Habitat connectivity improves reserve performance

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Abstract

Connectivity is now a common consideration in conservation planning, but we need further empirical evidence for the role of connectivity in catalyzing reserve function. We examined whether connectivity improved reserve performance by investigating how isolation between coral reefs and mangroves influenced fish assemblages inside and outside a reserve in Moreton Bay, Australia. Connectivity greatly enhanced reserve performance, with close reserve habitats supporting more harvested fish, and a greater abundance of both piscivores and herbivores than similar nonreserve locations. Close reserve habitats also contained fewer prey fish than nonreserve locations. In contrast, fish abundance in isolated reserve habitats did not differ from similar nonreserve locations. We demonstrate that connectivity can improve the performance of a reserve in promoting fish abundance. We highlight its importance for maintaining ecological processes in reserves and advocate the prioritization of areas of similarly connected habitat for conservation.

Introduction

The movement of organisms between habitats is vital for population persistence and productivity. This connectivity is of primary importance to ecosystem function and to the distribution and abundance of biota (Lindenmayer *et al.* 2008). It is assumed to confer ecosystems with resilience, as connected populations can recover from disturbance through the linking of populations, processes or food webs (e.g., Mumby & Hastings 2008). Consequently, enhancing connectivity has emerged as a favored option for conservation in the face of climate change (Hodgson *et al.* 2009). Connectivity is a prolific field in conservation (Grober-Dunsmore *et al.* 2009), but remains a complex, and much debated, area of ecology (Lindenmayer & Fischer 2007). Several studies have explored incorporating spatial ecological processes into conservation planning (e.g., Almany *et al.* 2009; Beger *et al.* 2010; Edwards *et al.* 2010) and we now need empirical evaluations of whether spatial processes, like connectivity, enhance the performance of reserves.

Broadly speaking, connectivity is a function of habitat area, quality and spatial arrangement, and the dispersal capabilities of individual species (Hodgson *et al.* 2009).

It can be conceived from a whole of landscape perspective, or visualized as linkages between particular habitats or populations. These flexible definitions, and the variety of metrics available for measurement, make connectivity a difficult concept to both interpret and assess. Here we define habitat as units of biophysical structure that are connected by migrating organisms, and focus on habitat connectivity, or the connectedness of habitat patches for particular taxa (Lindenmayer & Fischer 2007). Such connections are pervasive in ecology (Sheaves 2009), and their effects can be seen in many terrestrial and aquatic communities. Some connections that are known to influence population demography include: movement of birds among forest types (e.g., Wilson *et al.* 2009); migration of fish between coasts and rivers (e.g., Ray 2005); and movement of fish among tropical marine habitats (e.g., Grober-Dunsmore *et al.* 2009). In many cases, habitat connectivity is examined using structural metrics, which describe the spatial arrangement of habitat types, and are assumed to provide reasonable surrogates for multispecies conservation (Calabrese & Fagan 2004). This approach has been criticized for being overly simplistic (e.g., Nicholson *et al.* 2006), but it is this inherent simplicity that gives it great appeal for conservation planning

and assessment. However, at present, the scientific basis for such a strategy remains deficient (Hodgson *et al.* 2009). Given the existing impacts of habitat degradation and species exploitation, the impending effects of climate change, and the dearth of empirical evidence, a better understanding of the role for habitat connectivity in conservation is required.

We utilize subtropical marine habitats as a model system for assessing the value of prioritizing habitat connectivity in reserve conservation. These ecosystems are spatially heterogeneous seascapes, in which different habitats are connected by biological, physical, and chemical processes (Pittman *et al.* 2007). Many marine fish undertake migrations to utilize resources from different habitats, and consequently, patterns of species abundance are influenced by seascape composition (i.e., the presence and diversity of habitats) and configuration (i.e., the area, shape, and isolation of habitats) (Grober-Dunsmore *et al.* 2009). The role of habitat connectivity in marine systems is best appreciated for linkages between tropical coral reefs and adjacent habitats, which strongly influence fish populations on reefs (e.g., Mumby *et al.* 2004), in mangroves (e.g., Pittman *et al.* 2007), and over seagrass (e.g., Nagelkerken *et al.* 2008). These connections occur at the interface between terrestrial and marine realms and are essential for the persistence of many species and ecosystem functions (Beger *et al.* 2010). They might also be expected to improve the performance of marine reserves, but existing reserves generally fail to incorporate connectivity into their management frameworks (Almany *et al.* 2009).

Connectivity may also have consequences for the maintenance of ecological processes in reserves. For example, the role of herbivorous fish in removing algae and thereby promoting coral growth and reef resilience, or its capacity to absorb perturbations and regenerate without slowly degrading (Hughes *et al.* 2010), is now widely recognized. Connectivity with mangroves can enrich grazing on reefs near to mangroves (Mumby & Hastings 2008). When considered with herbivore recovery, ensuing reductions in algal cover and enhanced coral recruitment in reserves (e.g., Mumby & Harborne 2010), these responses may synergistically enhance the resilience of protected reefs near mangroves.

We test the hypothesis that connectivity between coral reefs and mangroves will enhance the performance of a reserve in promoting fish abundance, particularly harvested species, in the Moreton Bay Marine Park (MBMP) in eastern Australia. We show that connectivity can enhance reserve performance and recommend that connected habitats be considered as higher conservation priorities.
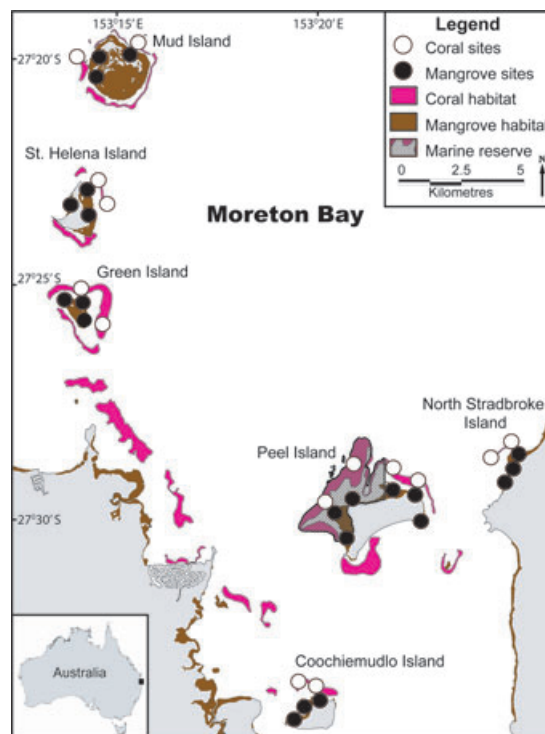
Figure 1 Mangrove and coral reef habitats of central Moreton Bay, Australia. Survey sites depicted as circles over mangrove and coral reef habitat.

Methods

Seascape analysis

We surveyed the fish assemblages of coral reef and mangrove habitats at seven locations in Moreton Bay, over the 2009–2010 summer (Figure 1). Each location supported a seascape of fringing coral reefs downshore of adjacent mangroves (Stevens & Connolly 2005). Only one effective no-take marine reserve protected these habitats in the MBMP at the time of our study, and we compared fish assemblages between this reserve (protected since 1997) and six unprotected control locations. At each location, we surveyed one site supporting close reef and mangroves, one with distant reef and mangroves, and one with isolated mangroves and no adjacent reef. Coral reefs without adjacent mangroves were not present in the system.

Connectivity was quantified from existing benthic habitat maps using ArcGIS (ESRI, Redlands, CA, USA; source: Queensland Department of Environment and Resource Management) as the edge-to-edge isolation distance between habitats. Importantly, seascape studies need to be scaled to the mobility of the species of interest (Grober-Dunsmore *et al.* 2009). A common method

for determining this spatial context is to scale studies by maximum distances traveled during routine daily movements (Pittman *et al.* 2007). Sites classified as supporting "close" habitats were, therefore, restricted to locations with a maximum separation of 250 m; habitats classified as "distant" were restricted to a minimum separation of 500 m. This scale encompassed daily home ranges of adult lutjanid (snappers), serranid (groupers), and sparid (sea bream) fish, which are large components of coral reef and mangrove fish assemblages in coastal Queensland (e.g., Sheaves 1993). Ideally, home ranges of other species would also be included when selecting a spatial context, but movement data are lacking for other fish families in the region.

Fish surveys

Fish on coral reefs were surveyed using underwater visual census (UVC) (following, Fulton *et al.* 2001). Five replicate 50 × 4 m transects were surveyed in mangrove and coral habitats at each site within 2 hours of high tide (when mangroves were inundated and accessible) and again in coral habitats at low tide (when mangroves were dry and not accessible). Adjacent transects were at least 50 m apart. Each census consisted of a diver swimming parallel to the reef slope and recording fish >5 cm total length (TL). Transects were positioned at depths of 1–3 m below Lowest Astronomical Tide.

Fish in mangroves were surveyed at high tide using UVC and fyke nets. UVC is appropriate for surveying large mobile species in mangroves with sufficient water clarity (Dorenbosch *et al.* 2009). Fyke nets are commonly used to sample smaller mangrove fish. The method of UVC was identical to that used in reef habitat, with transects positioned inside the mangrove fringe and surveyed within 2 hours of high water. In addition, three fyke nets (6 mm mesh fixed to 4 × 0.7 × 0.7 m frames and 2 × 6 × 0.7 m wings) were set inside the mangrove fringe at each site so openings faced landward. Fyke nets were set and retrieved, 2 hours before and after high tide, respectively. All fish captured were identified and released.

Fish assemblages occurring in reef and mangrove habitats were organized into the following groups: harvested fish, herbivores, piscivores, prey fish, and densities of selected individual species. Harvested species are most likely to respond to ecosystem protection; we used those listed as exploited by Rees *et al.* (2010). In Moreton Bay, fish are harvested in a commercial net fishery targeting *Acanthopagrus australis* (yellowfin bream) (Günther) and *Siganus fuscescens* (black rabbitfish) (Houttuyn), and by recreational fishers. Herbivores are a crucial functional group underpinning reef resilience by grazing on algae

(Hughes *et al.* 2010); herbivore density was calculated from the families Acanthuridae, Ephippidae, Kyphosidae, Pomacanthidae, Scaridae, and Siganidae (following Choat *et al.* 2002). The dominant herbivores of Moreton Bay are harvested by commercial net fishers and recreational spearfishers (Tibbetts & Townsend 2010). Piscivores are important in structuring marine food webs and influence trophic transfers among habitats (Valentine & Heck 2005); piscivore density was determined from species that commonly consume fish (following, Baker & Sheaves 2005). Prey fish densities were based on the abundance of *Atherinomorus vaigiensis* (common hardyhead) (Quoy & Gaimard) the only consistently abundant prey fish across both habitats. Harvested fish include species of herbivores and piscivores, whereas herbivorous, piscivorous, and prey fish represent independent guilds.

Data analysis

Reserve effects were evaluated using a modified Control-Impact design. Analysis examined interactions between connectivity and ecosystem protection through comparison of the reserve and six control locations with asymmetrical analysis of variance (Underwood 1992). The method for constructing an asymmetrical ANOVA involves combining sum of squares values from separate ANOVAs (described by Glasby 1997) to provide for contrasts between a single impact location and the average of multiple controls. The design properly accounts for variance and asks whether the single reserve location behaves differently to multiple controls. Replicates were grouped into five sites at each of the seven locations. Two of these were on coral reef (close and distant from mangroves) and three were in mangroves (close, distant, and isolated from coral reef). Two-factor ANOVAs were conducted for mangrove fish, and three-factor ANOVAs for reef fish. The factors were: connectivity (a fixed orthogonal factor), location (a random orthogonal factor), and tide (a fixed orthogonal factor used in reef analyses only). Data were log transformed to reduce heterogeneity of variances. Post hoc Student–Newman–Keuls tests were used to differentiate significant means.

To determine if connectivity influenced the composition of reef and mangrove fish assemblages, data were examined using nonmetric multidimensional scaling (nMDS) and analysis of similarities (ANOSIM) (Appendix S1).

Studies of spatial patterns in ecology can only infer causality after first testing and falsifying all potential alternative explanations (Mumby *et al.* 2004). We investigated whether observed patterns of fish abundance could be explained by covariation of habitat condition or area,
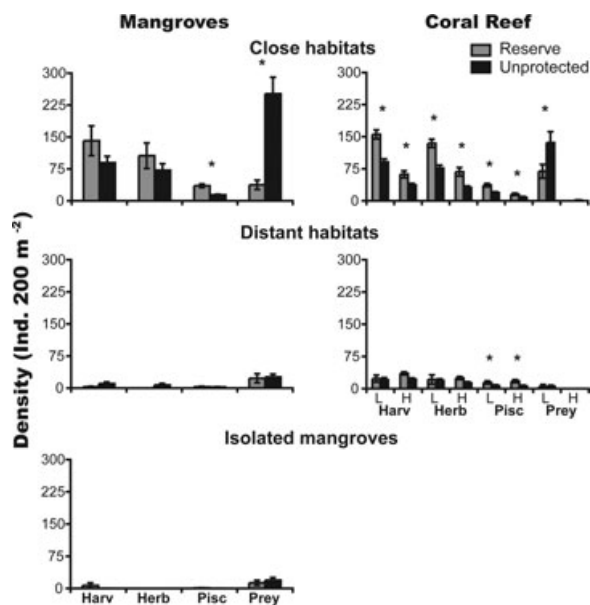
Figure 2 Density of harvested, herbivorous, piscivorous, and prey fish in mangroves and on coral reefs (mean ± SE). Harv, harvested fish; Herb, herbivorous fish; Pisc, piscivorous fish; Prey, prey fish; L, low tide; H, high tide. *represent significant differences between reserve and unprotected locations (identified by SNK *post hoc* analyses).

or water quality with habitat isolation, or by uneven fishing pressure within reserve and nonreserve locations (see Appendix S2).

Results

Connectivity enhanced reserve performance in promoting the abundance of harvested fish, as well as both piscivorous and herbivorous species. It had a negative effect on the abundance of prey fish.

Protection only influenced fish densities in mangroves that were close to reefs. Piscivorous fish were 147–156% more abundant in protected mangroves close to reefs, while prey fish were 496–701% less abundant in protected mangroves close to reefs (Figure 2, Table 1). Protection did not affect the abundance of harvested or herbivorous fish in mangroves (Figure 2, Table 1). Reserve status also had no influence on fish densities in mangroves located far from reefs, or with no fringing reefs downshore (Figure 2, Table 1).

Protection was most effective at influencing fish densities on reefs close to mangroves. Harvested and herbivorous fish were 68–71% and 76–120% more abundant, respectively, on protected reefs close to mangroves, regardless of tidal status (Figure 2, Table 1). Piscivorous fish were 87–187% more abundant on reserve reefs, regardless of their isolation from mangroves or the tidal

status (Figure 2, Table 1). Prey species, however, were 90–127% more depleted on protected coral reefs close to mangroves, but only at low tide (Figure 2, Table 1).

Habitat connectivity improved the performance of the reserve in promoting the abundance of three species; these were largely responsible for observed patterns in functional group abundances. *A. australis* were 133–147% more abundant in protected mangroves (at high tide) and 86–98% more abundant on protected reefs (at low tide) when both habitats were close together (Table 1). Similarly, *S. fuscescens* and *Lutjanus russelli* (moses snapper) (Bleeker) were 67–80% and 118–146% more abundant, respectively, on protected reefs close to mangroves, regardless of tidal status (Table 1).

Connectivity influenced the composition of mangrove and reef fish assemblages (Appendix S1). This reflected variation in the abundance of fish that use both habitats, and effects on reef assemblages were only detectable at low tide when tidally migrating species were concentrated on reefs.

The observed patterns of fish abundance could not be explained by covariation of habitat condition, area, or water quality with isolation, or by uneven fishing pressure within reserve and nonreserve locations (Table 2).

Discussion

Marine reserves are used throughout the world to conserve biodiversity and prevent overfishing, but uncertainty remains over strategies to optimize their design, productivity, and assessment (Claudet *et al.* 2008). This is paralleled in terrestrial ecosystems, where research is focused on identifying disproportionately important species, processes, and landscape elements for conservation (Pressey *et al.* 2007). The value of connectivity in conservation is particularly poorly understood (Lindenmayer *et al.* 2008). Our findings demonstrate that habitat connectivity can promote reserve performance, with connectivity between reefs and mangroves improving the performance of a reserve in promoting the abundance of harvested species. This result strongly supports recommendations for including habitat connectivity in reserve design (e.g., Almany *et al.* 2009; Beger *et al.* 2010). It corroborates the conclusions of Edwards *et al.* (2010), who incorporated connectivity between mangroves and reefs (through fish ontogenetic migration) into a reserve-selection algorithm and compared performance of generated reserve networks for the Belize Barrier Reef. They determined that connectivity had a weak influence on the biomass of commercially and ecologically important fish, and suggested that more striking results would be expected for fringing reefs, and those with more hard-bottom habitat. In contrast to the responses we detected

Table 1 Summary of asymmetrical analyses of variance examining spatial variation in the abundance of functional groups and fish species in mangroves and on coral reefs. df, degrees of freedom; C, connectivity; L, location; R, reserve locations; NR, nonreserve locations; T, tide; NS, nonsignificant; NR, not recorded in mangroves

Source of variation	df	Harvested fish	Herbivorous fish	Piscivorous fish	Prey fish	*Acanthopagrus australis*	*Siganus fuscescens*	*Lutjanus russelli*
Mangroves								
C	2	<0.001	<0.001	<0.001	0.003	<0.001	<0.001	NR
L	6	0.007	0.025	<0.001	<0.001	<0.001	0.025	NR
L (R vs. NR)	1	NS	NS	<0.001	<0.001	<0.001	NS	NR
L (NR)	5	0.006	0.015	NS	NS	0.017	0.015	NR
C × L	12	0.006	0.010	<0.001	<0.001	<0.001	0.010	NR
C × L (R vs. NR)	2	NS	NS	<0.001	<0.001	<0.001	NS	NR
C × L (NR)	10	0.004	0.006	NS	NS	NS	0.006	NR
Coral Reefs								
C	1	0.001	0.003	NS	0.037	<0.001	0.002	0.002
L	6	0.001	0.002	0.009	0.003	0.006	0.026	0.004
L (R vs. NR)	1	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
L (NR)	5	NS	NS	NS	NS	0.043	NS	NS
T	1	<0.001	<0.001	<0.001	0.031	0.002	<0.001	0.039
C × L	6	0.001	0.011	0.023	0.004	0.005	0.029	0.025
C × L (R vs. NR)	1	<0.001	<0.001	NS	<0.001	0.001	0.002	0.020
C × L (NR)	5	NS	NS	<0.001	NS	NS	NS	NS
C × T	1	0.005	0.004	0.003	0.040	0.005	0.004	0.042
T × L	6	NS	NS	NS	NS	NS	NS	NS
T × L (R vs. NR)	1	NS	NS	NS	NS	NS	NS	NS
T × L (NR)	5	NS	NS	NS	NS	NS	NS	NS
C × T × L	6	NS	NS	NS	0.005	0.036	NS	NS
C × T × L (R vs. NR)	1	NS	NS	NS	<0.001	0.015	NS	NS
C × T × L (NR)	5	NS	NS	NS	NS	NS	NS	NS

Table 2 Alternative explanations for increased fish abundance in close coral reef and mangrove habitats in the reserve

| Potential alternative explanations	Test	Result	Decision
1. Covariation of habitat condition or area with isolation	ANOSIM of habitat condition, area, and diversity variables	No difference ($P > 0.05$)[a]	Reject
2. Covariation of water quality with isolation	Asymmetrical ANOVA of water quality variables	No difference ($P > 0.05$)[a]	Reject
3. Uneven distribution of fishing pressure across unprotected locations	Compare fishing pressure between levels of isolation in unprotected locations	Fishing effort dispersed throughout available habitat (Kenyon *et al.* 2009)	Reject
4. Illegal fishing in reserve concentrated in isolated reserve habitats	Compare intensity of illegal fishing between levels of isolation	No difference ($P > 0.05$)[a]	Reject

[a]See Appendix S2 in Supporting Information for methods and results.

from harvested species, the lower abundance of prey fish in close reserve habitats suggests cascading effects of protection to lower trophic levels (*sensu*, Pinnegar *et al.* 2000). This highlights the variability of species responses to habitat connectivity, and indicates that increased connectivity in reserves is not beneficial to all organisms.

The positive responses of herbivores and piscivores to connectivity and protection suggest that connectivity may have important consequences for the maintenance of ecological processes in reserves. It is well-established that mobile organisms can link ecosystem functions across landscapes (e.g., Polis *et al.* 1997). An important implication of this concept is, however, that well-connected systems may behave differently (e.g., have higher productivity or resilience) to those that are more isolated (Lundberg & Moberg 2003). Our findings suggest that connectivity and protection may interact to affect the resilience, and trophic exchange among reefs and mangroves.
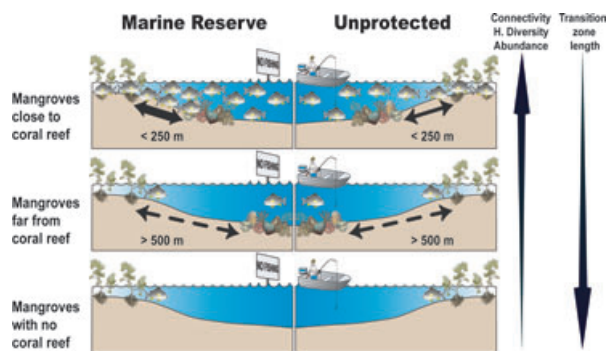
Figure 3 Conceptual diagram detailing the functional importance of reserve protection, habitat connectivity, habitat diversity, and transition zone length for harvested fish abundance on coral reefs and in adjacent mangroves. Arrow thickness depicts relative strength of connections, with dashed arrows representing weak connections (Symbols courtesy of the Integration and Application Network, ian.umces.edu/symbols/).

It can be difficult to separate the effects of habitat connectivity from those of habitat area, diversity, or value (Lindenmayer *et al.* 2008). Consequently, these simpler, more well-understood metrics are typically foci for conservation (Hodgson *et al.* 2009). Indeed, measures of habitat diversity and heterogeneity provide rudimentary proxies for connectivity and can improve reserve performance in both marine (Huntington *et al.* 2010) and terrestrial (Poulina *et al.* 2006) systems. We suggest that habitat connectivity may improve reserve performance by concentrating the positive effects of habitat diversity and the ecosystem services performed by mobile-link organisms (*sensu* Lundberg & Moberg 2003), which actively move across transition zones and can enhance ecosystem functioning in adjacent aquatic and terrestrial realms (Ewel *et al.* 2001; Beger *et al.* 2010). For example, in Moreton Bay fish populations that migrate tidally between coral reefs and mangroves are influenced positively by reserve protection, habitat connectivity, and diversity, and negatively by fishing and the length of tidal transition zones (Figure 3). We suggest that there might be a more general effect of high habitat connectivity and diversity enhancing the performance of conservation assets. It follows that failure to account for habitat connectivity when assessing reserve performance may underestimate the value of conservation efforts.

We recommend that, where other factors are equal, connected habitats be considered higher priorities for conservation. This connectivity can be evaluated most simply using isolation distances, with ecologically appropriate thresholds being scaled to organism mobility in the system of interest. For our study system, an appropriate threshold lies between 250 m and 500 m. To evaluate how this relates to the functioning of reserves

in similar seascapes at difference latitudes, or in other bioregions, we must consider the findings of other fish-seascape studies. At the broadest level, several recent reviews (e.g., Nagelkerken 2007; Grober-Dunsmore *et al.* 2009; Bostrom *et al.* 2011) point to ecological thresholds in mangroves-reef connectivity at the 100–1,000 m scale. This broad scale incorporates connectivity across juvenile and adult life stages and would be expected to narrow considerably where ontogenetic migrations are ignored. Indeed, Bostrom *et al.* (2011) infer the existence of a threshold at a scale of 100 m for adult reef fish. These scales are largely based on studies from the tropical Caribbean, but they correspond to the scale identified here in the subtropical Pacific. We therefore suggest that thresholds in mangrove-reef connectivity at scales of hundreds of meters may be more widely applicable for conservation. However, the broader utility of this potential threshold is in need of assessment, and would depend on other factors dictating mobility (i.e., home range, tidal amplitude, local hydrology, and bathymetry) in the system of interest. For example, larger thresholds for isolation might be expected in regions that experience larger tides or support species with greater home ranges.

Our findings demonstrate that connectivity can improve the performance of a reserve in promoting fish abundance and highlight its importance for maintaining ecological processes. We suggest that failure to incorporate connectivity into reserve assessment may undermine the value of conservation efforts and recommend that connected habitats be considered as higher priorities for conservation.

Acknowledgments

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1: Connectivity and assemblage composition.

Appendix S2: Testing potential alternative explanations.

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