

# Food or furniture: Separating trophic and non-trophic effects of Spanish moss to explain its high invertebrate diversity

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**Abstract.** Foundation species are typically suggested to enhance community diversity non-trophically by increasing habitat structure and mitigating physical stress, while their trophic role is considered of minor importance. Yet, there is little experimental evidence on the relative importance of trophic and non-trophic effects and the interaction with patch size. Here, we transplanted different festoon sizes of living *Tillandsia usneoides* (Spanish moss) and structural mimics assessing the trophic and non-trophic roles of this habitat-forming epiphyte in mediating the invertebrate community. Compared to bare branches, mimics enhanced species and feeding guild richness and abundances, but living festoons even more so, demonstrating that trophic and non-trophic effects jointly stimulated the community. Specifically, our results show that, independent of patch size, 40% of the total species richness and 46% of total guild richness increase could be contributed to habitat structure alone, while Spanish moss trophically stimulated these metrics by another 60% and 54%. As detritivores were particularly enhanced in living festoons, our findings suggest that trophic stimulation occurred primarily through the provisioning of Spanish moss detritus. Our results highlight that foundation species can facilitate their associated communities through both trophic and non-trophic pathways, calling for studies addressing their indirect trophic role via the brown food web.

**Key words:** brown food web; detritus; feeding guilds; food provisioning; foundation species; habitat complexity; habitat structure; non-trophic interactions; patch size; species richness; surface area.

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## INTRODUCTION

Foundation species are spatially dominant, habitat-forming organisms that enhance the richness and abundance of ecological communities (Bertness and Callaway 1994, Bruno et al. 2003).

Trees, freshwater macrophytes, seagrasses, reef-forming bivalves, and corals are all examples of such foundation species which create habitat for other species with their own body tissue (Jeppe- sen et al. 1992, Ellison et al. 2005, Coker et al. 2014, Christianen et al. 2016, van der Zee et al.

2016, Ali and Yan 2017). A major factor thought to underlie foundation species' enhancements of associated communities is their positive effect through their ability to modify their habitat (Govenar 2010). Habitat structure is suggested to enhance species richness through a number of potentially codependent non-trophic mechanisms (Kovalenko et al. 2012). First, it can enhance niche availability by creating new microhabitats (Cunha et al. 2012), modify predator-prey interactions (Klecka and Boukal 2014), and mitigate physical stress in harsh environments (Kovalenko et al. 2012, St Pierre and Kovalenko 2014). Secondly, habitat structure can also potentially increase productivity of secondary food sources, such as epiphyton or catching external detritus, that can further boost feeding guild richness and overall species richness (Kovalenko et al. 2012).

Next to these facilitative non-trophic pathways generated by increased habitat structure, foundation species may also increase biodiversity through their trophic role by acting as a food source (Strong et al. 1984). Although most studies on foundation species and species richness contribute their facilitative effects to their habitat-modifying properties (Bertness and Callaway 1994, Bruno et al. 2003), only recently a number of studies have focused on their role in the food web (Miller et al. 2015, van der Zee et al. 2016). These studies suggest that the direct trophic role of foundation species as a food source is of minor importance, compared to their non-trophic habitat-structuring role. Yet, the majority of these studies were correlative or theoretical studies (Miller et al. 2015, van der Zee et al. 2016) or studied the contribution of secondary food sources concentrated by the foundation species (Verweij et al. 2006, Gartner et al. 2013). Furthermore, only few studies limited to aquatic systems have directly compared artificial and natural structures to experimentally separate trophic and non-trophic contribution of the foundation species on total community and feeding guild responses (Taniguchi et al. 2003). Also, it remains unclear whether the relative importance of these trophic or non-trophic pathways shifts with the patch size of foundation species (Angelini et al. 2015). This may be important as larger patches can sustain similar species densities (Li et al. 2017), but edge effects may change species

dynamics and create non-linear community responses (Melo et al. 2016).

In this study, we experimentally tested the effects trophic and non-trophic contributions provided by habitat-forming plants on associated species and feeding guild diversity, and the effect of patch size. More specifically, we tested the hypothesis that habitat-creating properties of the vascular epiphyte, Spanish moss (*Tillandsia usneoides*, hereafter Spanish moss), are a stronger driver of species and feeding guild richness and abundances than its trophic role as a food source. Also, we hypothesize that, in line with earlier findings, invertebrate species number and abundance increase with patch size (Lawton and Schroder 1977, Taniguchi et al. 2003, Matias et al. 2010, Gartner et al. 2013).

Spanish moss is a rootless bromeliad distributed from North Carolina, USA, to central Brazil. It is common in the southeastern coastal plain of the United States where it prolifically and abundantly grows in the canopies of many trees including Southern live oaks (*Quercus virginia*, hereafter oak) and other trees (Garth 1964, Schlesinger and Marks 1977, Callaway et al. 2002). It grows in strands with alternating leaves that congregate in entangled clumps, called festoons, hanging from tree branches (Fig. 1). Through its festoon-forming structure, Spanish moss facilitates a wide range of invertebrate species—some of which exclusive to Spanish moss, such as the scale bug *Orthezia tillandsiae* and the jumping spider *Pelegria tillandsiae* (Rainwater 1941, Young and Lockley 1989). These epifauna benefit from Spanish moss's mitigation of temperature and humidity stress and reduction of predation pressure (Angelini and Silliman 2014). Garth (1964) also describes that “many species” use Spanish moss as an egg-laying site. Next to these non-trophic effects, Spanish moss may also serve a food source, as live plant tissue may attract herbivores and decaying plant tissue can serve as food for detritivores. However, as Spanish moss has a very low protein content with only 0.6% nitrogen content, we expected that its non-trophic contribution (i.e., providing habitat structure, capturing particulate organic matter, and mitigating stress) to species richness is more important, than its trophic contribution.

To test our hypothesis, we carried out a field experiment in which we compared bare

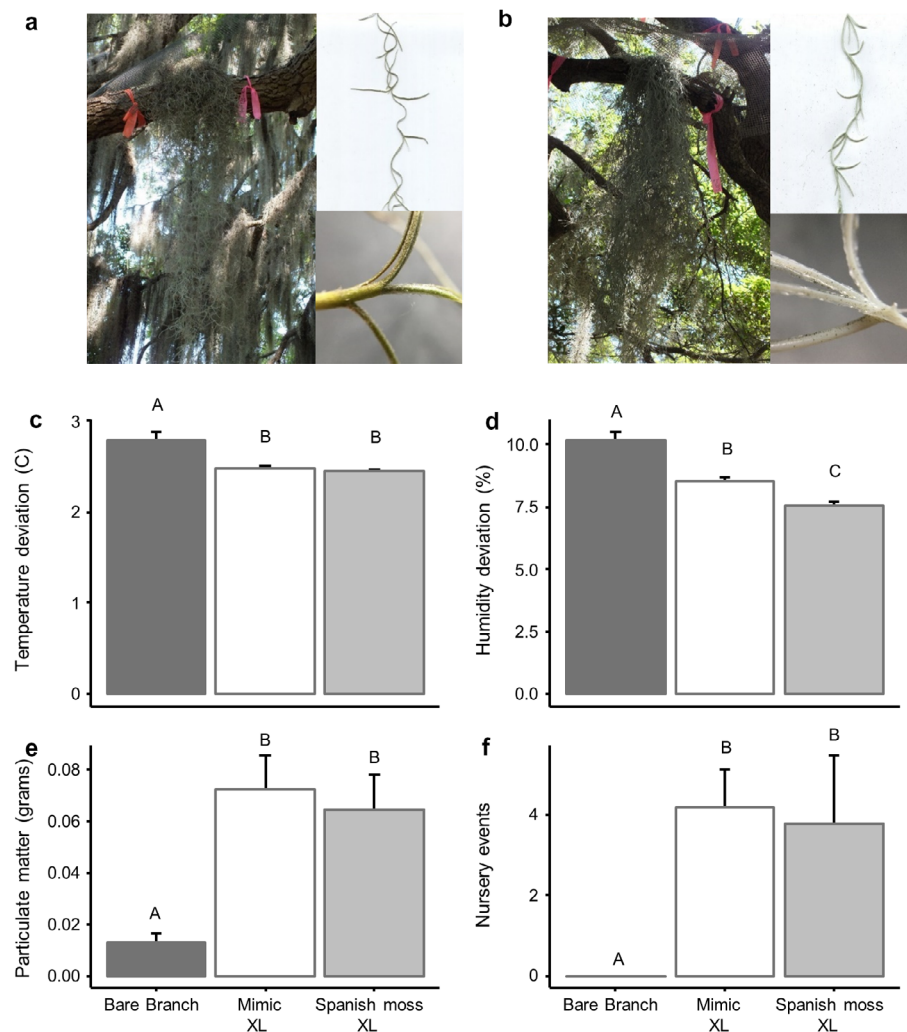


Fig. 1. Potential non-trophic services measured in Spanish moss and mimic festoons compared to bare branches. (a) Photo and close-ups of separate strands of the largest Spanish moss festoons and (b) the largest mimic festoons compared to bare branch. Non-trophic services: (c) temperature deviation from average, (d) humidity deviation from average, (e) particulate matter capture, and (f) nursery events (i.e., pupae and egg case incidences). Letters indicate post hoc grouping.

branches, to branches draped with living Spanish moss festoons and with plastic mimics of Spanish moss that do not provide live plant tissues to support invertebrates but can trap aeolian particulate matter. We also manipulated the sizes of both plastic and living festoons to explore the effect of patch size. We compared species number, invertebrate abundance, and feeding guilds as well as non-trophic effects, such as temperature, nursery function, and habitat complexity which we measured both as fractal dimensions

and as interstitial space. Our study reveals that trophic and non-trophic effects by foundation species can both have distinct effects on species richness and invertebrate abundances independent of patch size.

## METHODS

### Study site

The study was conducted in the subtropical National Estuarine Research Reserve on Sapelo

Island, Georgia, USA (31°24'49.1"N 81°17'19.4" W), from mid-April to mid-August 2014. In April, insect activity is expected to increase and overwintering adults will lay eggs and juvenile stages will become abundant. Peak activity is expected to be reached in July or August. The experiment was performed in savanna habitat dominated by live oaks (*Quercus virginia*) and Bahia grass (*Paspalum notatum*). The tree selected for the experiment was freestanding with its horizontal branches abundantly overgrown with Spanish moss (canopy diameter 28 m). Spanish moss, a vascular CAM-photosynthesizing plant that forms large entangled festoons, was chosen because of its easy manipulation, spatial dominance in the region, and its lack of a rhizosphere, leaving one sphere in which the species interactions take place.

### Experimental design

To elucidate the effects of habitat structure and food availability, we compared festoons of living Spanish moss ( $n = 5$ ; Fig. 1a) with artificial mimics ( $n = 6$ ) of Spanish moss (Komodo products, Syston, UK) with similar complexity commercially produced for use in vivaria (Fig. 1b), which were rinsed thoroughly with water before use. Living Spanish moss festoons were collected, after which all invertebrates and airborne particulate matter (dust) were removed by vacuuming each festoon for 60 s with a suction sampler (i.e., a Stihl BG55 leaf blower with vacuum attachment fitted with insect netting). Effectiveness of this method was tested by vacuuming the festoons twice and visually inspecting them, with no additional insects or eggs being recovered at the second sampling. To test the effect of patch size, we established four festoon size classes of 0.5, 0.8, 1.4, and 3.4 L for both living and mimic moss based on volume measured in a graduated cylinder. The smallest class was comparable in volume to small, newly grown festoons of Spanish moss, and the largest size class was comparable to some of the largest festoons found in the oaks (Fig. 1a; Appendix S1: Table S1; Angelini et al. 2015). Bare branches without any Spanish moss were used as a control. On the day of harvesting, the end volume of the festoons was measured again—three Spanish moss festoons (1 medium, 1 large, and 1 extra-large) had become smaller by shedding part of the festoon over time

and were reclassified to be a smaller, appropriate size class (see Appendix S1: Table S1).

Plots were set out on horizontal branches (branch diameter, 14 cm; SD = 7 cm) of the experimental oak between 1.5 and 3 m off the ground and between 2 and 3 m from the leaves. All Spanish moss within a 0.5-m distance from each plot was removed and all plots were fitted with a mesh roofing to prevent falling Spanish moss fragments from entering the plots and altering treatments. Treatments were randomly assigned to the plots and the Spanish moss and mimics were strapped to the tree using a cable tie. The bare branch control plots were also fitted with a cable tie and a mesh roof.

### Habitat complexity

Habitat complexity was interpreted in this study as the structural morphology of the plant. All festoons consisted of the same dichotomous strands typical for Spanish moss as the main complexity-generating element (Tokeshi and Arakaki 2012). By defining complexity, this way it can be studied independently of patch size (Taniguchi et al. 2003, Tokeshi and Arakaki 2012). To test whether habitat complexity of the mimics was equal to that of living Spanish moss, we measured and compared the fractal dimensions and interstitial space of both. To this end, strands of Spanish moss and plastic mimics were photographed on a white background and converted to black and white images using Photoshop CS6. Next, the fractal dimensions were analyzed using the fractal box counting tool in ImageJ 1.51k (Rasband 1997). Another proxy for habitat complexity, interstitial space, was calculated according to the method of Dibble et al. (1996) on the lowest festoon size classes. For this index, vertical and horizontal axes were randomly drawn on scans of living and mimic festoons ( $n = 3$ ; see examples in Appendix S1: Fig. S1) along which lengths and frequencies of interstices—gaps between stems and leaves—were measured, after which interstitial space ( $I$ ) was calculated as follows:

$$I_{hv} = \left( \frac{f_h}{l_h} \right) + \left( \frac{f_v}{l_v} \right)$$

where  $f$  is the mean frequency or the number of interstices, and  $l$  is the mean length (mm) of all interstices sampled along the horizontal ( $h$ ) or



vertical axes ( $v$ ). A higher  $I$  value means a higher frequency and smaller gaps in the structure. The fractal dimensions and interstitial space of the plastic mimics ( $1.16 \pm 0.001$  and  $5.4 \pm 1.06$ , respectively) were statistically indistinguishable from living Spanish moss ( $1.17 \pm 0.003$  and  $8.5 \pm 1.17$ , respectively; fractal dimensions:  $\chi^2 = 0.25$ ,  $P = 0.62$ ; interstitial space:  $F_{1,4} = 3.68$ ,  $P = 0.13$ ), and in our analyses, we therefore further assumed the treatments to be equal in complexity.

#### Temperature and humidity variation

Temperature and humidity were logged to  $0.5^\circ\text{C}$  accuracy every 15 min for 4 d using iButton data loggers (Hygrochron, Embedded Data Systems, Lawrenceburg, Kentucky, USA) to measure the effect of Spanish moss and the mimics on their environment. Due to the limited number of available loggers, iButtons were only glued to branch surfaces in the bare branch, the extra-large Spanish moss, and extra-large mimic treatments. The degree of environmental stability was approximated by using the average temperature and humidity overall measured value and calculating the absolute deviation from the total average temperature and humidity on each time step.

#### Invertebrate community sampling and dust collection

Four months after establishing the experiment, on the same day, we enclosed each plot in a 190-L plastic bag as quickly as possible, into which we placed the festoon (if present) and brushed the branch for 30 s to capture all present detritus and invertebrates (sensu Angelini and Silliman 2014). We collected all invertebrates and particulate matter by feeding the content of the bag over the suction sampler (i.e., a Stihl BG55 leaf blower with vacuum attachment fitted with insect netting; mesh size 0.5 mm; see also Angelini and Silliman 2014) and vacuuming each festoon for 60 seconds. All macroinvertebrates were stored at  $-20^\circ\text{C}$  until identification using a dissecting microscope at  $25\times$ . Identification was done to morphospecies (hereafter species sensu Angelini and Silliman 2014), and also, abundances were noted as well as feeding guild consisting of predators (carnivores), scavengers/omnivores, detritivores (detritus feeders), herbivores (plant eaters), or parasites (carnivores smaller in body

size than their host (feeding guilds were assigned according to literature, databases and expert knowledge) and life stage (juvenile/adult, on the basis of size and development of genitalia). All macroinvertebrates could be considered mobile in the sense that they either walk, crawl, or fly, although the scale bug *Orthezia tillandsiae* can be considered spatially bound to its host. The function of Spanish moss as a nursery was quantified as nursery events per festoon by counting the egg cases and pupae cases in the suction samples and by scanning the festoons for remaining egg and pupae cases. Each patch of egg cases was counted as one nursery event while pupae cases were counted individually.

Dust (i.e., airborne particulate matter) such as pollen and detritus may be an important food source to invertebrates. Hence, we measured the amount of particulate matter inside each festoon at the end of the experiment by collecting all the particles in an air filter behind the insect screen during the suction sampling (mesh size 0.2 mm). The dust sample was then transferred to a pre-weighted plastic bag and dried (24 h at  $60^\circ\text{C}$ ), after which biomass was determined.

#### Statistical analysis

All statistical analyses were done in R version 3.4.1. As a first step, we compared how extra-large living and mimic festoons compared to the bare branch treatment to test how the addition of structure alone in mimic festoons versus structure and food in living Spanish moss affected the non-trophic effects of Spanish moss (i.e., temperature, humidity, particulate matter, and nursery events as well as invertebrate community responses including species richness and evenness, and feeding guild richness and evenness). We used generalized linear models with a Poisson distribution for count data (i.e., nursery events, species richness, and guild richness data) and a Gaussian distribution for continuous data (i.e., particulate matter, temperature deviation, humidity deviation, species evenness, and guild evenness data). The models were analyzed using a one-way ANOVA with the car package in R, followed by Tukey post hoc tests to detect differences between the three treatments (bare branch, extra-large living festoon, and extra-large mimic).

In separate analyses, in which the bare branch treatments were not included, we then

investigated the effect of festoon patch size as a continuous variable and festoon type (living/mimic) as an independent factor. We used general linear models with festoon size class (i.e., volume in liters) and festoon type (i.e., mimic or living) as factors and invertebrate community responses (i.e., nursery events, juvenile abundance, species richness and evenness, feeding guild richness and evenness, feeding guild abundances of herbivores, detritivores, scavengers and predators, total particulate matter, particulate matter concentration, spider abundances, and web-weaving spider abundances) as dependent variables, and also, an interaction term was included for festoon size and type. Continuous variables (i.e., total particulate matter and particulate matter concentration, species evenness, and guild evenness) were checked for normality and log-transformed when necessary (particulate matter data were log-transformed to meet normality requirements). Count data (i.e., nursery events, juvenile abundances, richness data, feeding guild, and spider abundances) was analyzed using a Poisson distribution or negative binomial distribution when overdispersion was found (in the case of detritivores). These models were then analyzed in a two-way ANOVA type 3. Because we detected no interactions between festoon size class and festoon type, just the main effects are reported below. Temperature mitigation was analyzed using a linear mixed model (lmerTest in R) with treatment as fixed factor and time as a random factor.

## RESULTS

In total, 618 invertebrates were collected and 68 species were identified in the experiment. In the large festoons, up to 16 species were found. Of all species, 48% were predators (mostly spiders) and 33% were detritivores, which mostly consisted of isopods. Close to a 100 scavengers and herbivores were found (10% and 8% of the total abundance respectively), while only two parasites were identified. Parasites were therefore excluded from the feeding guild analyses.

### *Non-trophic interactions of Spanish moss and mimics*

Both living and mimic extra-large Spanish moss festoons stabilized temperatures relative to

bare branches, where temperatures varied 1.1 times more over the four days of iButton monitoring (Fig. 1c,  $F_{2, 3283} = 136.7$ ,  $P < 0.001$ ). The average humidity was 1.2 times more stable in the mimic festoons compared to bare branch, but even more in living Spanish moss (1.4 times; Fig. 1d,  $F_{2, 3283} = 53.7$ ,  $P < 0.001$ ). Secondary food resources in the form of aeolian particulate matter increased 5.3 times in both living and mimic festoons relative to bare branches ( $\chi^2_2 = 17.4$ ,  $P < 0.001$ ; Fig. 1e). Both festoon types acted as attachment substrate for egg cases and pupae (i.e., nursery events), increasing the amount of nursery events from 0 to 4 compared to the bare branch ( $\chi^2_2 = 32.5$ ,  $P < 0.001$ ; Fig. 1f).

### *Festoons versus bare branch*

The extra-large living and mimic festoons changed community metrics in various ways relative to bare branches, showing the strong potential for this foundation species to locally alter community structure and boost species richness. Species richness, expressed as the number of species, and guild richness (number of feeding guilds represented in the festoon community) were increased by the plastic mimics, but even more so by living festoons (species richness:  $\chi^2_2 = 57.6$ ,  $P < 0.001$ , guild richness:  $\chi^2_2 = 12.9$ ,  $P < 0.01$ ). Specifically, 6.7 times and 3.6 times, respectively, in mimic festoons compared to bare branch, while living festoons increased by 15.6 times and 6.7 times, respectively (Fig. 2a, c). Evenness increased 12.7 times in both festoon types (Fig. 2b,  $\chi^2_2 = 101$ ,  $P < 0.001$ ) and guild evenness was only significant for living Spanish moss, which increased 8.7 times compared to bare branch ( $\chi^2_2 = 25.8$ ,  $P < 0.001$ ). Comparing the smallest festoons to bare branch also shows the same statistical trends in biodiversity indicators, illustrating even smallest festoon is efficient to enhance species richness (Appendix S1: Fig. S2).

### *Effects of festoon type and size*

The number of nursery events increased with festoon patch size but did not differ between living and mimic festoons (Fig. 3a). The juvenile invertebrate counts also increased with festoon size but was significantly lower in mimics compared to living festoons (Fig. 3b). We found significant differences between living and mimic festoons for species richness, evenness, and guild

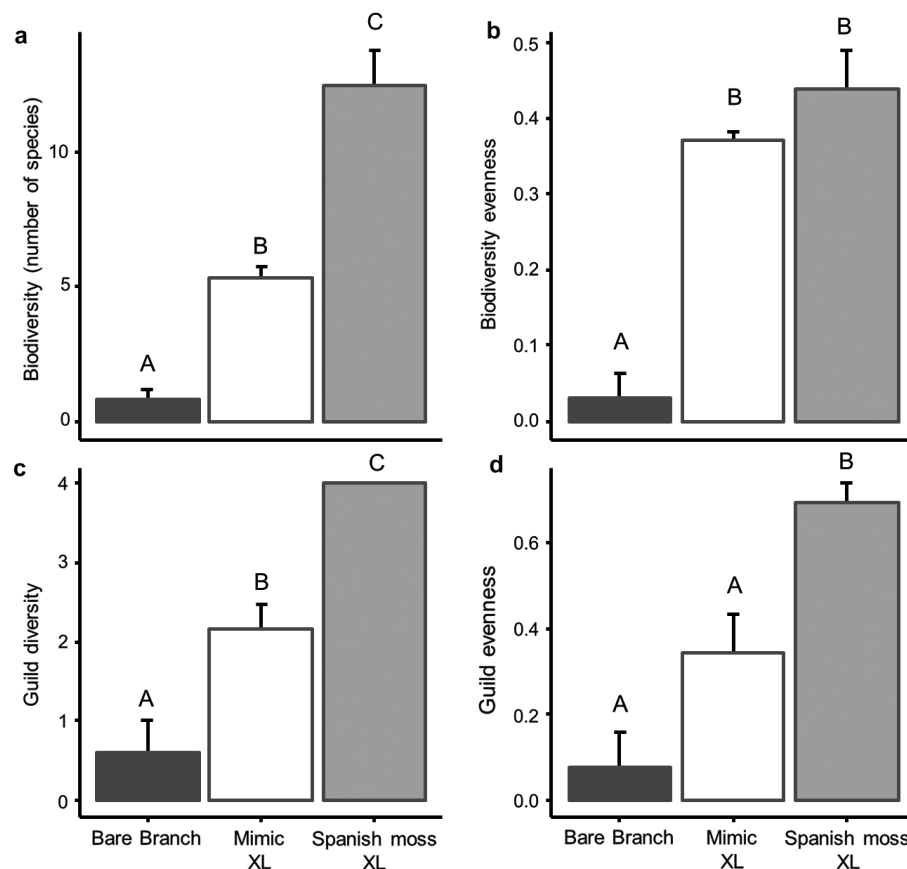


Fig. 2. Biodiversity indicators for the largest festoons of Spanish moss (light gray) and plastic mimics (white), with bare branch (dark gray) as a control. Letters indicate post hoc grouping. (a) Species richness expressed as the number of species, (b) species evenness, (c) guild richness, expressed as the number of guilds, (d) guild evenness.

evenness. Moreover, these were all dependent on festoon size, but without any interaction with festoon type (i.e., living or mimic; Fig. 3c, d, f). Species richness increased 1.9 times from smallest to the largest size class in the mimic festoons and 3 times in living Spanish moss. Evenness increased 1.5 times in the mimics and 1.6 times in Spanish moss (Fig. 3d). Guild richness was 1.8 times higher overall in Spanish moss compared to mimics. Finally, guild evenness did show a dependency on festoon size and type; mimics increased 1.6 times from smallest to largest while living Spanish moss increased 1.4 times (Fig. 3e).

Herbivores did not depend on festoon size or type and were less abundant than other feeding guilds (Fig. 4a). In contrast, detritivores, scavengers, and predators were all significantly affected by festoon size and festoon type

(Fig. 4b–d). Detritivores, which were 99% isopods, were rare in mimic festoons and only increased slightly in abundance with increasing festoon size (i.e., from 0 to 2 individuals per festoon in small versus extra-large festoons), in contrast to the living festoons increased 21.3 times in Spanish moss. Scavengers, which were mostly cockroaches and common scaly crickets, increased from 0 to 1.5 in mimics from small to extra-large and from 0.7 to 7 (i.e., by 10 times) in living Spanish moss. Predators, 98% of which were spiders, increased 2.7 times in mimics and 7 times in living Spanish moss.

## DISCUSSION

Our results show that the non-trophic role of Spanish moss festoons, as well as their role as a

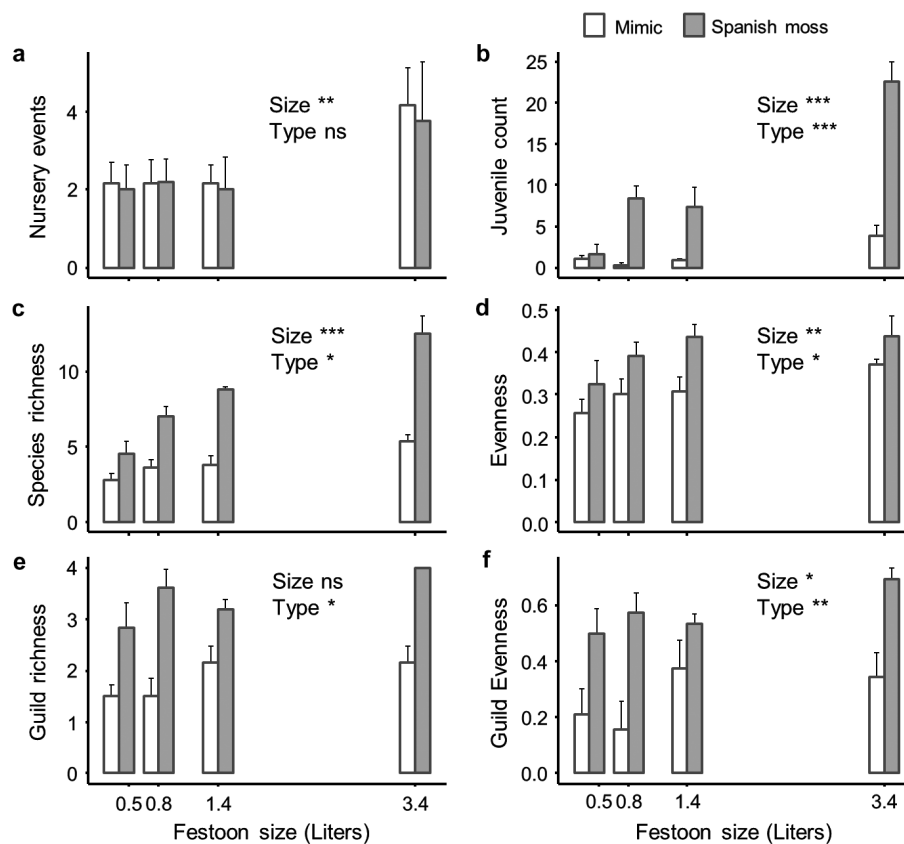


Fig. 3. Biodiversity indicators (mean  $\pm$  SE) for all festoon patch sizes and both festoon types (living or mimic) with statistics results, no interactive effects were found (statistics are reported in Appendix S1: Table S2). (a) Number of nursery events scored per festoon, (b) juvenile macroinvertebrates scored per festoon, (c) species richness as the number of species, (d) evenness of species, (e) guild richness expressed as the number of guilds present, and (f) evenness of guilds.

food source, both strongly increased the species and feeding guild richness and abundance of the invertebrate community with increasing patch size. Moreover, we found that trophic/non-trophic contributions (living vs mimic) stimulated community richness seemingly acted independently from patch size, since we did not identify any interactions. We found that non-trophic facilitation (structure) alone, as simulated by plastic mimic festoons, increased biodiversity indicators by 3.6–12.7 times compared to bare branch controls. Furthermore, in contrast to our hypothesis, species richness was stimulated much more within the living Spanish moss festoons. Specifically, our results demonstrate that, when added to the effect of habitat structure, the trophic role of Spanish moss increases

biodiversity indicators by 6.7–15.6 times. We therefore conclude that total species richness depends for about 40% on habitat structure and, on top of that, 60% depends on food provisioning by the festoons themselves.

Obviously, as our experiment lasted only 4 months, community composition may not yet have fully matured considering that the festoons and their associated communities can typically develop for years under natural conditions. A longer development period may have in particular have consequences for the amounts of accumulated detritus in real festoons and dust in both mimics and real festoons, both of which may in turn positively enhance abundances of species that directly or indirectly trophically depend on these resources. In addition, slow



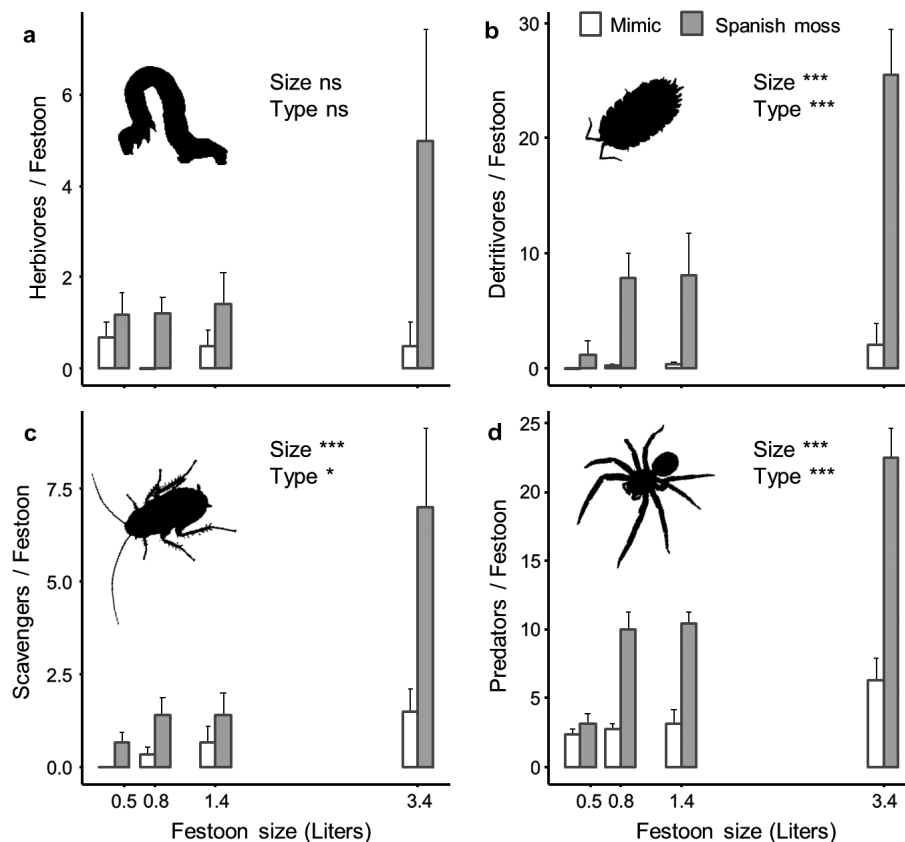


Fig. 4. Invertebrate abundances of different feeding guilds for all festoon patch sizes and both festoon types (living or mimic) with statistics results; no interactive effects were found (statistics are reported in Appendix S1: Table S2). (Bars represent mean  $\pm$  SE.) (a) Herbivores, (b) detritivores, (c) scavengers, (d) predators.

colonizers may have also been underrepresented in our experimental results. Overall, however, our results clearly highlight that facilitation by foundation species can be driven by the combined effects of their non-trophic, habitat-structuring role, and their trophic role in the food web, and that these effects are independent of patch size.

#### *Non-trophic, habitat-structuring, effects of Spanish moss*

We demonstrated that by generating habitat structure, Spanish moss strongly changes ecosystem functions and species richness. The results show that both the mimic and living festoons similarly mitigated temperature fluctuations, trapped similar amounts of particulate matter, and were also indistinguishable in their role as a nursery. The addition of habitat alone by the

mimic festoons resulted in a dramatic enhancement of species richness compared to bare branch. Moreover, even the smallest mimic festoons clearly stimulated species richness and community evenness compared to bare branches. Previous work from Angelini et al. (2015) suggests that together with the live oak on which it grows, Spanish moss forms a facilitation cascade, in which the moss acts as a secondary foundation species. In general, foundation species are suggested to enhance species richness by increasing habitat structure and mitigating physical stress (Bertness et al. 1999, Govenar 2010, van der Zee et al. 2015, 2016). Although our results show that Spanish moss indeed reduces temperature and humidity fluctuations, we found this mitigating effect to be relatively minor, that is,  $<0.5^{\circ}\text{C}$  temperature reduction in deviation from the average compared to bare branch and  $<3\%$

reduction in humidity deviation, and the difference in humidity deviation most likely caused by transpiration from the plant itself. Hence, we suggest that in our case, enhancement of habitat structure was likely more important in shaping the Spanish moss invertebrate community. Although the mechanism driving such a biodiversity–habitat complexity relationship is still not completely understood (Kovalenko et al. 2012), enhancement of niche availability through the creation of new (micro-)habitat and alterations in predator–prey interactions has been suggested as important factors (Bertness et al. 1999, Kovalenko et al. 2012, St Pierre and Kovalenko 2014). Additionally, habitat structure may also stimulate the community indirectly, by acting as a resource concentration mechanism (Kovalenko et al. 2012).

#### *Indirect resource concentration*

Apart from offering increased habitat structure, and mitigating physical stress, we found that both the mimic and living Spanish moss festoons increasingly trapped particulate matter with increasing festoon size (Appendix S1: Fig. S3a), while the amount captured per unit volume decreased with festoon size (Appendix S1: Fig. S3b). This suggests that virtually all of this accumulated matter originated from outside of the festoons. Hence, by trapping external resources Spanish moss festoons can indirectly fuel the food web through the indirect provisioning of resources, and this effect may differ depending on festoon size. For instance, rapidly moving organisms may benefit most from the sheer amount of dust collected by larger festoons, while slower moving species may profit more from the higher concentration found in the smaller festoons.

Although it is likely that the bulk of the dust originated from outside of the festoons, it is important to note these external resources may still also contain organic particles from neighboring festoons, from the host tree, or from other nearby trees. Therefore, to unravel whether secondary resource concentration is a truly non-trophically driven interaction, in-depth studies, such as isotopic analysis, will be necessary. In case of Spanish moss, we suspect it is indeed likely that collected dust within the festoons could in part consist of shredded trichomes from

the Spanish moss itself. Earlier work on the relationship between such secondary food sources and habitat structure yielded varying results (Taniguchi et al. 2003, Ferreiro et al. 2011, Verdonschot et al. 2012, Loke and Todd 2016). Patch size of plants has been positively linked with accumulation of external food sources (Taniguchi et al. 2003). Nevertheless, the extent to which these food sources drive biodiversity across ecosystems has yet to be disentangled from the other non-trophic effects of habitat structure. However, as an indirect trophic effect of foundation species, they may serve an important role for part of the food web (e.g., see Appendix S1: Fig. S3).

#### *Trophic effects of Spanish moss*

Compared to the mimics, living festoons clearly had a stronger facilitating effect on the community, which most likely resulted from the trophic role of the plants themselves, as we did not detect any differences in non-trophic effects (i.e., habitat complexity indices, temperature mitigation, particulate matter capture, and nursery function) between mimic and living festoons. Although Spanish moss thus appears to also have a direct trophic role next to its habitat-structuring (including resource-concentrating) role, the particular enhancement of the detritivores suggests that it serves primarily as an important food source in the form of detritus. Detritivores and scavengers were dramatically (4 and 15 times, respectively) increased in living Spanish moss compared to the mimics, whereas herbivores were unaffected and numbers were low compared to the other guilds. This stimulation of the brown food web, that is, food webs with detritus as the dominant carbon input rather than living plant matter that drive green food webs, indirectly also appears to facilitate predators, which were also much more dominant within living Spanish moss. As predators were dominated by spiders in our study system and web-weaving spiders in particular, we would expect that habitat structure would be of particular importance to this group (diminishing the effect of living vs mimic plants). In contrast, however, this group was greatly enhanced in living Spanish moss compared to the mimics (Appendix S1: Fig. S4) without any interaction with festoon size. These results thus suggest that

most predators in the festoons actually depend on local rather than external prey—probably mostly detritivores and scavengers—even in the case of web-weaving spiders.

Earlier studies by Lawton and Schroder (1977), Strong and Levin (1979), and Moran (1980) on herbivorous insects showed a strong dependency on plant size and plant structure. We did not find such a relationship in our data, probably as herbivores were strongly underrepresented in our dataset. The number of herbivores in live Spanish moss does seem to increase with patch size, although this effect is not significant. In the plant mimics, there was no effect of patch size on herbivore numbers, which is surprising since non-trophic interactions such as predator avoidance and nursery function will be important for herbivores. Herbivores in our dataset consisted mostly of granivorous beetles that are known to hibernate in Spanish moss (Rainwater 1941). Apart from *Orthezia tillandsiae*, the herbivores do not feed primarily on Spanish moss and can be considered as transient visitors. As Spanish moss only holds 0.6% N, protein levels and thus food quality are relatively low. Therefore, the contribution of live Spanish moss to the green food web, that is, food webs with live plant material as the main carbon input, will be minor. However, although not significant, herbivores do seem to prefer live Spanish moss over the mimics, suggesting that some species may supplement their diet with Spanish moss tissue. On the other hand, the absence of herbivores in mimic festoons may also indicate that species entering a new habitat may evaluate their microhabitat both on food availability and on habitat architecture (Lawton and Schroder 1977, Strong and Levin 1979, Romero and Vasconcellos-Neto 2005).

#### *Trophic versus non-trophic effects*

Recent empirical, but correlative, studies investigating the non-trophic and trophic roles of foundation species suggest that their non-trophic interactions are far more important than trophic interactions in facilitating other species (Miller et al. 2015, Christianen et al. 2016, van der Zee et al. 2016). These studies argue that foundation species are typically rather unpalatable and are therefore relatively unimportant as a food source. Although our experimental

manipulations indeed support the notion that Spanish moss, as a secondary foundation species (Angelini and Silliman 2014: Chapter 2) is relatively unimportant as living plant tissue, they also show that it has an important trophic role by stimulating the brown food web via decaying plant tissue. Although thus far hardly considered, such stimuli of the food web by foundation species may also be important in many other foundation species-structured ecosystems as well. For instance, studies on kelp trying to disentangle the contribution of detritus of kelp and phytoplankton seem to show a substantial contribution of kelp detritus to the diet of suspension feeders (Kaehler et al. 2000, 2006). This view is supported by earlier work showing that detritus is often pooled as one homogeneous food resource, rather than a separate compartment in food web studies, and emphasizes the urgent need to disentangle trophic pathways mediated by the brown web (Moore et al. 2004, Miller and Page 2012, Campaña-Llovet et al. 2017). In this study, we provide compelling evidence that foundation species, next to their structuring role, can significantly contribute as a food source via the brown food web.

## CONCLUSION

Overall, we conclude that foundation species can stimulate community-level biodiversity through multiple distinct pathways. First of all, our experimental results confirm the notion that foundation species, by increasing habitat structure, enhance both species and guild richness. Importantly, however, our results also provide unequivocal evidence that when their detritus is processed locally in the brown part of the food web, foundation species can greatly stimulate biodiversity. Moreover, we show that the effects of habitat structure and food availability may act independently of patch size to increase biodiversity.

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