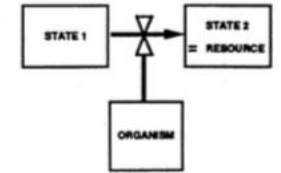
AUTOGENIC

ALLOGENIC

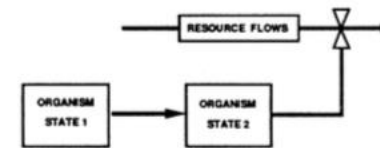


NOT ENGINEERING

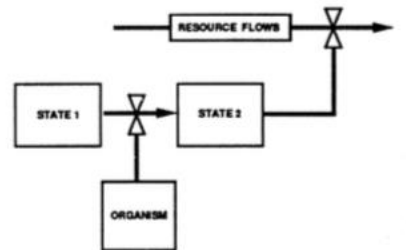
CASE 1



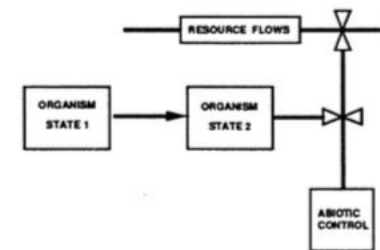
CASE 2



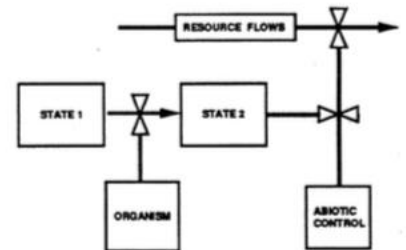
CASE 3



CASE 4



CASE 5



CASE 6

REVIEW

A global database and “state of the field” review of research into ecosystem engineering by land animals

Nicole V. Coggan¹  | Matthew W. Hayward^{2,3}  | Heloise Gibb¹ 

Number of sites per location



Engineer function

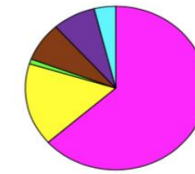


Habitat (climate) group

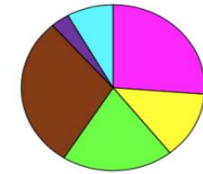


% of engineering functions researched in habitat (climate) groups

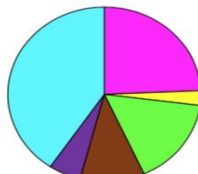
DRY/ARID
(50% of all studies)



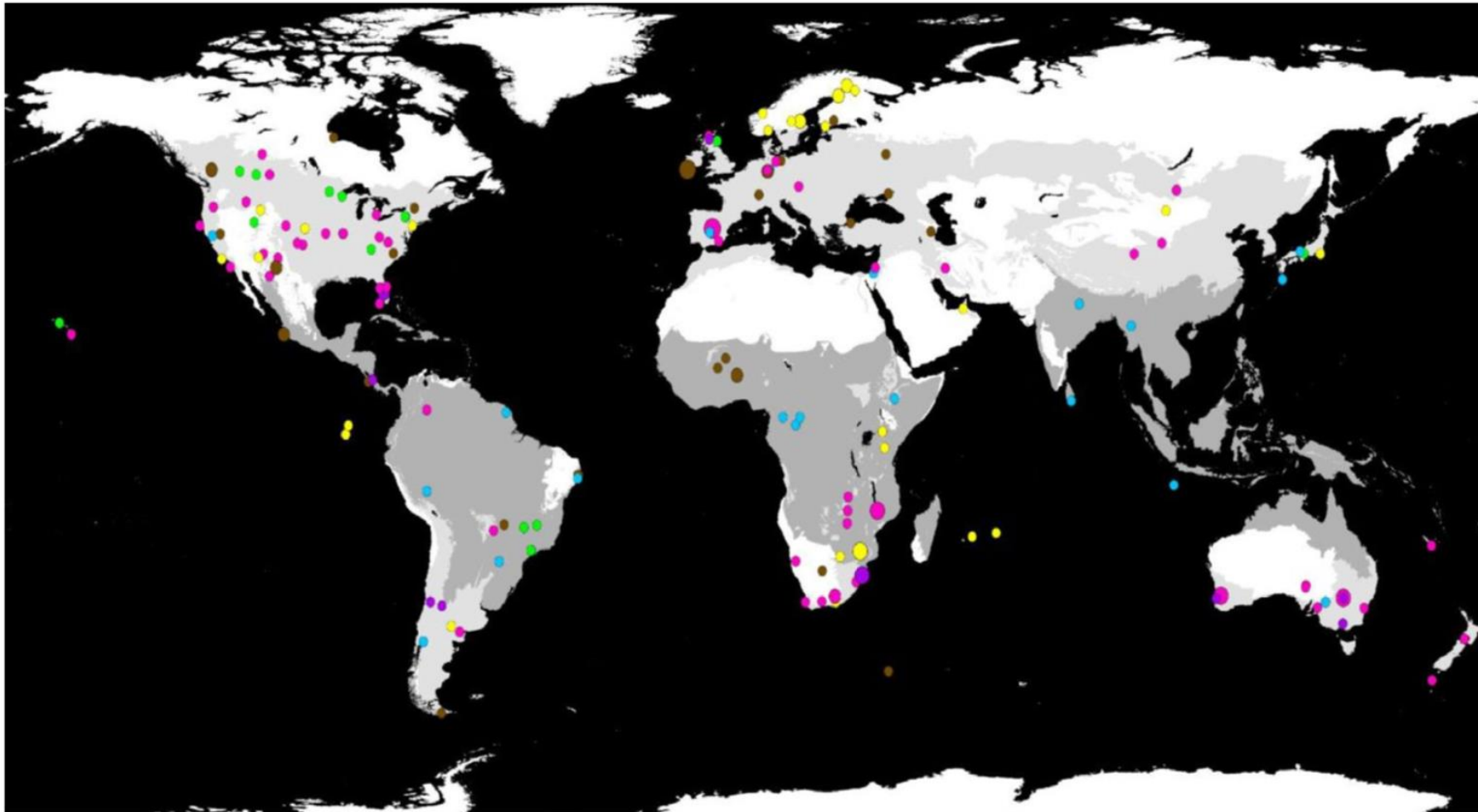
COOL/TEMPERATE
(31% of all studies)



TROPICAL/
SUBTROPICAL
(19% of all studies)



Global distribution of ecosystem engineering field research



A global database and “state of the field” review of research into ecosystem engineering by land animals

Nicole V. Coggan¹  | Matthew W. Hayward^{2,3}  | Heloise Gibb¹ 

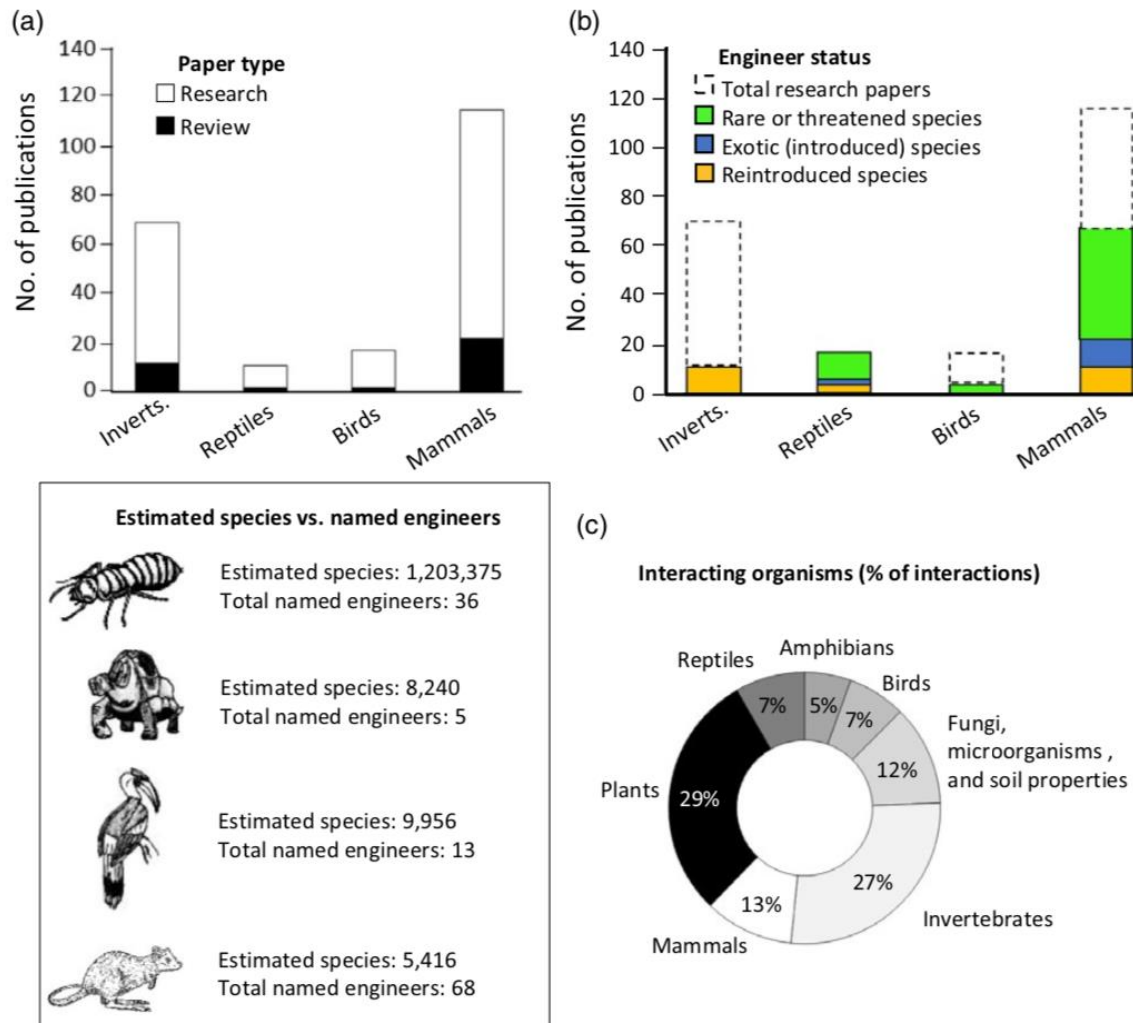


FIGURE 1 Summaries of (a) publications reporting or reviewing ecosystem engineering interactions, with global species estimates and number of named engineer species (n.b. some publications did not specify a species name), (b) count of publications where the engineer species is identified as rare, exotic or reintroduced and (c) proportion of interactions with other taxa reported by research [Colour figure can be viewed at wileyonlinelibrary.com]

Beavers and Their Dams



Justin P. Wright · Clive G. Jones
Alexander S. Flecker

An ecosystem engineer, the beaver, increases species richness at the landscape scale

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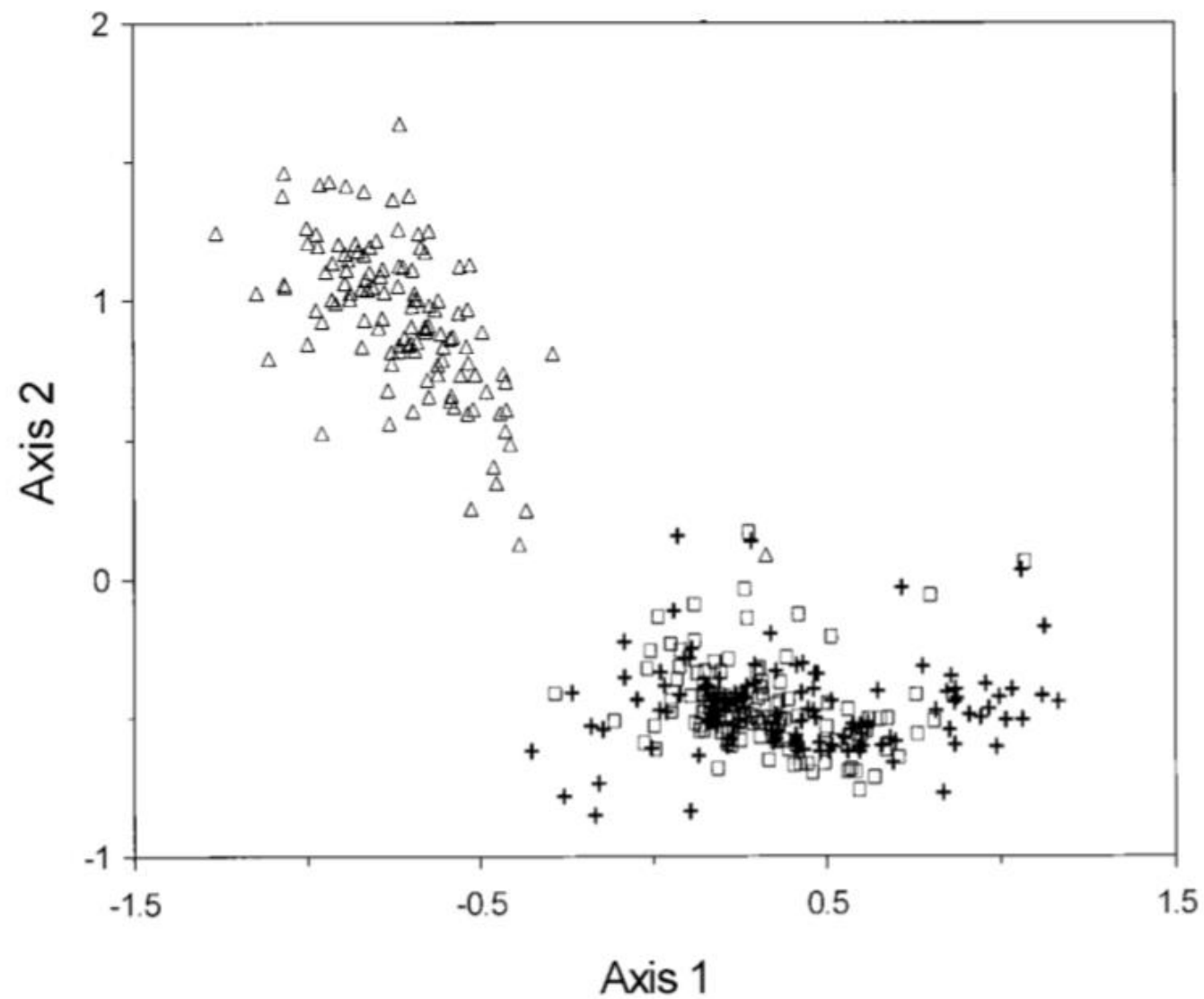


Fig. 1 Ordination of plant community composition between riparian zone habitats. Ordination of plots based on presence of species using non-metric multidimensional scaling. \triangle Forested riparian zone habitat, \square alder habitat, $+$ meadow habitat

Shit Happens (to be Useful)! Use of Elephant Dung as Habitat by Amphibians

Ahimsa Campos-Arcelz¹



Brief Introduction to Galls



Creosote gall induced by galling fly *Asphondylia auripila*



Maple Bladdergalls induced by galling mite *Vasates quadripedes*

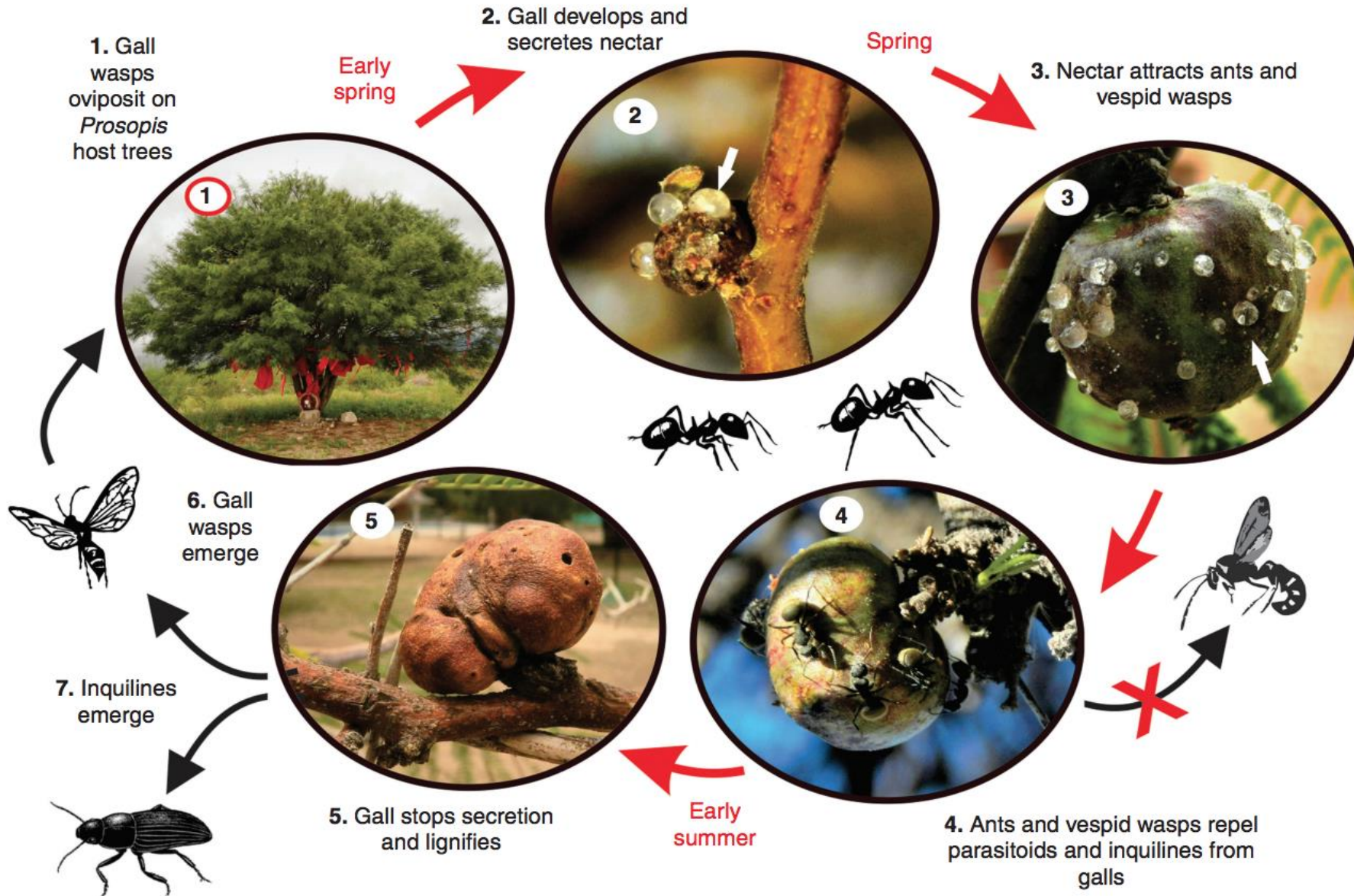


Horned Oak Gall induced by cynipid wasp *Callirhytis cornigera*



PART OF A SPECIAL ISSUE ON MORPHOLOGY AND ADAPTATION
Sugary secretions of wasp galls: a want-to-be extrafloral nectar?

Adriana Aranda-Rickert^{1,*}, Carolina Rothen¹, Patricia Diez², Ana María González³ and Brigitte Marazzi⁴



Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees

WILLIAM C. WETZEL^{1,4,7}, ROBYN M. SCREEN^{1,5}, IVANA LI², JENNIFER MCKENZIE^{3,6}, KYLE A. PHILLIPS^{1,3}, MELISSA CRUZ², WENBO ZHANG¹, AUSTIN GREENE¹, ESTHER LEE¹, NURAY SINGH¹, CAROLYN TRAN¹ AND LOUIE H. YANG²



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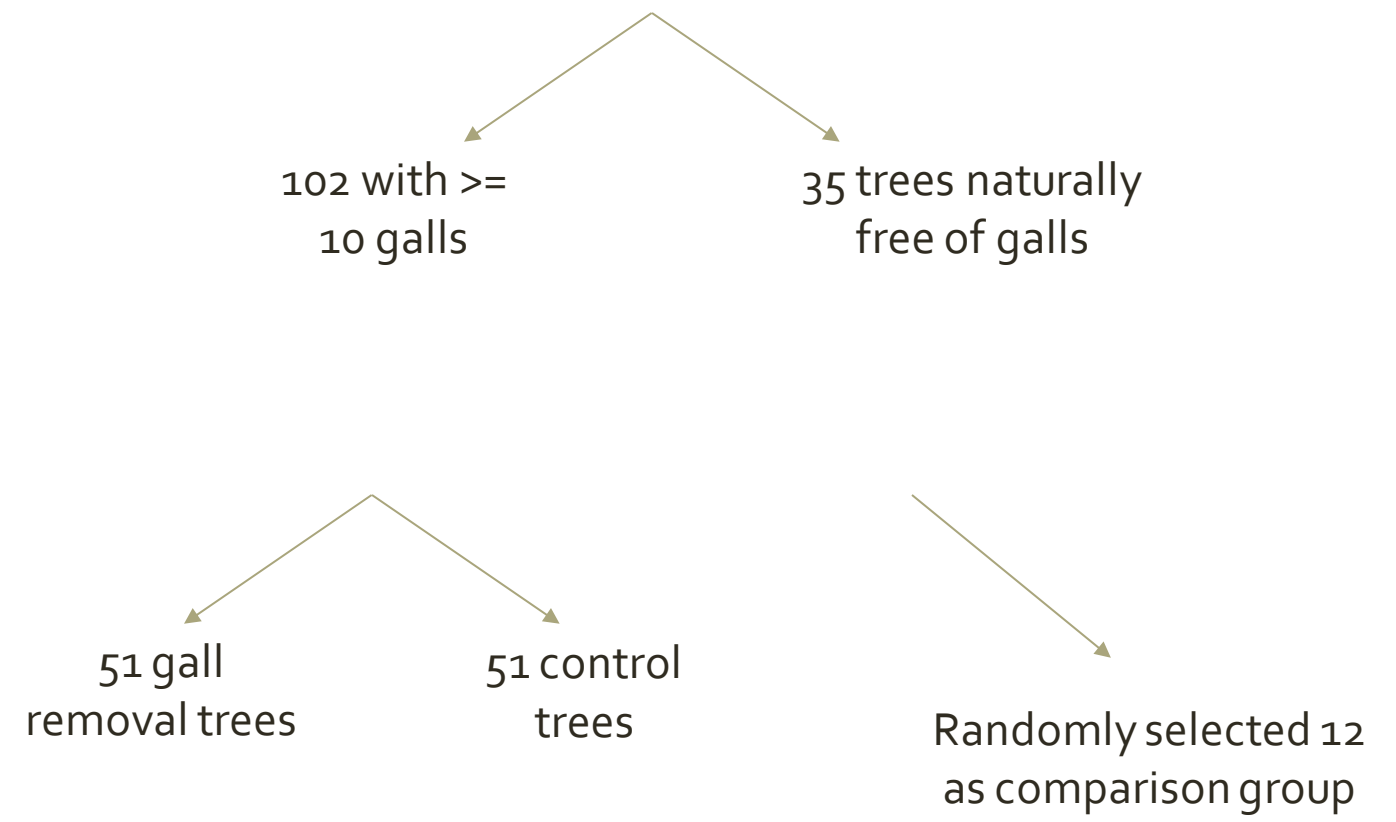
Research Questions

1. How does persistent habitat engineering influence community members that don't directly interact with the gall?
2. How does persistent habitat engineering influence the seasonal community assembly process?



Experimental Design

137 Oak Trees



Overwintering Inhabitants

- Evidence of *Salticid* spiders in 66% of senesced galls



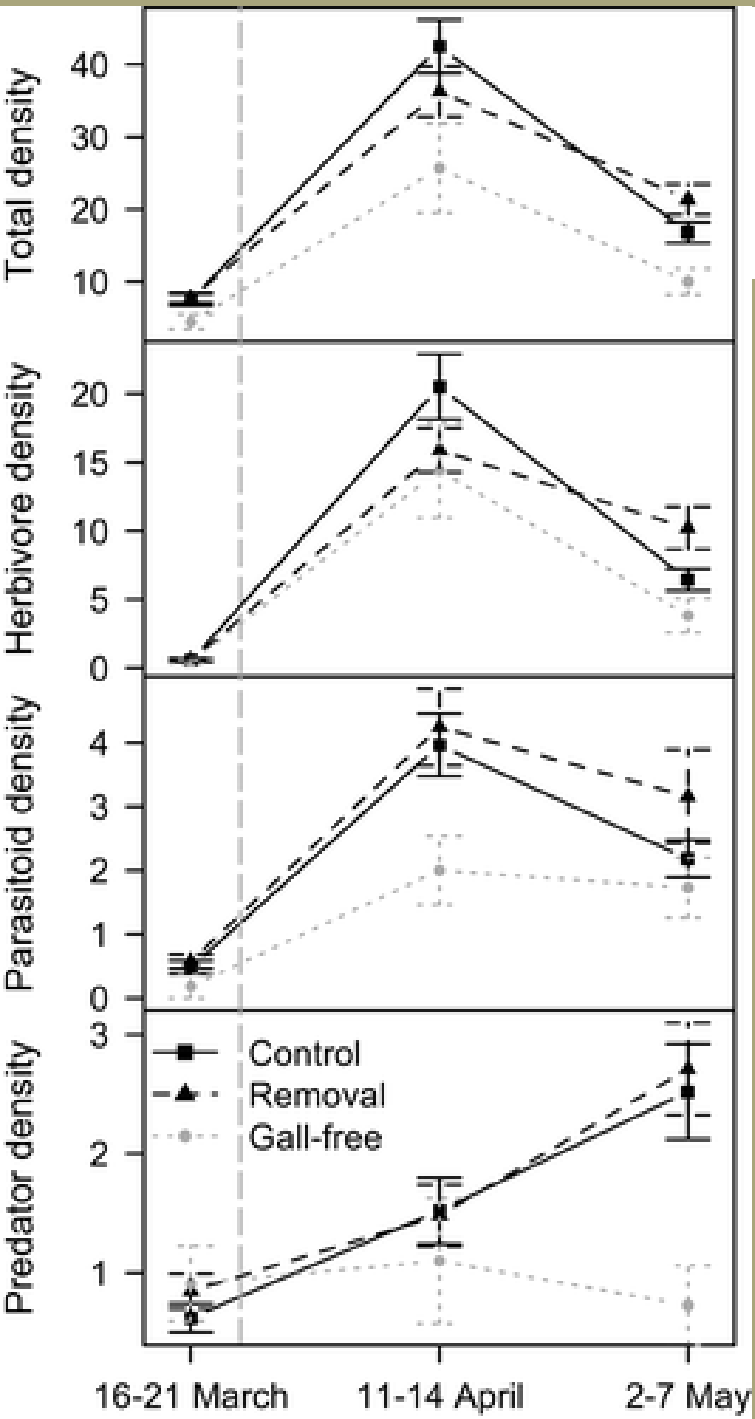
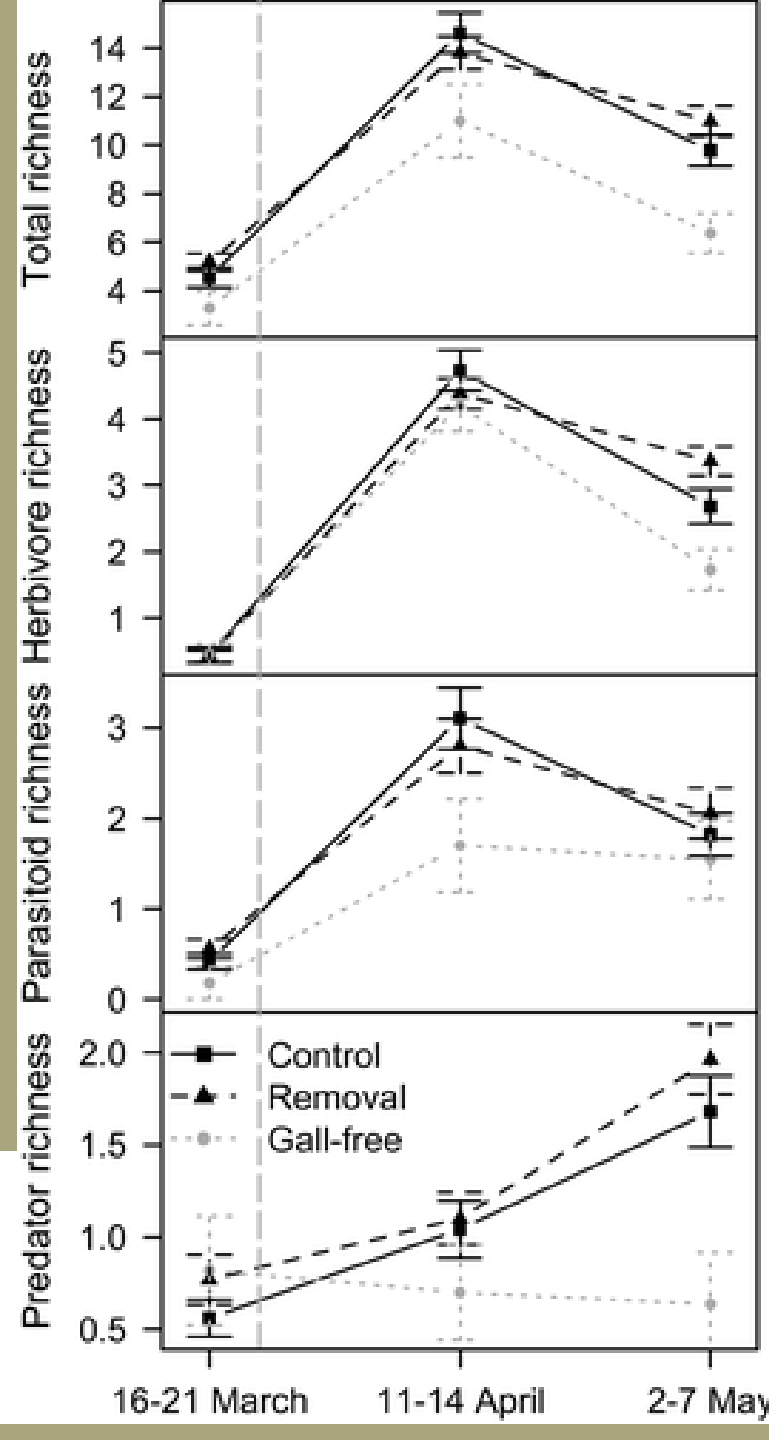


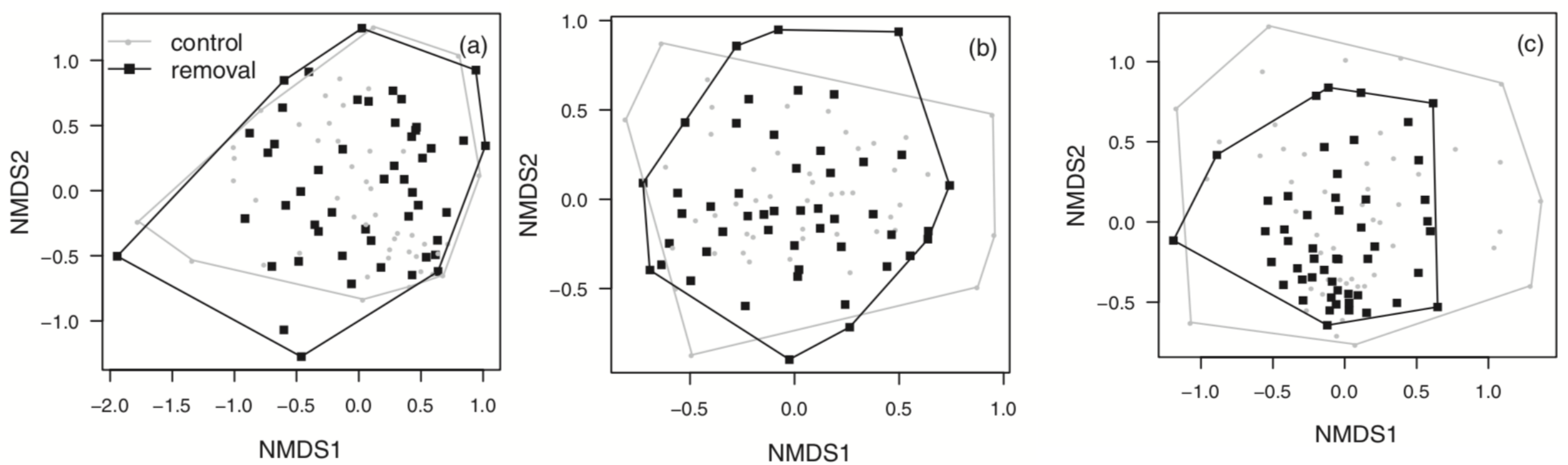
FIG. 2. Mean number of all arthropods, herbivores, parasitoids, and predators in sweep samples by treatment and time. Control trees are squares with solid lines, removal trees are triangles with dashed lines, and naturally gall-free trees are circles with gray dotted lines. Error bars are \pm SE. Vertical, gray dashes separate the pre-treatment/pre-budburst sample from the post-treatment/post-budburst samples.

Sampling Results

- Pre-Treatment, experimental trees had similar densities and richness
- Control trees had a significantly larger decrease in total arthropod and herbivore density and richness from 2nd to 3rd sample
- Naturally gall-free trees had significantly lower density and richness of herbivores and total arthropods than the experimental trees

FIG. 3. Mean arthropod, herbivore, parasitoid, and predator morphospecies richness in sweep samples by treatment and time. Control trees are squares with solid lines, removal trees are triangles with dashed lines, and naturally gall-free trees are circles with gray dotted lines. Error bars are \pm SE. Vertical, gray dashes separate the pre-treatment/pre-budburst sample from the post-treatment/post-budburst sample.





Pre-Treatment

Two-Weeks Post-Treatment

Five-Weeks Post-Treatment

Arthropod Community Composition

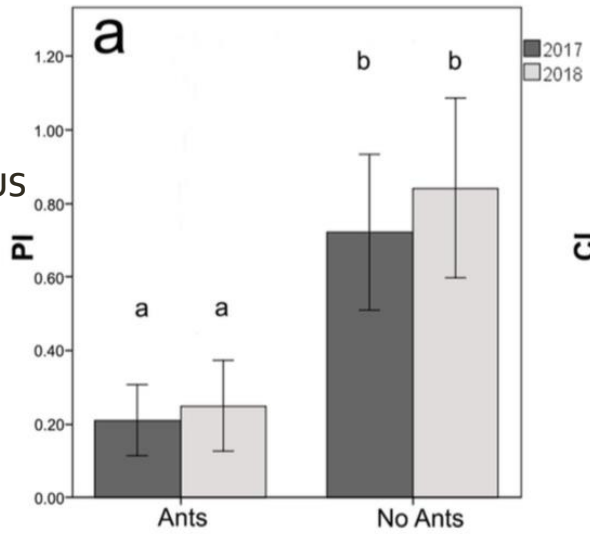
- Beta diversity was significantly higher among control trees compared to removal trees

FIG. 4. Nonmetric multidimensional scaling ordinations for arthropod communities on the removal and control trees in the (a) pre-treatment sampling and in the samplings (b) two and (c) five weeks post-treatment. Mean community composition did not differ between treatments in any sampling. In the third sample (c), control trees had significantly higher beta diversity (multivariate dispersion) than did removal trees. Three trees with communities >2 standard deviations from the mean were held out of each figure because those communities were so different they obscured variation among the rest of the communities. Inclusion or exclusion of these communities did not influence the outcome of analyses. Stress is 0.19, 0.25, and 0.23, respectively.

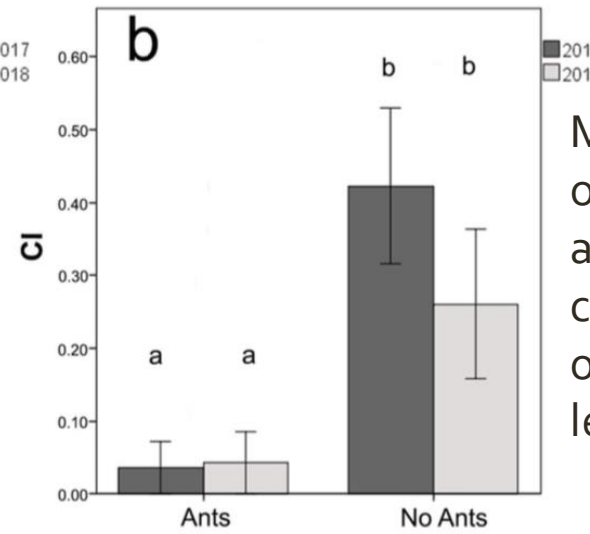
Conclusions

- By engineering galls in a summer, the gall wasp has an influence on the overwintering community on oak trees that cascades to ultimately change the arthropod community in future growing seasons, and these effects will remain present for as long as the gall stays attached to the tree.
- The increase in herbivore density after gall removal suggests that the jumping spiders commonly found in these galls play an important role in this community
- The consistently low densities of herbivores on gall free trees suggest that these trees may be poor-quality hosts for both herbivores and gall wasps

Mean # of
Phytophagous
Insects (a)



Mean proportion
of leaves
attacked by
chewing insects
on the total
leaves (b)



Giannetti et al.
2019

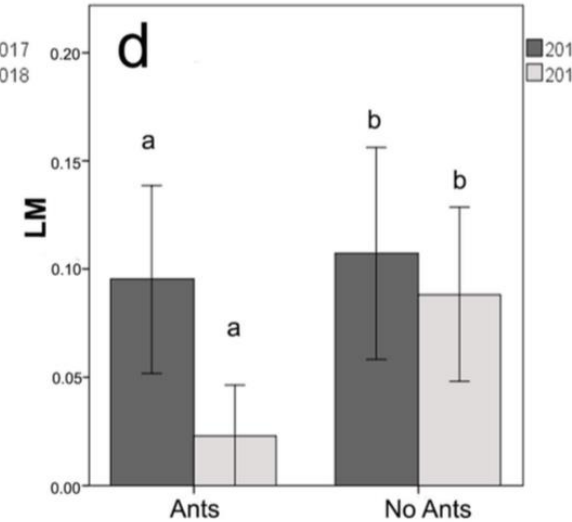
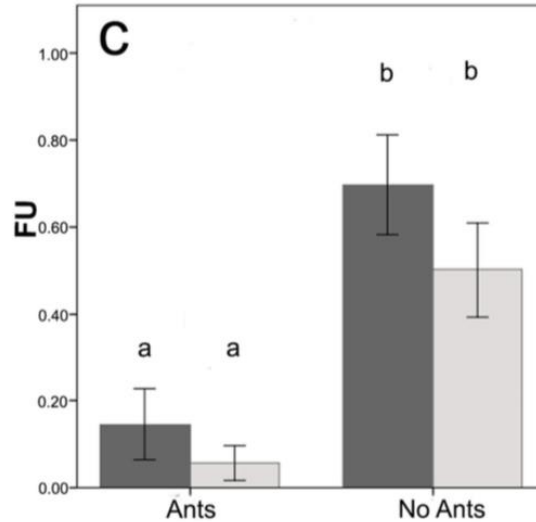



Figure 9. Effects of the ant presence on plant health. The effects are shown according to the two years of sampling (2017–2018). (a) PI: mean number of Phytophagous Insects, (b) CI: mean proportion of leaves attacked by chewing insects on the total leaves, (c) FU: mean proportion of leaves attacked by Fungi on the total leaves, (d) LM: mean proportion of leaves attacked by leaf miners on the total leaves. The SE interval is shown for each bar. The bars with the same letter are not statistically different (Two-way ANOVA, see text for further details).

Indirect effects of ecosystem engineering by insects in a tropical liana

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Research Questions

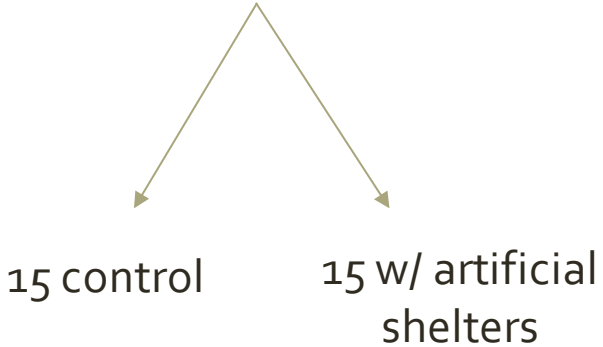
1. Does the presence of shelters increase the frequency, richness and abundance of arthropods on plants?
2. Does the type and number of shelters influence secondary colonization and use of shelters?
3. How does shelter presence and number influence herbivory levels experienced by plants?



Experimental Design

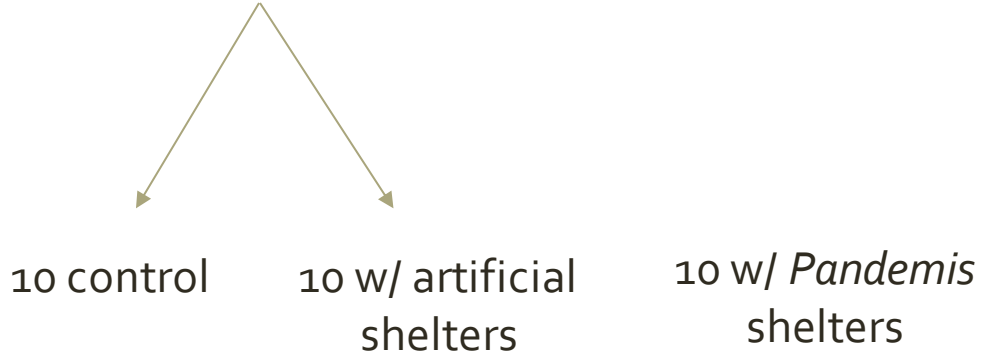
Experiment 1

30 plants w/o leaf rolls



Experiment 2

20 plants w/o leaf rolls



Experiment 1 Results

- Artificial Shelters had 2.2 times greater abundance and 1.5 times greater richness than control plants

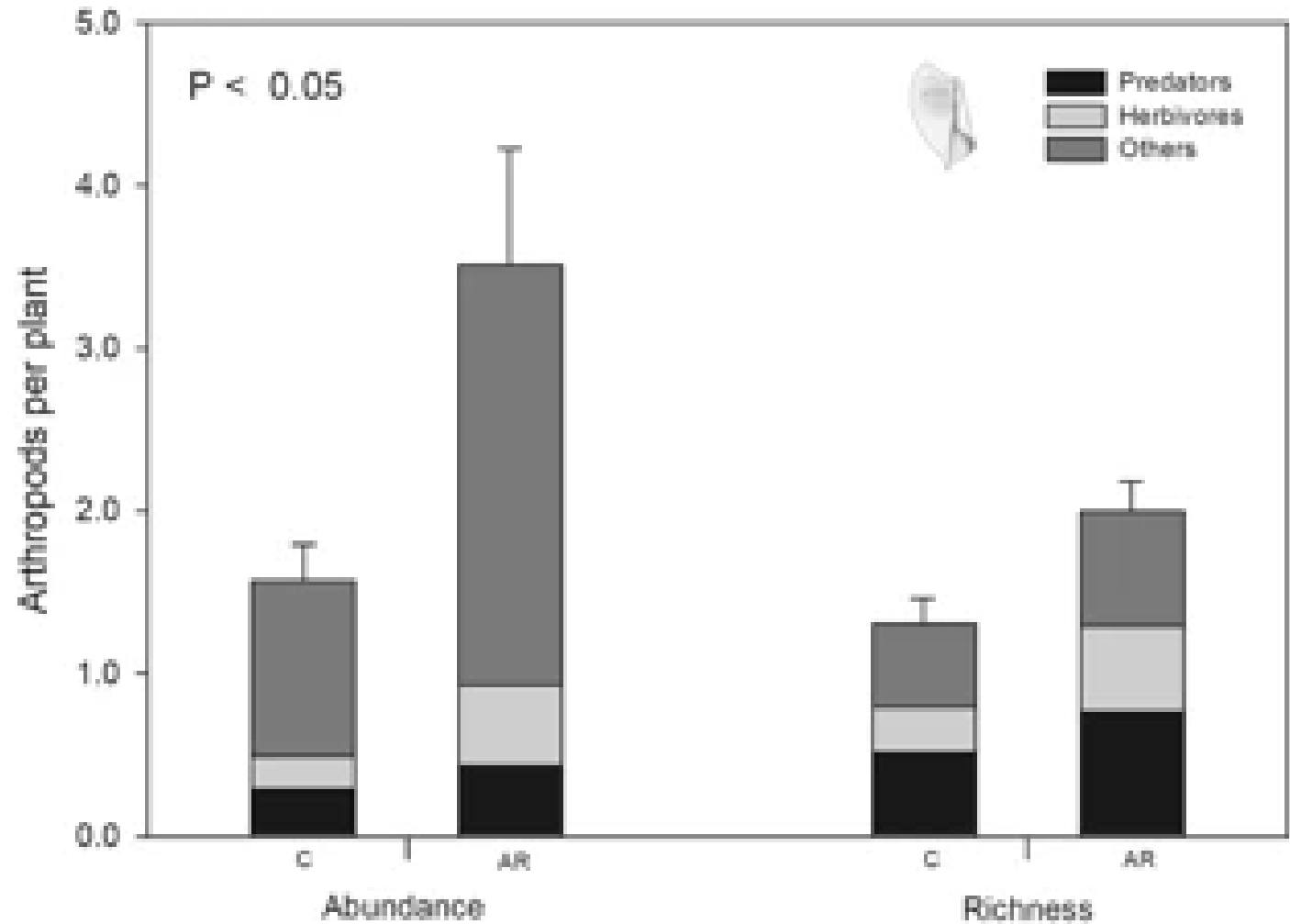


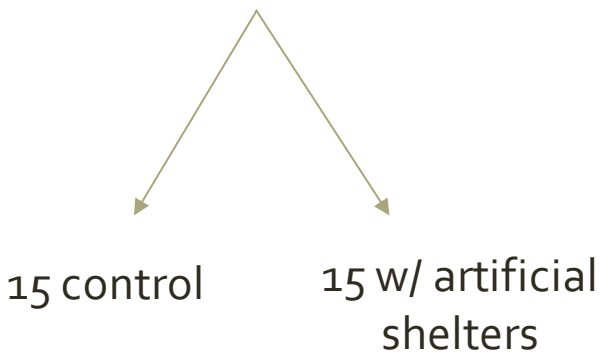
Fig. 1 Arthropod abundance and richness (mean \pm SE) in control plants (unaltered leaves) and artificially rolled leaves (shelters) of *Trigonostemon rotundifolius*. C control, AR artificial rolls. Other arthropods include detritivores, omnivores and parasites



Experimental Design

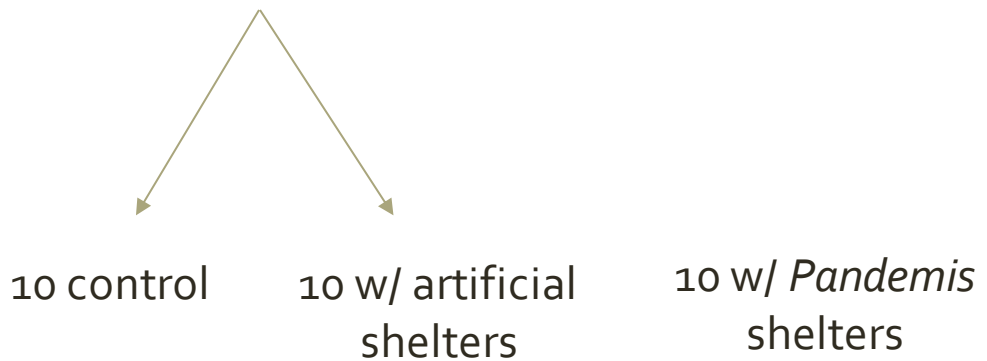
Experiment 1

30 plants w/o leaf rolls



Experiment 2

20 plants w/o leaf rolls



Experiment 2 Results

- Control plants have higher abundance than plants with either leaf roll
- Natural Shelters have significantly lower richness compared to Artificial Shelters

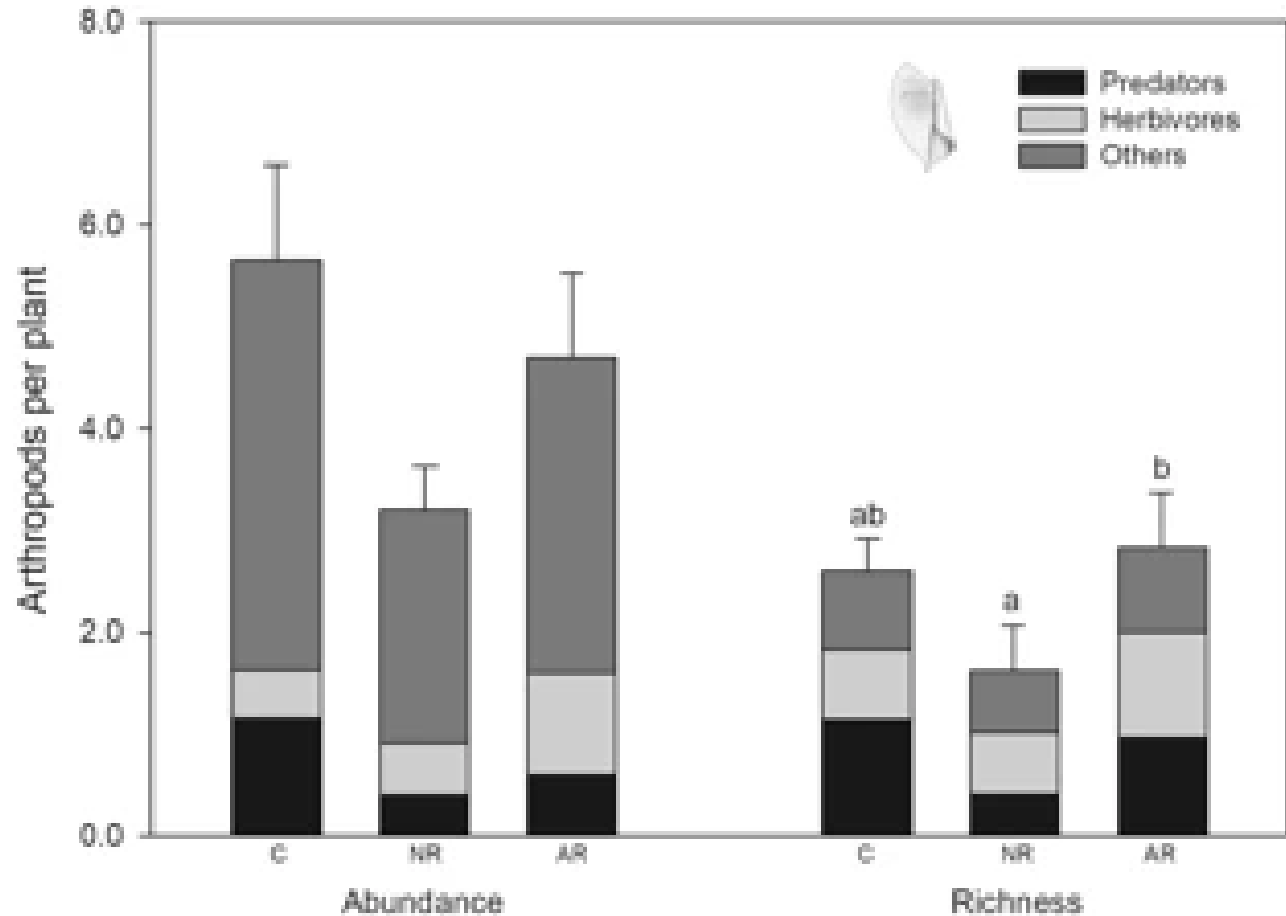


Fig. 2 Arthropod abundance and richness (mean \pm SE) in control plants (unaltered leaves), in plants with natural rolls (leaves rolled by *Pandemis* sp.) and in artificially rolled leaves (shelters) of *Trigonia rotundifolia*. Means followed by the same letters do not differ statistically from each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

Background Herbivory Rates

- Plants with 2 leaf rolls experienced 2.8 times higher herbivory

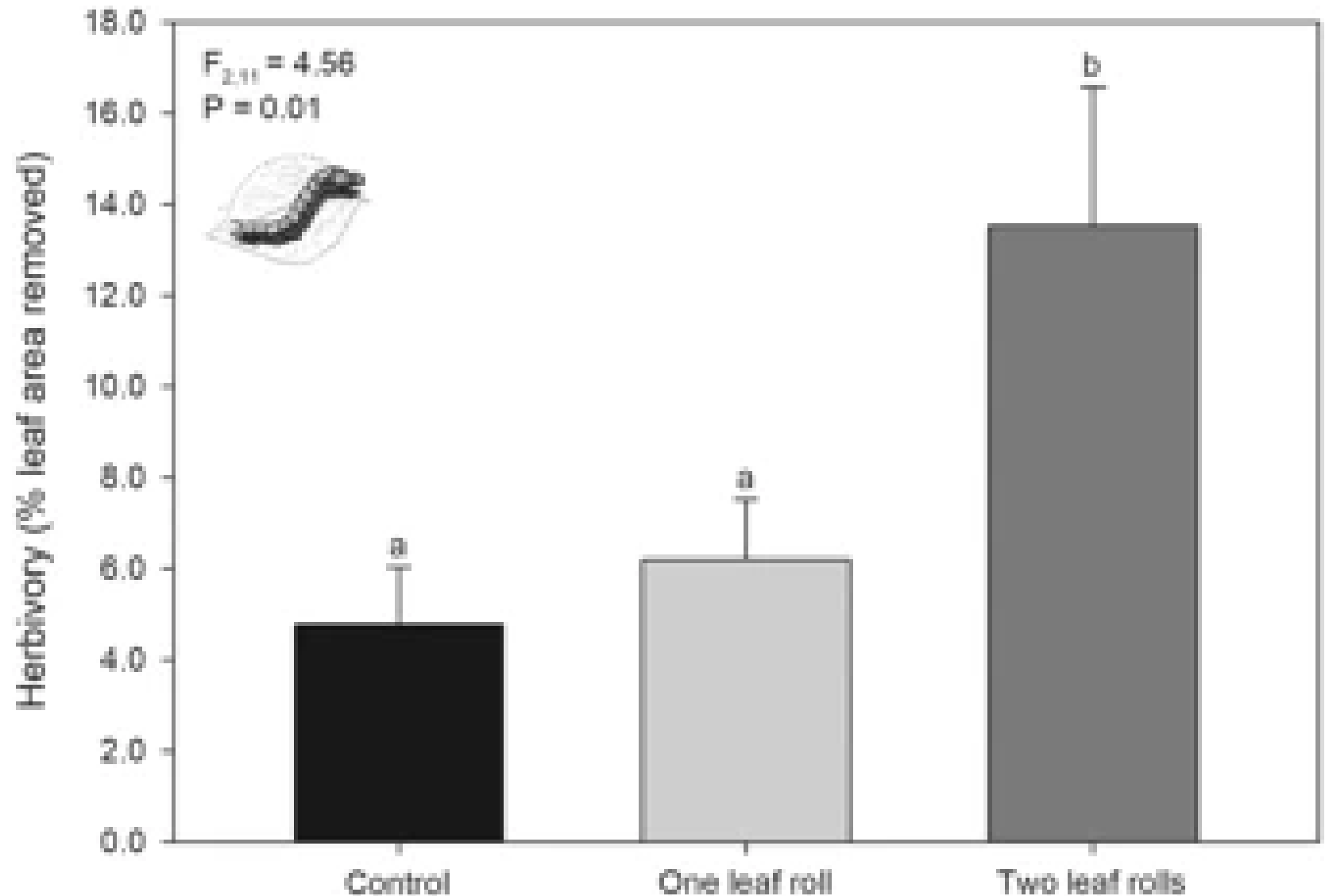


Fig.3 Herbivory (percentage of leaf area removed) in leaves of *Trigonía rotundifolia* without rolled leaves (control), with one natural leaf roll and two natural leaf-rolls created by *Pandemis* sp. Control plants and plants with one artificial roll did not differ in levels of herbivory

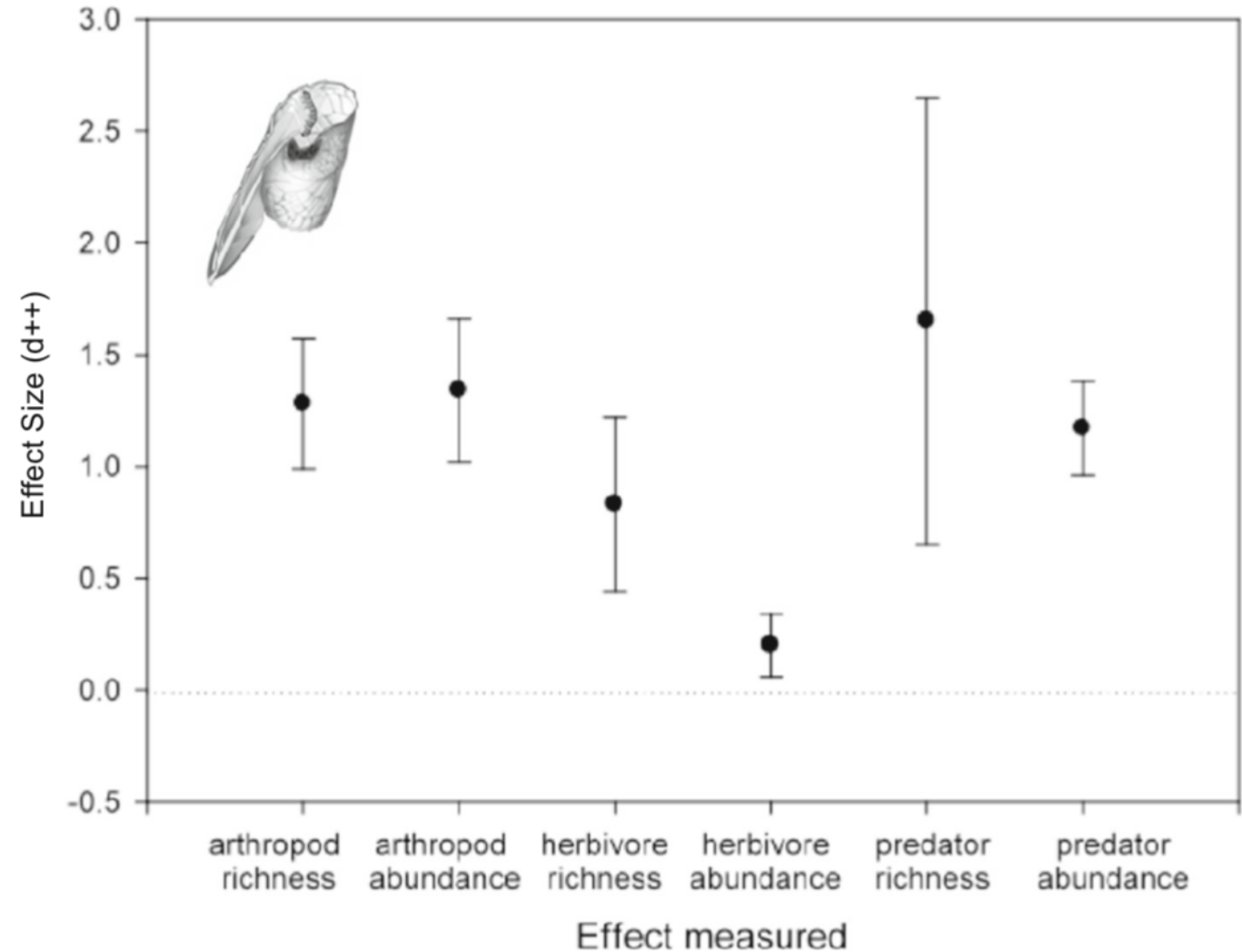
Authors' Conclusions

- The presence of these ephemeral and subtle leaf-rolling structures has a large impact on community structure and increases colonization rates and herbivory levels
- The major indirect effect of these shelters of increasing herbivory is fairly surprising because two main predators of herbivores, ants and spiders, composed of 61% of all arthropods sampled
- Natural leaf rolls did not influence abundance of arthropods, but caused a decrease in richness when compared to the artificial shelters

Shelter-Building Insects and Their Role as Ecosystem Engineers

T CORNELISSEN¹, F CINTRA², JC SANTOS³

Fig 3 Effects of shelters on local patterns of biodiversity from 12 studies that evaluated arthropod, herbivore, and predator richness and abundance inside and outside shelters or in plants with and without natural and artificial shelters. The cumulative effect size is reported for each effect measured with its 95% confidence intervals and effects are significant if confidence intervals do not overlap with zero.



Discussion Questions

1. These two habitat modifications are made of different plant materials in different locations on the trees, last on the tree for a drastically different amount of time, and are in different climates and different ecosystems, but both attract mainly predators as secondary colonizers. Why do you think this is? Do you think this is consistent with all shelters created by insects?
2. Shelters created by insects have been shown to have large effects on their host plant and the surrounding arthropod community, the outcomes of which depend on the ecological context and specific interactions that stem from that shelter.
 - a) Under what conditions would you expect the net effect on the host plant's fitness to be positive or negative?
 - b) How might the effects of these shelters on the surrounding arthropod community differ when the engineering organism still occupies the shelter as compared to after they have abandoned it? For example, do they attract different densities or species of arthropods, and is the mechanism behind the attraction different?
3. Throughout this class we have seen many examples of ant mutualisms facilitated by plant traits such as EFNs and domatia.
 - a) In what ways are the relationships mediated by senesced or developing galls similar or different to those from plant domatia and EFNs? Do you think one is more effective in indirectly reducing herbivory than the others? Would you expect them to attract the same arthropod assemblage?
 - b) The Rudgers 2004 paper we read earlier this semester showed evidence for and concluded that enemies of herbivores shape the evolution of plant EFN traits in wild cotton. With this example in mind how do you think natural selection has caused the evolution of nectar-secretion in galls?