

# Secondary foundation species as drivers of trophic and functional diversity: evidence from a tree–epiphyte system

CHRISTINE ANGELINI<sup>1</sup> AND BRIAN R. SILLIMAN

Department of Biology, University of Florida, Gainesville, Florida 32611 USA

**Abstract.** Facilitation cascades arise where primary foundation species facilitate secondary (dependent) foundation species, and collectively, they increase habitat complexity and quality to enhance biodiversity. Whether such phenomena occur in nonmarine systems and if secondary foundation species enhance food web structure (e.g., support novel feeding guilds) and ecosystem function (e.g., provide nursery for juveniles) remain unclear. Here we report on field experiments designed to test whether trees improve epiphyte survival and epiphytes secondarily increase the number and diversity of adult and juvenile invertebrates in a potential live oak–*Tillandsia usneoides* (Spanish moss) facilitation cascade. Our results reveal that trees reduce physical stress to facilitate *Tillandsia*, which, in turn, reduces desiccation and predation stress to facilitate invertebrates. In experimental removals, invertebrate total density, juvenile density, species richness and  $H'$  diversity were 16, 60, 1.7, and 1.5 times higher, and feeding guild richness and  $H'$  were 5 and 11 times greater in *Tillandsia*-colonized relative to *Tillandsia*-removal limb plots. *Tillandsia* enhanced communities similarly in a survey across the southeastern United States. These findings reveal that a facilitation cascade organizes this widespread terrestrial assemblage and expand the role of secondary foundation species as drivers of trophic structure and ecosystem function. We conceptualize the relationship between foundation species' structural attributes and associated species abundance and composition in a Foundation Species–Biodiversity (FSB) model. Importantly, the FSB predicts that, where secondary foundation species form expansive and functionally distinct structures that increase habitat availability and complexity within primary foundation species, they generate and maintain hot spots of biodiversity and trophic interactions.

**Key words:** biodiversity; community structure; facilitation cascade; food web; invertebrate; nursery habitat; positive interaction; predator–prey interaction; *Tillandsia usneoides*.

## INTRODUCTION

Experimental and comparative studies of habitat-forming foundation species (sensu Dayton 1972; see Bruno and Bertness 2001 for refined definition) have revealed time and again that these organisms can have positive effects on biodiversity by generating the structure and conditions within which other species and their interactions, such as competition or predation, occur (Bruno and Bertness 2001, Stachowicz 2001, Bruno et al. 2003). The overwhelming focus of this research has been on single foundation species (e.g., Douglas fir, *Pseudotsuga menziesii*; poplar, *Populus angustifolia* and *P. fremontii*; smooth cordgrass, *Spartina alterniflora*) or functional groups (e.g., nurse shrubs, corals, kelp) because these spatially dominant organisms are thought to be the primary drivers of community composition (Ellison et al. 2005, Whitham et al. 2006, Irving and Bertness 2012). Secondary, or dependent, foundation species can be among those organisms facilitated by a primary foundation species (e.g., ribbed

mussels, *Geukensia demissa*, within cordgrass), and, by creating significantly more structure or unique refuges from physical or biotic stress, may modify the number and identity of individuals in the local community (Altieri et al. 2007, Yakovis et al. 2008, Bishop et al. 2012, Dijkstra et al. 2012). Given that multiple habitat-forming species are present in many systems, secondary foundation species may be common, but currently underappreciated, drivers of biodiversity and ecosystem functioning (Thomsen et al. 2010, Angelini et al. 2011).

Ecologists interested in whole-community facilitation by foundation species (Bruno and Bertness 2001, Whitham et al. 2006, Rowntree et al. 2011) have documented higher abundance and richness of associated species where primary foundation species facilitate secondary foundation species (Altieri et al. 2007, Yakovis et al. 2008, Bishop et al. 2012, Dijkstra et al. 2012). This positive direct interaction among foundation species that gives rise to indirect facilitation of biodiversity has been coined a facilitation cascade (sensu Altieri et al. 2007). To date, no study has experimentally tested for the presence of facilitation cascades in terrestrial or aquatic systems, and few have extended their analyses of secondary foundation species' impacts beyond abundance and richness measures to include

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<sup>1</sup> E-mail: Choldredge@ufl.edu



FIG. 1. A potential example of a facilitation cascade is *Quercus virginiana* (Southern live oak) laden with *Tillandsia usneoides* (Spanish moss) in southeastern U.S. coastal savannas. Photo credit: Matthew D. Smith.

more functionally informative metrics of community structure (see Altieri et al. 2007, Dijkstra et al. 2012). To gauge whether the facilitation cascade concept holds broad utility, more research on foundation species' interactions in novel biomes is needed. Likewise, analyses that distinguish whether secondary foundation species simply enhance the size (i.e., support more individuals of the same species, feeding guilds, or life stages), and/or influence trophic structure (i.e., support new species and feeding guilds) and life stage diversity (i.e., support juveniles) of local communities, are critical to evaluate whether facilitation cascades also drive spatial patterns in food web complexity, species interactions, and nursery habitat, community characteristics that influence ecosystem functioning (Hooper et al. 2005). Beyond understanding the generality of facilitation cascades and their impact on community structure, we must also begin to construct conceptual models that formalize predictions for when and where these chains of positive interactions will generate hot spots of biodiversity and the more numerous and complex species interactions and ecosystem processes that can follow.

The association between trees and vascular epiphytes is a useful system in which to explore generality of facilitation cascades and the contribution of primary and secondary foundation species in regulating trophic structure and ecosystem function. Epiphytes, including thousands of charismatic species from Bromeliaceae, Orchidaceae, and Araceae families, are distributed throughout tropical and subtropical latitudes (Benzing

1990) and generate intricate structures within the broader architecture of host trees (Freiberg 2001, Stuntz et al. 2002). Although it is commonly assumed that epiphytes are intolerant of abiotic (e.g., high moisture, low light) and biotic (e.g., high consumer pressure) conditions on the ground (Nadkarni 1992, Matelson et al. 1993, Mondragón et al. 2004), ecologists have yet to use manipulative experiments to test if and how epiphytes depend on host trees (Zotz and Hietz 2001). In addition, epiphytes are commonly recognized as facilitators in metacommunity, tropical biodiversity, and community genetic studies, that is, they often form complex structures that support other organisms such as ants, frogs, protists, snails, spiders, and birds (Nadkarni 1989, 1994, Ellwood and Foster 2004, Dial et al. 2006, Cruz-Angón et al. 2009, Yanoviak et al. 2011, Zytynska et al. 2011). Despite these facts, they are not typically identified as foundation species (but see Thomsen et al. 2010 for discussion), and have never been studied as critical, intermediate links in facilitation cascades.

Here we explore the mechanisms that generate a facilitation cascade which likely organizes the most conspicuous tree–epiphyte assemblage in the southeastern United States: Southern live oaks (*Quercus virginiana*, hereafter, oaks) laden with the atmospheric bromeliad *Tillandsia usneoides* (commonly Spanish moss, hereafter *Tillandsia*; Fig. 1). Specifically, we test: (1) whether oaks and *Tillandsia* can act as primary and secondary foundation species, respectively, and collectively generate a facilitation cascade, and (2) if *Tillandsia*

enhances the density and diversity of species, feeding guilds, and life stages, and thus supports communities that are larger than and functionally distinct from those associated with oaks alone. We then compare invertebrate communities associated with oaks and both oaks and *Tillandsia* at sites distributed across the southeastern United States to test whether this epiphyte supports more complex food webs and generates nursery habitat wherever it overlaps with oaks.

#### METHODS

Field experiments were conducted in the National Estuarine Research Reserve on Sapelo Island, Georgia, USA (31°24'2" N, 81°17'4" W) in Bahia grass (*Paspalum notatum*) savannas interspersed with open-grown oaks (>30 cm crown diameter). This oak species was selected for this study because it is a common, "high-quality" epiphyte host (Callaway et al. 2002). *Tillandsia*, a CAM-photosynthesizing, rootless vascular plant that forms densely tangled clumps referred to as "festoons" was examined because of its extremely high abundance and widespread distribution in the southeastern United States (Benzing 1990). In this region, many other tree species host *Tillandsia* (Callaway et al. 2002) and other epiphyte species colonize oaks (Benzing 1990).

##### *Oak facilitation of Tillandsia: an experiment*

We first assessed whether *Tillandsia* depends on primary facilitation of trees by tracking the survival of festoons left on and removed from oak hosts. In May 2010, we identified a large oak at two sites and, within each oak, selected 15 festoons, standardized for volume (40 cm<sup>3</sup>), health (90–95% live tissue), and position (4 m off the ground, 5 m from canopy edge) on different branches and randomly assigned each to one of three treatments: oak limb control, procedural control, or oak limb removal [ $N = 5$  replicates per treatment per site]. For oak limb control treatments, we flagged but did not alter the position of festoons. For procedural control treatments, we removed and immediately replaced festoons on oak limbs to account for disturbance effects. For oak limb removal treatments, we removed and dropped flagged festoons on the ground. After 60 days, we assessed survival by saturating festoons in a bucket of water, refreshed after each replicate, and scoring plants for the percentage of live tissue. Wetting distinguishes live *Tillandsia* tissue, which is green when wet, from dead tissue, which is brown (Appendix: Fig. A1). The percentage survival data were arcsine (square-root) transformed to meet the assumptions of normality. We treated Site as a random factor, Oak Treatment as a fixed factor, and assessed their effect on festoon survival using mixed-effects analysis of variance (ANOVA).

We then tested the hypothesis that shading and elevation off the ground are two mechanisms by which host trees facilitate *Tillandsia*. To do so, we haphazardly assigned a Shade and Elevation treatment to each of 40, 40-cm<sup>2</sup> plots (four treatments: Shade/No Shade ×

Elevated/Ground,  $N = 10$  replicates) positioned within a Bahia grass patch located 75 m from a *Tillandsia*-laden oak in July 2010. We then air-dried and weighed 30-g *Tillandsia* transplants, collected from a single oak and standardized for live tissue (90–95%). We secured two layers of black mesh to corner stakes 60 cm above shade plots and left no-shade plots unmanipulated. To assess if shades mimicked the ~60% light attenuation provided by oak foliage in savannas (Appendix: Fig. A2), we monitored photosynthetically active radiation (PAR) in shade and no-shade plots on a cloudless day using a handheld light meter. To manipulate elevation, we positioned transplants 25 cm off the ground on grass turfs in elevated plots or directly on the ground in unmanipulated ground plots. We placed an iButton (Hygrochron, Embedded Data Systems, Lawrenceburg, Kentucky, USA), programmed to record one temperature reading per hour, in one transplant per treatment for the experiment's duration. After 3, 7, 14, 28, and 56 days, we monitored transplant survival as previously described. The effect size and significance of Shade, Elevation, and their interaction over time on the percentage of *Tillandsia* survival, transformed as previously described, was assessed with repeated-measures ANOVA.

##### *Tillandsia facilitation of invertebrates: the physical environment*

To assess whether *Tillandsia* functions as a secondary foundation species that moderates physical stress within oaks, we monitored temperature and humidity, factors known to influence invertebrate desiccation and survival (Wigglesworth 1945, Stuntz et al. 2002, Ellwood et al. 2011). In one oak at two savannas, we deployed three pairs of Hygrochron iButtons, programmed to record temperature and relative humidity hourly from 7 April to 17 May 2012. In each pair, one logger was positioned on a *Tillandsia*-colonized limb surface, and the other 0.5 m away on a limb of a similar size and elevation that lacked *Tillandsia*. This arrangement was used to minimize variation in canopy microclimate and thus isolate the effect of *Tillandsia*. For each pair, we calculated the difference (i.e.,  $Y_i = \text{Tillandsia-colonized}_i - \text{uncolonized}_i$ ) in mean daytime temperature, mean humidity, and the coefficient of variation (CV) of humidity. We assessed the CV in humidity because invertebrates have been shown to survive better in habitats characterized by stable (low-CV) humidity conditions (Bertrand and Wilson 1996). We then calculated the mean difference for each metric for each day at each site [ $Y_m = (Y_1 + Y_2 + Y_3)/3$ ] and used a  $t$  test to assess if mean differences in each metric significantly differed from zero.

##### *Tillandsia facilitation of invertebrates: survival*

To assess if *Tillandsia* is an effective foundation species and improves invertebrate survival within oaks, we conducted two experiments. First, to assess whether

*Tillandsia* increases invertebrate survival in the absence of predators and alleviates other potential sources of mortality within oaks, we constructed 30 × 60 cm mesocosms (diameter × length; Appendix: Fig. A3a) and stocked each with either a 25-cm limb draped with a vacuumed 25-g *Tillandsia* festoon, or a 25-cm limb without *Tillandsia* ( $N = 3$  replicates per treatment). We attached an iButton programed as above to each experimental limb and added 10 juvenile isopods (*Venezillo parvus*), which are common within oaks at our study site, to each mesocosm. Mesocosms were hung 4 m off the ground from limbs with similar light exposure within one oak. After seven days, we collected the iButtons, counted live isopods, and used a generalized linear model with a quasibinomial error function to test the effect size and significance of *Tillandsia* treatment on the number of live and dead isopods, using R version 2.15.1 (R Core Development Team 2012).

Next, to test if *Tillandsia* modifies predator foraging efficiency to enhance prey survival, we added either a 25-cm long oak limb and 25-g festoon, vacuumed to remove invertebrates, or a 25-cm limb without *Tillandsia* to 5-L arenas ( $N = 5$  replicates per *Tillandsia* treatment) positioned in the shade and stocked each with four juvenile field crickets (*Gryllus* spp.). We allowed crickets to acclimatize for two hours before adding one spider (*Gladicosa pulchra*) to each arena. Crickets and spiders were used as representative prey and predators because they are common and abundant in our study system. After 12 hours, we counted live crickets and inspected dead crickets for spider wounds to rule out other potential causes of death. The effect of *Tillandsia* treatment on the number of live and dead crickets was analyzed with a generalized linear model, as described previously.

*Oak–Tillandsia facilitation of invertebrates:  
community responses*

To test the hypothesis that *Tillandsia* not only increases invertebrate abundance and richness but also enhances food web structure (i.e., increases the number and diversity of feeding guilds) and functions as a nursery (i.e., supports juveniles) within oaks, we identified two, 1-m<sup>3</sup> *Tillandsia*-colonized plots standardized for limb diameter, height off the ground (4 m), festoon volume (30 cm long × 30 cm wide × 60 cm high), festoon health (90% live), and distance to adjacent festoons (2–3 m to nearest neighbor), in each of 15 oaks. In each oak, we randomly assigned a *Tillandsia* removal or control treatment to each plot: in removal plots, we extracted the festoon, leaving only the oak limb, and in control plots, we removed and immediately replaced the festoon. After eight weeks, we used a 190-L (50-gallon) plastic bag to envelop each plot, collect the festoon (if present), and capture all detritus and invertebrates that we brushed from each limb surface for 30 seconds. We ran each bagged sample over a vacuum (i.e., a leaf

blower equipped with an insect screen attachment) for one minute to isolate invertebrates. All macroinvertebrates were counted and sorted to morphospecies (hereafter, species), life stage (juvenile or adult, based on size and genitalia development), and feeding guild (predator, parasite, scavenger, detritivore, folivore, granivore, or nectarivore, assigned after consultation with experts at Florida Department of Agriculture and Consumer Services, Division of Plant Industries; see Appendix: Table A1 for species list).

To evaluate *Tillandsia*'s effect on different metrics of community structure, we assigned Tree as a random factor, *Tillandsia* Presence as a fixed factor, and used a mixed-effects ANOVA to assess their effect size and significance on invertebrate density (individuals per cubic meter), juvenile density (juveniles per cubic meter), species richness, species diversity (Shannon-Wiener,  $H'$ ), feeding guild richness, and feeding guild diversity ( $H'$ ). To investigate whether the composition of functional groups differed in *Tillandsia*-present and *Tillandsia*-removal plots, we calculated the proportional contribution of each functional group and conducted a multivariate ANOVA using the lme4 package in R (Bates et al. 2012). Significance of *Tillandsia* treatment was assessed with Pillai's trace test statistic (as in Jaschinski et al. 2009). We also rarefied our data to compare species and feeding guild richness metrics at a standard sample size (Gotelli and Colwell 2001) using the rich package in R (Rossi 2011). To evaluate the significance of *Tillandsia* treatment on rarefied richness metrics, we conducted 499 randomizations of our data, drawing samples with replacement, to calculate the probability,  $p$ , of observing differences between *Tillandsia*-present and *Tillandsia*-removal plots equal to or more extreme than observed differences in richness (Rossi 2011).

*Generality of oak–Tillandsia facilitation of invertebrates:  
latitudinal survey*

In September 2010, we surveyed invertebrate communities associated with oak or both oak and *Tillandsia* foundation species at six sites distributed from Harker's Island, North Carolina (34°42' N, 76°34' W) to Palm Coast, Florida (29°37' N, 81°12' W), to assess consistency in the strength of this potential facilitation cascade across a range in which live oaks and *Tillandsia* commonly overlap. At each site, we identified six oaks (only five in Palm Coast [FL1] because of time constraints) colonized by *Tillandsia*, and within each, selected one 1-m<sup>3</sup> uncolonized (*Tillandsia*-absent) limb plot and one 1-m<sup>3</sup> *Tillandsia*-colonized limb plot, and bagged, brushed, and vacuum-sampled invertebrates. Sampled invertebrates were stored in 70% ethanol. Using a microscope at 25×, we counted macro- and micro-invertebrates and categorized individuals as described in *Oak–Tillandsia facilitation of invertebrates: community responses* (see Appendix: Table A2 for species list). Since we had no a priori expectation that

communities would differ among trees within a site, we excluded Tree as a factor, nested *Tillandsia* Presence within Site, and assessed the effects of Site and Presence [Site] on the community metrics listed above using ANOVA. We used multivariate ANOVA to test the significance of Site and Presence [Site], assessed with Pillai's trace test statistic, on functional group composition. Within each site, we used randomization tests to calculate the probability, *p*, of measuring species and feeding guild richness differences between *Tillandsia*-present and *Tillandsia*-absent plots equal to or more extreme than our observed differences.

RESULTS

After two months, festoons assigned to oak control and procedural control treatments positioned on limbs survived (>85% live tissue), while those removed from trees (i.e., on the ground) died at both sites ( $\leq 17\%$  live, Oak Limb Presence:  $F_{2,26} = 357.6$ ,  $P < 0.0001$ ; Fig. 2a). In the experiment designed to test mechanisms of tree facilitation, *Tillandsia* positioned in control light and no-elevation ground plots experienced intensive light (Appendix: Fig. A2) and persistently high temperatures (Fig. 2b) and died rapidly (Fig. 2c). In contrast, *Tillandsia* survived for the 56-day experiment in treatments where transplants were both shaded and elevated (Time  $\times$  Shade  $\times$  Elevation:  $F_{5,32} = 20.7$ ,  $P = 0.0007$ ; Fig. 2c).

Monitoring revealed that daytime temperatures were typically cooler on *Tillandsia*-colonized relative to paired uncolonized limbs at our two sites (*Tillandsia* Presence,  $t_{40} > 8.6$ ,  $P < 0.0001$ , Fig. 3a). In addition, relative humidity was higher (*Tillandsia* Presence,  $t_{40} > 12.6$ ,  $P < 0.0001$ , Fig. 3b) and more stable (i.e., lower CV, *Tillandsia* Presence,  $t_{40} > 4.18$ ,  $P < 0.0001$ , Fig. 3c) on *Tillandsia*-colonized relative to uncolonized limbs.

In experimental mesocosms hung within an oak, *Tillandsia* increased juvenile isopod survival ( $77\% \pm 9\%$  vs.  $37\% \pm 9\%$  alive, *Tillandsia* Presence,  $T_4 = 2.81$ ,  $P = 0.0482$ ). Temperatures were lower and humidity higher in *Tillandsia*-present relative to *Tillandsia*-absent mesocosms (Appendix: Fig. A3b), as observed in canopy monitoring (Fig. 3). Similarly, *Tillandsia* significantly reduced spider predation to increase juvenile cricket survival (mean  $\pm$  SE,  $95\% \pm 5\%$  vs.  $60\% \pm 6\%$  alive, *Tillandsia* Presence,  $T_8 = 2.74$ ,  $P = 0.0256$ ). All dead crickets had spider wounds.

In our field experiment, all community metrics were higher in *Tillandsia*-present than in *Tillandsia*-removal plots (Table 1). *Tillandsia*-present plots not only contained 20 $\times$  more invertebrates, but also functioned as a nursery and supported 60 $\times$  more juveniles than *Tillandsia*-removal limbs (juveniles comprised 30% vs. 2% of the total community, on average, in each plot type). Similarly, *Tillandsia* increased species richness and species *H'* 6- and 10-fold, and feeding guild richness and *H'* 5- and 11-fold relative to removal plots. The composition of functional groups was also significantly different among treatments, such that detritivores,

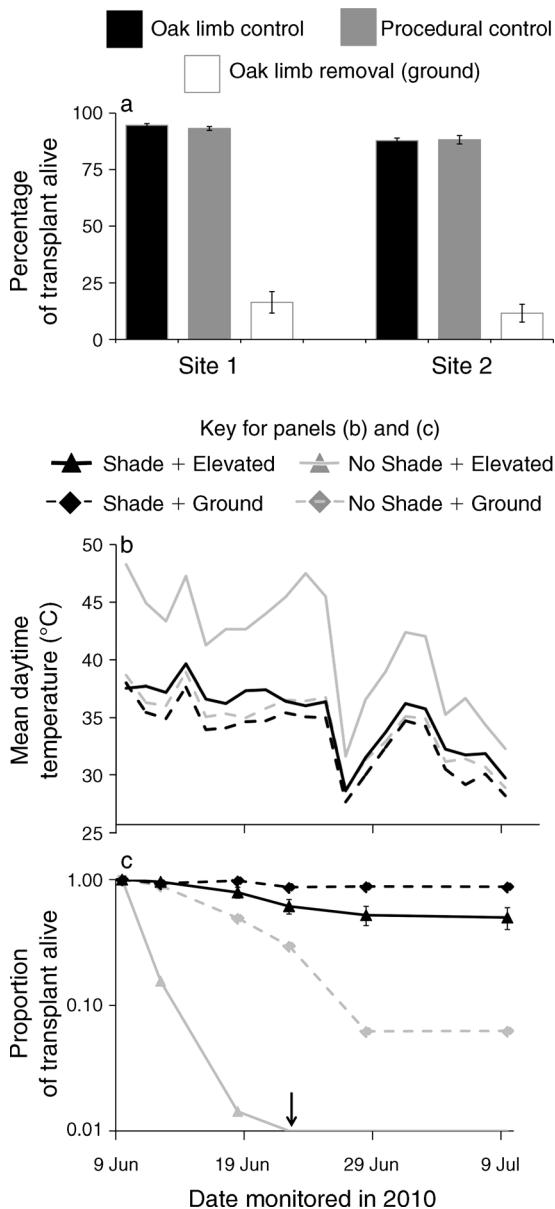


Fig. 2. Summary of two experiments testing the presence and mechanisms underlying oak facilitation of *Tillandsia*. (a) Effect of oak presence, meaning *Tillandsia* festoons were positioned on limbs (oak limb control and procedural control), and oak limb removal, meaning festoons were positioned on the ground, on survival at two sites. Effect of Shade and Elevation treatments on *Tillandsia* transplant: (b) mean daytime temperature and (c) survival, shown on a log scale, over the 2010 study period. In panels (a) and (c) data are shown as mean  $\pm$  SE. The arrow in panel (c) denotes when no transplants survived (0% survival).

omnivores, predators, and parasites were common in *Tillandsia*-present plots, while only detritivores were common in *Tillandsia*-removal plots (Pillai's trace = 0.61,  $F = 7.50$ ,  $P = 0.0002$ ). Rarefaction indicated there were approximately 2 $\times$  more species and feeding guilds on *Tillandsia*-present than *Tillandsia*-removal limbs.

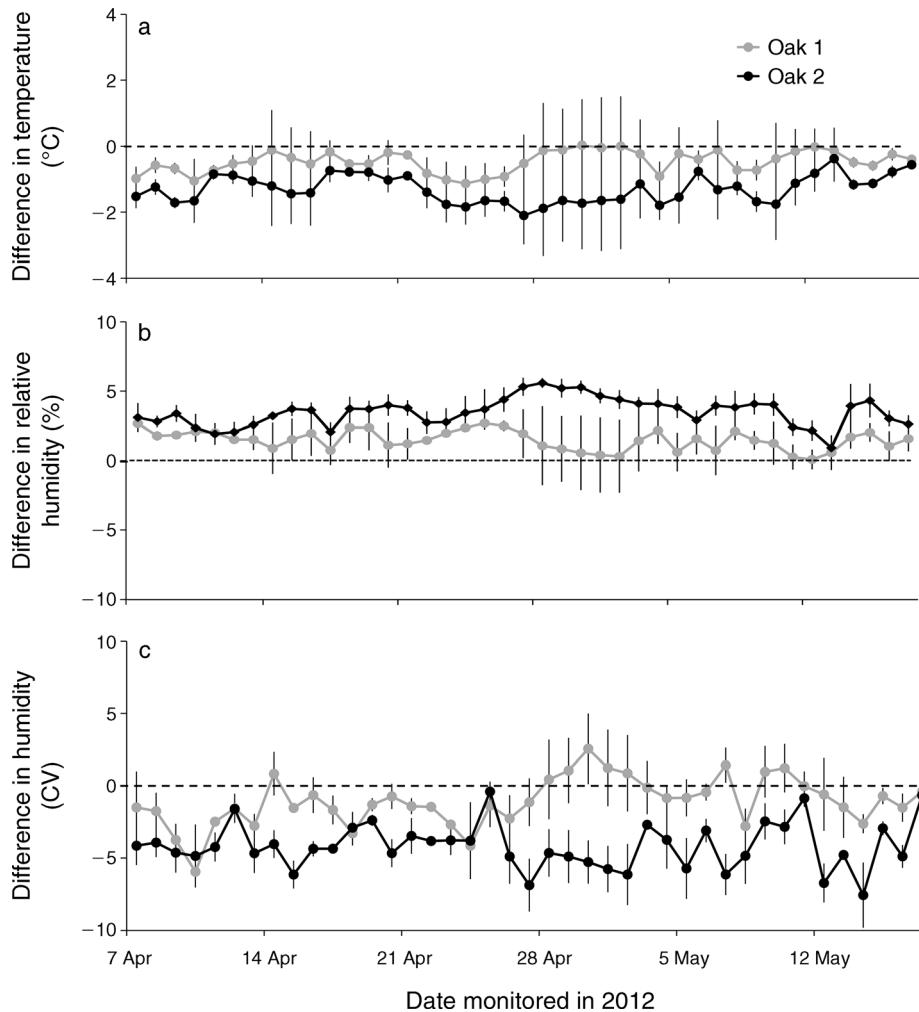


FIG. 3. Difference in (a) mean temperature, (b) relative humidity, and (c) the coefficient of variation in relative humidity between *Tillandsia*-colonized and uncolonized limbs in two oaks. Points below the dashed zero line denote days where mean temperature or humidity levels were lower and humidity more stable (i.e., less variable) on *Tillandsia*-colonized limbs relative to paired uncolonized limbs. Data are summarized as the mean difference in daytime mean ( $\pm$  SE) for three replicate iButton pairs per oak (see *Methods: Oak facilitation of Tillandsia: an experiment*).

TABLE 1. Summary of invertebrate community response to *Tillandsia* presence or removal. Data are shown as the mean (and standard error) for 15 replicates per treatment.

Response (per m <sup>3</sup> plot)	Present		Removed		$F_{1,14}$	$P$
	Mean	SE	Mean	SE		
No. individuals	22.5	4.7	1.1	0.3	20.7	0.0005
No. juveniles	6.1	1.1	0.1	0.1	30.7	<0.0001
Juvenile (%)	30	4.2	2.2	2.2	57.8	<0.0001
Species richness	5.9	0.5	0.7	0.2	100.7	<0.0001
Species $H'$ diversity	0.58	0.05	0.05	0.03	78.1	<0.0001
Feeding guild richness	3.5	0.2	0.7	0.2	125.7	<0.0001
Feeding guild $H'$ diversity	0.38	0.03	0.03	0.02	64.4	<0.0001
Rarefied species richness†	5.9	0.5	0.7	0.2	NA	0.01
Rarefied feeding guild richness†	3.5	0.2	0.7	0.2	NA	0.01

† Mean, standard error, and  $P$  value are based on 99 randomizations of *Tillandsia*-present and *Tillandsia*-removal plot communities conducted in R.

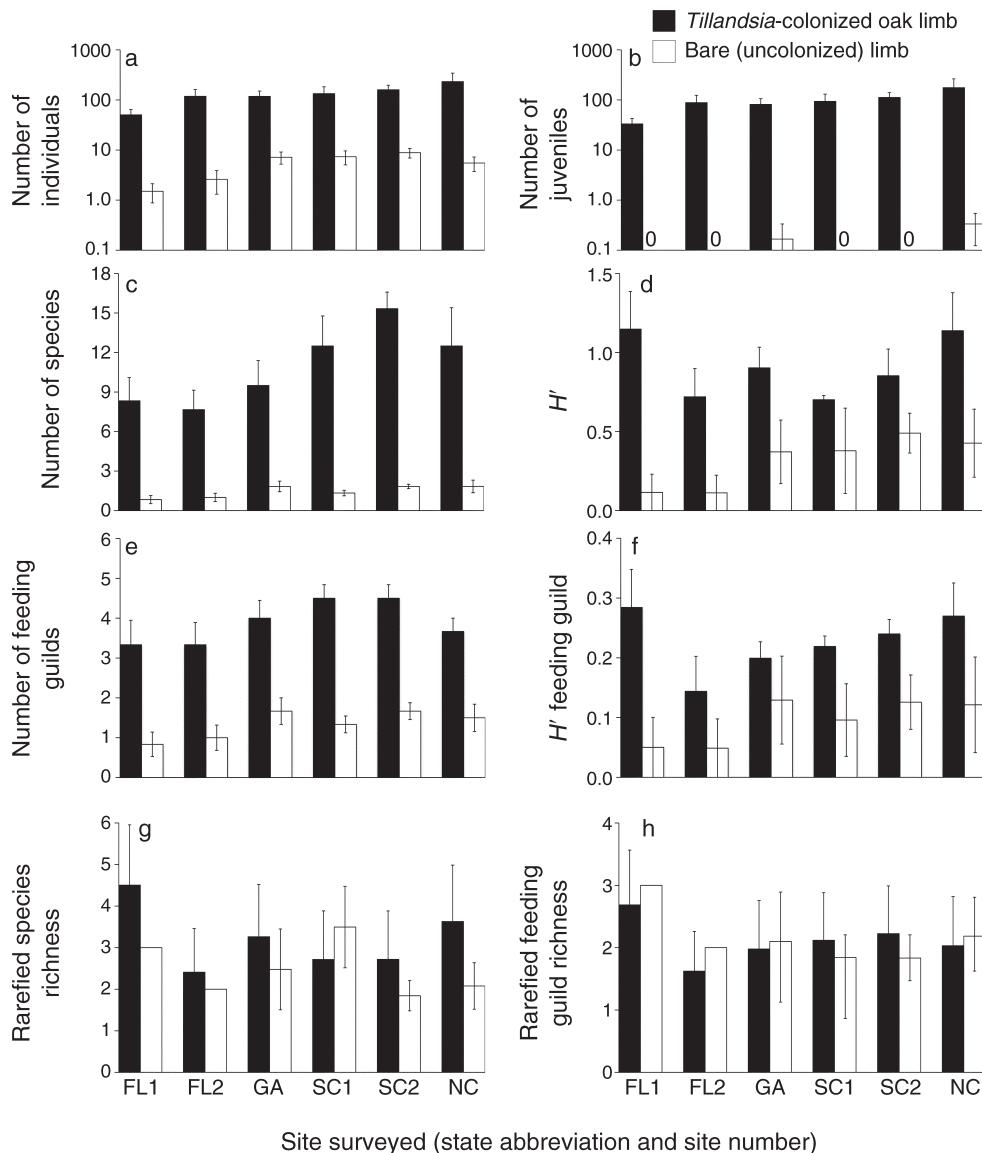


FIG. 4. (a) Invertebrate total density, (b) juvenile density, (c) species richness, (d) Shannon-Wiener  $H'$ , (e) number of feeding guilds, (f) feeding guild  $H'$ , (g) rarefied species richness, and (h) rarefied feeding guild richness on *Tillandsia*-colonized (black) vs. uncolonized (white) 1-m<sup>3</sup> live oak limb plots at six sites listed by state on the x-axis. Data are shown as mean  $\pm$  SE. Note the y-axis logarithmic scales in panels (a) and (b). Tables 2 and 3 report results from ANOVA and randomization tests.

In our survey, we found a significant effect of site on invertebrate density, richness, and diversity; the magnitude of between-site differences was minor relative to that of *Tillandsia* Presence effects within site, however (Fig. 4). Specifically, invertebrate density, species richness, and species  $H'$  were  $>16\times$ ,  $5\times$ , and  $1.7\times$  higher in *Tillandsia*-present plots than *Tillandsia*-absent plots. We found no juveniles in uncolonized limbs, and at the two sites where they were found in both plot types, *Tillandsia* increased average juvenile density from  $<1$  to  $>80$  individuals/m<sup>3</sup>. Feeding guild richness and  $H'$  were  $>2.4\times$  and  $1.5\times$  greater on *Tillandsia*-present

relative to *Tillandsia*-absent limbs. Invertebrates were largely detritivores and scavengers on bare limbs, while those on *Tillandsia*-present limbs often included detritivore (e.g., roaches, isopods, scale bugs), scavenger (e.g., ants, crickets), granivore (e.g., weevils), predator (e.g., ladybird beetles, spiders), and parasite (e.g., mite, parasitic wasp) guilds (Pillai's trace = 0.54,  $F = 10.35$ ,  $P < 0.0001$ ; Appendix: Fig. A4). Finally, rarefaction analyses indicated that communities were more species- and feeding guild-rich on *Tillandsia*-present vs. *Tillandsia*-absent limbs at five of our six sites (Fig. 4, Tables 2 and 3).

TABLE 2. Results from nested Analyses of Variance testing for the effect of Site and *Tillandsia* Presence within Site on six metrics of invertebrate community structure.

Response per m <sup>3</sup> plot	Site		<i>Tillandsia</i> Presence [Site]	
	<i>F</i> <sub>5,59</sub>	<i>P</i>	<i>F</i> <sub>6,59</sub>	<i>P</i>
No. individuals	3.7	0.056	33.57	<0.0001
No. juveniles	0.84	0.53	66.33	<0.0001
Species richness	3.97	0.0036	47.54	<0.0001
Species <i>H'</i> diversity	0.89	0.49	6.13	<0.0001
Feeding guild richness	2.99	0.02	22.03	<0.0001
Feeding guild <i>H'</i>	0.77	0.57	3.43	0.0057

#### DISCUSSION

Our results demonstrate that a facilitation cascade structures oak–*Tillandsia* invertebrate communities in southeastern U.S. coastal savannas. In this assemblage, oaks function as primary foundation species that ameliorate solar and temperature stress with their foliage and elevated limbs to facilitate *Tillandsia*. *Tillandsia*, in turn, functions as a secondary foundation species within oaks and further reduces desiccation stress and predator foraging efficiency to facilitate invertebrates. Importantly, our analyses reveal that *Tillandsia* supports communities that are not only larger and more species rich, but also contain far more juveniles and feeding guilds than those supported by oaks alone. Together with examples from marine and coastal systems, this study advances two ideas: (1) hierarchical organization of communities based on direct and indirect facilitation of multiple foundation species occurs across biomes, and (2) secondary foundation species can generate additional habitat and unique refuges within primary foundation species to locally enhance species abundance, food web complexity, and key ecosystem functions, such as nursery provision.

#### *Mechanisms maintaining tree–epiphyte facilitation cascades*

Although it is intuitive that host trees facilitate epiphytes (Zotz and Hietz 2001), the mechanisms underpinning these obligate associations have never been tested experimentally as far as we are aware. Studies that monitor the fate of dislodged epiphytes infer from observations that physical (e.g., low light, high moisture) and biotic (e.g., consumption by invertebrates, bacteria, and fungi) pressures not present in tree canopies are the likely drivers of plant death on the

ground (Nadkarni 1992, Matelson et al. 1993, Zotz and Hietz 2001). In our experiments, *Tillandsia* senesced when removed from host trees (Fig. 2a) suggesting that it is intolerant of temperature and light levels associated with the ground in the temporal and spatial context of our study, but survived for two months in the terrestrial environment if these specific physical stressors were relieved (Fig. 2c). In other seasons, habitat types, or latitudes, we suspect that *Tillandsia* depends on host trees for refuge from a number of other stressors, such as high moisture, given that its trichomes flatten and block CO<sub>2</sub> exchange when wet (Martin and Siedow 1981); nutrient limitation, since it acquires nutrients from tree leachates and atmospheric sources (Benzing 1990, Zotz and Hietz 2001); freezing temperatures; and fungal infestation (C. Angelini, *personal observation*). The broad conclusion here, that primary foundation species reduce multiple stressors to facilitate secondary foundation species, is consistent with other facilitation cascade studies (Altieri et al. 2007, Bishop et al. 2012), and highlights the fundamental importance of primary foundation species. Without their initial generation of habitat and modification of environmental conditions, most other species are unable to establish, and interactions among those species, including additional facilitation, fail to arise (Bruno and Bertness 2001, Silliman et al. 2011).

Within oaks, we found that festoons not only increase the amount of structure (Fig. 1), but also moderate two physical stressors, temperature and humidity (Fig. 3). Relative to bare limbs, *Tillandsia* extends periods of significantly lower temperatures and higher humidity for 4–5 days longer than bare oak limbs after rainstorms, which occurred during a trial iButton deployment (C. Angelini, *unpublished data*), but not during the persistently dry 2012 monitoring period. Prior studies have shown that elevating temperatures only a few degrees Centigrade can increase water loss from invertebrate larvae and pupae by an order of magnitude (Wigglesworth 1945); by inference, we suspect that the more favorable physical conditions within *Tillandsia* may be key to invertebrate survival. In fact, our results indicate isopods suffer higher mortality on drier, hotter, uncolonized limbs compared to moister, cooler *Tillandsia*-colonized limbs. Although this simple experiment did not test specific mechanisms by which *Tillandsia* facilitates invertebrates, it did show that *Tillandsia* and oak limbs generate a higher-quality habitat for isopods than oaks alone. Since many epiphytes, such as tank

TABLE 3. Results from randomization tests performed for each site assessing the effect of *Tillandsia* Presence on rarefied species and feeding guild richness.

Response parameter	<i>Tillandsia</i> Presence ( <i>P</i> value from randomization test)					
	FL 1	FL2	GA	SC 1	SC2	NC
Rarefied species richness	0.01	0.02	0.01	0.01	0.01	0.01
Rarefied feeding guild richness	0.07	0.01	0.04	0.01	0.01	0.01

bromeliads or bird's nest ferns, form large structures that modify moisture and temperature levels within trees (Nadkarni 1994, Ellwood and Foster 2004, Dial et al. 2006), we predict that they also function as secondary foundation species and support novel species, life stages, and feeding guilds that require buffered environmental conditions.

Our mesocosm experiment indicated that *Tillandsia* also affects the strength of predator–prey interactions and thus ameliorates biotic stress. Given the relative size of spiders (larger) and juvenile crickets (smaller), we suspect that crickets maneuver through the intricate structure of festoons more easily than spiders and therefore escaped from predation better in *Tillandsia*-addition than in *Tillandsia*-absent mesocosms (Persson 1995, Dijkstra et al. 2012). The outcome of this experiment could potentially be reversed if other predator or prey species were considered. For instance *Synema viridans*, the green crab spider, is a cryptic ambush predator that is common within *Tillandsia* (C. Angelini, unpublished data) and may catch prey more efficiently in festoons relative to bare limbs. The concentration of potential prey within *Tillandsia* also seemed to attract predators (e.g., up to 7 spider species and 15 individual spiders, respectively, in a single festoon), which may further influence the frequency and outcome of predator–prey encounters (Crowder and Cooper 1982). Regardless of whether *Tillandsia* increases the relative success of a given predator or prey, our results support classic studies that identify habitat structure as a key factor controlling species interaction strength (e.g., Crowder and Cooper 1982, Irlandi 1994, Persson 1995). Given that habitat structure is generated by foundation species that themselves evolve, grow, and interact with the environment and other species, as opposed to static nonliving or generically labeled “biogenic structure,” the relationship between habitat structure and species interaction strength is certainly more dynamic than often considered (Bruno and Bertness 2001). In our study system, for example, the architecture of oak limbs and morphology of *Tillandsia* festoons vary across savannas and forests and with plant age, features of this living habitat that likely elicit changes in both community composition and strength of species interactions.

#### *Secondary foundation species as drivers of trophic structure and ecosystem functioning*

Results from our removal experiment and latitudinal survey suggest that *Tillandsia* does more than simply increase the number of invertebrate individuals: instead, it facilitates a greater number of species, feeding guilds, and life stages across its range of overlap with oaks (Table 1, Fig. 4). Although patterns in community structure were similar between our experiment and all surveyed sites, inclusion of superabundant, tiny organisms in our survey counts modified our initial perception of *Tillandsia*'s impact based on the experiment in two ways: (1) since micro-invertebrates form a large portion of *Tillandsia*-associated communities, we likely underes-

timated *Tillandsia*'s facilitative effects by only including macroscopic species; (2) since invertebrate density was ~100×, rather than 20×, greater on *Tillandsia*-limb plots, we likely overestimated differences in rarefied richness between plot types. In other words, our survey revealed that *Tillandsia* communities are larger, more species rich, and less even than measured in the experiment. In addition, green anole lizards (*Anolis carolinensis*; C. Angelini, personal observation), Cuban tree frogs (*Osteopilus septentrionalis*; P. D. R. Silliman, personal observation), and northern yellow bats (*Lasiurus intermedius*; C. Bland, unpublished data) are often found in festoons, hinting that the impact of this facilitation cascade extends to larger organisms. Interestingly, folivores, which derive energy and nutrients from live plants, were rare in our samples, while detritivores, which assimilate resources from decomposing plants and transfer them to higher trophic levels, were common and abundant. Dominance of detritivores has been noted in many epiphyte studies (Nadkarni 1994, Ellwood and Foster 2004, Dial et al. 2006, Cruz-Angón et al. 2009) and may suggest that brown (detritus-based), rather than green (plant-based), food webs mediate energy flow in systems with high epiphyte cover.

*Tillandsia* also appears to function as a nursery. In the field, we often noted eggs, molts, and nests in festoons, and 3512 of the 3515 juvenile invertebrates, which included spiderlings, cricket and cockroach nymphs, and larval ants, counted in our survey were from *Tillandsia*-present plots. Other facilitation cascade studies have documented higher densities of juveniles within secondary foundation species as well (Altieri et al. 2007, Bishop et al. 2012, Dijkstra et al. 2012). The concentration of early life stages within secondary foundation species makes sense: these organisms are often susceptible to physical and biotic stress, and therefore benefit from the multiple levels of stress amelioration provided by primary and secondary foundation species. For the past decade, whole-community facilitation by foundation species has been recognized (Bruno and Bertness 2001, Bruno et al. 2003, Whitham et al. 2006, Rowntree et al. 2011), and what our study contributes to this concept is the idea that secondary foundation species can complement and magnify the facilitative effects of primary foundation species. In attracting novel species, life stages, and feeding guilds, secondary foundation species can increase the number and complexity of species interactions that occur, and likely increase the diversity of ecosystem services that the associated community can provide (e.g., pollination, nutrient cycling, pest control) to affect overall ecosystem functioning.

#### *Foundation Species–Biodiversity (FSB) model*

To date, facilitation cascade studies have focused on examples where layering of secondary foundation species within primary foundation species strongly enhances both species abundance and diversity. In many systems, facilitation cascades may have less dramatic

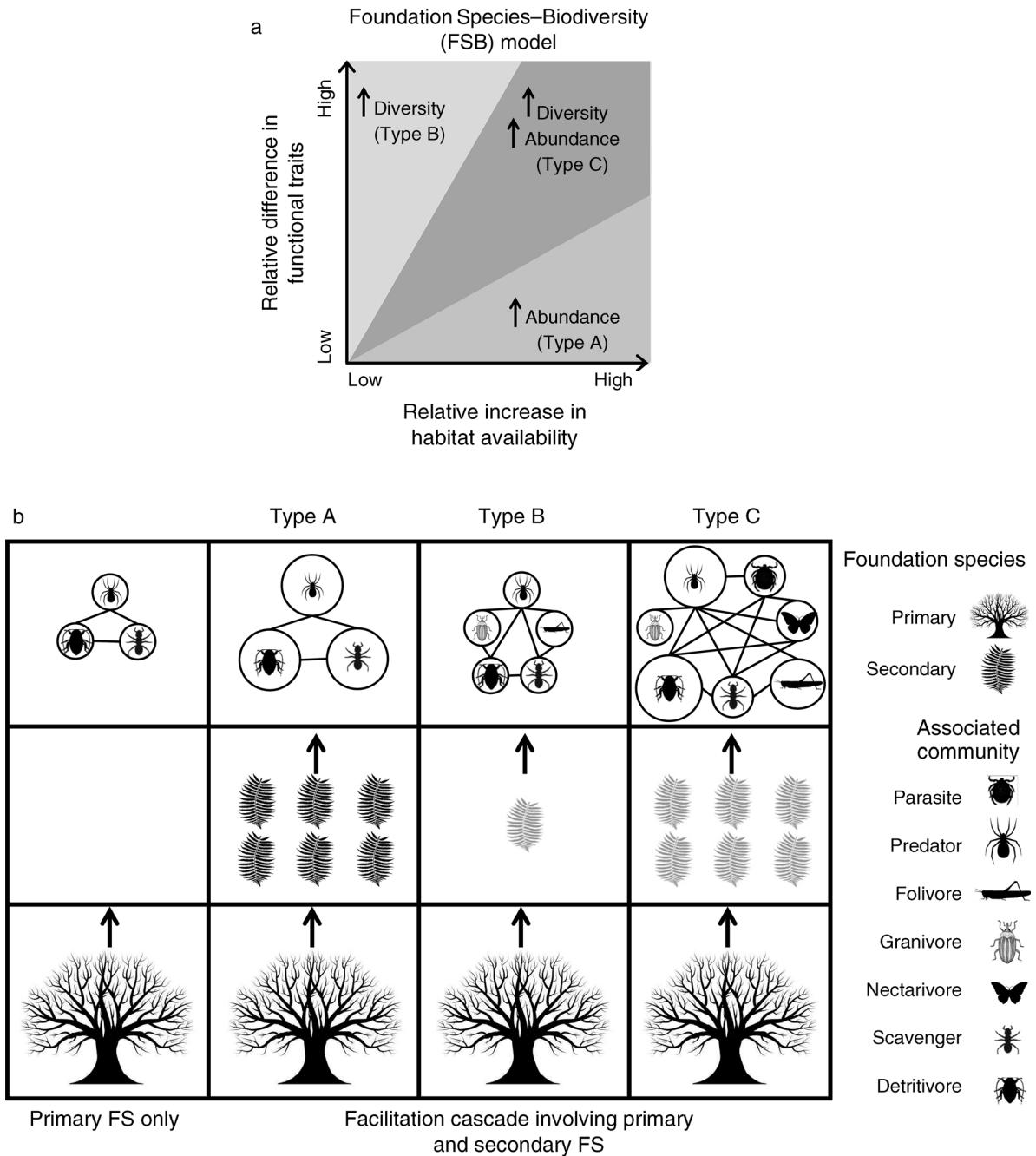


FIG. 5. (a) The Foundation Species–Biodiversity model and (b) visual diagram of the three types of facilitation cascades it predicts. Where secondary foundation species increase habitat availability within a primary foundation species, we predict they enhance abundance (Type A); where secondary foundation species exhibit functional traits different from those of the primary foundation species, we predict they enhance diversity (Type B); and where they both increase habitat availability and exhibit different functional traits, they enhance abundance and diversity (Type C). Abundance and diversity increases are relative to communities associated with a primary foundation species alone. Primary foundation species (tree icon) may directly facilitate communities, as shown in the left panel, or interact with secondary foundation species (fern icon) to indirectly facilitate communities in a Type A, B, or C facilitation cascade. The number of fern icons represents the relative increase in habitat availability generated by the secondary foundation species (many = large increase, one = small increase), and the shading of fern icons denotes whether they exhibit functional traits that are similar or different (black or gray, respectively) to those of the primary foundation species. Invertebrate icons refer to feeding guilds; node size represents abundance; and lines connecting nodes indicate species interactions.

effects on some, or all, metrics of community structure. The secondary foundation species may negligibly, or to a lesser extent, influence the amount of habitat that is available (e.g., they are uncommon or small), or generate habitat that is functionally redundant with that of the primary species (e.g., they exhibit similar structural attributes). In the Foundation Species–Biodiversity (FSB) model (Fig. 5), we integrate this context dependence and hypothesize that the size and functional traits of secondary foundation species, as the key, intermediate links in facilitation cascades, control their relative impact on associated species abundance and diversity.

Specifically, the FSB predicts that where secondary foundation species increase habitat availability, they provide the substrate and resources necessary to support the settlement, growth, and/or retention of more individuals of species that already occur in the community (Type A). A Type A facilitation cascade might occur, for example, where manatee grass (*Syringodium filiforme*) secondarily establishes within a meadow of structurally similar shoal grass (*Halodule wrightii*), and in increasing shoot density, significantly enhances the abundance, but not richness, of resident invertebrates and fish. Likewise, the FSB predicts that where secondary foundation species exhibit functional traits (e.g., surface texture, crevice size, chemical composition) that are very different from those of the primary foundation species, their generation of refuges from physical stress (e.g., via shading, baffling wave or wind stress, stabilizing humidity, providing hard substrate) or biotic stress (e.g., via forming smaller refuges for prey) facilitates the settlement and retention of new species, life stages, and feeding guilds (Type B). An example of a Type B facilitation cascade might occur where pen shells (*Atrina rigida*) settle within turtle grass (*Thalassia testudinum*) beds and, in providing stable substrate for other sessile invertebrates and complex shelter for egg-laying fish, enhance the species, life stage, and functional diversity of the resident community, but do not significantly alter the number of individuals. Where secondary foundation species increase habitat availability and exhibit functional traits different from those of the primary foundation species, like *Tillandsia* within trees (this study), mussel beds within cordgrass (Altieri et al. 2007), or oysters layered on mangrove roots (Bishop et al. 2012), they are predicted to increase both abundance and diversity (Type C). Alternatively, where secondary foundation species do not considerably increase habitat availability or functional trait diversity (Fig. 5a, bottom left), like encrusting lichens on trees, the FSB predicts that although they will increase species abundance and diversity to some extent, their facilitative effects will be small relative to those of the primary foundation species. Finally, the FSB predicts that, as secondary foundation species modify their functional traits in response to local conditions, and grow, the size and diversity of the associated community will change

accordingly (e.g., a facilitation cascade can shift from Type B to C across environmental stress gradients and over time).

In the future, experiments that manipulate the size and trait diversity of foundation species and use informative metrics to assess community responses are necessary to test whether the FSB predictions about where foundation species have maximal effects on biodiversity are indeed correct. Along with empirical studies, efforts to incorporate the powerful effects of foundation species into food web and metacommunity models will be essential in determining the mechanisms that cause community structure within foundation species to change over space and time. In closing, advancing our understanding of interactions among foundation species and context dependency in facilitation cascades is an exciting frontier for ecological research and theory, with important implications for conservation.

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## SUPPLEMENTAL MATERIAL

### Appendix

Three figures detailing experimental methods and two tables detailing invertebrate functional group, life stage, taxonomic information, and abundance ([Ecological Archives E095-017-A1](#)).