

# Modular mobile foundation species as reservoirs of biodiversity

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**Abstract.** The complex structure of biogenic habitats including coral reefs, hemlock forests, and seagrass meadows are widely recognized for the diverse communities they shelter. As human impacts accelerate the loss of such foundation species, we need to identify the general characteristics of previously unrecognized species that can also fulfill the role of habitat provider. We conducted surveys and experiments to test whether the slate-pencil urchin (*Eucidaris galapagensis*) acts as a foundation species on subtidal walls in the Galapagos archipelago. The spines of slate-pencil urchins are more than 90% encrusted with a diverse epifauna, and a single urchin can host over 20 species (e.g., sponges, ascidians, bryozoans, corals, molluscs, worms, and crustaceans). Like many other foundation species, urchins can provide substrate and a refuge from predators. Urchins are consistently abundant throughout the Galapagos subtidal, and the total surface area of urchin spines can rival that of the primary rock substrate, which is significant since substrate availability can limit small-scale species richness in this system. Our experimental manipulation of spine configuration and exclusion of predators revealed that urchins also enhance epifaunal diversity by providing a predation refuge. Unlike previously recognized foundation species, however, the urchin habitat is modular and mobile, and has the potential to redistribute associated epifauna. Characterizing how previously overlooked foundation species can act as reservoirs of biodiversity in ecosystems, such as the Galapagos where other foundation species such as coral have declined, has important implications for how we identify foundation species, predict ecosystem stability, and prioritize conservation efforts.

**Key words:** biodiversity; ecosystems engineer; epifauna; *Eucidaris galapagensis*; fouling community; foundation species; Galapagos; predation refuge.

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## INTRODUCTION

Many ecosystems including coral reefs, mangroves, hemlock forests, seagrass meadows, and salt marshes are defined by large, habitat-forming species. These foundation species (sensu Dayton 1972) enhance the diversity and abundance of associated species by creating habitat, modifying physical conditions, and mediating biotic interactions (Bruno and Bertness 2001, Stachowicz 2001). As a consequence, they have

large effects on ecosystem functions and are important providers of ecosystem services (Altieri and Van De Koppel 2013).

Despite their often large and fortified appearance, foundation species and the habitats they create are vulnerable to human impacts. For example, coral reefs have been heavily impacted by local activities and global change leading to over 80% loss in some regions (Gardner et al. 2003, Pandolfi et al. 2003, Hoegh-Guldberg et al. 2007), and their temperate analogs, oyster and

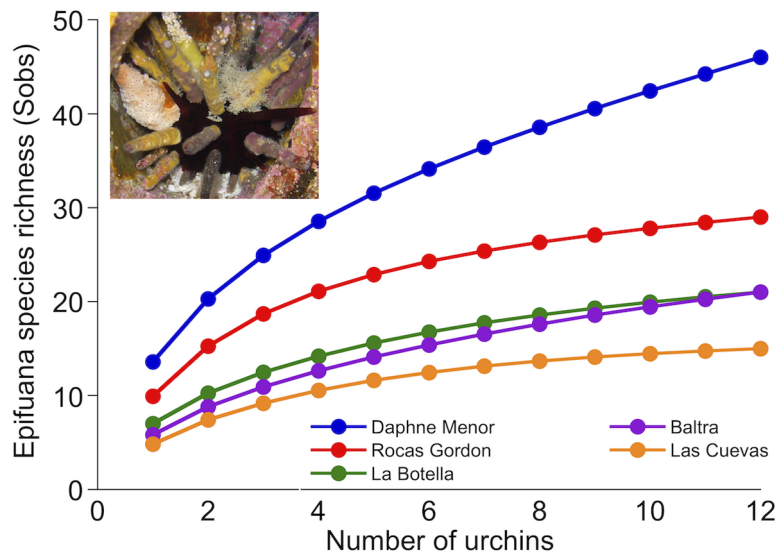


Fig. 1. Species accumulation curves based on species of epifaunal invertebrates observed on samples of 12 Galapagos slate pencil urchins (inset photo) at each of our five study sites that provide estimates of the species richness. Greater biodiversity with an increasing number of urchins sampled reveals that the emergent community of epifaunal invertebrates is apparent only when considering the aggregate habitat created by multiple urchins.

mussel reefs, have also declined because of overharvesting and declining water quality (Altieri and Witman 2006, Lotze et al. 2006, Beck et al. 2011). In some instances, loss of foundation species is clearly the direct result of activity such as shoreline development that converts marshes to urban terrain (Gedan et al. 2009). In other cases, human activities affect the persistence of foundation species in indirect ways, such as climate change that exacerbates parasites leading to the demise of hemlock forests in the US (Ellison et al. 2005), and the trophic cascade triggered by recreational overfishing that can lead to the collapse of salt marsh ecosystems (Altieri et al. 2012). These anthropogenic impacts threaten the diverse communities and related ecosystem functions and services that depend on foundation species.

Given the trajectory of decline suffered by these commonly recognized foundation species, we asked the question: are there other less recognized species that play the role of habitat-forming species worthy of study and protection for their function in creating habitat and enhancing diversity? One of the most conspicuous patterns on Galapagos subtidal rock walls is the

association between the abundant slate pencil urchins (*Eucidaris galapagensis*) and the diverse epifaunal community that consistently encrusts their club-like spines (Fig. 1). Moreover, *Eucidaris* is the most abundant species of urchin in the Galapagos archipelago (Brandt and Guarderas 2002; J. D. Witman, *unpublished data*). Because the urchins are small and mobile, they are different from classically recognized foundation species that are large and established features on the landscape. However, we hypothesized that urchins may be representative of previously unrecognized foundation species because they play a collective role as an important habitat.

To examine whether *Eucidaris* has characteristics typical of foundation species, we conducted a series of surveys and experiments in the subtidal ecosystem of the Galapagos to test the hypotheses that the urchins (1) create habitat, (2) enhance small-scale diversity, and (3) mediate species interactions by providing a predation refuge for epifauna. We considered two additional characteristics not typically associated with foundation species, but potentially important in their habitat-provisioning function, by testing the hypotheses that urchin habitat is (4) modular in

that discrete individuals contribute uniquely to diversity measures, and (5) mobile with the potential to redistribute other species.

## MATERIALS AND METHODS

### Site description

We conducted our study on subtidal, vertical rock walls in the Galapagos archipelago at a depth of 15–18 m. These walls are relatively productive due to currents that converge on the Galapagos and generate localized upwelling of nutrient rich waters, and are characterized by a mixed community of encrusting invertebrates (Witman and Smith 2003, Witman et al. 2004, Witman et al. 2010). Due to restrictions on industrial fishing practices within the Galapagos Marine Reserve, where all of our sites were located, the Galapagos are notable for the relatively intact food web including large consumers such as decapod crustaceans (e.g., lobsters and crabs), fish (e.g., triggerfish, hogfish, pufferfish), and snails (e.g., *Hexaplex princeps*) that feed on epifaunal invertebrates (Edgar et al. 2004, Witman et al. 2010). Our study included five primary sites located in the central Galapagos archipelago: Baltra (0°24'52" S, 90°16'27" W), Daphne Menor (0°23'42" S, 90°21'9" W), La Botella (1°18'1" S, 90°30'33" W), Las Cuevas (1°16'19" S, 90°21'13" W), and Rocas Gordon (0°33'57" S, 90°8'32" W). To highlight the general abundance of *Eucidaris* urchins and the availability of habitat created by their spines, we included urchin abundances from surveys conducted at an additional seven sites (see Witman et al. 2010 for map of all 12 study sites).

### Habitat provision

To quantify the area provided by urchins as substrate for epifaunal invertebrates, we haphazardly collected urchins from three sites in January 2004 for measurement: Rocas Gordon (n = 17), La Botella (n = 26), and Daphne Menor (n = 20). For all urchins, we quantified the number of the spines occupied by epifauna, distinguishing between spines that were completely encrusted, partially encrusted, or non-encrusted. For eight urchins at each site, we measured the test diameter and the surface area of spines (cylindrical in shape; calculated from their length and diameter). The aggregate habitat

area provided by *Eucidaris* was estimated by multiplying spine area per urchin by the average density of urchins (three 10 × 1 m transects/site) quantified at all 12 Galapagos sites.

### Species richness of epifauna

We evaluated the effect of urchins on epifaunal species richness by two methods in January 2004. First, we conducted a detailed assessment of epifaunal species richness on urchins by examining urchin spines with a binocular microscope in the lab. Second, we compared the species richness of epifauna on urchin spines to that on rock walls by analyzing images of both habitat types. Both of these methods allowed a more detailed examination of species richness patterns than in situ observation due to bottom-time limitations of working at 15–18 m depth. We limited the scope of our study to sessile epifauna so that our measures of species richness would not be confounded by potential loss of mobile organisms from urchins, or by horizontal transmission between urchins, during transport between field and laboratory.

For detailed assessment of urchin spine epifaunal diversity, we haphazardly collected 12 urchins from each of our five study sites for examination under a dissecting scope (40× magnification) in the lab. We identified and tallied the number of epifaunal species on the spines of each urchin. To estimate the relative contribution of individual urchins to total measures of epifauna diversity within the urchin habitat, we used presence/absence data of epifaunal species on each urchin to generate species accumulation curves from 1000 randomized poolings of urchins for each site using EstimateS software (Colwell 2013).

To compare the species richness of epifaunal communities on spines with that on rock walls, we haphazardly selected 12 urchins and 12 adjacent areas of rock wall habitat at each of three sites (Daphne Menor, La Botella, and Las Cuevas) to photograph with a high-resolution digital camera (Coolpix 5000 camera, Nikon, Melville, New York, USA) that included a scale bar in the field of view of each image. To standardize the area in which we examined epifaunal species richness, we measured the area of spine substrate on each urchin facing the camera, and then marked the equivalent area

(130–155 cm<sup>2</sup>) in the corresponding photograph of adjacent rock surface. We then identified and censused the number of epifaunal species on urchin spines or rock surface in each photograph. Differences between urchin spines and rock surface in the average species richness (species density) were analyzed by a nested ANOVA where habitat type (urchin or rock wall) was nested within site. We tested for habitat (urchin spine, rock surface) and site differences in the species composition of the epifaunal communities using non-metric multi-dimensional scaling (nMDS) followed by a permutational analysis of variance (PERMANOVA) using PRIMER (v6) and PERMANOVA+ (PRIMER-E, UK) software.

A Kulczynski resemblance coefficient was used for the presence/absence data which was analyzed with a more conservative Type III sum of squares in PERMANOVA to account for the unbalanced data set where some samples contained no epifaunal invertebrate species.

#### *Predation refuge*

We conducted two experiments to test whether urchins enhance species richness by providing a predation refuge among their spines. In the first experiment, we tested the hypothesis that the species richness of epifauna on a spine is increased if that spine is surrounded by other spines. This was done by fastening defaunated spines to 10 × 10 cm PVC plates with Z-Spar Splash Zone marine epoxy (Kop-Coat, Rockaway, New Jersey, USA) perpendicular to the surface of the plate in one of two configurations with 8 replicates per treatment. Spines were either solitary on a plate, or in a group surrounded by 8 other spines in a regular grid pattern (n = 16 total replicates, spaced >2 m apart). Spines in groups were spaced 2 cm apart which was the average distance between spines at their midpoint on 10 haphazardly collected urchins. The replicate plates were bolted flush to the surface of rock walls in November 2004 at Daphne Menor. Defaunated spines for the experiment were collected from beaches on Santa Cruz Island where they had been washed ashore, sand-scoured, and sun-dried. At the end of the experiment in June 2005, the plates were collected and the diversity of epifauna on solitary spines and the central spine within groups was quantified in the laboratory. We were not able to

measure the diameter of epifauna, as in the second experiment (below), due to unreliable measurements associated with fusion of epifauna between adjacent spines in the group treatment. The difference in average number of species on spines in the two treatments was analyzed by ANOVA.

In the second experiment, we tested whether elevated epifaunal diversity observed on spines surrounded by other spines in the first experiment could be explained by a predation refuge effect by using cages to exclude predators from urchin spines. Two defaunated spines were attached to replicate loops (20 cm circumference) of polypropylene rope that were fastened to the rock wall with stainless steel bolts. Eight replicate loops were assigned to each of three treatments: full cage, procedural control cage, or no cage (n = 24 total replicates, spaced >2 m apart). Full cages had roofs and four walls (12 × 12 × 12 cm) and were constructed of vinyl coated galvanized steel (mesh size 4 cm). Control cages were similar to full cages except that two opposite walls were removed to allow predator access. Two spines were inserted in each replicate cage as insurance against accidental breakage of the spines due to handling and rough sea conditions at the site. We started the experiment in June 2005 at Rocas Gordon, and at the end of the experiment in January 2006 we quantified the number of species on each spine and measured the diameter of encrusting invertebrates extending from each spine (proxy for biomass). Where both spines persisted to the end of the experiment, the species richness and diameter values for the two spines were averaged together for a single value in each replicate cage. Differences in both the average number of species and the diameter of encrusting organisms on the spines in the three treatments were analyzed by ANOVA.

Since *Eucidaris* is a generalist consumer, and may simply provide a refuge to epifauna from their own predation, we assessed the intensity of urchin grazing by quantifying the area of urchin grazing scars in each of the rock wall photographs (described above in *Species richness of epifauna*) using image analysis software (ImageJ v1.47, NIH, USA). Scars were identified by characteristic markings of Aristotle's lantern determined from an urchin enclosure experiment (Brandt et al. 2012).



### Movement of urchins

*Eucidaris* are often stationary in recessed shelters during the day, and emerge to move about the substrate at night (Dee et al. 2012). To investigate whether urchins return to their home refuge or if there is net movement of urchins on a diurnal basis that could potentially redistribute epifaunal species across rock walls, we conducted a tagging experiment at La Botella in January 2006. We tagged 50 urchins with uniquely numbered tags fastened to the base of their spines, and then measured the distance between each urchin and two fixed points to triangulate the location of each urchin on the wall. Four days later we located all tagged urchins within 15 m of the original tagging area, and measured the distances between urchins and fixed points again to determine net distance moved. Using this approach we were also able to distinguish vertical and horizontal movement rates, and to test if there was a tendency towards vertical or horizontal movement with a paired t-test. To estimate tag retention rates, we tagged 20 urchins within a  $3.0 \times 1.5 \times 1.0$  m (L  $\times$  W  $\times$  D) concrete outdoor tank at the Charles Darwin Research Station supplied with flowing seawater and determined the number of urchins with tags remaining after day 4. The tank was stocked with piles of rock rubble in which the urchins hid during the day, emerged at night, and scraped their spines and tags as at the study site.

## RESULTS

### Habitat provision

We found a high occupancy of epifauna on urchin spines, with an average ( $\pm$  SE) of  $91\% \pm 2\%$  of urchin spines completely encrusted with epifauna across all sites (Daphne Menor  $90\% \pm 1\%$ , La Botella  $95\% \pm 1\%$ , Rocas Gordon  $88\% \pm 2\%$ ). Partially encrusted spines were observed at only one of the sites (Rocas Gordon) where they accounted for less than 2% of spines. We noted that spines not encrusted by epifauna tended to be smaller than others in the same position on the urchin, suggesting they were newer and in a process of regrowth. The average surface area of all spines on individual urchins was  $316 \pm 31$  cm<sup>2</sup> (Daphne Menor  $377 \pm 24$  cm<sup>2</sup>, La Botella  $291 \pm 16$  cm<sup>2</sup>, Rocas Gordon  $280 \pm 15$  cm<sup>2</sup>). When scaled to the total number of urchins per site

using survey data from 12 sites over a 7-year period (2003–2010) that found an average density of  $7.4 \pm 0.8$  urchins/m<sup>2</sup> (J. D. Witman, *unpublished data*), we estimate an average of  $2338 \pm 253$  cm<sup>2</sup> spine area for every 1 m<sup>2</sup> of rock habitat. The importance of urchin substrate is underscored further when considering extreme *Eucidaris* densities of 50 individuals/m<sup>2</sup> (Glynn et al. 1979), in which case we estimate the surface area of urchin spines would exceed that of rock with 1.6 m<sup>2</sup> of urchin spines for every 1 m<sup>2</sup> of primary rock substrate.

### Diversity of epifauna

Using a microscope to inspect invertebrate epifauna on the 12 urchins from each of the five replicate sites, we found a total of 56 species from eight phyla: Annelida (5 spp.), Arthropoda (1 sp.), Bryozoa (18 spp.), Chordata (7 spp.), Cnidaria (4 spp.), Mollusca (5 spp.), Porifera (15 spp.), and Sipuncula (1 sp.). There was an average of  $8.3 \pm 1.6$  epifaunal species per urchin, and  $27.0 \pm 5.3$  species per site. Species accumulation curves at four of the five sites began to asymptote within our samples of 12 urchins (Fig. 1), indicating adequate sample size for estimates of epifaunal species richness at study sites and for detecting differences between urchins and rock in our photographic analysis. For all five sites, the estimated species richness for a sample of 12 urchins was at least threefold higher than for a single urchin, revealing an emergent effect on the diversity of the epifaunal community generated by the collective urchin habitat. Although we did not quantify mobile epifauna, we did note small fish, brittle stars, crabs, sea spiders, isopods, nudibranchs, and snail egg masses utilizing the space among spines.

Our photographic analysis revealed that diversity was consistently higher on urchin spines (Fig. 2A) than on equivalent areas of adjacent rock walls (Fig. 2B) at all three sites ( $F_{3,66} = 42.82$ ,  $P < 0.0001$ ; Fig. 2C). Epifaunal community structure differed across sites and substrate types owing to a significant interaction between the two (pseudo- $F_{2,59} = 3.71$ ,  $P = 0.001$ ; Fig. 2D). Across all sites, we found a total of 33 epifaunal species, of which six were unique to urchin spine habitat, and only three were unique to rocky substrate.

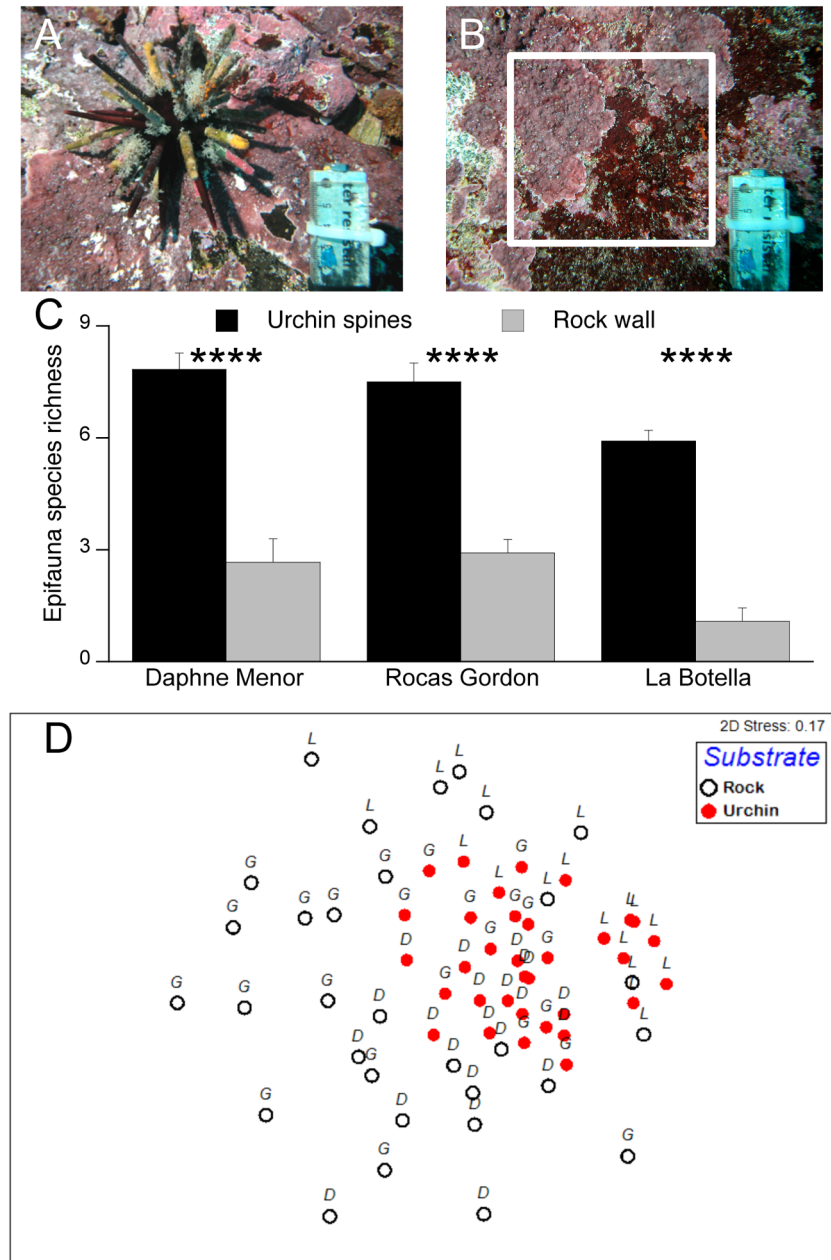


Fig. 2. Photographs of (A) typical *Eucidaris galapagensis* urchin with spines covered by epifauna, and (B) nearby rock wall habitat covered with coralline algae and largely devoid of epifauna. Photos include scale bar used to set sample area on rock (white square) equivalent to urchin spine area. (C) Average species richness of epifauna on urchin spines and equivalent area of nearby rock wall. Data are means  $\pm$  SE. \*\*\*\*  $P < 0.0001$ . (D) Differences in epifaunal community structure across sites and substrate types (rock vs. urchin spine) are apparent in the nMDS plots based on species presence/absence in replicate photos. Symbol labels: L = La Botella, G = Rocas Gordon, D = Daphne Menor.

### Predation refuge

In the first predation experiment, we found species richness was significantly higher on spines in the protection of surrounding spines than on solitary spines ( $F_{1,12} = 6.71$ ,  $P < 0.001$ ; Fig. 3A). In the second predation experiment, we found that predation reduced species richness in the open and control cages relative to predator exclusion cages ( $F_{2,14} = 4.78$ ,  $P < 0.05$ ; Fig. 3B). Similarly, we found that the extension of encrusting invertebrates from the surface of spines (a proxy for epifaunal biomass) was greater in the absence of predators than in open or control treatments ( $F_{2,14} = 28.60$ ,  $P < 0.0001$ ; Fig. 3C). Our analysis of rock wall images suggested that rates of urchin grazing were relatively low. Across our three study sites,  $44\% \pm 10\%$  of photos had signs of urchin grazing, but only  $2\% \pm 1\%$  of rock surface had grazing marks.

### Movement of urchins

Urchins demonstrated significant movement over a short period of just 4 days ( $t_{1,41} = 2.96$ ,  $P < 0.01$ ), with an overall net distance moved of  $61 \pm 21$  cm in the tagging experiment. This low average belies a greater potential for movement since the maximum distance a single *Eucidaris* urchin moved was 664 cm in 4 days. Moreover, our estimates of movement rates are conservative since there were likely urchins that moved beyond our 15-m search radius as we recovered only 43 of the 50 tagged urchins in the field (86% recovery rate). It was unlikely that these unrecovered urchins were caused by tag loss since we found only 1 of 20 urchins in the laboratory control populations lost their tag in the equivalent 4-day period. When we partitioned urchin movement into vertical and horizontal components, we found a propensity for movement in both vertical ( $45 \pm 16$  cm) and horizontal ( $34 \pm 12$  cm) directions with no significant tendency toward either ( $t_{1,41} = 1.32$ ,  $P = 0.19$ ).

## DISCUSSION

We found that Galapagos slate pencil urchins (*Eucidaris galapagensis*) function as a mobile foundation species that increase the species richness of invertebrate communities in subtidal rock wall ecosystems. The urchins fit the definition of foundation species because they are an

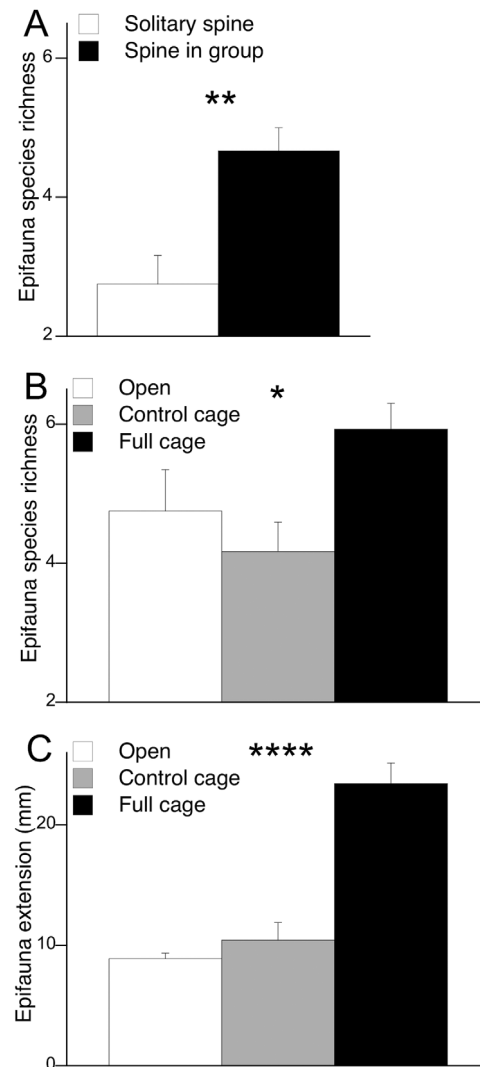


Fig. 3. (A) Species richness of the epifaunal community was higher on spines amongst other spines than spines that were alone, suggesting that spines offer a refuge from predators. The importance of a predation refuge for the spine epifaunal community was evident in the caging experiment in which experimental protection from predators led to (B) species richness which was higher when protected from consumers, and (C) lateral extension of epifauna (proxy for biomass) which was greater when not cropped down by consumers. Data are means  $\pm$  SE. \*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*\*  $P < 0.0001$ .

abundant species that facilitates a diverse community by at least two mechanisms: substrate provision and predation refuge. They also have two attributes not traditionally associated with

foundation species: they are mobile, and they are modular in that each is a discrete unit that harbors only a subset of the associated community and moves independently of one another rather than forming a static structure as other habitats created by aggregations of individuals (e.g., hemlock forests, kelp beds, coral reefs).

Substrate provision is a primary mechanism by which urchins facilitate epifauna, given that ~90% of urchin spines are entirely encrusted with a diverse invertebrate community, and urchins are consistently abundant throughout the Galapagos, adding hundreds of square centimeters of substrate for every square meter of rock substrate. The additional living space provided by urchins is especially important on subtidal Galapagos rock walls since previous work in the system has found that diversity is space-limited (Witman and Smith 2003). Such provision of secondary substrate is a widely recognized function of foundation species that enhances diversity in both marine and terrestrial ecosystems as classically illustrated for intertidal mussel epifauna (Suchanek 1986) and tree epiphytes (Benzing 1990) communities. Moreover, all space is not created equal, as we found that community structure differed between urchin and rock substrates, and that a given urchin had double the species richness found on an adjacent, equivalent area of rock.

We found one reason that urchins host an elevated diversity of epifauna is that predation limits species richness, and that urchin spines provide the epifauna with a refuge from predation. These associational defenses where host anti-predator defenses benefit smaller inhabitants are most commonly observed between macrophyte hosts and their invertebrate inhabitants such as acacia trees and thorn-dwelling ants (Janzen 1966) and noxious algae that host crustaceans (Hay 1992) but also include the crevice space among the calcified structures of mussels (Witman 1985) and corals (Idjadi and Edmunds 2006) that shelter diverse communities of invertebrates.

*Eucidaris* is a generalist consumer that feeds on rock surfaces (Brandt et al. 2012), so the urchins themselves likely contribute to the limitation of diversity on rocky substrate and the dependence of epifauna on the predation refuge among urchin spines. Several lines of evidence suggest

that other consumers drive this pattern as well. First, other urchin species in this system (e.g., *Lytechinus*) have relatively greater consumption rates and impacts on benthic community composition (Brandt et al. 2012). Second, we found evidence of grazing by urchins to be relatively rare on rock wall substrate in our photographic analysis. Third, epifaunal diversity was enhanced by our experimental exclusion of consumers from spines that were suspended above the rock substrate, suggesting that other predators capable of foraging above the rock surface (e.g., fish or decapod crustaceans) limit epifaunal diversity on substrates not protected by urchin spines. If the pattern of higher diversity among urchin spines than rock surface is partly driven by urchin foraging on the rock walls, then the system is analogous to intertidal algae in South Africa that finds refuge from limpet grazing on the shells of the limpets themselves (Branch 1981).

Although each urchin is a discrete unit of substrate unto itself, the role of urchins as a habitat-creating foundation species is evident when considering the emergent community of sessile invertebrates collectively supported by the population of abundant urchins at a given site. The aggregate epifaunal species richness on a dozen urchins sampled at a given site was over threefold higher than the average richness on a single urchin. Moreover, the total species richness of invertebrates occupying urchin habitat at a site was likely higher than our estimate given that species accumulation curves were beginning to asymptote but had not leveled off in our samples. The urchins can therefore be considered a modular foundation species because each urchin is a habitat unit that independently contributes to overall species richness, and because the urchins are mobile and move independently of one another.

Mobility is an important attribute of urchins that affects their function as a foundation species with important potential consequences for overall community structure. We found that urchins exhibited net movement over a relatively short period of time which has three important implications. First, urchins can alter overall community composition patterns since urchins move vertically and the community composition and diversity of rock wall epifauna varies with



depth in the Galapagos (Witman and Dayton 2001, Witman et al. 2010). Second, the urchins can act as dispersal vectors for epifauna since many of the organisms (e.g., ascidians, bryozoans, and sponges) found on urchin spines can reproduce by fragmenting and re-attaching. Urchins could seed new areas of rock with epifauna, or pass epifauna onto other urchins they contact. Third, urchin movement behavior is responsive to stimuli including predators and light (Dee et al. 2012), and so changes in biotic or abiotic environmental conditions could affect urchin movement with cascading consequences for the distribution of the spine inhabitants.

Interactions between foundation species are increasingly recognized as common and important, but competition and facilitation have been considered as the primary interactions to occur among foundation species (Angelini et al. 2011). We suggest that predation could also be an important interaction since *Eucidaris* consumes live coral (Glynn et al. 1979, Glynn and Wellington 1983) and co-occurs on rock walls along with Pocilloporid corals which are another foundation species supporting a diverse community of motile and sessile epifauna (Rhoades 2009). Predation by urchins could thereby limit the scope of facilitation and habitat modification by corals. Even if urchin and coral interactions are inconsequential, the co-occurrence of two foundation species has important implications for functional redundancy and community stability. We predict that the importance of urchins in sustaining diversity as a foundation species will increase if corals continue to decline due to disturbances such as El Niño Southern Oscillations (Glynn 1990) that cause coral thickets to shed epifaunal species (Rhoades 2009).

The Galapagos Archipelago is changing rapidly due to increased human activity, with increased fishing intensity in recent decades (Bustamante et al. 2002). *Eucidaris* behavior and abundance is influenced by secondary consumers (e.g., hogfish, triggerfish and sea stars) (Dee et al. 2012; N. H. N. Low and J. D. Witman, unpublished data) and may be more abundant in areas where those species are fished (Edgar et al. 2010). Thus, the role of urchins in sustaining patterns of diversity as shown here, and the indirect link between fishing and urchin populations in the Galapagos, suggests the importance

of urchins as foundation species could increase, and that the role of exploitation and trophic dynamics in determining diversity patterns deserves greater attention.

Are there other habitat-providing species that fit into this class of non-traditional foundation species defined by *Eucidaris* that are abundant but small and mobile? One of the best cases has been made for murex snails in the Sea of Cortez (Prescott and Cudney-Bueno 2008), although their study did not quantify how diversity of epifauna on murex differed from the primary substrate, nor did it identify mechanisms of facilitation other than observed substrate provision. Other potential examples include mudsnails (Thomsen et al. 2010), horseshoe crabs (Patil and Anil 2000), and decorator crabs (Wicksten 1980) that are commonly encrusted with algae and invertebrates and can be locally abundant, as well as sloths whose fur can be inhabited by a diverse community of algae and arthropods (Gilmore et al. 2001). Many other previously unrecognized foundation species will be appreciated as such once their common characteristics are identified, and they are evaluated for their effects on diversity and potential for dispersing other organisms. More broadly, we suggest that as ecosystem change leads to species loss and phase shifts, a refined concept of foundation species will drive awareness of previously unrecognized habitat-forming species that act as reservoirs of diversity worthy of study and conservation.

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