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Quantifying the role of colonization history and biotic interactions in shaping communities –a community transplant approach

Chun-Yi Chang and Dustin J. Marshall

C.-Y. Chang (http://orcid.org/0000-0003-4672-7427)(changcy.mlml@gmail.com) and D. J. Marshall, Centre for Geometric Biology/School of Biological Sciences, Monash Univ., Victoria, 3800, Australia.

The role of colonization history and subsequent biotic interactions in determining the species composition in communities has long been the subject of debate in ecology. While one narrative has emphasized deterministic assembly rules, another has emphasized historical contingency. One problem lies in approach: community studies are typically either manipulative but somewhat unnatural, or observational but lacking manipulation. Furthermore, while most ecologists now recognize that both historical and biotic factors shape communities, too few studies have moved beyond qualitative descriptions of their roles. Here we use a manipulative approach that leverages natural variation to provide quantitative estimates of the relative contributions of colonization history and the subsequent biotic interactions. 384 communities were developed on artificial substrata in a homogeneous environment before undergoing reciprocal transplantation. We then compare community structure before and after transplantation as proxies for colonization history and biotic interactions. We found that the importance of history and the ensuing biotic environment differed at different times in community development. Early transplantations resulted in the local environment modifying community history faster compared to postponed transplantations. With a four-week difference in age, colonization history explained 20% more of the variation in older communities than in younger communities. Biotic interactions were able to modify colonization history at the age of 16 weeks, but older communities showed more resistance to the changing biotic environment. Our method provides a manipulative and quantitative approach for understanding the relative contributions of colonization history and biotic interactions to community in natural systems.

Colonization history and the subsequent biotic interactions among local populations are two key determinants of community structure (Tilman 1982, Cornell and Harrison 2014). Colonization of available habitats involves localized dispersal from near-by populations or migration from the regional species pool (Cornell and Harrison 2014). Once settled, organisms appropriate resources and interact with each other either through competition or facilitation (Connell and Slatyer 1977, Tilman 1982). For a long time in ecology, biotic interactions were hypothesized to be a main determinant of local community structure: succession could be predicted regardless of colonization history, because species' niche differences govern their competitive dominance (Clements 1916, Goldberg and Barton 1992, Silvertown 2004). Nevertheless, a counter-narrative states that colonization history may also set the course of succession in some communities when biotic interactions fail to modify colonization history (Gleason 1926, Chase 2003, Fukami 2015). This is often documented when member species are more tolerant to environmental change (Connell and Slatyer 1977), or in areas without distinctive environmental gradients (Egler 1954). The relative contribution of history and biotic interactions in shaping local species assemblages has inspired much research in ecology because such an understanding can ultimately shed light on the cause and maintenance of biodiversity (Hutchinson 1959).

Past observations on plant communities showed that, to a first-order approximation, when similar resources and habitat conditions are present among patches, local assemblages will have relatively low patch-to-patch variation (Whittaker 1972, Chase 2003). However, more recent observations revealed that when colonization history is unpredictable and more resistant to the modifications of biotic interactions, greater inter-patch variation may emerge even under identical habitat conditions (Drake 1991, Samuels and Drake 1997). Although there are ways to mechanistically explain why a greater-than-expected variation might occur during succession (Chase 2003, Chase and Myers 2011, Vannette and Fukami 2014), methods to quantify the relative contributions of history and biotic interactions can sometimes fall short of our expectations when challenged with observations from natural communities. We have reduced well-known methods into three very broad categories. First, studies have used observational community data combined with null models, testing if the local assemblage is largely a random subset of species found in the regional pool, therefore

identifying patterns generated by biotic interactions such as competitive exclusion (Cavender-Bares et al. 2009, Ulrich and Gotelli 2013). The second category of studies also used observational community data, but additional environmental variables are incorporated to carry out multivariate variance partitioning (Anderson et al. 2011). The third category of approach studies colonization history directly by assembling communities under controlled environments (Drake 1991, Fukami et al. 2005, Sams and Keough 2012). All three approaches have various advantages (Mayfield and Levine 2010, Götzenberger et al. 2012). However, they are either manipulative but somewhat unnatural, or observational and lack manipulation. These limitations arise because it is often difficult to reproduce or manipulate colonization history in natural communities in sufficient detail (Fukami et al. 2005, Vellend et al. 2014). A hybrid of the above approaches would combine both strengths: a field experiment that is both manipulative and detailed enough to account for different levels of natural variability in colonization history. Such a hybrid may offer a quantitative, direct, and more realistic way to disentangle the relative significance of history versus biotic interactions.

One way to manipulate community-wide history and biotic interactions is via transplants of intact communities. By transplanting communities, past studies have revealed how plant communities react to novel abiotic and biotic environments such as those introduced by climate change (Alexander et al. 2015). When transplanting among locations with different patch connectivity or species dispersal potential, historical information such as colonization frequencies or species turnover rates may be inferred from results of the transplantation (Cottenie and De Meester 2004). With marine sessile communities, studies have used transplantation of multispecies assemblages to investigate the drivers of structural variation across long environmental gradients (Cifuentes et al. 2010, Ralston and Swain 2014). With the recent shift in research focus from deterministic factors towards neutral stochasticity (Vellend et al. 2014), empirical experiments should now advance toward manipulating dispersal or colonization history, instead of manipulating abiotic environmental gradients alone. Patterns generated by colonization and post-colonization biotic interactions are intrinsically entangled (Chase and Myers 2011). If colonization history and biotic interactions are not manipulated simultaneously, it is not possible to estimate their relative contribution to community assembly. Our approach thus transplanted communities among patches known to have different levels of variability in species colonization and subsequent biotic environment, creating a mismatch in the variability between early and late assembly. Importantly, all patches are located in a small marina with rather homogeneous environment. This allowed us to decouple the effects of colonization from the effects of biotic interactions that may covary with colonization.

The relative importance of colonization history versus biotic interactions may change over time (Zhou et al. 2014). Factors known to influence the relative importance include resource availability (Kardol et al. 2013), disturbance (Chase 2007), and habitat connectivity (Cottenie and De Meester 2004). These factors can change depending on the time and stage of assembly (Menge and Sutherland 1987). For example, imagine a landscape with a mosaic of discrete patches connected by dispersal, forming a metacommunity. Now suppose a mass dispersal event took place among some patches because of phenological events such as mast seeding in forests, or mass spawning in corals. With more abundant dispersers, the connectivity of these patches may become higher than the landscape average because of the migration of primary colonizers (Connell and Slatyer 1977). Over time, the connectivity may slowly return to average due to increasing competitive exclusion and resource limitation faced by secondary and tertiary colonizers. These temporal changes have been shown to shift the relative contribution of dispersal and local interactions (Zhou et al. 2014); however, such phenological events may be difficult to track with non-manipulative approaches. By altering the timing of transplantation, our approach provides a way to assess the time evolution of the underpinnings of community assembly.

We conducted the experiment with marine sessile invertebrates inhabiting underwater hard substrata. Marine sessile community is a model system that is suitable for our purpose because there has been a strong tradition in the marine literature focusing on mechanistic aspects of community dynamics (Paine 1966, Sutherland 1974, Connell 1978). In the current study, young communities were recruited within their natural habitats before undergoing reciprocal transplantation. Importantly, the translocation from an origin patch to a destination patch was done at different community ages. We then partitioned the variation in transplanted communities into variation explained by their origin patch versus their destination patch, as proxies for colonization history and biotic environment. This is a strictly phenomenological approach and represents a departure from other community assembly studies that are more mechanism-focused.

Material and methods

Experiments were conducted at Blairgowrie Marina (38°21′31″S, 144°46′23″E) near the southern tip of Port Philip Bay, Victoria, Australia. The marine fouling community of the study region consist of species that require unoccupied substrate for vegetative growth, and competition for space, food and oxygen can be intense. Pilot studies at this site showed that species composition varied considerably from patch to patch. In general, species composition varied twice as much among patches than it did within patches (Chang 2016). We therefore created mismatches between history (the origin of a community) and biotic environment (its location) by transplanting intact communities among different patches.

General experimental setup

Underwater patches were created using PVC panels (55 × 55 cm) for fouling communities to establish. There were 16 plots per patch, each plot was 121 cm^2 in area (11 × 11 cm). Plots in a patch were 2 cm apart from each other. Surface of plots was roughened with sandpaper to encourage settlement of propagules. Patches were hung on a floating pontoon, submerged 1 m below the water surface facing downwards horizontally. Patches were randomly spaced but were on

average 3 m apart from one another. The floating pontoon was 3 m wide, 180 m long. The water depth ranged from 5.5 to 6 m. From a regional perspective, the marina represents a local community embedded within the regional species pool of Port Philip Bay. However our field site is likely the source of local recruits because the connectivity with other marinas are likely to be low since the surrounding shoreline (>5 km) is comprised of sandy beaches that isolate local fouling communities.

Field programme

Experiments began in November 2013 with unoccupied plots. After allowing communities to develop for a period of time, four replicated plots each carrying intact communities were transplanted away to a destination patch that was novel to the communities. As such, all plots received both an Origin treatment at the beginning of the experiment, followed by a Destination treatment. Communities shaped by their Origin patch were designated as a proxy of colonization history; subsequent development in their Destination patch was designated to be due to biotic interactions, and thus a proxy of the biotic environment. In order to maximize the number of transplants and therefore the statistical power, the transplantation from an Origin to a Destination was always reciprocal. For example, four replicates were transplanted from patch 1 (Origin) to patch 3 (Destination), meanwhile another four replicates were transplanted from patch 3 (Origin) to patch 1 (Destination). Note that when plots received the same treatment for Origin and Destination, they served as baseline communities for that patch. For example, when plots (n = 4 as replicates) in patch 2 were still assigned to patch 2 as Destination, they were moved to different positions in patch 2 and served as patch 2 baseline. Blocking was necessary because 16 was the maximum number of plots one patch can accommodate; a block consisted of four patches (see Fig. 1A for design schematic of a block). A full experiment was comprised of three blocks, therefore contained 192 plots in total (3 blocks × 4 Origin × 4 Destination × 4 replicates). The number of patches and replicates in a block was chosen in order to maximize the number of reciprocal transplants.

To formally estimate the relative importance of colonization history versus biotic interactions at different stages of assembly, we carried out two parallel transplant experiments. Both experiments followed the above steps, but the transplantation took place at week 4 in one experiment (the early transplant experiment, three blocks 192 plots), and week 8 in the other (the late transplant experiment, three blocks 192 plots). We followed the assembly of communities and investigated how results of variance partitioning changed with the timing of transplant. To achieve this, we followed the percent cover of each species in all 384 plots. Sampling of the plots in the early transplant took place when they were 8 and 12 weeks old. Sampling of the plots in the late transplant took place when they were 12 weeks and 16 weeks old (refer to Fig. 1B for the experiment schedule). At each sampling time point we photographed all plots in situ non-destructively. Computer software (Coral Point Count with Excel extensions, Kohler and Gill 2006) was used to generate 75 randomly distributed points over each plot. All visible

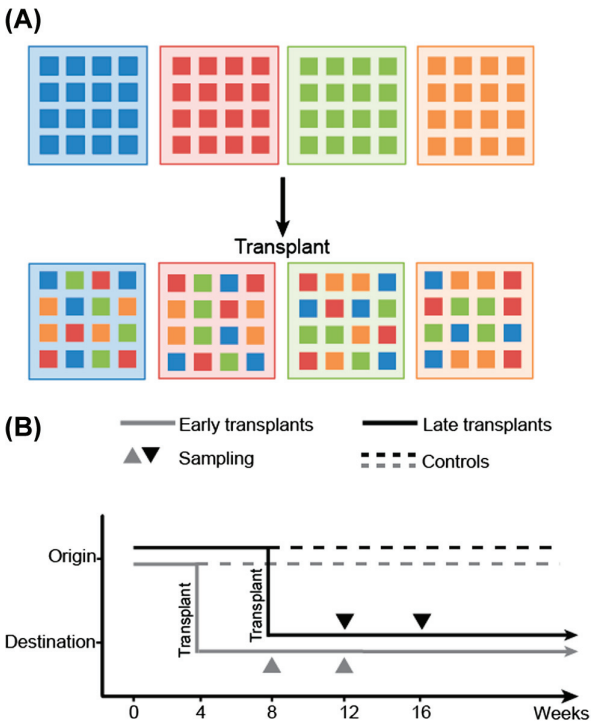

Figure 1. Schematic of the transplantation design and sampling schedule. (A) Example of a single experimental block consisting of four patches. Color of patches and plots (larger and smaller squares respectively) reflects their origin. Reciprocal transplantation (the direction of the arrow) created a fully factorial structure, in which each patch had their representative plots in all other patches. (B) Assembly commenced in November 2013 when empty plots were submerged. The path of the grey arrow represents the early transplant experiment; the path of the black arrow represents the late transplant experiment. Broken lines represent the control plots, they remained at their origin throughout the experiment. Triangles label the time point when samples were taken from both the baseline and the transplanted communities.

fouling species under the points were recorded to generate percent cover estimates.

Statistical analysis

Using the percent cover of each species, we calculated four summary statistics to describe our communities: species richness, Shannon index, loadings from correspondence analysis (CA) axis 1, and loadings from CA axis 2 (Oksanen et al. 2016). CA is a multivariate approach commonly used for analyzing species abundance data (Legendre and Legendre 2012). Species abundance here was quantified in terms of frequencies, and CA preserved the χ^2 distances among sampling units (plots); this ensured that the influence of rare species was not overlooked. Community structure was fitted to a linear mixed effects model. Four summary statistics (response variables) were modeled separately. There is no single best summary statistics for community structure, therefore we view CA1 and CA2 as two complementary ways to describe a community, acknowledging that they are not independent of each other. Model fitting was done with restricted maximum likelihood in the MIXED procedure of SAS ver. 9.4 (SAS Inst.). Main effects Origin and

Destination, and interaction Origin × Destination were all modeled as random factors nested within the random blocking factor (block). These random effects were tested using likelihood ratio tests. Our main goal was to detect changes in the relative contribution of historical and biotic effects at different assembly stages, therefore we analyzed data from early and late transplants separately.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.nt6bq> (Chang and Marshall 2016).

Results

In total we recorded 39 species, belonging to eight phyla; all were sessile organisms that require free space and hard substrata for vegetative growth. Overall, the eight most abundant species groups (over 2% space coverage) were the encrusting bryozoan *Watersipora subtorquata* (30.3%), upright red algae (10.0%), arborescent bryozoans *Bugula* spp. (6.0%, including four species), *Hydrozoan* (6.0%), tubeworms (4.1%, including three species), the oyster *Anomiidae* sp. (3.7%), colonial ascidians (4.2%, including five species and three morphospecies), and other encrusting bryozoans (3.2%, including five species). Although there was still unoccupied space even during our last sampling, it was mostly finely scattered under canopies of arborescent species where successful establishment of juveniles was unlikely. Furthermore, the larval settlement rate on nearby bare surfaces became very low 4–6 weeks after experiments commenced (Chang and Marshall unpubl.). We therefore consider our communities after the transplantation to be saturated in terms of larval settlement, and that very few ongoing colonization event can take place thereafter.

In the early transplant, Destination always explained more of the variation in communities than did Origin (Fig. 2A–B). At week 8, approximately 9.0% of the variation in community structure was explained by Origin (Table 1A, four summary statistics averaged), whilst around a quarter was explained by Destination (24.6%; Table 1A). By week 12, signal of Origin decreased to 7.4%, whereas Destination still explained 26.0% of total variance (Table 1B). There were no significant interactions between Origin and Destination in the early transplant (Fig. 2A–B).

Community structure in the late transplant was initially dominated by Origin effects (Fig. 2C). With a four-week difference in the timing of transplantation, colonization history explained 20% more of the variation in the late transplant than in the early transplant (contrast Fig. 2A with 2C; note that they were both four weeks post-transplantation). At week 12, 29.0% of variation was explained by Origin, whilst only 8.7% were explained by Destination (Table 1C, four summary statistics averaged). By week 16, three of the summary statistics did not contain any Origin signal (Fig. 2D); interactions were present but none was significant (species richness, Shannon index, and CA2). For CA1, most of the variance was still explained by Origin.

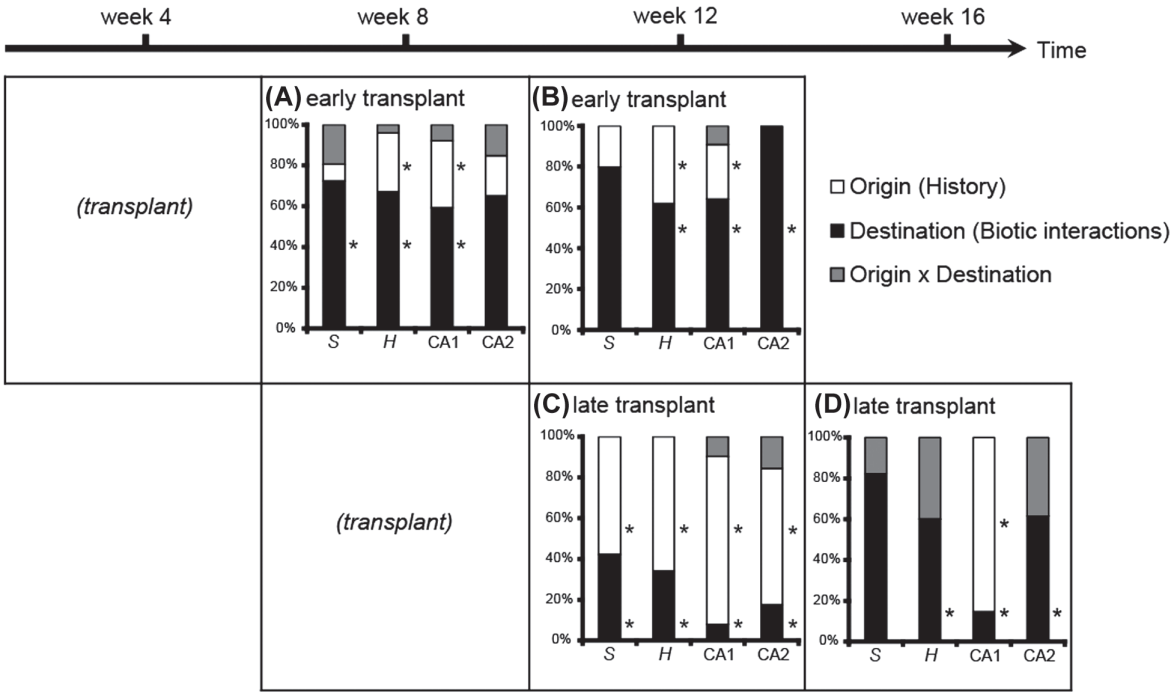

Figure 2. The variation in community structure explained by Origin (proxy for history), Destination (proxy for biotic interactions), and their interaction. (A) and (B) are results from the early transplant experiment. (C) and (D) are results from the late transplant experiment. *S*, species richness; *H*, Shannon index; CA1and CA2, correspondence analysis axis 1 and 2. Asterisks indicate significant effects tested using likelihood ratio tests ($p < 0.05$). Note that these bars report only explained variances; see Table 1 for block effects and unexplained variances.

Table 1. Partitioning of the variation in the four community summary statistics. VAR = variance explained by the CA axes. Numbers in bold represent statistically significant terms ($p < 0.05$), tested using likelihood ratio tests. Sections (A), (B), (C) and (D) of the table correspond to those labeled in Fig. 2.

	Species richness		Shannon index		CA1		CA2	
Source	Estimate	%	Estimate	%	Estimate	%	Estimate	%
(A) early transplant					VAR = 18.0%		VAR = 8.5%	
Origin	0.15	1.9	**0.02**	**11.7**	**0.03**	**13.1**	**0.01**	**9.2**
Destination	**1.31**	**17.2**	**0.05**	**27.4**	**0.05**	**23.5**	**0.03**	**30.4**
O × D	0.35	4.6	0.00	1.7	0.01	3.1	0.01	7.1
Block	**2.45**	**32.3**	0.05	29.9	0.05	23.5	0.00	0.0
Residual	3.32	43.8	0.05	29.3	0.07	36.7	0.05	53.3
(B) early transplant					VAR = 22.6%		VAR = 14.2%	
Origin	**0.27**	**5.9**	**0.01**	**10.3**	**0.04**	**13.5**	0.00	0.0
Destination	**1.07**	**23.2**	**0.02**	**16.7**	**0.09**	**32.6**	**0.04**	**31.3**
O × D	0.00	0.0	0.00	0.0	0.01	4.7	0.00	0.0
Block	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Residual	3.27	70.9	0.10	73.0	0.14	49.2	0.10	68.7
(C) late transplant					VAR = 26.0%		VAR = 12.4%	
Origin	**0.85**	**14.2**	**0.02**	**21.5**	**0.14**	**48.1**	**0.04**	**32.0**
Destination	**0.62**	**10.4**	**0.01**	**11.2**	**0.01**	**4.7**	**0.01**	**8.4**
O × D	0.00	0.0	0.00	0.0	0.02	5.7	0.01	7.4
Block	0.00	0.0	0.00	0.0	0.00	0.0	0.00	0.0
Residual	4.51	75.4	0.07	67.3	0.12	41.5	0.07	52.2
(D) late transplant					VAR = 28.3%		VAR = 18.2%	
Origin	0.00	0.0	0.00	0.0	**0.17**	**55.9**	0.00	0.0
Destination	0.33	5.8	**0.01**	**7.8**	**0.03**	**9.6**	**0.02**	**11.9**
O × D	0.07	1.3	0.01	5.2	0.00	0.0	0.01	7.4
Block	0.28	5.0	0.01	4.0	0.00	0.0	0.00	0.0
Residual	4.93	88.0	0.12	82.9	0.11	34.5	0.16	80.6

Discussion

Our experiments quantified the relative roles of both colonization history and subsequent biotic interactions in shaping communities. Taken together, the results from early and late transplants demonstrate that assemblages with similar colonization histories diverged once they experience different biotic environments, and communities that were once different converged after experiencing the same biotic environment. This can be seen in the last sampling of both early and late transplant (Fig. 2B, 2D). At this stage, assemblages in both early and late transplant were readily dominated by the Destination signal, suggesting that colonization history has been modified by subsequent biotic interactions. Note that this is true regardless of patch identity, since patch identity represents a random factor in our experiment. For example, communities that were moved from patch 1 to patch 3 became more similar to patch 3 than to patch 1, and those moved from patch 1 to patch 4 became more similar to patch 4 than patch 1. Furthermore, communities that were transplanted earlier converged to a destination assemblage more quickly than communities that were transplanted later (contrast Fig. 2A to 2C). Four weeks after our manipulation, assemblages in the early transplant already lost most of the Origin signal (Fig. 2A), whereas assemblages in the late transplant still retained most of the Origin signal (Fig. 2C). Communities that were transplanted later not only maintained their pre-transplant configuration for a longer period of time, but also showed a more noticeable interaction between colonization history and subsequent biotic environment (contrast Fig. 2D to 2B). In other words, we found quantitative evidence that the influence of history on assemblage pattern was proportional to the time since succession began, with communities who spend longer times at their origin having a more robust historical signal. Biotic interactions in subsequent succession depended partly on its historical legacy.

Both colonization and biotic interactions play a role in the assembly of fouling communities. While other studies in this system have suggested both processes are important (Sutherland 1974, Menge 1991), few have explored both simultaneously and quantified their relative contributions. When compared with the early transplant, we found relatively larger interaction terms in the late transplant during the last sampling (Fig. 2D). Although interaction terms in the model were not significant, we believe that their general increase is indicative because the increase was seen across different biological organizations including species richness, Shannon index and CA2. This colonization–postcolonization interaction suggests that, although the biotic environment can determine which species survived and thrived in their plot (as seen in the early transplant), the initial species composition cannot be overlooked. Recruits dominating early assembly stages are mainly species with fast reproduction and weak competitive ability. Simply by arriving first to open substrata allowed them to exploit resources for a short period of time. In terms of the demand for space to survive, they are considered species with large resource requirements. Post-colonization biotic interactions could likely affect these species more than others – species with larger space requirements may suffer disproportionally higher mortality early in succession when existing recruits have begun expanding through lateral growth (Hart and Marshall 2012). For example, young *W. subtorquata* settlers (large space requirement)

were rarely seen in our plots after *Bugula* spp. colonies (fast lateral growth) had established. This biotic filter may have favored early-spawning species and 'opportunistic' colonizers during early assembly, which then transformed the resident populations through competitive exclusion and selective facilitation during later stages of assembly (Amarasekare 2002, Valiente-Banuet and Verdú 2007, Cavender-Bares et al. 2009).

The insights provided by our transplant experiments are relevant to studies concerning the timing of species colonization. The timing of colonization has been demonstrated using phytoplankton species in microcosms. By varying the timing of species introduction, subsequent species composition changed even when the order of introduction remained the same (Robinson and Edgemon 1988). Furthermore, species need not be in the same trophic level to have a historical timing contingency. Using a protist–bacteria predator–prey system in microcosms, Olito and Fukami (2009) showed that the timing of predator arrival plays a key role in determining the long-term dynamics of prey community. These past studies lead to the generalization that the trajectory of community assembly can be altered by biological forcing even when the abiotic environment remained constant. For instance, a mass spawning event in some taxa may shift the trajectory of community assembly over time in the same location (Sutherland 1974). In our study, we manipulate the timing of transplantation, instead of the timing of colonization, as a way to manipulate history in a more realistic fashion. Suppose a scenario in which a mass spawning event occurred during the four-week gap between our early and late transplant, that is, it took place after the early transplant but before the late transplant, we would expect it to contribute to the strong Destination (biotic environment) signal in the early transplant. In contrast, for the late transplant, the event will contribute to the Origin (colonization history) signal. There are of course other possible scenarios where such phenological events or external disturbances occur at different time points, and could shift assembly trajectories differently. For the purpose of this study, we do not attempt to link patterns to processes, therefore, no attempt was made to document any specific event. Regardless, any event that affect assemblage structure will register their signature in our plots, and we will be able to estimate their collective influence relative to the timing of transplantation.

Our results indicate that natural levels of variation in colonization history are sufficient to influence subsequent assembly over a time scale relevant to the reproductive schedule of fast-growing 'opportunistic' species, generating community-level priority effects in a small homogeneous area such as the marina in this study. Theory predicts that priority effects should be strong when early-arriving species strongly affect the environment of the late-arriving species (i.e. wide impact niche) and when resource use is highly overlapped (Vannette and Fukami 2014, Fukami 2015). The most relevant studies testing these predictions have manipulated species colonization order as a putative stochastic driver of initial community difference (Robinson and Edgemon 1988). However there have been repeated calls for empirical studies to accommodate natural variation in colonization history (Vellend et al. 2014). We would argue that our results are particularly relevant to this discussion as we use natural variation in colonization rather than more structured approaches (Olito and Fukami 2009, Sams and Keough 2012).

While environmental factors, such as climate or nutrient enrichment, are important in determining community structure, assembly is not always predictable from environmental data (Lawton 1999). Stochastic events can generate patch-to-patch variation even under identical (or very similar) environmental conditions. Our study capitalized on the spatial variation of community structure occurring in a rather homogeneous environment. This setup provided a post-colonization environment that was (almost) free of abiotic environmental differences among plots and patches. However, our setup also imposed limits to our ability to make inferences: we are likely working with a relatively small amount of systematic variation. In our experiment, the amount of variation in community structure to initiate assembly is entirely introduced by larval dispersal, settlement choices, and post-settlement mortality. This variation may be largely stochastic because of identical artificial substrata and homogeneous abiotic environment. Comparing with other transplant experiments in which communities were moved across sharp environment contrasts (Cifuentes et al. 2010, Ralston and Swain 2014, Zhang et al. 2016), the variation between Origin and Destination in our study may contain relatively smaller amounts of systematic signal. We tackled the problem with a complete random-effects variance partitioning and a large number of replicates. Nonetheless, the unexplained variation at week 16, our last sampling point, can be as high as 71.5% (Table 1D). It is desirable to lower the unexplained variance and extend the length of the inference period, particularly when the ecological process under investigation needs more time to unfold (e.g. species range shift). Hierarchical Bayesian models have the capacity to draw inference on complex stochastic processes and are suitable for estimating their influences (Clark 2005). Improving the inference power of the statistical model with a better experiment designed specifically for quantifying stochastic components is one possible solution. At its current state, this study should be viewed as a first step towards exploring the utility of manipulative experiments in variance partitioning.

One could argue that short experiments might not be able to represent ecological succession at longer time scales. We believe it is more useful to clearly identify the ecological processes of interest. If one wishes to study the effect of initial colonization of pioneer settlers versus the effect of subsequent competition for space, then an experiment within one generation's time would suffice the purpose. In contrast, if one is interested in species' range shift in response to climate change or the invasion of novel competitor, then colonization history and biotic interactions documented across multiple generations would be needed to make such inference. Moreover, previous studies on the same sessile community at nearby locations showed that it is still unclear as to what constitutes an 'endpoint' of succession, since there was still substantial turnover of space even after two years of monitoring (Kay and Butler 1983). Within a small spatial and temporal scale relevant to our focus, we have demonstrated that whole-community transplantation is useful for

partitioning the variation in community structure into components of sequential events in time. The strength of this methodology is the ability to provide temporal snapshots of the relative contribution of assembly events, and it holds promise for quantifying the roles of natural variation of both the history and biotic interactions of communities in the field.

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