MONASH University

Deterministic and stochastic effects underlying marine benthic communities

Chun-Yi Chang
M.Sc.

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Contents

Chapter One General Introduction

Background

The history of species arrival to a habitat and their ensuing interactions with the biotic and abiotic environment shape the abundance and distribution of organisms in ecological communities. Ecology has traditionally focused on the effect of species interactions –the mutualistic and antagonistic interactions among organisms and their adaptation to the surrounding habitat were once thought to have paramount importance in shaping natural species assemblages. The majority of these interactions take place in a local area that allows individuals to interact with one another directly.

Nevertheless, there has long been a counter-narrative that colonization history of the habitat can substantially influence subsequent organism interactions in that area and alter the structure of assemblage. This perspective radically expands the local picture of species interactions into a broad-scale regional perspective. The history of species arrival to a local habitat is the joint outcome of multiple forces that operate over both large and small areas. The task of predicting patterns of colonization is therefore difficult, if not insurmountable.

A consensus is emerging which suggests that both arrival history and the interactions among extant community members are consequential, but their relative dominance over one another can be anything between historical effects overwhelms that of species interactions, or species interactions completely modify the pattern of colonization history. It has been suggested that the best practice to start understanding a given community is to first determine the relative importance of these two factors (Chase and Myers 2011, Vellend et al. 2014).

The research in this thesis builds on our understanding of the *variability* in natural communities. In essence, community ecology is the study of how abundances of organisms vary in space and time. At the basis of all community observations are species identity and

their abundances, often called species composition or community structure (in other studies, the term community structure can refer to distributions of phenotypic trait values or functional diversity, but in this thesis I use the term interchangeably with species composition and refer only to species composition). When many patches are sampled at the same time, the species composition may vary across space; this variation can be summarized using a mean species-composition and its variance. Studies aimed at explaining why species composition varies among patches can be grouped into three categories. In the first category, studies use observational species composition to test if observed patterns of variation obey certain theoretical predictions. Null models are a common tool for this task (e.g. Ulrich and Gotelli 2013). The second category of studies are also based on observational data, but additional environmental variables are incorporated to partition observed variances (e.g. Legendre and De Cáceres 2013). This is carried out under the premise that the surrounding environment shapes community structure. When environmental variables include spatial information such as connectivity or dispersal patterns, historical information such as colonization frequencies or species turnover rates could be inferred. These two categories are indirect studies because they infer underlying processes from observed pattern, therefore strong assumptions are necessary to link process and pattern. Trying to avoid indirect approaches, the third category of research investigated community structure directly by manipulating communities under controlled environments (e.g. Drake 1991, Fukami et al. 2005). This approach is often used to study whether similar communities can develop under identical environments. All three approaches have advantages and limitations (Hille Ris Lambers et al. 2012), yet they are typically either manipulative but somewhat unnatural (category three), or observational but lack manipulation (category one and two). Furthermore, too few studies have moved beyond qualitative descriptions of the relative importance of history and environment (i.e. is the effect of each ‘significant’). As an alternative, a manipulative field experiment that leverages

natural variation during community establishment may offer a quantitative, direct, and more realistic approach to disentangle the relative significance of historical versus environmental effects. In this thesis, I first focus on quantifying levels of species compositional variation that are naturally occurring in the field. I then manipulate these levels of natural variability as a way to manipulate community history. I explore the community-level consequences of the manipulations and their implications. Specifically, I explore ways of manipulations (1) as experimental designs to partition community variations; (2) as ways to detect principal drivers behind converging or diverging succession; (3) to obtain empirical expectations to inform theoretical predictions, regarding how replicated assemblages within a homogeneous habitat would react to varying initial recruitment history.

Study system

Marine benthic assemblages of sessile or sedentary organisms are well known to be heavily shaped by propagule colonization history and intense local competition among colonizers (Connell 1961, Sutherland 1974, Keough 1984). Transplanting individual fouling species has helped the establishment of some fundamental ecological principles such as population resilience and species range shifts (Paine 1976, Connell 1980, Palumbi 1984). However, the range of questions that can be addressed by using whole-community transplants have never been fully explored in this system.

Significance of this thesis

The goal of the research in this thesis is to provide a synthesis in approach, which preserves the advantages from various studies while addressing their limitations. When studying the historical and environmental effects on communities, an ideal approach is able to provide quantitative estimates of their relative influence, but still offer a direct way that manipulates

history or environment. Moreover, it is essential to manipulate communities at their natural levels of variability and complexity. This is usually difficult because natural history is complex, with addition and removal of species, abiotic perturbations, and predation constantly taking place at arbitrary intensities and between random time intervals. However, from lessons learnt in controlled laboratory experiments, we understand that even slight difference in the fitness, fecundity, or arriving sequence of initial founder populations can lead to very different species composition, a phenomena known as priority effects (Drake 1991, Young et al. 2001). Therefore, in Chapter Two I quantify the variation in species composition of a marine sessile community, at both early and late stages of community development. I concentrate on identifying two different spatial scales that differ in their natural magnitude of compositional variation, and report the time progression of this variation. Capitalizing on this information and the same model community, in Chapter Three, I demonstrate an *in situ* manipulative experiment that formally incorporated natural variability in initial recruitment processes as causal explanations to the variations in the subsequent succession trajectories. This has been repeatedly called for in past syntheses but has never been realized. With the experimental design, I also demonstrate variance partitioning using mixed effects modelling, variability of initial recruitments are modelled as random deviations from a fixed population mean.

From lessons learnt in controlled laboratory experiments, we now know that testing the cause of convergence or divergence in natural assemblages has to satisfy two requirements. First, colonization history has to be manipulated in ways that separate the effects from other assembly processes; second, the manipulation has to be replicated in identical (or nearly identical) habitats. Addressing these requirements in the field has proven rather difficult because colonization history is often unpredictable, generating greater patch-to-patch variation despite absence of habitat heterogeneity. In Chapter Four, I transplanted replicated

communities to different patches, so that these communities could interact with others that were otherwise beyond the reach of local interactions. The design extracts and utilizes natural sources of random variability that are often present over different spatial scales. The idea can be traced back at least to Schluter (1986). Instead of a manipulative experiment, Schluter (1986) proposed a comparative approach in which convergence (or lack thereof) is tested by comparing the variance between replicated communities within habitats to the variance between different habitats, assuming that communities in different habitats share more similar history. With the transplant experiment, the assumption would not be necessary. If the transplanted communities show more divergent trajectories than the non-transplanted ones, then assembly history could be concluded to drive succession.

A common feature of recent community models is conserved stochastic components that introduce random variation into community structure. Importantly, stochasticity not only results from higher-dimensional processes such as dispersal and colonization histories, but can also take place when dispersal or history interacts with niche-based processes (May 1976). Overlooking differences in initial history may lead to unanticipated community divergence, because variable colonization history may give rise to heterogeneous variance structure among treatment communities even in the absence of habitat heterogeneity (Fukami et al. 2005, Houseman et al. 2008). This is consequential because recent community assembly models rely heavily on the pattern of variation within and among treatment communities (i.e., beta-diversity) to determine the degree of assembly predictability, whether the ‘treatment’ is planned manipulation (e.g., Inouye and Tilman 1995) or unplanned natural gradients (e.g., Bernard-Verdier et al. 2012). In Chapter Five, I use a transplantation approach that brings together assemblages from different recruitment regimes to a homogeneous environment in order to assess how their adult compositional variation responds to variable recruitment. This

approach, which is more realistic than artificially assembled colonizers, can bring new insights into our current understanding of community assembly.

In Chapter Six, I provide a synthesis with the results from each Chapter and discuss new insights and ecological implications revealed by these experiments.

Chapter Two The spatio-temporal distribution of marine fouling populations within a metacommunity

Abstract

Linking ecological processes to the spatial scale on which they operate remains difficult in community ecology. Our understanding of ecological communities cannot advance if we do not distinguish large scale processes from smaller ones. Identifying the spatial scales that capture the most variability in community structure is a reasonable starting point to begin our investigation. Marine fouling communities are strongly shaped by both the supply of larvae and direct resource competition among colonizers –two processes that operate on distinctly different scales. Here I demonstrate how community structure varies with spatial scale in a fouling metacommunity in temperate Australia, and identify the spatial scale that captures this variability. Community structure was quantified with both univariate (species richness and diversity) and multivariate (species dissimilarity) indices. Variation in fouling community structure was unevenly distributed between the two spatial scales examined. On average, the fouling community structure varied twice as much among patches than it did within patches. The magnitude of temporal fluctuation in populations was much greater than community-level fluctuations. Furthermore, some populations showed a significant but inconsistent correlation on both scales. My findings show that both larval supply and local competition are important in shaping local communities within this metacommunity.

Introduction

A major goal in ecological research is to identify patterns in biodiversity and understand how they are generated. To achieve this in community ecology, one must first explain how communities vary in space (Underwood et al. 2000). However, ecologists are concerned about very different spatial scales. Choosing spatial scales that are appropriate for a given question is difficult, and 'the problem of scale' has been highlighted in ecology by many authors (Levin 1992, Huston 1999, Godfray and Lawton 2001). For example, in several early theoretical explorations, MacArthur and co-workers highlighted the importance of trait-environment relations at local scales (MacArthur and Levins 1967), but dismissed the importance of these relations when studying larger spatial scales (MacArthur and Wilson 1967). More recently, findings have suggested that *scale dependency* is the key to disentangling patterns in community structure (Holyoak et al. 2005, Chase and Myers 2011, Boulangeat et al. 2012).

Identifying the spatial scale at which the greatest variation lies can be informative. It allows us to focus on the principal processes that are the most important across habitats. It is not uncommon for ecologists to summarize multi-dimensional biological patterns using a few variables. For example, instead of studying the entire community, one could focus on a few principal axes that explain the most variance in species composition (Legendre and Legendre 2012). A certain ecological process may operate predominantly on one scale, whilst still exerting minor influences on other scales. For example, facilitated dispersal among moss patches reduced the loss of microarthropod species from local populations that are otherwise less likely to persist (Gonzalez et al. 1998). The relative importance between local and regional factors may be a unique feature of each community. Finding a spatial scale that captures the most variance within a multi-species community is therefore a simplification we make in order to understand complex patterns in nature.

A widely practiced approach in spatial ecology is to explain the relations between biodiversity and environmental gradients. However, these studies are concerned with *mean* biodiversity changes; less attention has been given to the *variance* around the mean of diversity, especially in the absence of environmental gradients (Legendre et al. 2005, Tuomisto and Ruokolainen 2006, Chase and Myers 2011). For example, beta-diversity (the difference in species richness among sites) is often quantified along an environmental gradient axis (e.g., productivity gradient, habitat size gradient), it is then explained by these environmental differences. The unexplained part, that is, diversity variation in the absence of gradients, is often concluded to be 'artificial', due to minor differences in uncontrolled factors, or pure sampling error (e.g. Olivier and van Aarde 2014). The view that biodiversity is constantly fluctuating in space seems equally plausible, however challenging to verify. This challenge is due, at least partly, to limitations in statistical techniques. Hierarchical mixed-effects modelling suitable for ecological datasets have only become available over the past three decades, and are yet to be widely implemented in ecology (Bolker et al. 2009). Hierarchical variance partitioning is a useful way to separate scale-dependent ecological processes. For example, barnacles compete for planktonic food sources directly with their neighbors within a 0.01-0.1 m range, but produce free-swimming propagules that disperse and interact with other populations over a distance of 10 000 m. Seed dispersal in terrestrial plants represents a similar example (Myers and Harms 2009). These ecosystems are thus hierarchical in structure and should be analyzed as such (e.g. MacNeil et al. 2009).

Marine sessile invertebrate species inhabiting underwater hard substrata (the fouling community) have several general as well as specific features which make them an advantageous model system for ecological studies. The adult life stage is exclusively sessile, whilst the larvae life stage is not. Swimming larvae are released by adults into the ambient water. As most larvae are limited in their swimming ability, some dispersal is obligatory

caused by passive transport of water movement. In this regard, life-history traits involving fertilization, reproduction, dispersal, and settlement are comparable between marine sessile communities and terrestrial plant communities (e.g. Myers and Harms 2009). However, specific to marine communities relative to plant communities, is the occurrence of faster life cycles and shorter time periods to sexual maturity; both of which are desirable qualities for ecological studies such as hierarchical variance partitioning. In order to obtain reliable variance estimates, hierarchical experimental design usually requires more replication of the same treatment compared to traditional ANOVA experimental designs. Juveniles of marine invertebrates can be recruited quickly in the field with high temporal synchrony, which minimizes the effects from other uncontrolled factors if juveniles were to recruit from different cohorts.

The goal of this study is to investigate the compositional variation in a marine fouling community on two different spatial scales—one is a few centimeters apart, and the other can span up to 100 m. Based on previous studies, the factors generating variations on these scales are different. Using hierarchical variance partitioning, we will separate the compositional variation into different components representing different spatial scales. After investigating the scale dependency of the variation, we will also infer underlying ecological processes with different species. Specifically we will ask (1) what are the spatial patterns of fouling species percent cover? (2) Are these patterns due mainly to variations among patches? (3) Are species' abundance distributions similar (or dissimilar) across scales?

Methods and materials

Study site and the fouling community

Experiments were conducted within Blairgowrie marina (38°21’31”S, 144°46’23”E) near the southern tip of Port Philip Bay, Melbourne, Australia. The marine fouling community of the study region consists of species that require unoccupied substrata for vegetative growth and competition for space, food and oxygen can be intense in some cases (Ferguson et al. 2013, Svensson and Marshall 2015).

Experiment setup

PVC settlement plates (11×11 cm) were attached to larger PVC backing panels (55×55 cm) for fouling communities to establish. Each backing panel carried 16 settlement plates which were placed 2 cm apart. The surface of the settlement plates was roughened with sandpaper to encourage settlement of propagules. Backing panels were hung horizontally off a floating pontoon 1 m below the water surface facing downwards. The floating pontoon was 3 m wide, 180 m long, with an average water depth of 5.5 m.

Backing panels can be viewed as empty patches randomly created under the pontoon (and referred to as ‘patch’ hereafter). Settlement plates were thus equivalent to replicated plots (and referred to as ‘plot’ hereafter) and were randomly located within each patch.

Field programme

In this study we took a strictly phenomenological approach; that is, in our experimental design we did not include any treatment assumed to be related to a particular mechanism. The only treatment subjected to the community was the spatial arrangement of patches, and this ‘patch effect’ was treated as a random factor. However, we assumed that the entire marina was within an area small enough so that physical and hydrological conditions within the marina were homogeneous. This assumption allowed us to attribute any unexplained variance purely to biological causes.

To quantify the spatial variation, we monitored 14 patches over a period of three months. We visited each patch regularly during the austral summer (from December 2012 to the end of February 2013). Once every month, four randomly chosen plots from each patch were brought back to the laboratory and photographed. The abundance of a species in a plot was quantified in terms of its percent cover: the area occupied by a species divided by total area. Computer software (Coral Point Count with Excel extensions, Kohler and Gill 2006) was used to generate 100 randomly distributed points over each plot and all visible, sessile species under the points were recorded in order to generate percent cover estimates.

From our samples we isolated three of the dominant taxa, representing functional groups with distinct growth forms and reproductive strategies. We then examined their spatial distribution in detail. *W. subtorquata* is an invasive bryozoan and is now commonly found in southern Australia. Their planktonic larvae are typically among the first to colonize available spaces early in summer. With an encrusting growth form, young colonies take over spaces quickly and become reproductive within eight weeks. Soon after reproducing, part or all of the adult colonies may begin to senesce, freeing up space for succession of other species. *W. subtorquata* represents the functional group with a more opportunistic larval stage and larger resource requirements (space) as adults. Arborescent bryozoans have tree-like growth forms and are more abundant during mid- and late-community stages. With a different growth form, they exploit a different resource niche relative to the other encrusting species and thus rely less on being a fast grower and an opportunistic colonizer. They represent the functional group with smaller resource requirements and a slower growth rate. Colonial ascidians represent a competitively dominant functional group with larger resource requirements.

Modelling community structure variation

Using the percent cover data, we calculated four summary statistics to describe our community: species richness (*S*), Shannon Index (*H*), loadings from Correspondence Analysis Axis 1 (CA1), and loadings from Correspondence Analysis Axis 2 (CA2). CA can be used to analyze community structure when species abundances are quantified in terms of frequencies. CA preserves the chi-square distances among sampling units, which ensures that the influence of rare species is not overlooked. These summary statistics were then modelled using a hierarchical mixed effects model, fitted using restricted maximum likelihood (MIXED procedure of SAS 9.4, SAS Institute, Cary, NC). The model had no fixed term, and estimated the patch effects based on the random deviations of summary statistics from the fixed population means. The total variation was partitioned into those due to patch and those due to error terms. Significance tests for patch effects were done using likelihood ratio tests. In order to visualize the dissimilarity between plots that were either located within a patch or among different patches, we calculated chi-square distances between all pairs of sampled plots using the raw species percent cover data, and presented the results of within- and among-patch pairs separately.

We also modelled the abundance and distribution of selected representative taxa with the above model.

Results

Throughout the sampling period, we recorded 33 taxa in the fouling community; of which 31 were invertebrate animals and two were algae. Most community members could be identified to the species level; for those that could not be identified to their species using a digital photograph, morphospecies were assigned based on their morphological features (a list of common taxa along with their adult growth form can be found in Table 1).

Abundance and distribution of dominant taxa

The abundance of dominant taxa changed over time (Fig. 1). Tubeworms were the most conspicuous taxon throughout the experiment. They covered *c.* 30% of the space at week 4 and 8, and were over-grown by other organisms only until week 12. The solitary ascidians (includes three morphospecies) and the dominant encrusting bryozoan *Watersipora subtorquata* increased steadily in their space coverage with time. At week 12, *W. subtorquata* occupied *c*. 17% of the space while solitary ascidians had a space coverage of *c*. 10%. Arborescent bryozoans (includes four species) and colonial ascidians achieved their maximum cover in week 8 (34% and 25% respectively) and had less cover at weeks 4 and 12. For the three representative functional groups, their abundance appeared to have significant spatio-temporal variation at the level of the observation unit, that is, plot. Spatial variability of *W. subtorquata* increased in time with its overall percent cover, with the greatest variation observed at week 12. In contrast, arborescent bryozoans and colonial ascidians both showed the highest amount of inter-plot variation during mid-succession, at week 8.

Patterns in community structure

Similar to the patterns in the population of functional groups, community structure also appeared to vary significantly over space and time (Fig. 2b & c). At week 4, we recorded 22 taxa marina-wide ($S = 22$). The expected S in any given plot was, however, only 7.5. At week 8, marina-wide S peaked to 28, with an expected S for a given plot to be 13. At week 12, both marina-wide and plot-expected S decreased slightly to become 21 and 12.5, respectively. H showed a temporal pattern similar to S where the community was the most diverse during mid-succession (Fig. 2c). Both S and H had similar amount of spatial variability over time since the size of each box was similar over time. Nonetheless, the H observed in each plot at week 4 appeared to tend towards smaller values, suggesting that plots at this stage were mostly colonized by only a few common taxa.

Patch-level vs. plot-level variability

Results of the variance partitioning showed that patch differences were sometimes important in maintaining the spatial variation in the abundance and distribution of the major functional groups. However, this depended on the identity of the functional group (Fig. 3). For the distribution of *W. subtorquata*, the observed among-plot variability at week 4 (early succession) was similar even when comparing two plots from distant patches. Models with and without patch identity as a random factor, fitted the *W. subtorquata* data equally well under our likelihood ratio tests (Fig. 3a week 4). At week 8 and 12, the model with patch identity as a random factor performed significantly better in explaining *W. subtorquata* distribution than the model without patch information. For the distribution of arborescent bryozoans (Fig. 3b), the model with patch random effect always had a better fit than the model ignoring patch identity, regardless of the timing of sampling. For populations of colonial ascidians (Fig. 3c), aggregation at the patch level was only significant at week 8 (mid-succession). During early and late succession, their spatial distribution did not show an obvious pattern following patch identity.

Patch effect was also able to account for a significant portion of the community-level variation (Fig. 4). At week 4 and 12, patch effect was significant in all community summary statistics. At week 8, patch effect was only important when *S*, CA1, and CA2 were considered, and was not influential for *H*.

The dissimilarity between any two plots first decreased from week 4 to week 8, and then finally peaked at week 12 (Fig. 5). Nonetheless, the plot-plot dissimilarity among patches were always significantly higher than those within patches (Fig. 5).

Discussion

Community structure (species richness *S* and Shannon Index *H*) showed significant spatial variation. This is interesting because patches were located within a small marina, with a

rather homogenous environment. *S* and *H* varied significantly among patches (distributed across the 100 m^2 field site). *S* and *H* varied less within each of the 0.3 m^2 patches. Multivariate ordination analysis of the full dataset of community percent cover further confirmed this patch effect. Spatio-temporal variation was also an important feature at the site. *S* and *H* stayed low until week 4, mounted to their highest at week 8, and then decreased slightly at week 12.

Community dissimilarity on both the patch scale and the site scale changed in a similar way over time. The dissimilarity first showed a decrease from week 4 to week 8; it then increased from week 8 to the highest at week 12. This pattern indicates that the assemblage first converged then diverged. The convergence was largely driven by both the tubeworm *Pomatocerus* and *Bugula* spp., occupying over 65% of the space at week 8. Other species increased gradually towards week 12, causing the assemblages to further diverge. Communities at the study site may be more driven by stochastic assembly. Considering recent results from other studies in the same region, four in five of the community assembly experiments reported failure of convergence in community structure (Sams and Keough 2013). Therefore, the fouling community does not appear to have a long-term deterministic pattern of assembly, which echoes the findings in other parts of the world (Sutherland 1974).

Similar to the community-level attributes, percent cover of abundant populations showed significant spatio-temporal variation at a patch scale. However, the magnitude of fluctuation of populations was much greater than the magnitude of fluctuation due to community-wide diversity attributes. There are other systems known to have similar contrasts of community vs. population variability. Tilman (1996) reported that year-to-year variation of a grassland total community biomass was relatively stable compared with population abundance variation. Our results demonstrate that the contrast can be observed on shorter, within-generation time scales. Whether the same set of principal mechanisms are in operation

between long and short time scales is not clear at this point. In our observations, there seems to be complementary space occupiers. For example, in a given community, when arborescent bryozoans failed to establish, colonial ascidians such as *Botrylloides* or *Didemnum* were very likely to take over the free space. Thus, so long as this complementary relationship holds among species, there will be relatively little variation. However, the coarse taxonomic resolution used in our study should be interpreted with caution. Major colonial ascidian populations were lumped into functional groups because identification at the species level was problematic with photography sampling. Therefore, it is possible that our analysis underestimates the total community variance if populations varied more at the *species* level than at other coarser levels. Nevertheless, it is clear that spatial variation among patches was significant at both population and community levels employed in the current study.

Many of the biological interactions and trait differences among species could affect the observed population patterns, which would in turn affect the overall community pattern. The three most important drivers of population-level variation in our system are: differential investment in life-history strategies (tradeoffs), difference in dispersal, and difference in species interactions. Tradeoffs between life-history traits have long been regarded as an important mechanism that maintain diversity in communities (Tilman 2004). A classic example among fouling communities is the colonization-competition tradeoff (Sousa 1979), in which different species invest differently in the larvae and post-recruitment stages. If species rely heavily on the larval period, they may have phenotypes such as better larval dispersal ability or rapid sexual maturity. Meanwhile, other species investing in post-recruitment stages may grow slower, but may also eventually become better competitors for resources (e.g. space). The tubeworm *Pomatocerus* may adopt the former strategy, since we observed a single huge pulse of settlers that distributed relatively evenly over the study site, and then quickly occupied over 30% of the space in less than a month. On the contrary,

solitary ascidians such as *Pyura* may adopt the latter strategy, since they were hardly found in the first month, but gradually overgrew other species as succession occurred. Dalby (1995) also reported that *Pyura* colonize steadily throughout the year but rarely dominate settlement events. Such segregation in phenology may be an important way in which diversity is maintained (Butler and Chesson 1990).

Another factor driving different population patterns is dispersal. Dispersal is a broad concept referring to the movement of organisms from one place to another (Vellend et al. 2014). Various processes are involved in shaping the dispersal pattern of an organism. For fouling communities, lengths of larval period, swarming behavior, habitat choice, and surrounding fluid dynamics are all important. Because of its complex nature, small-scale dispersal variability is often modelled as a stochastic component in community assemblages (Edwards and Stachowicz 2011). Here, the spatial scale is considered 'small' if the landscape (e.g. temperature, flow regime, resource availability) within this scale is rather homogenous. In this sense, our study site is likely to be considered a 'small' area, and thus propagule dispersal should only contribute stochastic variation to the community structure. However, as argued by Vellend et al. (2014), high mean dispersal combined with high dispersal variance should lead to high predictability in initial species composition in empty patches. High mean dispersal indicates that many propagules arrive per unit time, and high variance indicates that there are many more propagules of some species compared to others. Our observational data coincide with the above argument; during early colonization (week 4), the abundance of 2 (out of 3) species examined can be predicted affectively by patch effects. Although the above predictions given by Vellend et al. (2014) were originally focused at the community level, our results imply that the predictions could extend to generate population-level hypotheses.

The third important factor driving different population patterns is differences in species interactions. The study of species interactions has its pivotal role in the construction of the

niche concept and has been unambiguously regarded as a deterministic ecological process (Chase and Myers 2011). Even so, species interactions are known to be asymmetrical and non-uniform among taxa, and their combined effects on the community assembly may have complex interactions with local environment (Sams and Keough 2012). The larvae of some species with high space demand have been shown to avoid settling near large space-occupying competitors (Grosberg 1981, Gaines and Roughgarden 1985), such as *Pyura* in our study system. Meanwhile, in other studies, *Pyura* have also been shown to facilitate adjacent bryozoan larval settlement and colony growth (Sams and Keough 2013). Moreover, depending on resource availability, interactions within taxa may propagate to the community level with completely opposite effects. For example, if the patch is already crowded, then the facilitated *Bugula* spp. settlement by *Pyura* may not last long enough to affect succession at later stages, because *Bugula* are short-lived. However, if there is plenty of free space, *Bugula* spp. have the potential to alter the community structure through direct interactions with colonizers of longer-lived species (Menge 1995).

Conclusion

The factors discussed above can be broadly grouped into two categories; with respect to the most influential point of a fouling-species life-history. I call the first category ‘historical factors’ because dispersal and colonization interactions take place predominantly during the early stages of community assembly. The second category I call ‘environmental factors’ because biological inhibitive and facilitative interactions are all part of the ‘environment’ organisms experience. Additionally, organisms also change the distribution of resources and abiotic factors around them ('impact' niche, sensu Soberón 2007). All of the above proposed processes are simply speculative at this point; an essential next step is to understand the relative significance of both historical and environmental factors to the structuring of

community composition. A manipulative experiment at the community level may be informative. As it is concluded that the community structural variation was the strongest at the scale of the entire field site, future manipulative experiments seeking to explore community-wide patterns should be designed accordingly.

Table 1. List of common taxa found in our fouling community. Commonness is defined as having a percent cover equal to or more than 2% in at least one patch. The growth form of each species is also described: A-arborescent; E-encrusting; C-colonial; S-solitary.

Taxa	Growth form
MACROALGAE	
Bryopsis plumosa	A
Asparagopsis armata	A
ANNELIDA	
Hydroides elegans	S
Pomatocerus taeniata	S
Spirorbis spirorbis	S
BRYOZOA	
Bugula dentata	AC
Bugula stolonifera	AC
Bugula flabellata	AC
Bugula neritina	AC
Schizoporella spp.	EC
Membranipora membranacea	EC
Watersipora subtorquata	EC
Celleporella hyalina	EC
Microporella ciliata	EC
CNIDARIA	
Hydroidae sp.	A
ASCIDIAN	
Ascidiella aspersa	S
Botrylloides leachi	EC
Botryllus schlosseri	EC
Didemnum sp.	EC
Ciona intestinalis	S
Pyura stolinifera	S
Diplosoma listernium	EC
PORIFERA	
Sycon ciliatum	AS

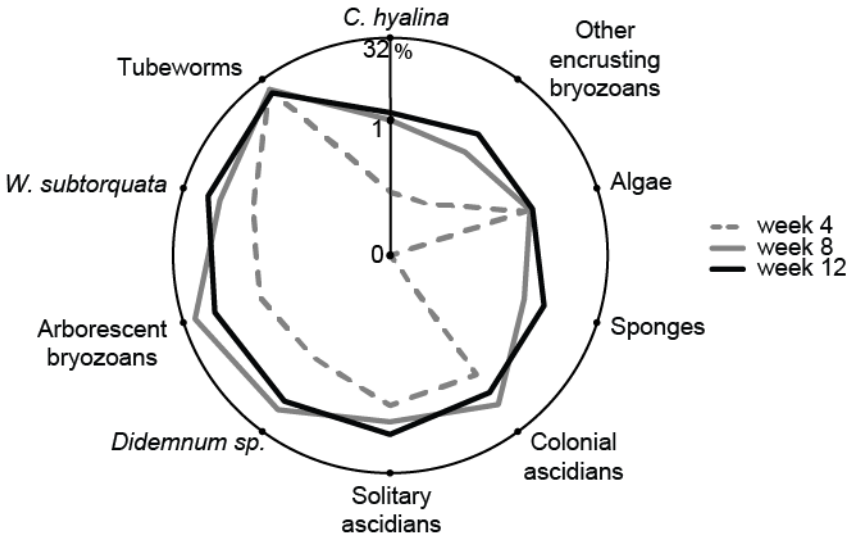

Figure 1. Ten most abundant taxa and their temporal changes in abundance (percent cover). Species are arranged clockwise with increasing total abundance, from *C. hyalina* (least) to tubeworms (most). Abundance axis is in log scale. Refer to Appendix A for growth forms of each taxon.

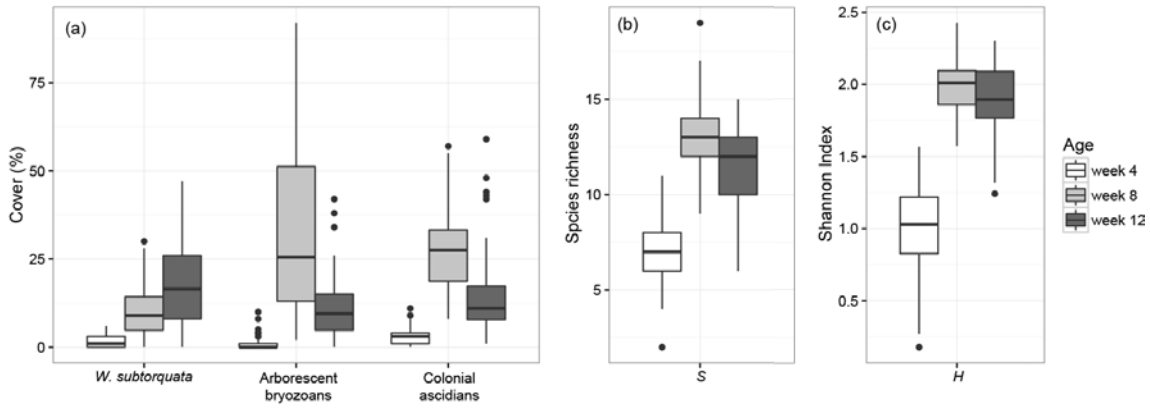

Figure 2. Spatial variation in abundance of *W. subtorquata*, arborescent bryozoans, and colonial ascidians (a). Spatial variation in species richness *S* (b). Spatial variation in Shannon diversity *H* (c). Observations at the plot level is presented and thus the size of the boxes represents plot-level variation. Thick lines in boxes represent medians; lower and upper hinges of boxes correspond to first and third quartiles of the observation; lower and upper whiskers span through the 3/2 interquartile range; observations beyond the end of the whiskers are outliers (solid circles).

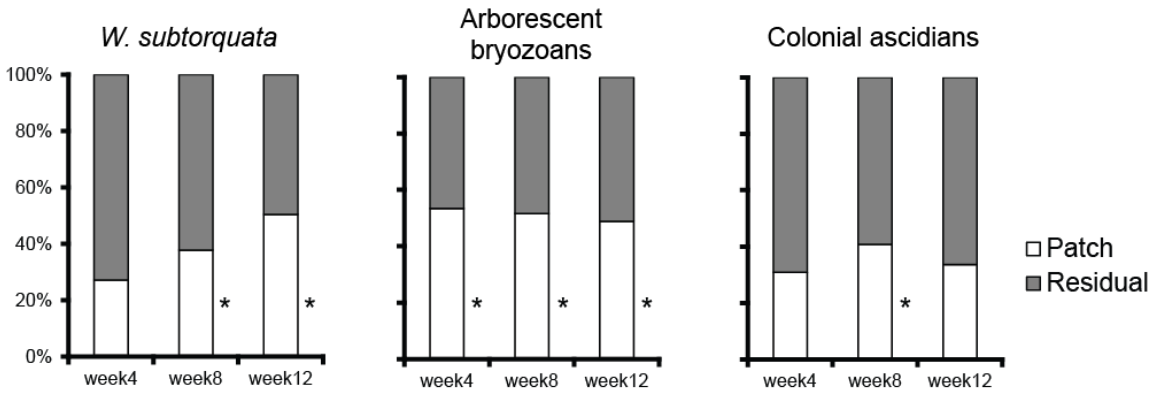

Figure 3. Spatial variation in abundance of *W. subtorquata*, arborescent bryozoans, and colonial ascidians partitioned into those explained by patch identity, and those explained by plots within patches (residual). An asterisk next to each bar indicates that the model with patch information explained the distribution significantly better than the null model (one without patch information) at a significance level of $p = 0.05$.

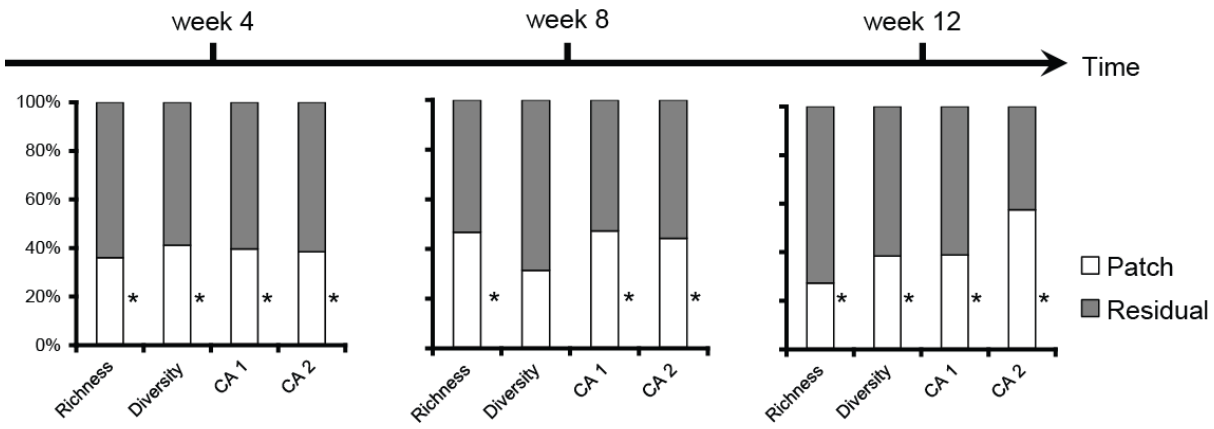

Figure 4. Spatial variation in community structure partitioned into those explained by patch identity, and those explained by plots within patches (residual). Community structure is quantified in four ways: species richness (*S*), Shannon Index (*H*), and the first two axes of correspondence analysis (CA). An asterisk next to each bar indicates that the model with patch information explained the distribution significantly better than the null model (one without patch information) at a significance level of $p = 0.05$.

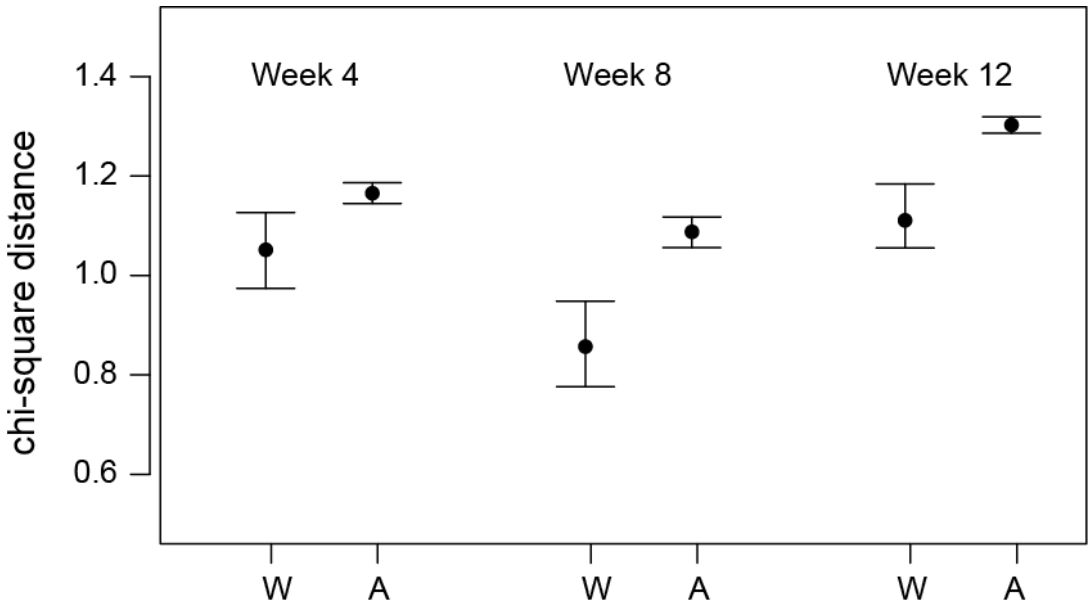

Figure 5. Structure variation of whole community partitioned into within (W) and among (A) patch components. Chi-square distance is the dissimilarity among two communities being compared. Lower distance indicating communities being more similar. Dots and error bars represent the estimated mean and 95% confidence interval around the mean. Note that the intervals at week 4 are not overlapping.

Chapter Three Quantifying the role of history and environment in shaping communities

Abstract

The role of history and environment in determining 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. However, one problem lies in both these approaches: community studies are typically either manipulative but somewhat unnatural, or observation but lack manipulation. Furthermore, while most ecologists now recognize that both historical and environmental 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 history and environment. 384 communities were developed within their natural habitats before undergoing reciprocal transplantation. We then partition the variance in community structure explained by origin, destination, and their interaction as proxies for history and environment. We found that the importance of history and environment differed at different times in community development. When we transplanted young communities early in development, local environment modified community history much more rapidly than it did when we postponed the timing of transplant. In older communities, history provides more resistance to a changing environment. Overall, we demonstrate how an understanding of community assembly could benefit from an explicit consideration of history-environment interactions.

Introduction

Colonization history and consumer-resource interactions are two key determinants of community structure (Tilman 1982, Gaines and Bertness 1992). Colonization of available habitats involves localized dispersal from near-by populations or migration from the regional species pool. Once colonized, organisms appropriate resources and interact with each other via mutualistic or antagonistic interactions. Traditionally, consumer-resource interactions were widely appreciated because their effects on ecological succession can be either directly observed or can be revealed by competition experiments (Paine 1969, Tilman 1982). These effects could be collectively called *environmental effects* because organisms not only respond to changing resource levels, but experience the biotic environment among their neighbors (requirement and impact niche; Chase and Leibold 2003). For a long time in ecology, environmental effects were hypothesized to be a main determinant of community structure: succession could be predicted without information on colonization history, because species niche differences govern their performances (Clements 1916, Silvertown 2004).

Nevertheless, a counter-narrative states that colonization history may also set the course of succession in some communities, when environmental effects fail to modify *historical effects* (sensu Fukami et al. 2005) set by the colonization history (Gleason 1926, Connell and Slatyer 1977, Shmida and Wilson 1985). This is often documented in areas without distinctive environmental gradients (Egler 1954), or when member species are more tolerant to environmental change (Connell and Slatyer 1977). The relative contribution between history and environment in shaping biodiversity has inspired much research endeavor in ecology because understanding the relationship between history and environment can ultimately shed light on the cause and maintenance of patterns in biodiversity (Hutchinson 1959).

Past observations on plant communities showed that, to a first-order approximation, when similar resources and abiotic conditions are present among patches, local assemblages will have relatively low patch-to-patch variation (Whittaker 1972; cf. Chase 2003). However,

more recent observations revealed that when colonization history is unpredictable and more persistent than environmental effects, greater inter-patch variation may emerge even under identical abiotic 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, Vannette and Fukami 2014), methods to quantify the relative contributions between history and environment 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 environmental effects (e.g., 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 (e.g., Anderson et al. 2011). The third category of approach, studies colonization history directly by assembling communities under controlled environments (e.g., Drake 1991, Fukami et al. 2005, Sams and Keough 2012). All three approaches have various advantages and limitations (Götzenberger et al. 2012): they are either manipulative but somewhat unnatural, or observational that 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 detail 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 historical versus environmental effects.

One way to manipulate community-wide history and environment is via transplants of intact communities. By transplanting communities along environmental gradients, past studies have

revealed how plant communities react to novel abiotic and biotic environments such as those introduced by climate change (e.g., Alexander et al. 2015). When the environmental gradient involves spatial characteristics (e.g., habitat connectivity or species dispersal potential), historical information such as colonization frequencies or species turnover rates may be inferred from results of the transplantation (e.g., Cottenie and De Meester 2004). Among the works done with marine communities, transplants of individual species have helped the establishment of fundamental ecological principles such as community resilience and species range shifts (Paine 1976, Connell 1980). More recent studies have used transplantation of whole communities to investigate the drivers of structural variation across long environmental gradients (Cifuentes et al. 2010, Ralston and Swain 2014). We are not aware of any studies that simultaneously explore sources of variation in historical and environmental effects, without which it is not possible to estimate the relative contribution of history and environment in community structure. Our approach thus took colonization history into consideration. We transplanted communities among patches known to have different levels of variation in species colonization and subsequent environmental effects, creating a mismatch in the variability between history and environment. This allowed us to decouple the effects of colonization from environmental effects that covary with history.

We conducted the experiment with marine sessile invertebrates and macroalgae inhabiting underwater hard substrata. Marine sessile communities are 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 the community dynamics (Connell 1980, Gaines and Bertness 1992, Caley et al. 1996). In the current study, young communities were recruited within their natural habitats before undergoing reciprocal transplantation. We then partitioned the total variation in transplanted communities into those explained by their origin habitat and their

destination habitat. This is a strictly phenomenological approach and represents a departure from other community assembly studies that are more mechanism-focused.

Methods and materials

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 unpublished thesis). We therefore created mismatching colonization history and the ensuing environment by transplanting intact communities among different patches.

General experimental setup.

PVC settlement plates (11×11 cm) were attached to larger PVC backing panels (55×55 cm) for fouling communities to establish. Each backing panel carried 16 settlement plates, these plates were 2 cm apart from each other. The surface of settlement plates was roughened with sandpaper to encourage settlement of propagules. Backing panels with plates were hung to a floating pontoon and were submerged 1 m below the water surface facing downwards horizontally. 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. Our field site is the likely source of recruits in the community because the connectivity with other marinas are likely to be low since the surrounding shoreline (> 5km) is sandy beach that isolates local fouling communities. Backing panels attached to the pontoon can be viewed as randomly formed empty patches

(and referred to as ‘patch’ hereafter). Settlement plates were thus equivalent to replicated plots (and referred to as ‘plot’ hereafter) randomly located in each patch.

Field programme.

New patches carrying empty plots were submerged at random locations along the pontoon in November 2013, following the general setup described above. After allowing communities to develop for a period of time (4 and 8 weeks, see next paragraph), replicated plots carrying intact communities were transplanted away to a destination patch that was novel to the communities. Specifically, plots all received an Origin treatment from the beginning of the experiment, and then received a Destination treatment. In order to maximize the number of transplants and therefore the statistical power, the transplantation from an Origin to a Destination was always reciprocal. Such transplantation is equivalent to a fully factorial design with two factors (Origin and Destination); both factors had four levels (patch 1 to 4). In practice, patches at the study site were assigned into groups of four; each group represented an experimental block. When transplanting, plots in a patch were randomly reassigned, in groups of four as replicates, to another patch in the block (e.g., four plots were transplanted from patch 1 [Origin] to patch 3 [Destination]). This was done for all patches. Plots were never moved among blocks. Note that when plots received the same treatment for Origin and Destination, they served as baseline communities for that specific patch. For example, when plots (n = 4 as replicates) in patch 2 were reassigned to patch 2, they were moved to different positions in patch 2 and served as patch 2 baseline (refer to Fig. 1A for design schematic). A full experiment comprised three blocks, therefore contained 192 plots in total (3 block × 4 Origin × 4 Destination × 4 replicates). Blocking was necessary because 16 was the maximum number of plots one patch could accommodate; number of patches and replicates in a block were chosen in order to maximize the number of reciprocal transplants.

Patches were randomly spaced, but on average were 3 m apart from one another; on average blocks were 20 m apart along the pontoon.

We were also interested in whether the relative importance of history versus environment changed at different stages of assembly, so we repeated the transplant experiment at two different times in succession. Both experiments followed the above steps, but the transplantation took place at week 4 in the first experiment (the early transplant experiment, ET) and week 8 in the second (the late transplant experiment, LT).

We followed the assembly of communities after transplantation to estimate the relative contribution of historical and environmental effects, and asked if their contribution changed through time. To achieve this, we estimated percent cover of each species through time. Sampling of the plots in ET took place when they were 8 and 12 weeks old. Sampling of the plots in LT 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 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 (*S*), Shannon Index (*H*), loadings from Correspondence Analysis (CA) Axis 1, and loadings from CA axis 2. 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 chi-square distances among sampling units (plots); this ensures that the influence of rare species is not overlooked. These summary statistics were modeled using a linear mixed effects

model, fitted with restricted maximum likelihood in the MIXED procedure of SAS 9.4 (SAS Institute, Cary, NC). Main effects Origin and Destination, and interaction Origin × Destination were all modeled as random factors nested within the random blocking factor (block). Random effects were tested using likelihood ratio tests. Our main goal was to detect the changes in the relative contribution of historical and environmental effect at different successional stages, but was not to determine how each stage affects one another. We therefore analyzed data from different successional stages separately.

Results

In total we recorded 39 species, belonging to 8 phyla; all were sessile organisms that require free space and hard substrate for vegetative growth. Overall, the eight most abundant species groups in terms of percent space cover were the encrusting bryozoan *Watersipora subtorquata* (30.3%), arborescent red algae (10.0%), arborescent bryozoans *Bugula* spp. (6.0%, including 4 species), *Hydrozoan* (6.0%), tubeworms (4.1%, including 3 species), the oyster *Anomiidae* sp. (3.7%), colonial ascidians (4.2%, including 5 species and 3 morphospecies), other encrusting bryozoans (3.2%, including 5 species). Although some space was still unoccupied during our last sampling event, the unoccupied space was mostly finely scattered sections 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, personal observation). We therefore believe that our communities after the transplant were saturated in terms of larval settlement and that very few ongoing colonization events can take place thereafter.

In the ET, Destination always explained more of the variation in communities than did Origin (Fig. 2A and B). At week 8, approximately 9.0% (Table 1, four summary statistics averaged) of the variation in community structure was explained by Origin, while around a quarter was

explained by Destination (24.6%; Table 1). At week 12, signal of Origin decreased to around 7.4%, while Destination could still explain a quarter of the total variance (26.0%). None of the Origin × Destination interaction in the ET was significant (Fig. 2A and B; Table 1).

In contrast to the ET, community structure in the LT was dominated by Origin effects (Fig. 2C). At week 12, 29.0% of variation was explained by Origin, while only 8.7% were explained by Destination (Table 1, four summary statistics averaged). At week 16, although Origin effects diminished, more interaction terms became important. Results from *S*, *H*, and CA2 were more consistent (Fig. 2D), while most of the variance in CA1 was still explained by Origin (Fig. 2D). Results of CA across different sampling time points were summarized in Fig. 3.

Discussion

Our experiments quantified the relative roles of both colonization history and subsequent consumer-resource interactions in shaping communities. Taken together, the results from ET and LT experiments demonstrate that assemblages with similar colonization histories diverge once they experience different environments (and communities that were once different converged upon experiencing the same environment). Communities that were transplanted earlier converged to a destination assemblage more quickly than communities that were transplanted later. Communities that were transplanted later not only maintained their original configuration for a longer period of time, but also showed a stronger interaction between colonization history and environment. In other words, we found quantitative evidence that the influence of historical effects on assemblage pattern were proportional to the time since succession began, with communities who spent longer times at their origin having a more robust historical signal. The influence of the environment in subsequent succession depended partly on the historical legacy. Natural levels of variation in colonization history are sufficient

to generate community-level priority effects, even in a small area such as the marina in this study.

Both colonization and resource competition play a role in the assembly of fouling communities; while other studies in this system have suggested both processes are important, few have explored both simultaneously and quantified their relative contributions. We found relatively larger interaction terms in variance decomposition for LT during the last sampling compared with ET (Fig. 2D). Although interaction terms in the model were not tested to be significant, we believe that their general increase is indicative because the increase was seen across different biological organizations such as species richness, Shannon Index, and CA2. This history-environment interaction suggests that, although the biotic environment can determine which species survived and thrived inside the arena (as seen in ET), the initial set-up of the arena cannot be overlooked. Nonetheless, biotic environment could likely affect some species more than others: species with large resource requirements may suffer disproportionally from higher mortality early in succession (Hart and Marshall 2012). In other words, the biotic filter may have favored a certain group of species, which in turn transformed the resident populations through interference competition (Amarasekare 2002, Hart and Marshall 2012).

The insights provided by the transplant experiment are relevant to studies concerning the timing of species colonization and priority effects. Priority effects have been demonstrated using phytoplankton species in microcosms by varying the timing of species colonization. Subsequent species composition changed even when the order of colonization 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 a prey community. In our study, there was

little evidence of predation at our study site (e.g. partially eaten colonies or newly bare patches), nor did we see sedentary predators (e.g. predatory nudibranchs) active on patches when they were sampled. The interaction between history and environment revealed by the transplant experiment therefore is most likely the result of interactions within the same trophic level (e.g. niche preemption). As demonstrated in previous studies (Yodzis 1988, Wootton 1992), indirect effects are pervasive among species, and can be a major source of ecological complexity. Indirect effects result when one species affects the abundance of a second by changing the abundance of a third species (Menge 1995). Interestingly, the concept of indirect effects echoes the arguments made by Robinson and Edgemon (1988) and Olito and Fukami (2009), that is, that ephemeral interactions can propagate through 'spring-board' species (species that pass the influence of previous interactions on to late-arriving species) and have long-lasting community consequences. Regardless of the underlying mechanisms acting to structure sessile marine communities, our experimental design revealed the different strengths of history and environment in community assembly at different successional time points.

Ecological succession is rarely predictable at the level of species composition (Fukami et al. 2005, Vellend et al. 2014) despite the hope that deterministic assembly rules can be deduced (Connell and Slatyer 1977). Recently, the central argument regarding succession has advanced from a firm dichotomy between deterministic and stochastic processes, to a more inclusive spectrum that seeks to determine when succession is more or less predictable, and under what circumstances (Chase 2003, Vannette and Fukami 2014). When there is a strong interaction between colonization history and priority effects, the community succession trajectory can appear to be historically contingent. Recent theory predicts that priority effects should be strong when early-arriving species greatly affect the environment of the late-arriving species (wide impact niche) and when resource use is highly overlapped (Vannette

and Fukami 2014). The most relevant studies testing these predictions have manipulated species colonization order as a putative stochastic driver of initial community difference. However, there have been repeated calls for empirical experiments to accommodate natural variation in colonization history (Vellend et al. 2014). Our results support the contention that both history and environment play a role. We argue that our results are particularly relevant to this discussion, as we use natural variation in colonization, rather than more structured approaches (e.g., Olito and Fukami 2009, Sams and Keough 2012).

We have demonstrated that whole-community transplants are useful for partitioning the variation in community structure into components of sequential events in time. The strength of this method is the ability to provide temporal snapshots of the relative contribution of succession events. Nonetheless, this study has several limitations, and should be viewed as a first step towards exploring these concepts via *in situ* transplant experiments. Several factors could significantly influence the inference power of our study. First, the method requires a significant amount of assemblage variation among transplanting units, without which the power of the model could decrease rapidly with time. Second, it is unclear as to what natural 'endpoint' in community succession is represented in this system (Kay and Butler 1983). Therefore when to end the experiment could be an arbitrary decision. Nevertheless, we believe this method holds promise for quantifying the roles of natural variation of both the history and environment of communities in the field.

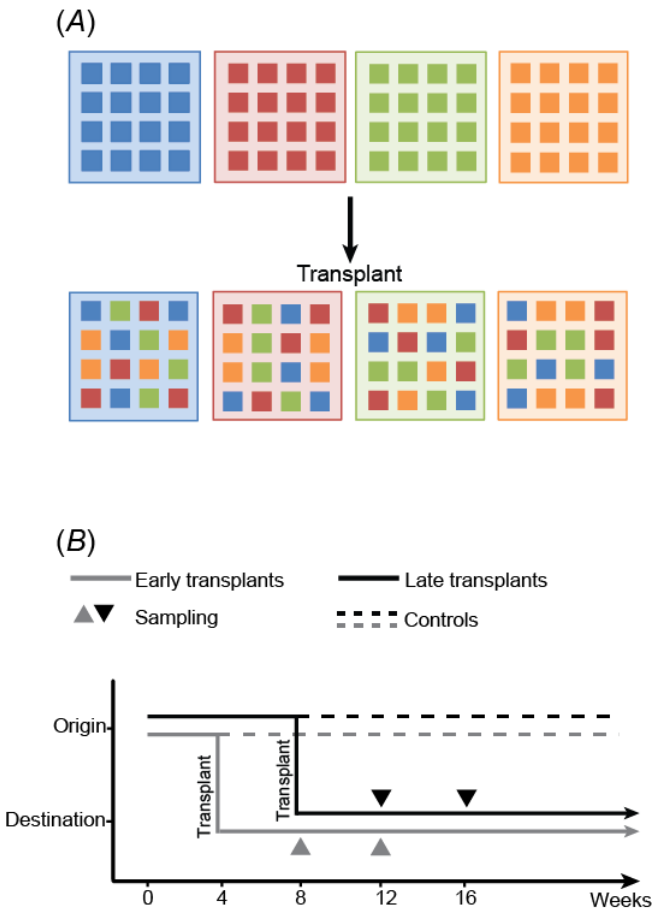

Figure 1. Schematic of the transplantation design and sampling schedule. (*A*) Example of a single experimental block consisting of four patches. Color of patches and plots (larger and smaller squares respectively) reflects their origin. Reciprocal transplantation (the direction of the arrow) created a fully factorial structure, in which each patch had their representative plots in all other patches. (*B*) Succession 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 where samples were taken from both the controls and the transplants.

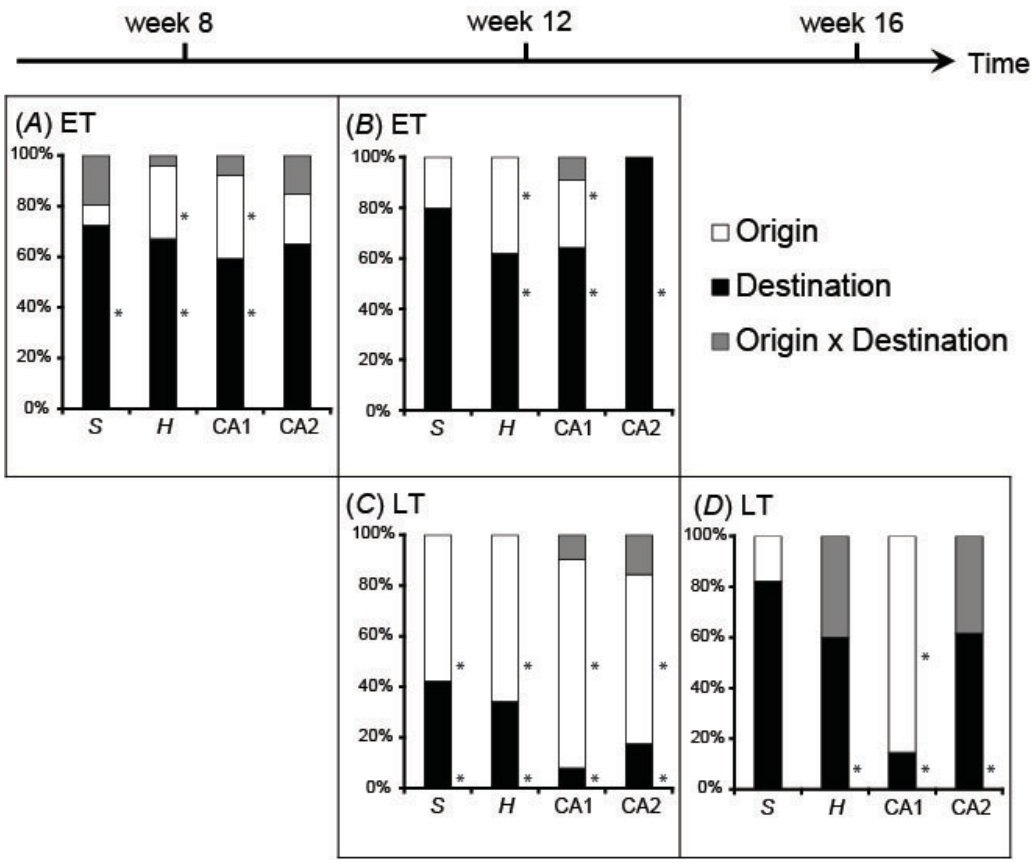

Figure 2. The resulting variation in species composition explained by Origin, Destination, and their interaction. Community structure sampled at different time points after the transplantation is summarized in different panels. (*A*) and (*B*) are results from the early transplant experiment. (*C*) and (*D*) are results from the late transplant experiment. *S*, species richness; *H*, Shannon Index; CA1and 2, correspondence analysis axis 1 and 2. The asterisk next to each effect indicates that the effect is statistically significant ($P < 0.05$). Note that these bars include only variance explained by main effects; see table 1 for block effects and unexplained variances.

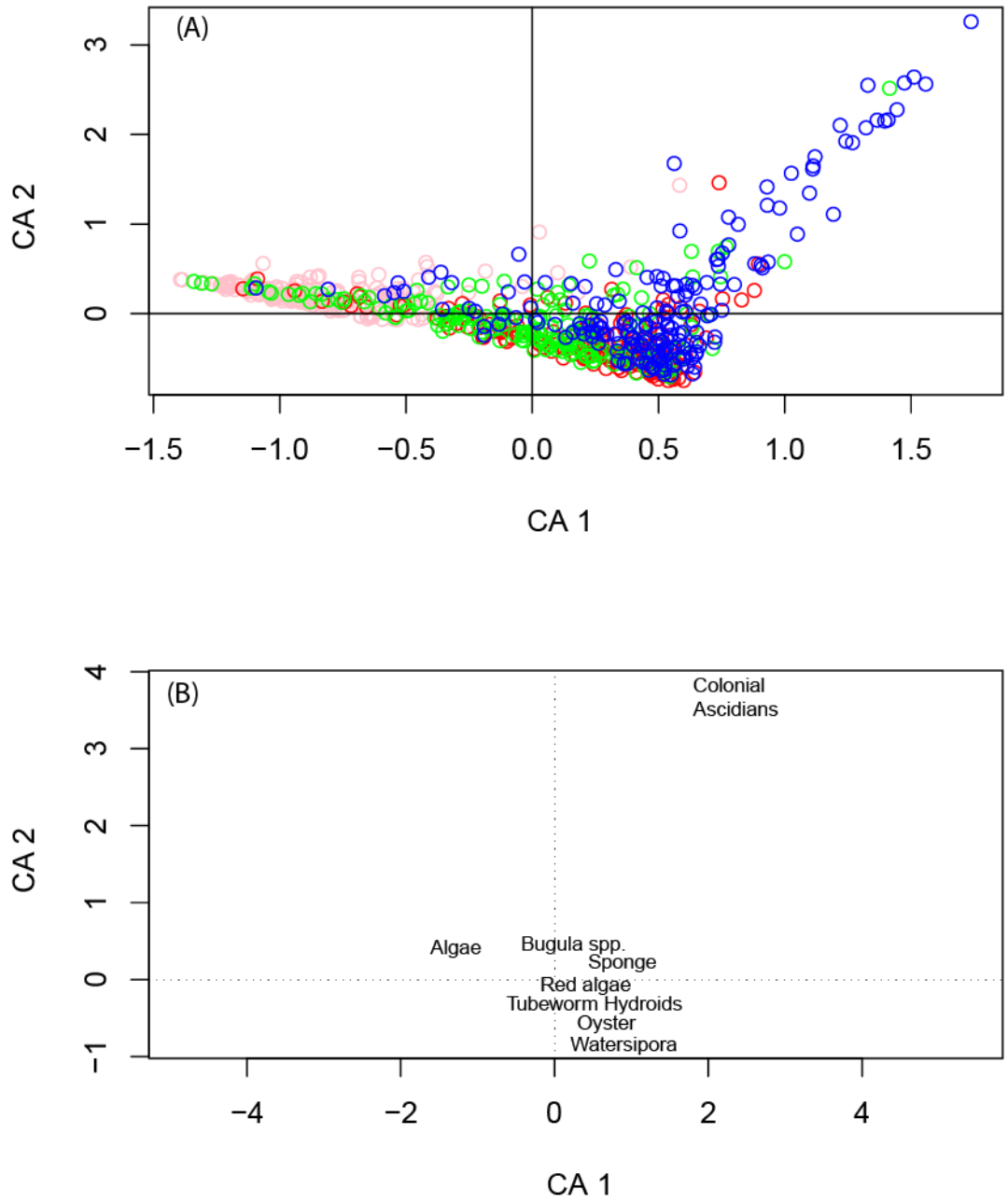

Figure 3. Summary plots of the Correspondence Analysis, showing results from axis 1 and 2. (A) Relative position among communities. Pink: ET week 8. Red: ET week 12. Green: LT week 12. Blue: LT week 16. (B) Species scores.

Table 1. Partitioning of the variation in the four community summary statistics (*S*, richness; *H*, Shannon Index; CA1 and CA2, correspondence analysis axes 1 and 2). Numbers in bold represent statistically significant terms ($P < 0.05$), tested using likelihood ratio tests. We use O (Origin) and D (Destination) as proxies for history and environment. Sections *A*, *B*, *C*, and *D* of the table correspond to different sampling time points, as those used in fig. 2.

	S		***H***		**CA1**		**CA2**	
Source	Estimate	%	Estimate	%	Estimate	%	Estimate	%
(*A*)					*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*)					*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*)					*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*)					*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

VAR = variance in the multivariate species composition data presented in the CA axis.

Chapter Four Do similar communities develop in similar patches? A manipulative natural experiment

Abstract

One useful way to empirically determine the relative importance of colonization history versus environmental filtering in driving community succession is to manipulate history and examine whether similar communities always assemble under similar environmental conditions. Direct manipulation of assembly history in the field has proven to be rather difficult in many systems. This is because succession trajectories are extremely sensitive to small differences in initial community states, such as those generated by the timing of species arrival, a property introduced by priority effects. It is therefore important that differences in the history of communities be realistic. Here, I manipulated colonization history of marine fouling communities across levels of naturally occurring complexities, and documented the succession trajectories in a homogeneous environment. Species composition of the fouling communities gradually diverged over time and the divergence was non-directional, suggesting a lack of deterministic directional selection. Furthermore, communities sharing similar history followed trajectories that were less variable than communities that did not. My findings show that community structure can be divergent even in a small and uniform habitat, and that the divergence in this metacommunity is likely to be driven solely by variable colonization history.

Introduction

Communities on different continents but living in habitats with similar environmental conditions often show parallels in community structure (Clements 1916). Such global-sale comparisons are conceived on the premise that similar environments lead to similar communities because the environment determines possible species compositions (Hutchinson 1959). The concept of ecological succession was originated largely from this premise and states that local assemblages are the deterministic outcome of local ecological processes (Clements 1936, Connell and Slatyer 1977). Accordingly, this deterministic framework predicts that communities which develop under similar environments have a tendency to converge on a common structure (Samuels and Drake 1997).

In order to understand the drivers of community assembly and test deterministic succession, ecologists examine whether similar communities always assemble under similar environmental conditions (e.g. McCune and Allen 1985). Rather than surveying biological similarities across continents, the focus is now upon manipulating community replicates under identical abiotic environments. In replicated beakers containing identical growth medium, Robinson and Dickerson (1987) demonstrated that the sequence of freshwater plankton addition to the beakers determined the community structure and richness. In a set of related microcosm experiments, the time interval between species addition was found to also control plankton community structure (Robinson and Edgemon 1988). They extrapolated these observations and suggested that in real ecosystems, habitat connectivity and invasion frequency together shape the natural community structure. Motivated by the seemingly ever-increasing number of assembly rules, Drake (1991) used similar microcosm experiments to decompose assembly rules, however, he did so in a more mechanistic framework. Drake found that histories are unique in their nature and effects on each system, and suggested that the historical event that introduced divergence and variation may determine which other ecological factors are subsequently important. Therefore the sequence and frequency of species addition and removal, as well as the sequence of predation and other abiotic disturbances all contribute towards the influence of history (Samuels and Drake 1997). Based on these insights,

Fukami (2001) showed that the sequence of drought events (a form of disturbance) and predator arrival can determine the structure of freshwater protist communities. Later, the population dynamics in microbial microcosms were showed to be influenced by varying only the time interval of predator arrival (Olito and Fukami 2009). These investigations provide mixed support for both convergence and divergence of species composition under similar abiotic environments. Assembly history is thus recognized to be indispensable in shaping future succession trajectories. With this knowledge, it is now hard to defend the view that community assembly represents a predictable and inevitable response to the abiotic environment (Ejrnæs et al. 2006).

From the lessons learnt in controlled laboratory experiments, we now know that testing the cause of convergence or divergence in natural assemblages has to satisfy two requirements. First, colonization history has to be manipulated in ways that separate the effects from other assembly processes; second, the manipulation has to be replicated in identical (or nearly identical) habitats. Satisfying these requirements in the field has proven rather difficult for two reasons. First, when colonization history is unpredictable and interacts with habitat conditions, greater patch-to-patch variation may emerge despite the absence of habitat heterogeneity. A common feature in community assembly resulting from this interaction is called a priority effect (Cornell and Harrison 2014, De Meester et al. 2016). Priority effects can occur simultaneously with other assembly processes, such as directional selection caused by competition asymmetry. This can cause the assemblage pattern to be highly contingent upon both history and the extant environment. Therefore, direct manipulation of the history over assembly-relevant time scales is essential for verifying priority effects. However, this also leads to the second difficulty, that is, how well do artificial histories represent natural histories of communities? Artificial manipulation of the chronological sequence of assembly events, such as species addition or removal, is usually far more simplified than the natural history. Natural history is complex, with the addition and removal of species, abiotic perturbations, and predation constantly taking place at arbitrary intensities and between random time intervals. Certainly, the combination of these events is so vast, that efforts

devoted to documenting each individually seems counter-productive. Therefore, most experiments manipulating artificial histories have focused on the *mean intensity* of assembly events (e.g., 1000 cells of bacterivore protist introduced to treatment one; 2000 cells introduced to treatment two). This research program overlooked the effect of *variation* as a causal explanation for the observed pattern (e.g., 1000±100 cells of bacterivore protist introduced to treatment one; 1000±500 cells introduced to treatment two). Variability has been repeatedly emphasized as a genuine property of communities and needs to be properly incorporated in community assembly studies (Butler and Chesson 1990, Underwood et al. 2000, Benedetti-Cecchi 2003, Vellend et al. 2014). In practice, incorporating natural variance of colonization history into explanatory experiments and models necessitates the understanding of how processes vary in space, and how natural variance drives succession trajectories within these explicit spatial scales.

One potential way to achieve this goal is to replicate experiments in space, an approach that extracts and utilizes natural sources of random variability that are often present over different spatial scales. Different spatial scales should be chosen to differ in the levels of natural variability in assemblage structure, but should also harbor habitats that are similar in abiotic conditions. When combined with transplant experiments, which move assemblages across these scales, different community responses can be attributed to the habitat in which they experienced early history. The idea is similar to that advocated by Schluter (1986), in which convergence (or lack thereof) is tested by comparing the variance between replicated communities within habitats to the variance between different habitats, assuming that communities in different habitats share more similar history (Schluter 1986). In my study, community trajectories within a scale are compared to those transplanted to a different scale, so that the effect of variable colonization history (due to different spatial scales) can be isolated from contemporary influences. For example, if transplanted communities showed more divergent trajectories than non-transplanted ones, then assembly history may be the likely driver of succession, and priority effects should be expected to be pervasive.

Here, I study the patch-to-patch variation in marine fouling assemblages in order to provide empirical data to address the issues discussed above. Benthic assemblages of sessile or sedentary organisms are well-known to be heavily shaped by propagule colonization history and intense local competition among colonizers (Connell 1961, Sutherland 1974, Keough 1984). Transplanting individual fouling species has helped the establishment of some fundamental ecological principles such as population resilience and species range shifts (Paine 1976, Connell 1980, Palumbi 1984). However, the range of questions that can be addressed by transplanting intact communities has never been fully capitalized upon in this system. Therefore, I investigate the convergence (or lack thereof) in species composition by tracking sampling plots through time. I ask (1) whether the community is converging or diverging in species composition on scales with different levels of natural variability? (2) Whether the community trajectory is contingent upon different variability in history?

Methods and materials

Study site and the fouling community

Experiments were conducted at Blairgowrie marina (38°21'31"S, 144°46'23"E) near the southern tip of Port Philip Bay, Australia. The marine fouling community consists of species that require unoccupied hard substrate for vegetative growth. They compete heavily for space on underwater hard substrates, including rock surfaces, shells, hard parts of other organisms, and man-made underwater structures. In old and undisturbed patches, solitary ascidian species dominated most of the space (~ 85 % space coverage) and usually had the greatest biomass. These solitary ascidians grow relatively slow and have longer life-history cycles compared with other groups in the community. With their hard tunic, they can nearly always overgrow other adjacent species, which in turn contributes to the complex three-dimensional structure of the fouling community. Arborescent bryozoans, sponges, and brown algae are the next most abundant groups in old patches (together having ~ 10 % coverage). These species share the common feature of an up-right growth form, and

thus all have a relatively low space requirement of the substrate. Arborescent bryozoans grow into tree-like formations; once colonies reach a certain size and density, they form thick layers of 'canopy' that can effectively capture food and oxygen from a wider range of water column. Tubeworms and oysters can also be abundant in old patches, but layers of overgrowth of other species often cover their calcified cases. Usually, only the openings of their cases could be seen from the surface of the community, but underneath they form the base structure for other species to settle and attach to.

In newly formed, unoccupied patches, succession can be rapid. Tubeworms (e.g. *Pomatocerus taeniata*) and bryozoans (e.g. *Watersipora* sp. and *Bugula* spp.) are the most dominant animal groups on newly formed bare surfaces. Together they can sometimes cover over 40% of the free space within a month. Arborescent brown and red algae are also early colonizers of newly freed spaces due to their fast growth rates (~ 10 % after the first month). However they have a relatively weak ability to persist in such patches and are often 'bulldozed' off by other invertebrate competitors. Colonial ascidians (e.g. *Botrylloides leachi*) can sometimes rapidly increase their biomass and overgrow other species, causing mass mortality However, in general colonial ascidians are weaker competitors. Five other encrusting bryozoans can be found at the study site, but all in low abundances. Like *Watersipora* sp., these encrusting species expand horizontally and have high a demand for space in order to persist; therefore, they are less common in late successional stages. Solitary ascidians are the minority in newly formed patches (usually ~ 1 % space cover after the first month), mainly due to their slow-growing life history.

General experiment setup

PVC settlement plates (11×11 cm) were attached to larger PVC backing panels (55×55 cm) for fouling communities to establish. Each backing panel carried 16 settlement plates; these plates were 2 cm apart from each other. The surface of settlement plates was roughened with sandpaper to

encourage settlement of propagules. Backing panels were positioned horizontally below the water surface facing down, hanging off a pier. Panels did not have any physical contact with surrounding hard surfaces, thus the only way for propagules to colonize was by dispersing through the water column. The pier was 3 m wide, 180 m long, with an average water depth of 5.5 m.

From a regional perspective, the marina represents a local community embedded within the species pool of Port Philip Bay. However, the marina is likely to be the only source of local recruits because the connectivity with other communities outside of this marina is likely to be very low (the surrounding shoreline of > 5 km radius is sandy beach that isolates this marina). Although some member species produce larvae that are still competent to settle after hours of swimming, most larvae prefer to settle within minutes upon release. Therefore, under normal weather conditions, I take the simplifying assumption that all arriving species are from communities within the marina. These communities which occupied nearby but discrete piers form the metacommunity of my study site. Backing panels randomly attached to the pier can be viewed as randomly formed empty patches (referred to as 'patch' hereafter). Settlement plates were thus equivalent to replicated plots (referred to as 'plot' hereafter) randomly located in each patch.

Field programme

Previous monitoring of the study site showed that species composition varied considerably on the scale of patches, i.e., patch to patch. In general, species composition of the fouling community varied twice as much among patches than it did within patches (see Chapter 1 results). For this reason, I chose to transplant plots among patches; meanwhile, some plots served as controls and were never transplanted. This design essentially brings together assemblages with different histories into the same patch, creating patch communities that are otherwise similar in history.

New patches carrying vacant plots were submerged at random locations along the pier in November 2013, following the general setup described above. At week 4, replicated plots (n = 4) in each patch were transplanted to a destination patch that was novel to them. The transplantation between patch-

pairs was reciprocal in order to maximize the number of transplants (see appendix 1 for design schematic). Transplanted plots remained in their destination patches until the end of the experiment. In any given patch there were also control plots (n = 4) that were never transplanted, so they were native to their patch. I followed the community structure by sampling these plots repeatedly over time. In total, the entire community was sampled three times, at weeks 8, 12, and 16. The number of weeks throughout this manuscript refers to time since new patches were first submerged. I collected data on the percent cover of each species. At each sampling time point, I photographed all plots *in situ* non-destructively. A computer program (Coral Point Count with Excel extensions, Kohler and Gill 2006) was used to generate 75 randomly distributed points over each plot. All visible, sessile species under the points were recorded to generate percent cover estimates.

Data analysis

39 marine fouling species were recorded in total throughout the experiment period; of which 37 were sessile invertebrates, 2 were algae species. Fouling community composition was quantified using the percentage of free space covered by each species. Species that collectively covered less than 2% of the total surveyed area were considered as rare species. The abundances of rare species were merged with close relatives into higher taxa in order to minimize the effect of double-zeros when computing dissimilar metrics (Gauch 1982, Legendre and Legendre 2012). As a result, the final community dataset describing each plot contained 9 species groups. It is acknowledged that merging the abundance of individual species into higher taxa may sometimes obscure the unique functional role of each species (e.g. Bevilacqua et al. 2012). Therefore, before starting the main analysis of this chapter, the effect of merging abundance was first examined. This was done by comparing the ordination results before and after the merging. First, the dissimilarity among each community before the merging was calculated using both Euclidean distance with Hellinger transformed raw data (followed by Principal Component Analysis, PCA) and chi-square distance with untransformed raw data (followed by Correspondence Analysis, CA). PCA and CA are

statistical tools that reduce many variables (e.g. species) to a small number of newly derived variables (commonly 2 or 3 to facilitate visualization) that summarized the original information. PCA preserves the Euclidean distance among sampling plots, thus the distance among points in the biplot represent the absolute difference between sampling plots. CA on the other hand preserves chi-square distances among sampling plots, which is less sensitive to rare and absent species. The same transformation and ordination procedures were also applied to the dataset after merging. The ordination results before and after merging were then compared using Mantel test (e.g. Anderson et al. 2006), which reports the probability of two matrices being the same configuration. Result of the Mantel test showed that the dissimilarity among each sampling plot were statistically identical before and after the merging, and that PCA and CA yield qualitatively similar conclusions. I thus conclude that the merged abundance is adequate to represent the original data.

Species compositional convergence or divergence over time

With the merged dataset (the abundance of 9 species groups), I tested whether the species composition was converging or diverging over time. This was done by testing for homogeneity of multivariate dispersion (Anderson et al. 2006). In practice, the variability of species composition among plots was tested for equality over time. The variability of a group of plots can be measured as the average multivariate dispersion from individual plots to the group centroid. I used the Hellinger distance to quantify the dispersion (Legendre and Gallagher 2001). The test for homogenous multivariate dispersions is a multivariate analogue to Levene's test of the equality of variances. In this multivariate analogue, an *F*-statistic was calculated to compare the average distance of plots to their group centroids; a *P*-value was then obtained by permuting least-squares residuals. If an overall difference among sampling time points was statistically significant, pairwise comparisons between time points were then carried out using Tukey's Honest Significance Difference test.

Drivers of species compositional variability

After investigating the convergence/divergence in community succession, I further asked what is driving the succession trajectory. Is it a consequence of the degree of variability in assembly history, or is it due to deterministic habitat filtering? To test this, I repeated the previous analysis and tested homogeneity of multivariate dispersion over time, but split the plots into two groups and tested their temporal changes separately. The first group consisted only of plots that were never transplanted and therefore experienced their history and contemporary environment with the same degree of variability. The second group consisted of transplanted plots as well as their respective control plots and therefore represented communities that experienced different histories. This way, the only difference between the two groups was whether or not the communities had history from different patches. After calculating their magnitude of dispersion separately, I calculated the difference in dispersion between the two groups. The difference was tested using a linear mixed-effect model, in which the grouping was modelled as a fixed effect; patch inconsistencies that caused random deviations around the Group means were modelled as a random effect. Any detected difference between the two groups would indicate that history played a role in driving succession. By contrast, a lack of difference would imply that post-transplant habitat filtered out “forbidden species combinations” (Diamond 1975) that were created by colonizing history.

Results

The succession of fouling communities at the study site showed gradual species compositional divergence over time. Replicated plots were initially more similar to one another, but gradually moved further away from their group centroid (Fig. 1a). The average distance to the group centroid was the smallest at week 8 (0.42); plots sampled at week 12 had an intermediate average distance (0.58); the greatest average distance was observed at week 16 (0.76). The test for homogeneity of variances gave support to an overall unequal variance among sampling time points (Table 1). Pair-wise comparisons between sampling time points showed that replicated plots have significantly different and increasing variances over time (Table 1), and thus suggesting divergence. The ordination result clearly illustrates the correspondence between fouling species and time points

where they showed highest percent cover. The assemblage during early succession at week 8 appears to be a group of algae species and *Bugula* early colonizers (Fig. 1b). The green, brown, and turf algae were the earliest colonizers of bare surfaces. They grew rapidly to reach a high percent cover, then quickly completed their life-cycle by producing spores into the water column, which wait for free space to be released from occupation. Another four species became common at week 12. These species include the arborescent red algae, a group of polychaete tubeworms (including three species), the encrusting bryozoan *Watersipora*, and an oyster. The rest of the species showed strong a signal in the first quadrant of the ordination. These were hydroids, a group of sponges (including three species), and a group of colonial ascidians. These populations reached their peak abundance later than the others did, because the plots sampled at week 16 are driven in this same direction and are separated from the other sampling time points.

The divergence did not appear to be driven by any deterministic directional selection. The assemblage in each patch was nearly equally different to one another (Fig. 2), without any detectable direction.

Although the overall variability of species composition increased with time, separating the plots into those sharing similar history and those that do not, revealed that the transplant plots had a tendency of being more variable than the control plots (Fig. 3). This tendency was not obvious during earlier succession (week 8 to 12), but became significant afterwards (from week 12 to 16; likelihood ratio test L = 1.06, $P < 0.02$).

Discussion

Before I go deeper into the implication of my results, one important assumption must be first identified –patches were environmentally homogeneous. Like many other natural experiments, the current study addresses the question: will similar communities develop in similar environments? This has been examined with plants by replicating experimental communities in closely adjacent

plots. A well-known example is the soil nitrogen addition experiment conducted on the native savanna in Minnesota (Inouye and Tilman 1995). The experiment was critically based on the assumption that the field was small enough, so that adjacent plots were similar in every possible way, except in the manipulated nitrogen levels. In another example which bears higher resemblance to the current study, Fukami and colleagues manipulated the initial composition of grassland communities at a site of *c*. 2,000 m^2; the authors argued that such small area would preclude most abiotic differences and only allow for the operation of initial biotic variation (Fukami et al. 2005). Based on the same logic, the current study was conducted in an area deliberately chosen to be small and low in wave energy (on a single pier in a marina); therefore, I did not collect data on environmental variables (e.g. temperature). This is in direct contrast with gradient analysis (e.g. diversity—productivity experiments), in which community structure is examined along environmental gradients. Gradient analysis operates under theories that predict a change in community structure as ecological processes change with environment (e.g. Inouye and Tilman 1995); whereas in the current study, experiments were conducted in a homogeneous habitat. My data on community spatial structure support the homogeneous-environment assumption. At any given time point, species compositions of patches showed random deviations from the site-wide composition, with no evidence of directional change along the pier (Fig. 2). However, on the scale of individual patches, species composition varied twice as much among patches than it did within patches. This suggests that as larvae dispersed from their surrounding source populations, they most likely followed some form of a distance-decay function, which may be different depending on patch locality.

The experiment commenced from bare surfaces in all patches, which simulates the regeneration of open gaps within an existing metacommunity. Colonizers arrive to these new resources by dispersing through the water column from existing nearby communities. The connectivity between existing and new patches is therefore the foremost factor that determined species arrival and initial composition in new patches. From the data I collected, the connectivity within this metacommunity

is likely to be similar among existing communities and new experimental patches, since a similar set of species can be found in most local communities (within patches) during early succession. After the early recruitment stage, patch connectivity seems to be less important in altering local assemblages because young settlers were always absent from my surveys on the established communities. Nonetheless, site-wide assemblage diverged with time. How are these patterns generated in a uniform environment? Such community assembly seems to be initially driven by dispersal, and subsequently maintained by the biotic environment in each patch. Under this scenario, there are two alternative explanations to the observed pattern. First, the pattern of divergence can be generated solely by a dispersal-driven community assembly. Priority effects introduced by stochastic colonization history, which was then followed by strong biotic filtering, could lead to differentiating community structure (Shurin et al. 2004). Second, the pattern of divergence could have been generated by undocumented patch differences in niche factors. Here, one potential cause of difference is predator-prey interactions with predator species that are external to the focal community. For example, non-consumptive effects of fish predators can cause larvae to actively alter the environment they colonize, in order to counter predation risk (Kraus and Vonesh 2010). Additionally, some species are also known to avoid habitats near conspecifics to avoid competition of common resources (Almany 2004). This effect could accumulate over successional phases and eventually generate patterns in the distribution of conspecifics and competitors (Binckley and Resetarits Jr 2003).

Result from the reciprocal transplants show that the metacommunity at my study site is largely a history-driven one, corresponding to the first explanation above. Communities that were assembled under a more different historic background diverged more than those that shared similar histories (Fig. 3), suggesting that colonization history from earlier a stage retains the potential to influence community assembly at later stages. Furthermore, as discussed earlier, the spatial pattern of colonization at any one time appeared stochastic on the scale of the entire site. Taken together, these results suggest that by stochastically altering abundance and composition of assembling

communities initially, colonization history drives the biotic environment divergence for the subsequent succession.

The result of the manipulation provide an empirical observation on the community-level divergence in a uniform habitat. Ecology has a strong background in studying community structure along extrinsic gradients. For example, community organization has been shown to vary with nutrient availability (Inouye and Tilman 1995, Steiner 2014), primary productivity (Waide et al. 1999, San Martin et al. 2006), disturbance rates (Sousa 1979, Violle et al. 2010), and connectivity (Cottenie et al. 2003). Colonization history, on the other hand, has been viewed as an intrinsic property rather than a gradient; after all, the history of colonization was once part of the ongoing succession progress, which can itself be driven by various biotic and abiotic factors. However, recent syntheses on patterns across spatial scales have resulted in a common question that asks whether similar communities develop in similar sites (McCune and Allen 1985, Samuels and Drake 1997, Jenkins and Buikema 1998, Fukami et al. 2005). This is an important step forward because previous gradient analyses largely concentrate on keeping the feedbacks of assembly process constant while investigating the focal gradient (e.g. null models). An opposite approach would be to directly investigate the feedbacks of assembly in the absence of external forcing (Vellend et al. 2014). When community assembly is studied within a narrow range of abiotic conditions, the opportunity for structural variation due to a changing environment is limited to its minimum, and historical priority effects predominate (McCune and Allen 1985). Multiple lines of evidence suggest that assembly history is a causal explanation to succession trajectories (McCune and Allen 1985, Drake 1991, Cornell and Lawton 1992, Zhou et al. 2014); this current study adds to the growing evidence and further provides empirical data on the community-level response to history manipulations at realistic complexity.

Although I found evidence that history drives patterns of subsequent assembly, I also found a history-independent period during which the treatment had no effect. From week 8 to week 12, there is no evidence for a difference in the amount of divergence between groups with different

historical background (Fig. 3); the site-wide assemblage still diverged during this time period, but there is no indication that the divergence was due to dissimilar colonization history. Indeed, there is no reason to expect effects of colonization history to be constant over time when at least some aspects of the habitat are being modified by the resident species (Vannette and Fukami 2014). In groundwater microbial communities, the importance of assembly history in controlling succession trajectories was found to be time dependent (Zhou et al. 2014); the presence of the same predator may produce different outcomes due to different timing in community assembly (Chase et al. 2009, Kraus and Vonesh 2010). Although these examples are rather recent, the idea is not a new one. The concept of impact niche (Leibold 1995) describes such phenomena where organisms consume and modify the surrounding resources. The feedback effects of community assembly on itself may be the cumulative modification by all individuals of all species. For example, although it is already assumed in this study that the abiotic environment of the study site does not have obvious spatial structure, neither do resources distribute unevenly across patches (e.g. space and substrate topology was identical in every patch). Early colonizers nevertheless modify the habitat based on their impact niche and generate a heterogeneous biotic environment (Shurin et al. 2004). In this study, one most easily-quantified such modification is the reduction of free space that forced new settlers into a situation of increased competition and less available space. Faced with this biotic heterogeneity, a potential settler may alter their settlement choice, and a potentially successful colonizing attempt may become unsuccessful, leading to site-wide priority effects (Shurin et al. 2004).

How well could the results of the current study be generalized to predict community assembly at longer time scales? The time span of the sampling period may appear be one major limitation to the current study. The major reason is that even though free space have been occupied completely, succession cannot be considered to have reached its climax. On the other hand, past studies in similar marine habitats have shown that communities can still be in a dynamic changing state even after several years of succession (Kay and Keough 1981, Kay and Butler 1983), because the surrounding environment is never in a steady state. Therefore, the question ‘how long is long

enough for assembly experiments' may have different answers depending on the ecological processes of interest. If the question of interest is focused on whether a single pulse colonization event could have an effect on the immediate biotic environment of the community, then my data clearly showed that it can. On the other hand, if the question is about other long-term ecological events such as population range shifts, then the experiment may also need to be extended to include appropriate scales in time.

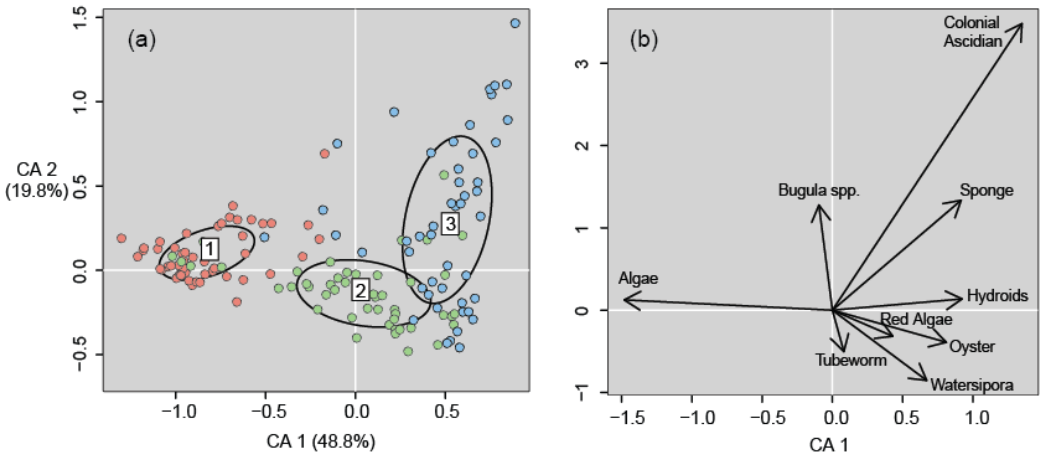

Figure 1. (a) Site-wide species compositional variability changed over time. Each circle represents the mean assemblage in a set of replicated plots (n = 4). The closer the circles are, the more similar they are in terms of species percent cover. Groups 1 to 3: week 8 (red), week 12 (green), and week 16 (blue). Major axes of dispersion ellipses represent group standard deviation. Group labels are located at group centroids. The first two axes of the ordination result is plotted. The eigenvalues associated with the first two CA axes explained 68.5% of the total variance. The variance homogeneity test does not support the null hypothesis that groups have equal variance (F = 16.88; P < 0.001). (b) Result from the same analysis as in (a), but showing contributions of each species (tip of arrowheads). Any circle found near a species is likely to contain a high mean percent cover of that species.

Table 1. Species compositional variability: pair-wise comparisons between sampling time points using Tukey's HSD. The comparison always subtracted the earlier time point from the later, and the difference is always positive, suggesting that the variance is constantly increasing.

Comparison[†]	**Difference**	**Lower bound**	**Upper bound**
(2)-(1)	0.163*	0.035	0.290
(3)-(1)	0.348**	0.220	0.476
(3)-(2)	0.185*	0.058	0.313

[†]Numbering followed Figure 1a: (1): week 8, (2): week 12, (3): week 16.
*$0.001 < P < 0.05$; **$P < 0.001$

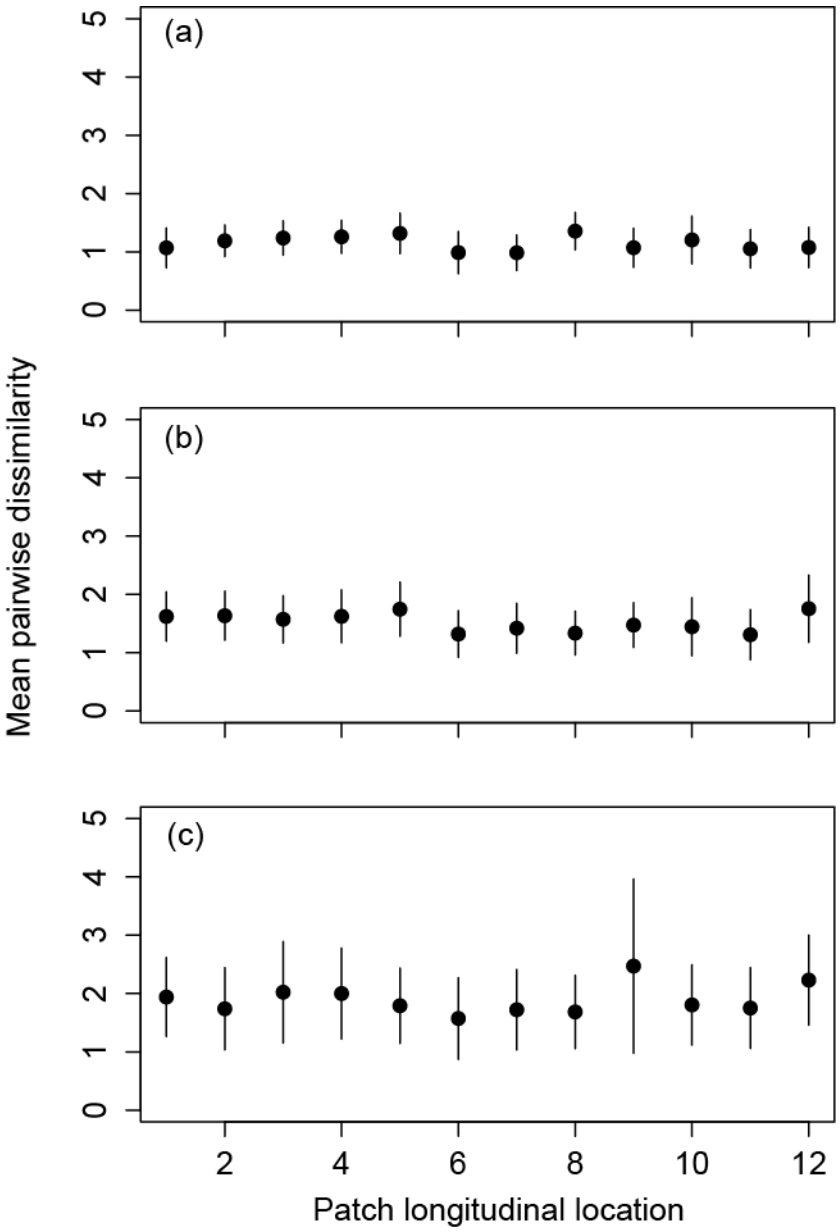

Figure 2. Mean pairwise dissimilarity of assemblages of a patch to all other patches. (a) week 8; (b) week 12; (c) week 16. Patch location corresponds to the actual ordinal location along the pier. A directional change in community structure along the pier would result in a directional change in the mean pairwise dissimilarity.

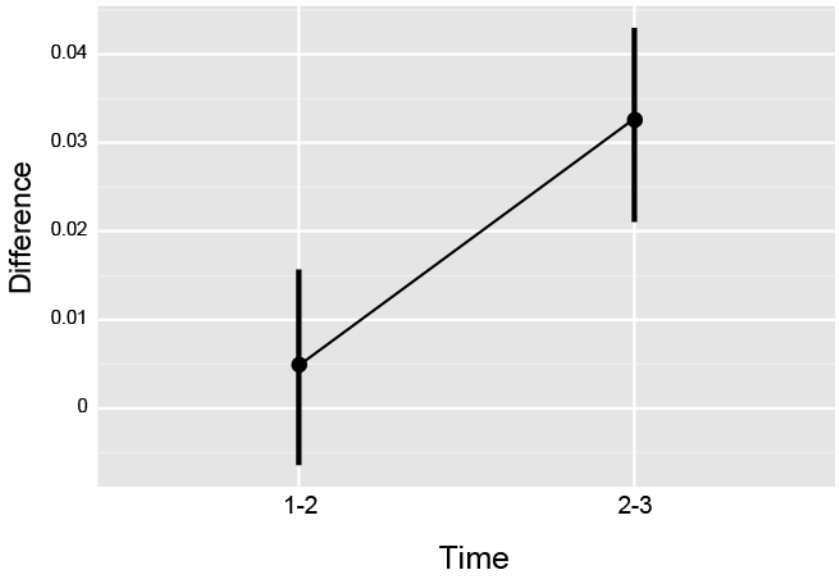

Figure 3. The difference between control and transplant assemblages over time (± standard error). Assemblages were grouped according to whether they shared similar history or not, and the magnitude of difference between groups was quantified by calculating the distance between two group centroids. Time 1-2: the magnitude of difference between sampling time point 1 and 2. Time 2-3: the magnitude of difference between sampling time point 2 and 3.

Chapter Five Explaining the unexplained: the magnitude of variation among communities in a uniform environment

Abstract

Recent models of community assembly emphasize the importance of stochastic factors that introduce random variations into community structure. Testing these models with field observations is challenging because one must examine whether similar communities always assemble under similar environments. Common to all ANOVA-based approaches, high (and low) similarity is judged in a relative sense using the variability of the residual as baseline, however in nature, heteroscedasticity is common. Although statistical models are capable of incorporating heteroscedasticity in explicit-spatial designs, homogeneous variance are usually assumed in homogeneous environments and thus modelled as such. Evidence against this assumption is accumulating, but empirical field data is still lacking. Here I conduct a manipulative field experiment that brings together marine fouling assemblages from different recruitment regimes into a homogeneous environment in order to assess community-level baseline variability. I show that, even closely adjacent communities living in nearly identical habitats can have enough heterogeneity in their community structure to overshadow differences caused by differences in their initial recruitment regimes. The magnitude of variation in older communities developed in proportion to their initial recruitment variability, even in a homogeneous habitat. My findings imply that the usefulness of model predictions about the convergence or divergence of natural communities critically depends on the structure of residual variation even in a homogenous habitat, which is in turn determined by the stochasticity of assembly history.

Introduction

A classical paradigm for explaining the composition of communities holds that community assembly is determined by biotic and abiotic selection forces, such that similar assemblages will develop in similar habitats (Clements 1936, Tilman 2004). An opposing view arises from the observation that variable colonization history can lead to multiple community configurations, even in identical habitats (Egler 1954, Sutherland 1974). Models of community assembly now incorporate the more pluralistic perspective that the history of species arrival, and the subsequent selection via biotic and abiotic interactions, together shape ecological communities in nature (Adler et al. 2007).

A common feature of recent community models is that they all contain a stochastic component that introduces random variations into the community structure. Importantly, the stochastic component exists not only in dispersal and colonization histories, but also in the niche-based processes that interact with the history. For example, under an identical physical environment and resource density, an invading consumer species consisting of individuals with different fitness's was able to alter community assembly to a very different trajectory (Drake 1991). Contingent assembly trajectories were sensitive to even minor variations in founder-population variables such as number of survivors and their fecundity. Each death and reproduction event in a population might have deterministic niche-based causes, however, if their sequences occur randomly with respect to species identity (Vellend et al. 2014), even deterministic processes will give rise to stochastic priority effects (May 1976).

Despite the recognition of the issues above, the degree to which assembly proceeds in a deterministic manner is challenging to estimate in natural communities –one must examine whether similar communities always assemble under similar environments. An informative empirical approach is to manipulate replicated communities with identical abiotic environmental conditions and species pools (e.g., Samuels and Drake 1997). Many of our early insights come from freshwater plankton communities in highly controlled microcosms (Robinson and Sandgren 1983, Robinson

and Edgemon 1988, Drake 1991, Steiner 2014). Empirical data from field experiments is gradually accumulating in systems such as plankton communities of freshwater ponds (Cottenie and De Meester 2004), underground microbial communities (Stegen et al. 2012, Zhou et al. 2014), and grassland plants (Fukami et al. 2005, Ejrnæs et al. 2006, Houseman et al. 2008). By manipulating the history of species arrival, most field studies found evidence supporting a synergistic effect of both colonization history, and adult-adult interactions. However, across most of these studies community assembly was studied under simple recruitment patterns (relative to recruitment patterns in nature). This simplification represents a trade-off between the degree of natural variability and experiment tractability. While manipulating replicated communities has the advantage of being a direct approach which investigates the effects of variable recruitment, the approach must sacrifice a degree of natural variation in colonization history in order to initiate controlled assembly. Such an approach therefore risks over- or under-estimating the variance in colonization histories, and therefore their relative importance.

Overlooking such stochastic drivers in initial community differences may lead to unanticipated community divergence, because variable colonization history may give rise to heterogeneous variance structure among treatments even in the absence of habitat heterogeneity (Fukami et al. 2005, Houseman et al. 2008). This is consequential because recent assembly models rely heavily on the pattern of variation within and among treatment communities (i.e., beta-diversity) to determine the degree of assembly predictability, whether the 'treatment' is planned manipulation (e.g., Inouye and Tilman 1995) or unplanned natural gradients (e.g., Bernard-Verdier et al. 2012). Specifically, according to a recent synthesis, when communities are replicated within a homogeneous habitat, compositional variation among replicates should be low under strict niche assembly, because species membership is determined solely by their niche requirements and local habitat conditions (Fig. 1a). In contrast, high compositional variation in the absence of habitat heterogeneity signifies stochastic assembly (Fig. 1b; Fukami 2010, Chase and Myers 2011, Vellend et al. 2014). Importantly, low and high variations are defined here in a relative sense using the variance *within*

replicates as a baseline (variability 1 and 2 in Fig. 1a and b; i.e. the residual). Most manipulative experiments have the implicit assumption that this baseline remains constant among different levels of treatments (e.g. Fig. 1a and b), and thus were therefore tested using statistical models with an unstructured residual variance. This obviously contradicts existing evidence that some assembly trajectories are sensitive to "founder effects" and can be highly variable even when replicated under identical history and abiotic conditions (Drake 1991). Therefore, heteroscedasticity may prevail even when different treatments show broad-scale convergence (Fig. 1c). Likewise, heteroscedasticity may obscure the "boundary" between treatment levels, making it challenging to discern between deterministic divergence and purely stochastic assembly (compare Fig. 1d and 1e), and can potentially lead to erroneous conclusions regarding the relative importance of history and environment as assembly drivers. However, it is not clear how often heteroscedasticity would occur within homogeneous environments in the field, because few studies have manipulated natural history with enough detail and tracked the ensuing community-level variability simultaneously in the field.

Here, I use a transplantation approach that brings together assemblages from different recruitment regimes to a homogeneous environment in order to assess how their adult compositional variation responds to variable recruitment. In the case of marine sessile invertebrates, direct experimental data is still rare regarding how variable recruitment can affect community-level assembly. The majority of marine studies examine how recruitment affects population dynamics or pairwise species interactions (Underwood and Denley 1984, Fairweather 1988, Menge 2000). However, there are good reasons to anticipate that recruitment variation have effects that are more complex at the community level. Studies that manipulated recruitment and tracked whole-community response generally found contingent patterns where the adult environment can heavily modify patterns generated by recruitment in some cases, but not in others (Bingham 1992, Forde and Raimondi 2004, Sams and Keough 2012). A more realistic approach that is able to manipulate natural

variation in recruitment and accommodate heterogeneous responses within a homogeneous environment can provide new insights to our current understanding of community assembly.

Methods and materials

Study site and the fouling community

Experiments were conducted at a long-term monitoring site located within Blairgowrie marina (38°21’31”S, 144°46’23”E) near the southern tip of Port Philip Bay. The marine subtidal hard bottom of the region is typically dominated by macroalgae and sessile epifauna, together they form the fouling community. The fouling community consists of species that require unoccupied hard substrate for vegetative growth. They compete heavily for space on underwater hard substrates, including rock surfaces, shells, hard parts of other organisms, and man-made underwater structures. In old and undisturbed patches, solitary ascidian species dominate most of the space (~ 85 % space coverage) and usually have the greatest biomass. These solitary ascidians grow relatively slow and have longer life-history cycles comparing with other groups in the community. With their hard tunic, they can nearly always overgrow other adjacent species, which in turn contribute to the complex three-dimensional structure of the fouling community. Arborescent bryozoans, sponges, and brown algae are the next most abundant group in old patches (together having ~ 10 % coverage). They share a common feature of an up-right growth form, which has a relatively low space requirement of the substrate. Arborescent bryozoans grow into a tree-like formations; once colonies reached certain size and density, they form thick layers of ‘canopy’ that can effectively capture food and oxygen, leaving very little resources for the organisms underneath. Tubeworms and oysters can also be abundant in old patches, but layers of overgrowth of other species often cover their calcified cases. Usually only the openings of their tubes could be seen from the surface of the community, but underneath they form the base structure for other species to settle.

In newly formed, unoccupied patches, succession can be rapid resulting in a dynamic species composition. Tubeworms (e.g. *Pomatocerus taeniata*) and bryozoans (e.g. *Watersipora* sp. and *Bugula* spp.) are the most dominant animal groups on newly formed bare surfaces. Together they can sometimes cover over 40% of the free space within a month. Arborescent brown and red algae are also early colonizers of newly freed spaces due to their fast growth rate (~ 10 % after the first month). However, they have a relatively weak ability to persist and are often 'bulldozed' off by other invertebrate competitors. Colonial ascidians (e.g. *Botrylloides leachi*) can sometimes rapidly increase in biomass overgrowing other species, causing mass mortality; but in general, they are also weaker competitors. Five other encrusting bryozoans can be found at the study site, but all in low abundances. Like *Watersipora* sp., these encrusting species expand horizontally and have high demand for space in order to persist; therefore, they are less common in late successional stages. Solitary ascidians are the minority in newly formed patches (usually ~ 1 % space cover after the first month) mainly due to their slow-growing life history.

General experiment setup

PVC settlement plates (110×110 mm) were attached to a larger PVC backing panel (550×550 mm) for fouling communities to establish. Each backing panel carried 16 settlement plates; these plates were 2 cm apart from each other. The surface of settlement plates was roughened with sandpaper to encourage settlement of propagules. Backing panels were hung horizontally off a floating pontoon below the water surface facing down. The floating pontoon was 3 m wide, 180 m long, with an average water depth of 5.5 m.

From a regional perspective, the marina represents a local community embedded within the species pool of Port Philip Bay. The connectivity with other communities outside of this marina is likely to be low, since most reefs and peers are kilometers apart and isolated by sandy bottoms. The disperse kernel of most larvae are within 0.01 to 0.1 kilometers, and hence our field site is therefore a source of local community. Backing panels randomly attached to the pontoon can be viewed as randomly

formed empty patches (referred to as ‘patch’ hereafter). Settlement plates were thus equivalent to replicated plots (referred to as ‘plot’ hereafter) randomly located in each patch.

Field program

The entire study spanned over two consecutive summers. During the first summer from December 2012 to March 2013, a monitoring experiment (*Experiment 1*) was conducted to document the natural community variation among depth. I reported how natural fouling assemblages change along a depth gradient. During the second summer from December 2013 to April 2014, a transplant experiment (*Experiment 2*) was conducted to determine if variation in juvenile recruitment along this gradient was the main driver of the different fouling assemblages.

Experiment 1

I will first show that natural larval recruitment and the subsequent species composition of the fouling community differed between depths. For this purpose, 30 new unoccupied patches were created following the method outlined in *General experiment setup*. 15 were located at 1 m depth; the other 15 were located at a depth of 3 m. The locations of the shallow patches were randomly chosen along the jetty, but the deeper patches were always located directly below the shallow one. This setup greatly reduced the difficulties of the fieldwork. I monitored the patches over the period of *Experiment 1* by recording the percent cover of each species at week 4, week 8, and week 12. Species percent cover of any given patch was estimated by taking the species percent cover from four randomly chosen plots in that patch. Plots were brought back to the laboratory and photographed with a digital camera. An overlay of 100 points were randomly distributed over each photograph with a computer program (Coral Point Count with Excel extensions, Kohler and Gill 2006). All visible fouling species under the points were identified. The percent cover (p_i) of species *i* in a plot is calculated as

$p_i = (C_i / 100) \times 100$ %,

where C_i is the number of points (out of 100) having landed on species i.

I describe the community structure of the fouling assemblage in three ways. The first two are common summary statistics of biodiversity: species richness (S) and Shannon Index (H). S is simply the number of species present in a plot; H of a plot is calculated as

$$H = -\sum_{i=1}^{S} p_i \times \ln p_i.$$

The third method describes the variation in species composition within a patch (*var*). It is based on Q-mode dissimilarity measurements (Q-mode meaning investigating the relationship among sampling units) that are commonly used with multivariate community datasets (Legendre and Legendre 2012). This can also be viewed as a way to quantify beta-diversity among sampling units (Whittaker 1960, 1972, Legendre et al. 2005). In practice, an n by n Euclidean distance matrix was first calculated from the original data of species composition (n by S data table, where n was the number of sampling units and S the number of species). This matrix represents all pairwise distances among the row vectors (plots) of the original data table. In the current design, $n = 4$, since each patch was represented by a sample of four replicated plots. The distance matrix I chose to use preserved the Pearson's χ^2 correlation among plots, since each plot was described by a series of event frequencies (the frequency of points landing on each species). A measure of *variance* among replicated plots within a given patch could then be calculated as the *mean* of squared Euclidean distances of their distance matrix (Anderson 2001).

Different amounts of information in the original data of species composition are preserved in different summary statistics. I chose these three indices of community structure because they cover a range of abstraction to the original data, and thus different degrees of information loss; regardless, they are all very common in the literature. Species richness S is the simplest and most common descriptor of biodiversity found in the literature. In essence, it is a summary of binary data (presence-absence) and preserves the least amount of information in the original species

composition. Species *identity* and *abundances* are irrelevant and thus rare and dominant species have the same influence over *S*. Shannon Index *H* is based on the *abundance* data, and takes into account both species richness and how evenly abundance is distributed among these species. Both high species richness and very even abundance distribution across fewer species could contribute to high *H* values. Nevertheless, species *identity* is irrelevant to the calculation of *H*. The multivariate technique that determines the resemblance between sampling units preserves the most information collected from the field observation. The *n* by *n* distance matrices carry information concerning all pair-wise comparisons of samples, and the calculation takes into account both the proportion of shared species (therefore species *identity*) and their *abundance* differences.

Experiment 2

With this experiment, I will investigate the principal factor creating assemblage patterns along the depth gradient. As introduced earlier, colonization history and consumer-resource interactions are two main categories of factors creating patterns in natural communities. Colonization history, in particular, can have very complex pattern of spatial variation. The kernel of dispersal can differ with species; even within the population of a single species, it can differ still according to microclimate, weather, and seasonality. Here, I ask specifically if variation in larval recruitment drives variation in fouling assemblages along the depth gradient. I use the transplant experiment to test the null hypothesis: patterns along the depth gradient were not caused by difference in larval recruitment pattern. A failure in rejecting the null hypothesis would indicate that environmental differences, which may be correlated with depth, are otherwise responsible for the difference in fouling assemblages. Monitoring the community structure of transplants eliminates differences in environmental forcing on post-recruitment stages, and allows us to infer whether larval supply and recruitment jointly influence community formation.

24 new unoccupied patches were created at the study site following the method outlined in *General experiment setup*, 12 were located at 1 m depth, the other 12 were located at 3 m depth. The locations of the shallow patches along the jetty were randomly chosen, but the deeper patches were always located directly below the shallow one. This setup greatly reduced the difficulties of my fieldwork. From each shallow patch, I transplanted replicated plots (n = 4) to the deep patch directly below it during early successional stages, to assess whether shallow assemblages were able to remain different to their deeper counterpart. One question remains, that is, how should I define 'early stages'? Conceptually, I refer to 'early successional stage' in this study as the period of time starting from when empty patches first appeared at the study site, until the stage when it becomes relatively difficult for new settlers to successfully recruit to the adult community. The competitive ability of fouling species to appropriate resources is known to be positively related to their age and body size. Late arriving larvae therefore suffer from the compounded disadvantage of being smaller in body size, and having to compete for rarer resources. Therefore, the number of successful new recruits decreases with time (age of the community). Juveniles recruited within this period of a benign time 'window' could all contribute to subsequent community formation. In field observations, this does not imply that new recruits are blocked out from the community completely after the early successional stage has passed. Mortality in the adult community caused by intense competition, predation, or disease can free up preoccupied space for new recruits to establish. However, these dynamics are more appropriately considered to be within the mid- or late-successional stages. To address the uncertainty concerning the early stage time window, two different sets of replicated plots were transplanted from each shallow patch to the deep patch immediate below it. One set (n = 4) was transplanted at week 2 (*early-recruitment stage*), the other (n = 4) at week 4 (*late-recruitment stage*); together they consisted of the *recruitment stage* and post-recruitment stage, which comes after the *recruitment stage*. To serve as reference control plots to the transplants, replicated plots (n = 4) in each of the deep patches were picked up and then returned to the patch. Figure 1 shows the schematic of the experiment design.

I monitored the deep patches over the period of *Experiment 2* by recording the percent cover of each species at week 4 and 20. At week 4, species percent cover of all plots was recorded just before they were being moved. To sample the community, plots were brought up to the dry dock and placed in a tank filled with seawater. Digital photographs of individual plot were taken while submerged. Species percent cover of each plot was obtained by placing an overlay of 75 points randomly distributed over each photograph with a computer program (Coral Point Count with Excel extensions, Kohler and Gill 2006). All visible fouling species under the points were identified. The percent cover (p_i) of species *i* in a plot is calculated as

$p_i = (C_i / 75) \times 100\ \%$,

where C_i is the number of points (out of 75) having landed on species *i*. The community structure was summarized with the same three descriptors as described in *Experiment 1*, namely, species richness (*S*), Shannon Index (*H*), and variation in species composition using distance matrices.

Data analysis

The goal of *Experiment 1* was to investigate whether fouling assemblages were different between shallow patches and deep patches at the recruitment stage and subsequent successional stages. *S*, *H*, and *var* were each analyzed using a linear mixed-effects model, fitted with restricted maximum likelihood using the *nlme* package of R, version 3.0.2 (R Development Core Team 2011). The model had *depth* (with two levels, shallow and deep) as fixed effect, and estimated the among-patch variances based on the random deviations of descriptors from the fixed population means. The goal of *Experiment 2* was to assess whether the shallow transplants remained different to the deep controls, or whether shallow transplants and deep controls converged in community formation. For this purpose, *S*, *H*, and *var* were each analyzed in a linear mixed-effects model identical in model structure to that used in *Experiment 1*. Instead of *depth*, the model had *treatment* (with three levels: controls, *early-recruitment stage* transplants, and *late-recruitment stage* transplants) as fixed effect, fitted with the same procedure as in *Experiment 1*. Note that all parameter estimates reported in

results were fitted using restricted maximum likelihood. However, in both *Experiment 1* and *2*, the fixed effect of all models was tested for significance using likelihood ratio tests, where both the target and null models were fitted under the maximum likelihood framework (Zuur et al. 2009). Where relevant, means ± 1 standard error of the summary statistics are present throughout.

Results

Pattern of mean diversity

Results from *Experiment 1* and *2* jointly suggest that the pattern of initial recruitment was largely unrelated to the ensuing differences in species richness and Shannon diversity between shallow and deep patches. From the results of *Experiment 1*, it is concluded that shallow patches usually had higher diversity than deep patches during various successional stages (Fig. 3; Table 1). In other words, higher number of species accumulated and persisted in the shallow community over time. Persistence was not observed in *Experiment 2*, where transplants coming from shallow patches had higher diversity initially, but gradually became indistinguishable from deep controls (Fig. 5). It thus appeared that post-recruitment processes heavily modified initial recruitment pattern. This is likely to be the mechanism that was in operation because of the following observations. First, in both *Experiment 1* and *2*, and in both shallow and deep patches, diversity continued to increase after the *recruitment stage* (Figs. 3 and 5). Second, the transplants in *Experiment 2*, however, only increased to a level similar to the controls (week 4 to 8, Fig. 5). Third, the final diversity in *Experiment 2* across treatments all resembled those observed in *Experiment 1* deep patches, but not the shallow ones (the final observations of Figs. 3 and 5). Combining these observations and acknowledging that the initial recruitment diversity was indeed different across treatments in *Experiment 2*, effects of post-recruitment modification became apparent.

Pattern of diversity variation

Results from *Experiment 1* and *2* jointly suggest that initial recruitment pattern was responsible for the subsequent difference in the patch assemblage variability between shallow and deep patches. The results of *Experiment 1* show that communities in shallow patches usually had lower levels of variation than deep patches (Fig. 4; Table 2). The results of *Experiment 2* show that the diversity variation among treatments became systematic and different over time, showing no sign of converging (Fig. 6). The controls, which received all their recruits from the deep patches, had the greatest variability; the transplants, which received their recruits from both shallow and deep patches, always had lower variability than the controls. This hierarchy lies in agreement with those observed in *Experiment 1* (Fig. 4). Initial recruitment difference between depths is thus evident to have strongly driven community structure.

Discussion

My results show that similar communities can develop under similar environmental conditions, but the variability among each experimental replicate can be significantly heterogeneous. In a relatively homogeneous environment, the magnitude of residual variance developed in proportion to the initial recruitment treatment irrespective of the post-recruitment environment. In contrast, the post-recruitment environment strongly controlled the mean state and mean diversity of communities regardless of recruitment histories.

Although similar levels of mean diversity were observed, adult communities of different recruitment treatments have unequal amount of residual variance that showed heteroscedasticity. Changes in variability among treatments has often served as evidence to convergence or divergence (Houseman et al. 2008). Such evidence has been observed in manipulative experiments where communities along an environmental gradient were monitored. The environmental gradient of interest can either be a planned manipulation or unplanned natural gradient, including nutrient enrichment (Inouye and Tilman 1995), abiotic disturbance (Bernard-Verdier et al. 2012), patch connectivity (Chase and Ryberg 2004), and predation (Germain et al. 2013). In most cases, if

divergence is observed without a difference in the gradient, the result is attributed to minor differences in uncontrolled factors (Vellend 2010). However, most of these earlier studies have seldom considered the potential effect size of historical contingencies, nor the ecological implications of heterogeneous variance in the absence of gradient difference. Consequently, as communities were replicated along the gradient, the background variability due solely to subtle historical differences remained unchecked. Results reported here demonstrated that even under experiment-wide community convergence, replicates within each treatment level can still diverge and have very different "unexplained" residual variances.

Reports of elevated variance among replicates in field experiments is not uncommon, but were often presented in the form of a non-rejection of the null hypothesis (Forde and Raimondi 2004, Sams and Keough 2012). Failure to reject the null hypothesis directly indicates that the residual variance is relatively high (or not low enough) relative to the variance among treatments. However, the implications behind these "failed" hypothesis tests usually received little interpretation. Recent empirical studies that investigated the role of colonization history and nutrient enrichment simultaneously, have demonstrated that their interactive effect can significantly alter the community variability, relative to their independent effects (Inouye and Tilman 1995, Fukami and Morin 2003, Houseman et al. 2008, Steiner 2014). Results from the current study join these earlier findings, and further demonstrated that naturally occurring differences in recruitment pattern can cause heterogeneous variance structure in absence of an obvious environmental gradient.

In my study, limiting niche factors may impose an upper limit on the total diversity because most species could access both shallow and deep patches, yet diversity is constantly lower in the deep. In many cases, such niche factors co-vary with the abiotic environmental gradient (e.g. depth), creating habitats with different available niche spaces among depths. Within a depth, if the environment is relatively homogeneous, convergent selection may drive the diversity pattern. Such niche factors can be either biotic or abiotic (Pianka 1966). Convergence in diversity of adult communities have been observed in transplant experiments where patch exposure to wave energy

and local hydrology was influential (Menge 2000). Habitat morphological characteristics are also often invoked as a diversity determinant (McKindsey and Bourget 2001, Rule and Smith 2007). Subtle changes in the morphology of natural habitats can strongly affect the structure of associated assemblages (Rule and Smith 2007, Smith et al. 2014), and substrate complexity can directly or indirectly determine diversity. Effects of these abiotic factors may all contribute to the converging mean diversity in this study because the site is entirely within a low wave-energy area such that the post-recruitment individuals were unlikely to be damaged or swept away by currents. Furthermore, my experimental design minimized the effect of substrate complexity since artificial settlement plates all have simple and identical surfaces. Therefore, effects of substrate morphology should be homogeneous and neutral across all treatments and replicates.

I determined the effects of initial recruit composition by directly gathering natural recruits using settlement plates without changing initial environmental conditions. As such, I can attribute convergence in mean diversity to the experimentally generated variation in initial composition. An alternative potential explanation for my results is that similar mean diversity resulted because the transplantation simply subjected plots to very similar pools of colonizers, such that there was a fundamental divide between shallow and deep habitats. However, most species were recorded in both depths over the course of my experiment. I can thus eliminate the possibility that limited dispersal alone caused diversity convergence. Therefore, the invariant mean diversity across treatments strongly points to the operation of biotic controls on mean diversity in the study region, such as inhibition or facilitation (Connell and Slatyer 1977). Initial recruits directly or indirectly affected the potential of later immigrants to establish, and these priority effects collectively caused the gradual increase in the variability difference among plots of different recruitment treatments. Convergence in species diversity has been observed in other communities where biotic interactions predominate (Sousa 1979, Hille Ris Lambers et al. 2004). In structurally simple environments such as my study site, competition can control diversity more strongly than other factors, mainly through competitive exclusion (Hart and Marshall 2012, Sams and Keough 2012). Directional selection is

thus likely to act on interspecific trade-offs in life-history traits that differentiate species' competitive hierarchy, excluding species with higher resource requirements and cause convergence.

Despite recent conceptual shifts in other parts of community ecology, the philosophy of experiments for marine sessile communities did not move very far away from deterministic standard models (but see Aiken and Navarrete 2014). Based on the philosophy, with increasing recruit density, the influence of density-dependent selection (e.g., per capita rate of death, reproduction, and predation) would also increase to modify post-recruitment population (Connell 1985). However, these deterministic models overlooked historical contingencies. The strength of recruitment-postrecruitment relationships can be contingent upon species combinations, local patch characteristics, and regional hydrology (Caley et al. 1996). The consequence of overlooking these new lines of evidence is reflected on the mixed results of determinism-driven studies that adult environments can heavily modify patterns generated by recruitment in some cases, but not in others (Menge 2000, Forde and Raimondi 2004, Sams and Keough 2012). To reverse the general perception that (marine) community ecology is inundated with contingencies and exceptions, conceptual models for community assembly should adopt more holistic views that incorporate both niche and neutral predictions. Importantly, creative experiments are needed to verify theoretical predictions empirically.

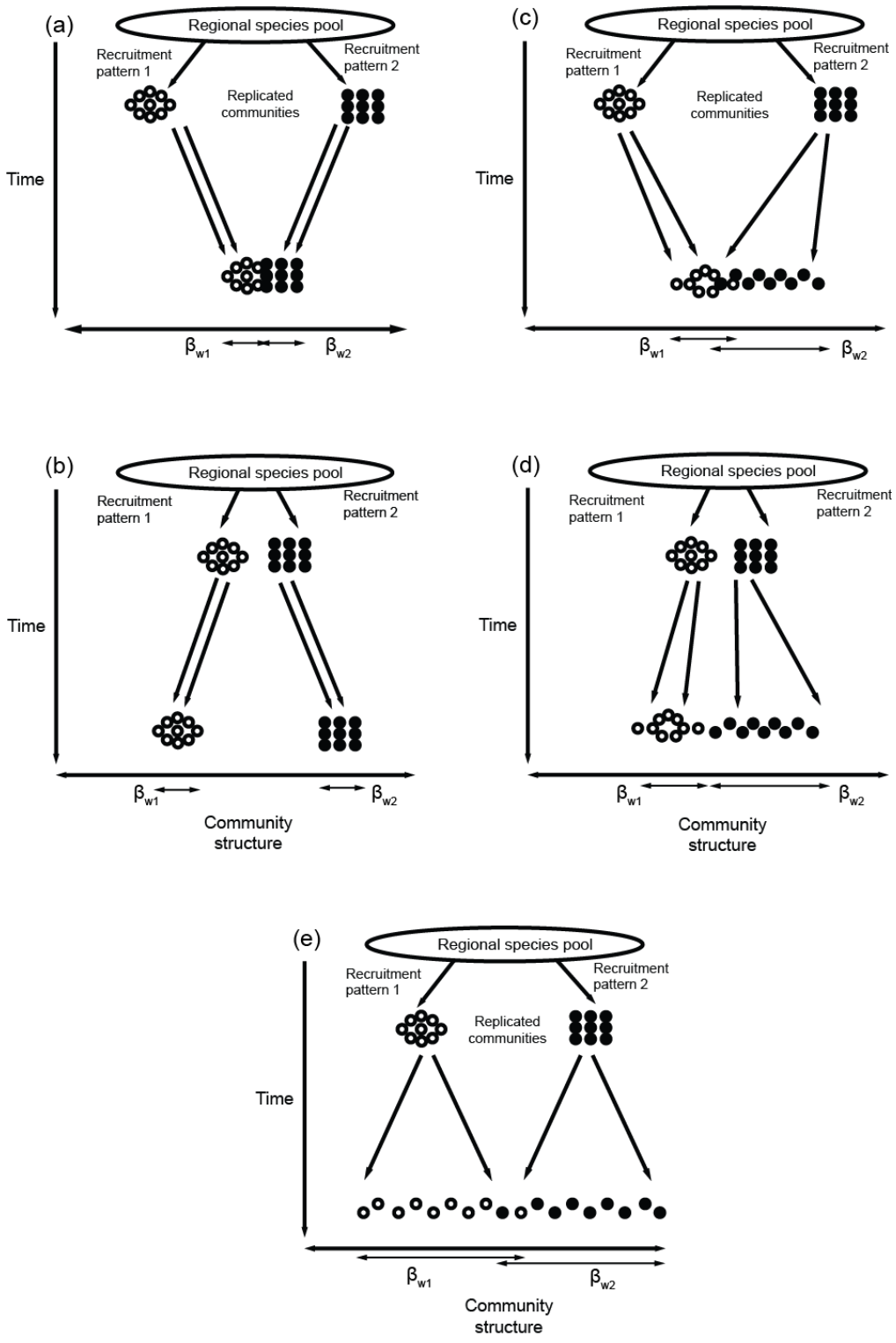

Figure 1. Will similar communities develop in similar sites? Graphical models of experiments to identify convergent assembly (a & c), divergent assembly (b & d), and purely stochastic assembly (drift; e). Initial community differences were generated by different recruitment patterns. In (a), under convergent selection, β-diversity at the end of experiment is low in both within (β_w) and among treatments (treatments = recruitment patterns). In (b), under divergent selection, β_w is lower

than those among treatments. However, (a & b) both assume that recruitment history has no effect on the subsequent trajectory. Under strong historical priority effects, there are no clear relationship between β_w and those among treatments (c & d), making it challenging to distinguish directional selection from drift. (a), (b), and (e) are modified from Vellend et al. (2014).

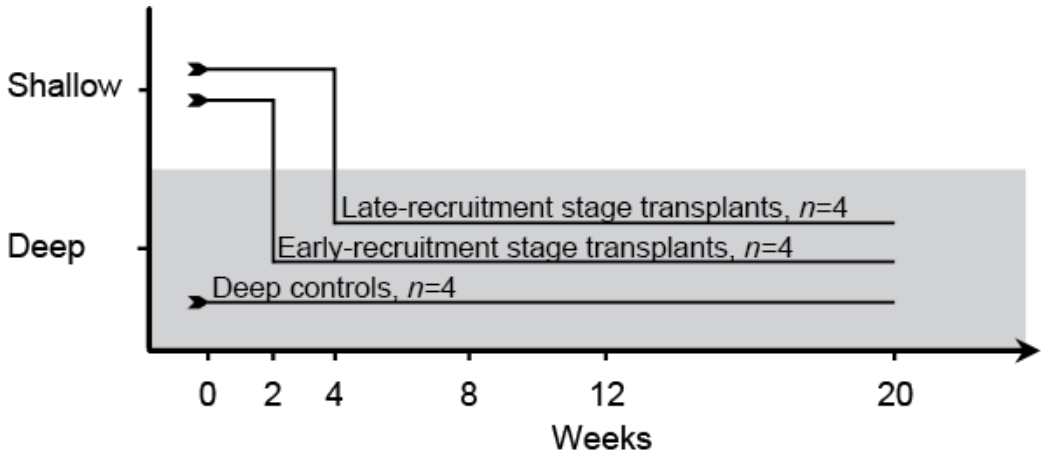

Figure 2. Design of *Experiment 2* transplantation in a patch. Each line represents a treatment and the movement of four replicated plots. The time points with sampling taking place are labelled (as weeks after first deployment).

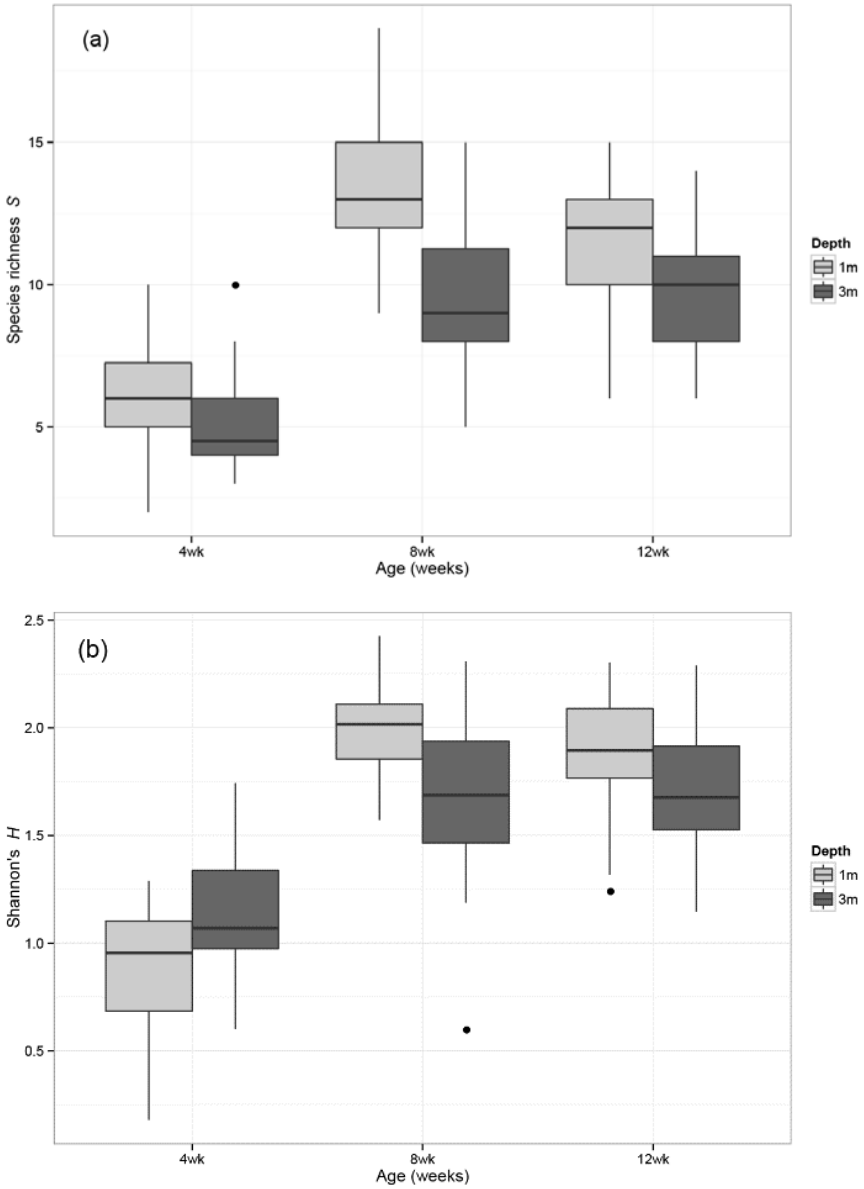

Figure 3. Box-and-whisker plot showing the difference between shallow and deep assemblages in (a) species richness *S* and (b) Shannon Index *H*. Boxes with different shades highlight the difference between shallow and deep, as well as illustrate the sampling distribution. *S* and *H* were measured on the scale of patch.

Table 1. Likelihood ratio test for the difference in *S* and *H* between depths at different sampling time points. Results for the fixed effect (*depth*) and its interaction with the random effect (*patch*) is presented.

Age	***S***		***H***	
	Depth	*Depth×Patch*	*Depth*	*Depth×Patch*
4 weeks	**13.94****	1.83	**5.09***	**4.21***
8 weeks	**29.07****	1.67	**16.71****	1.10
12 weeks	**5.18***	**5.90***	**3.82***	**12.67****

*$0.001 < P < 0.05$; **$P < 0.001$

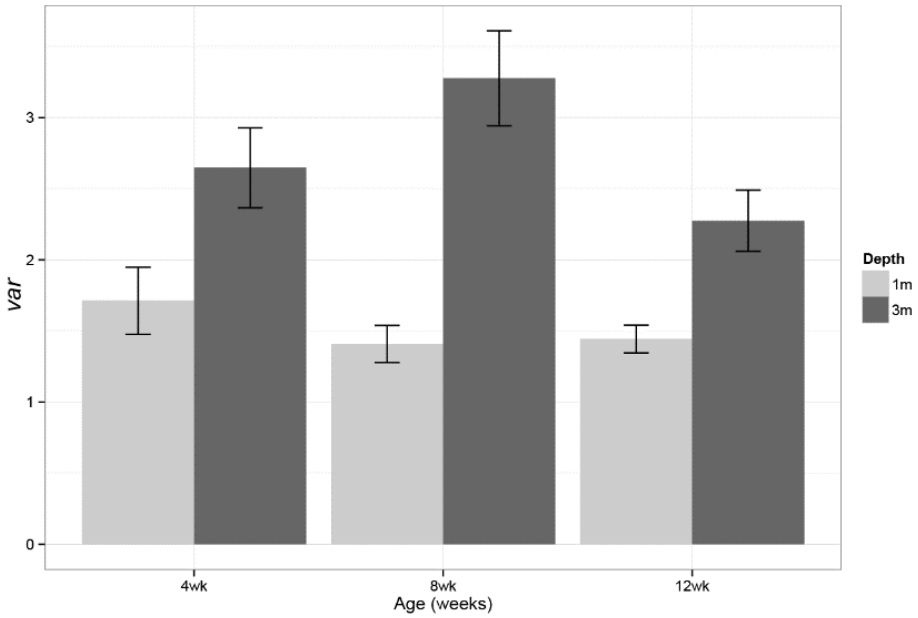

Figure 4. Within-treatment variation among replicated plots (*var*). Bars with different shades highlight the difference between shallow and deep. Error bars represent ± 1standard error.

Table 2. Likelihood ratio test for the difference in *var* between shallow and deep patches.

Age	***var***	
	Depth	*Depth×Patch*
4 weeks	2.64	**11.55****
8 weeks	**4.98***	**17.42****
12 weeks	**3.88***	**15.97****

*0.001 < *P* < 0.05; **P* < 0.001

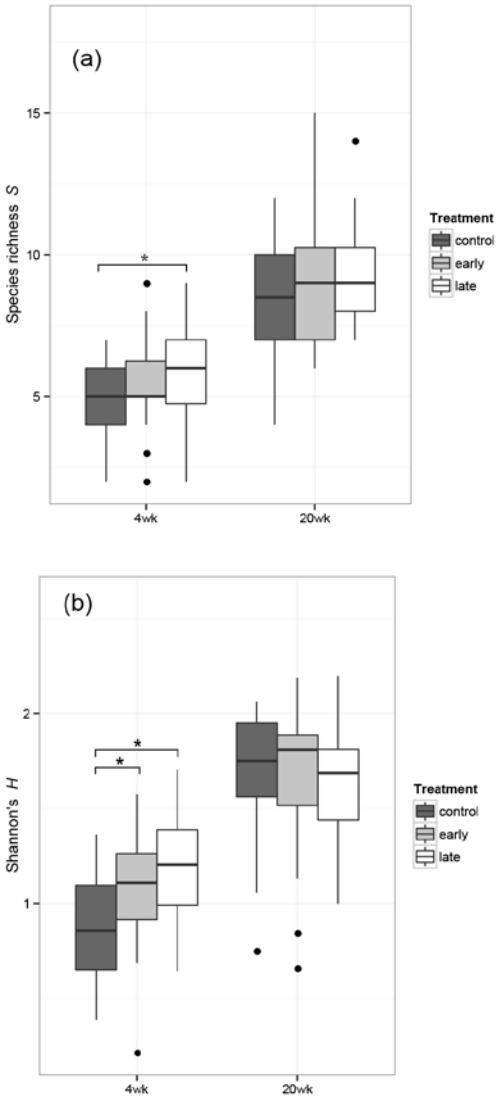

Figure 5. Difference among assemblages receiving different treatment, in terms of (a) species richness *S* and Shannon Index *H*. Downward square brackets above boxes indicate pairs with significant difference (with at least 95 % confidence). Control = deep communities; early = *early-recruitment stage* transplants; late = *late-recruitment stage* transplants. Note that no comparison was made between the means among sampling time points, see Results for justification.

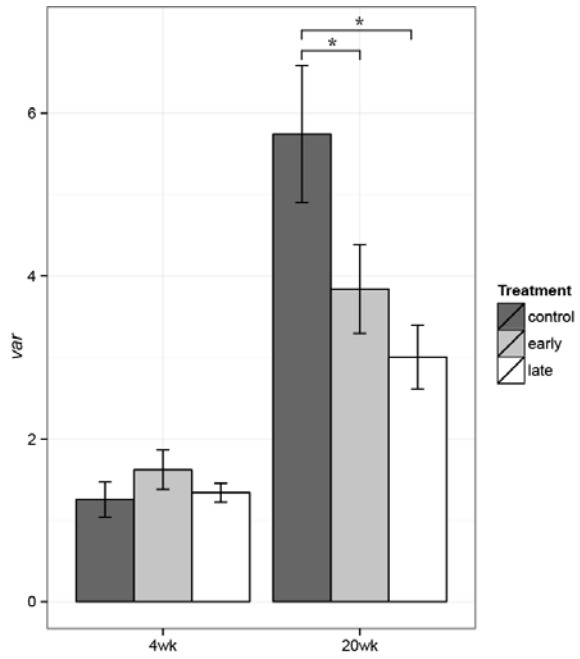

Figure 6. Difference among assemblages receiving different treatment, in terms of within-treatment variation (*var*). Downward square brackets above boxes indicate pairs with significant difference (with at least 95 % confidence). Error bars represent ± 1 standard error. Control = deep communities; early = *early-recruitment stage* transplants; late = *late-recruitment stage* transplants. Note that no comparison was made between the means among sampling time points, see Results for justification.

Chapter Six General Discussion

Our understanding of the nature of biological communities has advanced from an exclusively local (or exclusively regional) one, to a comprehensive panorama that advocates the comparative study of local and regional patterns. 'The problem of scale' in ecology (Levin 1992) is now less of a problem, but more a framework that facilitates the study of community structure. In its broadest sense, the study of community structure concerns those on the scale of entire continents, and the type of questions asked here are most often biogeographic in nature (Schluter and Ricklefs 1993). When studying colonization history and the effect of contemporary environment on this broad scale, the length of history considered spans geological time scales, where 'history' refers to speciation and species range shifts due to geological events (e.g. tectonic shifts or climate change).

On a smaller scale, a continent may encompass a range of geographical or ecological landscapes. When physical barriers are present, each landscape may hold a unique species pool that is rather isolated from others (Cornell and Harrison 2014). A landscape is thus a smaller spatial scale than continental, but still includes many habitats that vary widely in their environmental condition. Studying colonization history and contemporary environment on this scale was initiated by the theory of island biogeography (MacArthur and Wilson 1967), and also known as the local versus regional control over community structure (Schluter and Ricklefs 1993). Within a landscape, a set of local communities that are linked by dispersal of multiple (potentially) interacting species are collectively studied using the concept of metacommunity. In contrast to island biogeography theory, metacommunity models treat regional processes (e.g. dispersal among localities) as operating on a similar time scale to that of local ones (e.g. predation, competition). The issues investigated in the current thesis fit nicely into the metacommunity research, in that discrete patches are imbedded in a pool of species that is itself a regional source of species (Chapter Three). Patches are connected by varying degree of dispersal. Furthermore, one important additional simplification in my study design is that patches are embedded in a rather homogeneous regional environment. This would narrow down the number of metacommunity processes involved. For example, a homogeneous

environment would simplify the patch-dynamic and mass-effect aspects of the metacommunity models, and allow me to focus solely on the biotic environment (i.e., those modified by species' impact niche), such as the colonization history and the ensuing biotic environment generated by recruitment.

By comparing the pattern of community assembly across different scales in space, old and new ecological concepts can be put into perspective and examined under a unified framework of an interactive metacommunity. The observational study conducted in Chapter Two capitalized on the metacommunity framework, and investigated the pattern of structural variation on two different scales in space. Two categories of models are often invoked to explain the observed patch-to-patch variation. First, patches may have different communities because of environmental heterogeneity. Patches may differ in their abiotic habitat conditions that directly limit the number of species or their relative abundances. For example, in plant communities, different patches that vary in their soil fertility or microclimate may have different capacity for biodiversity (e.g., Inouye and Tilman 1995). Likewise, for marine fouling communities that inhabit hard surfaces, the microstructure of hard substrates often covary with wave exposure or water depth (e.g., Rule and Smith 2007). Of all the species in the region, if species are well adapted to different patch conditions, community structure will show patch-to-patch variation (Whittaker 1960). Therefore, differences in community assembly mechanisms along environmental gradients is not a requirement to explain variation in community structure.

Second, different patches are thought to have different communities because of difference in niche occupancy (e.g., Myers and Harms 2009). If local niche space (requirement niche) is only loosely filled with species, then the local community is said to be unsaturated. The effects from the regional species pool, mediated via dispersal, are more important in unsaturated communities; by contrast, a saturated community in which species are densely packed into niche spaces will show little influence from the species pool (Cornell and Lawton 1992). If the fouling communities at my study site were unsaturated, then communities at the smaller local scale and the larger regional scale

should engage in some type of metacommunity dynamics (Leibold et al. 2004). In contrast, if the fouling communities were saturated with species, then resources should be observed to be constantly and fully used by residents, and colonizers coming from a larger species pool should have little or no effect on local community structure.

The first environmental heterogeneity model is unlikely to be responsible for the observed structural variation in my data, because such models usually operate under the premise that communities are approaching or have reached a dynamical equilibrium (Connell 1978). In the first year of my study (Chapter Two), even from the data obtained at the last census time point, there was still 15 to 20% of patch space unoccupied, suggesting that the system still retained high potential to alternate between colonization-competition trade-offs and species-sorting dynamics (Tilman 2004), and they were far from equilibrium. Although space has been traditionally assumed to be the sole limiting resource in this system, this is an assumption that is increasingly under challenge. Based on empirical experiments, oxygen limitations (Lagos et al. 2015) and food limitations (Svensson and Marshall 2014) can significantly alter patterns of larval settlement and recruitment. With these environmental gradients present, one important feature of the environment heterogeneity model is that local communities track these gradients (Whittaker 1967). In my experimental design, the artificial substrates deployed for communities to develop have homogeneous surface features across patches, which eliminated topological differences as an abiotic factor and forced species to compete in a homogeneous two-dimensional arena; in addition, the experiment was conducted inside a small marina area that further minimized abiotic differences among experimental patches. Results from the reciprocal transplant experiment indicate that the change in community structure was non-directional, that is, I am able to model the magnitude of variation within and among patches, but not the mean (Chapter Four). The precise species composition of each patch appeared to be the result of a random draw from the surrounding regional pool of species.

Considering the second, niche occupancy model, the key issue is whether or not the fouling community at my study site is saturated (Cornell and Harrison 2014). Results from the reciprocal

transplant experiment (Chapter Three) provide direct empirical evidence that supports an unsaturated community structure. The historical community structure generated by initial colonizers can still be identified after 16 weeks of successional changes. The fouling community structure depends significantly on the initial colonizing patterns (Chapter Three), which is mediated by a largely stochastic larval transportation among patches at the environmentally homogeneous study site (Chapter Four). After recruitment, local community members undergo deterministic selection that is mediated by resource competition with their adjacent neighbours (niche occupancy). Both history and the ensuing biotic environment play an important role in driving the succession trajectory (Chapter Three).

Other than providing support for an unsaturated community, results from the cross-depth transplant experiment further suggest that a synthesis of the two common metacommunity models –patch-dynamic and species-sorting model, is the likely template for the community structure in my study system (Chapter Five). In the patch-dynamic model, local patches do not differ in any respect except for species composition in space; the species-sorting model considers the effects of local abiotic features on population state variables such as fecundity and death rates (Chase and Leibold 2003). Results from Chapter Five highlight the effects of 'biotic environments' on succession trajectories, which is the combined results of the two models. I show that, for an unsaturated community where colonization history is stochastic and has significant interaction with the ensuing biotic environment, deterministic processes such as resource partitioning can result in unpredictable succession trajectories, even in homogeneous-abiotic habitats.

Marine fouling communities offer an excellent opportunity for *in situ* transplant experiments of intact communities to manipulate historical and environmental aspects of assembly. By transplanting intact communities among localities *in situ* where the pattern of community structure varies significantly, we can simultaneously investigate both historical and environmental causes of variation in communities. Plant ecologists have used whole-community transplant techniques to simulate species range shifts, and empirically study its influence to community assembly under

climate change (Alexander et al. 2015). Such experiments represent a direct approach in that communities are moved to different localities, and therefore, this directly manipulates the environment experienced by communities. By observing how communities with similar colonization histories respond to different environments (or how communities in the same environment but different histories), the relative strength of history and environment can be estimated.

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