

Temporal variation in dispersal modifies dispersal–diversity relationships in an experimental seagrass metacommunity

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ABSTRACT: Dispersal is a key force driving patterns of biodiversity. However, temporal variation in dispersal due to seasonality, weather, and other stochastic forces is an understudied aspect of the dispersal–diversity relationship. Metacommunity theory predicts temporal variation in dispersal can alter species distributions across patches. We empirically tested the hypothesis that variation in dispersal can modify the nonlinear dispersal–diversity relationship. Using a mesocosm experiment, we factorially manipulated variation in and intensity of dispersal in invertebrate grazer communities associated with nearshore seagrass ecosystems. Higher dispersal intensity led to higher grazer abundance, higher species richness (alpha diversity), and—when dispersal was variable—lower compositional similarity among patches (higher beta diversity). Within each dispersal intensity treatment level, temporal variation in dispersal decreased alpha diversity and increased beta diversity, with strongest effects at low- and intermediate-intensity dispersal. Our results provide the first empirical evidence that temporal variation in dispersal can substantially modify the well-described dispersal–diversity relationship for both alpha and beta diversity. Broadly, our results provide increasing evidence for the effects of spatial and temporal variability in modifying the role of the ecological processes driving marine metacommunity structure.

KEY WORDS: Community assembly · Jensen's inequality · Larval supply · Seagrass · Metacommunity

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1. INTRODUCTION

Dispersal is a key driver of population dynamics (Roughgarden et al. 1988) and diversity (Palardy & Witman 2011, Palardy & Witman 2014) in marine communities. Dispersal among habitat patches can strongly influence species richness and compositional similarity at local and landscape scales (Aiken & Navarrete 2014, Stier et al. 2014, Valdivia et al. 2015). In many marine systems, such as coral reefs, kelp forests, and rocky shores, life histories that include passively dispersing larval stages are relatively common, and dispersal during this life stage can affect population persistence (Botsford et al.

2001, Byers & Pringle 2006). Though population-level effects of dispersal have been the focus of much study, community-level consequences such as diversity patterns across habitat patches in marine systems are less understood (Boström et al. 2006, Caro et al. 2010, White & Samhouri 2011, Heino et al. 2015).

Ecological theory predicts communities connected by high dispersal rates will exhibit greater similarity in species composition than communities linked by less frequent dispersal events (Hastings & Gavrilets 1999, Loreau 2000, Amarasekare & Nisbet 2001, Mouquet & Loreau 2002, Mouquet & Loreau 2003, Cottenie & De Meester 2004, Urban 2006). A suite of observational and experimental studies support this

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prediction (Harrison 1997, 1999, Forbes & Chase 2002, Chase 2003, Chase & Ryberg 2004, Kneitel & Chase 2004, Cadotte & Fukami 2005, France & Duffy 2006, Östman et al. 2006). Two alternative explanations exist for these common patterns. First, when competition is weak, high dispersal can homogenize community structure in discrete patches, because all species can reach all patches and persist (i.e. 'mass effects' [Shmida & Wilson 1985] or 'rescue effects' [Brown & Kodric-Brown 1977]). In contrast, in communities structured by interspecific competition, high compositional similarity in heavily connected patches is often attributed to an increase in the supply and density of competitively dominant species. When competitively dominant species are released from dispersal limitation, their persistence in patches can homogenize species composition across locations by excluding inferior competitors (Mouquet & Loreau 2002, Chase 2003, Mouquet & Loreau 2003).

To date, most evidence for the importance of dispersal in driving diversity patterns has come from tests and theory that assume a single (or average) dispersal rate among all patches or for all species in a spatially structured competitive metacommunity. When this mean dispersal rate increases, compositional similarity increases (Myers & Harms 2009, Matias et al. 2013, Catano et al. 2017). Further, there is evidence that this relationship is often nonlinear, with compositional similarity decreasing exponentially with an increase in mean dispersal rate.

With increasing appreciation that variability in ecological processes can have distinct effects relative to changes in the mean (Bertocci et al. 2005, Benedetti-Cecchi et al. 2006, Bernhardt et al. 2018), it is critical we consider how temporal variability in dispersal affects the dynamics and distribution of species in spatially structured communities. Two lines of evidence suggest that temporal variation in dispersal can produce unique biodiversity patterns. This evidence includes: (1) theory explicitly manipulating temporal variability in dispersal and measuring how biodiversity patterns change (Matias et al. 2013), and (2) the mathematical relationship known as Jensen's inequality whereby variation in a nonlinear process can produce effects that would not be predicted by focusing on mean conditions alone (Ruel & Ayres 1999, Denny 2017).

Recent theory predicts that temporal variation in dispersal should alter spatial patterns of biodiversity in spatially distinct communities connected by dispersal (i.e. a metacommunity). Using a source-sink model, Matias et al. (2013) built temporal variability in dispersal into a previous model by Mouquet &

Loreau (2003) and demonstrated how temporal variability in dispersal events interacts with the intensity of dispersal, or the number of individuals arriving in a dispersal event, to drive alpha and beta diversity. This model assumes species exhibit a trade-off between competitive ability and dispersal frequency. Under this assumption, the Matias et al. (2013) model predicts that temporal variability in dispersal can produce unique patterns of alpha diversity—the diversity within a patch—and beta diversity—the compositional dissimilarity among patches. Specifically, the model predicts that when dispersal has zero temporal variability (i.e. is constant in time), there will be a hump-shaped relationship between dispersal intensity and alpha diversity and a nonlinear decline in beta diversity with increase in dispersal intensity. When the model introduces temporal variability in dispersal, it produces a shift in peak alpha diversity to higher dispersal intensity and a more shallow decline of beta diversity as dispersal intensity increases. This effect on beta diversity can be large, with temporal variability in dispersal increasing beta diversity by >10-fold the spatial turnover predicted in the absence of variability (Matias et al. 2013). Matias et al. (2013) hypothesize these patterns emerge because the importance of competition as a driver of local diversity shifts with different dispersal regimes. When dispersal intensity is high, top competitors are present in nearly all patches and competitively exclude other species, lowering diversity both within and between patches because only competitively dominant species persist. Variability in dispersal amplifies this effect because pulses of high dispersal intensity facilitate rapid competitive exclusion by dominant species.

The second reason why temporal variation in dispersal likely affects the dispersal–diversity relationship is Jensen's inequality (Denny 2017). Jensen's inequality states if $f(x)$ is nonlinear, then the mean of the function is not equal to the function evaluated at the mean. For decelerating nonlinear functions (i.e. the 2nd derivative is negative), the inequality predicts $\bar{f}(\bar{x}) > f(\bar{x})$. Since beta diversity is typically a decelerating nonlinear function with an increase in dispersal intensity (Cadotte 2006, Matias et al. 2013), the inequality predicts that variability around any mean dispersal (\bar{d}) will increase species turnover relative to a patch with fixed dispersal (i.e. $\bar{f}(\bar{d}) > f(\bar{d})$) (Fig. 1). While this prediction is qualitatively similar to the one made by Matias et al. (2013), it is a statistical property of nonlinear functions, not a product of competitive dynamics.

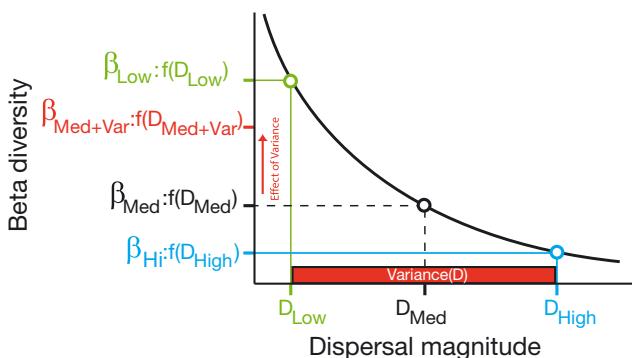


Fig. 1. The role of Jensen's inequality in producing greater expected beta diversity in the presence of variable and fixed dispersal rates. Beta diversity is theoretically predicted to be a decelerating nonlinear function of dispersal. Expected beta diversity at Low (β_{Low}), Medium (β_{Med}), and High (β_{Hi}) is shown for 3 invariant dispersal rates: (1) Low Dispersal (D_{Low} ; green), (2) Medium Dispersal (D_{Med} ; black), and (3) High Dispersal (D_{High} ; blue). The introduction of variation in dispersal around D_{Med} (represented by the red bar) produces an expected beta diversity ($\beta_{\text{Med+Var}}$; red) that is greater than the expected beta diversity for the same average dispersal magnitude with no variance (β_{Med}). The positive effect is because $\beta_{\text{Med+Var}}$ is equal to the average of β_{Low} and β_{Hi} . For simplicity, we show the expected effect of variability in dispersal for a single mean; however, Jensen's equality operates for all dispersal magnitudes and will have positive effects on dispersal for all dispersal magnitudes

In this study, we empirically quantify the dual contribution of the intensity and temporal variability in dispersal as drivers of biodiversity patterns in seagrass-associated epifaunal communities commonly found worldwide in coastal marine ecosystems. Seagrasses form spatial networks of meadow habitat separated by sand, mud, or other substrates, supporting grazer populations that are connected demographically by movement and dispersal. Most seagrass-associated epifauna are mobile as adults with non-dispersing juvenile stages; these include isopods, amphipods, and many of the gastropod grazers, although some epifaunal gastropods do have dispersing larval stages. Spatial and temporal variability in dispersal, as well as variation in dispersal intensity, are likely primary drivers of alpha and beta diversity in seagrass ecosystems. There is, however, no direct evidence yet for how dispersal patterns could contribute to the spatial biodiversity patterns observed across seagrass meadows within regions (Carr et al. 2011, Barnes & Ellwood 2012, Yamada et al. 2014, Whippo et al. 2018). Our study builds on previous work by Lee & Bruno (2009), which demonstrated that intensity and variability of grazer dispersal has a strong influence on grazer abundance, alpha diversity, and species composition.

The quantitative predictions of the Matias et al. (2013) model are difficult to test empirically in seagrass epifaunal communities. Competitive dynamics are poorly understood, and field logistics limit our ability to match the long iteration length of the model. Moreover, as noted above, the adult dispersal strategy of many organisms in the seagrass community differs from the assumed larval dispersal in many metacommunity models examining dispersal–diversity relationships. Indeed, many empirical tests of metacommunity theory fail to effectively match the assumptions of metacommunity models (Logue et al. 2011). Therefore here, inspired by Matias et al. (2013), the predictions we have generated from Jensen's inequality, and empirical patterns quantified by Cadotte (2006) and Cadotte & Fukami (2005), we take an empirical approach to test the qualitative hypothesis that the dispersal–diversity relationship depends on variation in dispersal using grazer metacommunities associated with a coastal seagrass *Zostera marina* epifaunal system.

2. MATERIALS AND METHODS

2.1. Approach

To examine how temporal variability in dispersal mediates the effects of dispersal intensity on grazer alpha and beta diversity, we re-analyzed data from Lee & Bruno (2009). We specifically tested 2 hypotheses: (1) dispersal intensity has positive effects on alpha diversity and negative effects on beta diversity, and (2) temporal variability in dispersal alters the strength of these effects.

The Lee & Bruno (2009) experiment factorially crossed levels of dispersal intensity with dispersal variability (additional details in Section 2.2) and measured the response of grazer abundance, species composition, and diversity. Our approach extends the analysis of Lee & Bruno (2009) in 2 ways. First, we consider how different types of dispersal affect beta diversity, while the previous study primarily focused on alpha diversity. Second, we consider the role of sampling effects in biasing estimates of biodiversity. Specifically, estimates of alpha and beta diversity can be affected by changes in abundance (Gotelli & Colwell 2001, Stier et al. 2016), and estimates of beta diversity can depend on changes in alpha diversity (Chase et al. 2011); therefore, we re-report abundance and alpha diversity from Lee & Bruno (2009), then use rarefaction to test whether changes in grazer alpha and beta diversity linked to changes in

dispersal intensity and variability are driven by changes in grazer abundance. Specifically, we quantified 5 response variables that describe how grazer abundance and diversity shifted in patches experiencing varying levels of grazer dispersal intensity and variability: (1) total abundance of all grazer species (hereafter abundance) in each local community, (2) grazer alpha diversity measured as species richness (the number of species within a patch uncorrected for differences in abundance), (3) grazer alpha diversity measured as rarefied species richness (the number of species within a patch corrected for abundance), (4) grazer compositional dissimilarity measured as beta diversity based on species incidence (the Jaccard index: a metric focused on the gain or loss of a species taking into account species identity, estimated as the median distance to centroid [i.e. the distance between each replicate's multivariate location and the multivariate location of the mean community composition per dispersal treatment]), and (5) grazer compositional dissimilarity measured as beta diversity based on species incidence estimated as the rarefied Jaccard index.

2.2. Dispersal manipulations

Diversity estimates are from 6 wk experimental communities in mesocosms at the University of North Carolina's Institute of Marine Sciences in Morehead City that were established in June 2004. Additional detailed experimental methods are described by Lee & Bruno (2009). They manipulated intensity (4 levels of intensity: small, medium-low, medium-high, large) and variability of grazer propagule additions (2 levels of variability: single and multiple additions) in a fully factorial design ($n = 6$). The high variability treatment had a single pulse of propagules early in the 6 wk experimental period, and the low variability treatment had weekly grazer additions. An analysis of 3 sampling dates suggests weekly additions were nearly identical in species identity and rank abundance (see Table S1, Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m613p067_supp.pdf). The experiment was performed in 4 l flow-through mesocosms to control potentially confounding factors such as sampling scale, habitat complexity, and flow regime and to ensure homogeneity of resources.

The researchers also included control mesocosms in which no additional grazers were added to developing communities. Every mesocosm included an artificial seagrass mimic, and all mimics were preconditioned with filtered seawater to allow epiphytic algal propag-

ules to settle and provide food for grazers. Unlike many marine organisms that disperse as minute larvae, the amphipods and isopods in the system are iteroparous brooders that disperse primarily as juveniles and adults, thus allowing manipulation of the propagule supply by adding juveniles and adults collected from algae in the field. Grazers were collected from the field and placed in a large holding tank and added to experimental mesocosms according to assigned treatments by volume (i.e. medium-low, medium-high, and large treatments received 2-, 4-, and 8-fold the volume of grazers added to small treatments, respectively). Samples of propagule additions were preserved and later identified ($n = 20$). Grazers were added in the single and multiple frequency mesocosms in volumes determined by assigned level of supply intensity. Grazers were experimentally added to mesocosms on a weekly basis in multiple treatments. Throughout the experiment, the ratio between supply intensity treatments remained the same, although the total volume varied with availability. Thus, the mean number of dispersers was roughly the same between the treatments with and without variable dispersal, with the exception of minor changes in the species pool through time. Some grazer and algal propagules also colonized all mesocosms naturally via the sea water supply, thus providing a continual source of food for grazers and allowing invertebrate grazer communities to develop in no-addition controls. At the end of 6 wk (2 to 3 generations for most grazer species), all grazers were collected and preserved. Grazers were identified to the lowest possible taxonomic group; some common species were lumped by genera because of the large number of juvenile individuals.

These experimental manipulations of the intensity and frequency of grazer additions are used to simulate dispersal. Hereafter, we use 'dispersal' synonymous with the grazer additions. Although the spatial scale at which grazer dispersal occurs remains an active research question, grazer density does vary at the scale of both meters and kilometers (Whippo et al. 2018), which is likely a product of both grazer movement and grazer reproduction. However, we note that large pulses of grazers may also occur in seagrass communities due to local grazer blooms (Whippo et al. 2018). Therefore, while we concentrate on how this experiment mimics different levels of dispersal from one isolated patch to another, the experimental results could also be interpreted as the biodiversity impacts of grazer blooms within a patch. Additionally, we note that as with many metrics of biodiversity, the concept of scale is paramount.

Implicit in our approach is that the different replicate mesocosms within a given grazer addition treatment are representative of discrete patches of seagrass that are connected via dispersal. We refer to the average diversity within a given replicate mesocosm as alpha diversity and variation in species composition between replicate mesocosms as beta diversity.

2.3. Statistical analysis

Here, we used a 2-factor analysis of variance (ANOVA) to test the effect of dispersal intensity and variability on grazer abundance, richness, and rarefied richness. We are unaware of existing methods for the factorial analyses of beta diversity. Therefore, we analyzed the effects of dispersal intensity and variability on beta diversity using 2 separate 1-factor analyses using PERMDISP, a multivariate permutation test of dispersions (Anderson et al. 2006, 2011). To do this, we conducted 2 independent tests on beta diversity in response to dispersal intensity and compared beta diversity in high-variability versus low-variability treatments. We then estimated and visually examined the median multivariate distance to centroid of the dispersal intensity and variability for all treatments to determine how dispersal intensity and variability affected beta diversity and rarefied beta diversity.

Because dispersal treatments differed in alpha diversity, and beta diversity estimates can be sensitive to variable alpha diversity (Chase et al. 2011), we also used the same method to estimate beta diversity using the modified Raup-Crick index (Chase et al. 2011). The modified Raup-Crick dissimilarity index ranges from 0 to 1 and is interpreted differently from Jaccard's dissimilarity. The values of the modified Raup-Crick index can provide insight into the processes governing community assembly. Values approaching zero are representative of communities that are assembled deterministically (i.e. unlikely to have been assembled by chance), whereas values that approach 1 are less dissimilar than expected by chance (Chase et al. 2011) and are more likely to be assembled through stochastic processes. The index is non-metric, but can be interpreted similarly to other dissimilarity metrics used to compare beta diversity adjusting for differences in alpha diversity (Chase 2010). For visualizing this metric, we calculate the median and standard error of the estimated distance to centroid of the modified Raup-Crick index.

Finally, patterns of alpha and beta diversity are highly sensitive to shifts in abundance, yet most stud-

ies of dispersal–diversity relationships tend to ignore this underlying expectation. Here, we used rarefaction to adjust diversity for abundance effects because we expected mesocosms with larger numbers of grazers would also have higher species richness (Gotelli & Colwell 2001) and lower beta diversity (Cardoso et al. 2009) due to sampling effects. Specifically, we used individual-based rarefaction to estimate rarefied species richness and rarefied beta diversity. For additional details on rarefaction, see Gotelli & Colwell (2001) for alpha diversity and Stier et al. (2016) for beta diversity (additional details for beta diversity rarefaction are in Text S1 in the Supplement). All diversity indices were estimated using the vegan package in R (Oksanen et al. 2017).

For Jaccard and modified Raup-Crick beta diversity metrics, we also conducted 2 types of post-hoc comparisons. First, we compared the effects of temporal variance in dispersal at each dispersal intensity treatment. These contrasts are orthogonal, but we conservatively Hochberg-corrected the p-values. Second, we compared all possible combinations of treatments and corrected using Tukey's honestly significant difference corrections to adjust p-values. All post-hoc results are reported in Tables S2–S4 in the Supplement.

3. RESULTS

Increasing the intensity of dispersal (number of individuals per dispersal event) increased abundance for the low variability treatment (Fig. 2), alpha diversity (Lee & Bruno 2009) and rarefied alpha diversity (Fig. 3) and reduced beta diversity when dispersal occurred in a single event (Figs. 4 & 5). While abundance had a minor positive effect on diversity estimates, both dispersal intensity and variability had clear, but independent effects on rarefied species richness (intensity: $F_{3,40} = 2.7$, $p = 0.05$; variability: $F_{1,40} = 4.0$, $p = 0.05$, Fig. 3). There was, however, no statistical evidence for an interaction between dispersal intensity and variability, despite overlap in rarefied species richness that emerged at high dispersal intensity (rarefied richness: $F_{3,40} = 0.6$, $p = 0.59$; Fig. 3).

PERMDISP indicated a significant positive main effect of dispersal variability on beta diversity measured as the Jaccard index ($F_{2,55} = 4.67$, $p = 0.013$), with higher beta diversity in treatments when dispersal was variable compared to when dispersal was fixed (Fig. 4). However, there was no detectable main effect of dispersal intensity on beta diversity meas-

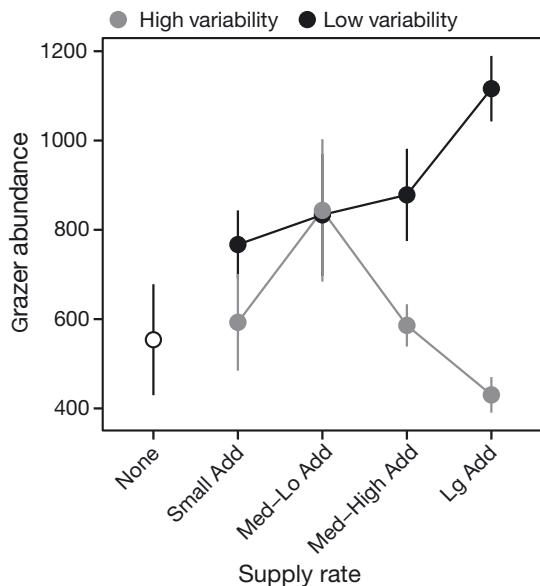


Fig. 2. Mean (± 1 SE) grazer abundance (ind. l^{-1}) in seagrass mesocosms with variation in intensity and variability of dispersal. Points and lines correspond to no dispersal (white), a single pulse of propagules (high variability; grey), and a more frequent pulse of propagules (low variability; black)

ured as Jaccard's index ($F_{2,55} = 1.26$, $p = 0.292$). On average, beta diversity was higher for a single pulse of dispersers (high temporal variability) compared to pressed treatments with multiple dispersal events (low temporal variability), but this effect diminished as dispersal intensity increased (Fig. 5) and was statistically significant for the Jaccard index at the lowest dispersal intensity treatment (see Table S4). Patterns of higher beta diversity in temporally variable dispersal event treatments compared to low-variability dispersal treatments were consistent for beta diversity estimated as both observed (Fig. 5A) and rarefied beta diversity (Fig. 5B) measured as the Jaccard index. Additional nonmetric multidimensional scaling plots show alternative representations of differences in beta diversity among dispersal treatments (see Fig. S2 in the Supplement).

Patterns of beta diversity measured as the modified Raup-Crick index also largely support the hypothesis that beta diversity is higher when dispersal is more variable, with the exception that at high dispersal intensity, the low-variability treatment had higher beta diversity than the high-variability treatment (Fig. 4C). PERMDISP identified significant main effects of both dispersal variability ($F_{2,55} = 6.84$, $p = 0.007$) and dispersal intensity ($F_{2,55} = 7.30$, $p = 0.001$) (Fig. 4C). Post-hoc contrasts found significant differences at all levels of dispersal intensity ($p < 0.01$) with the exception of the lowest dispersal intensity which

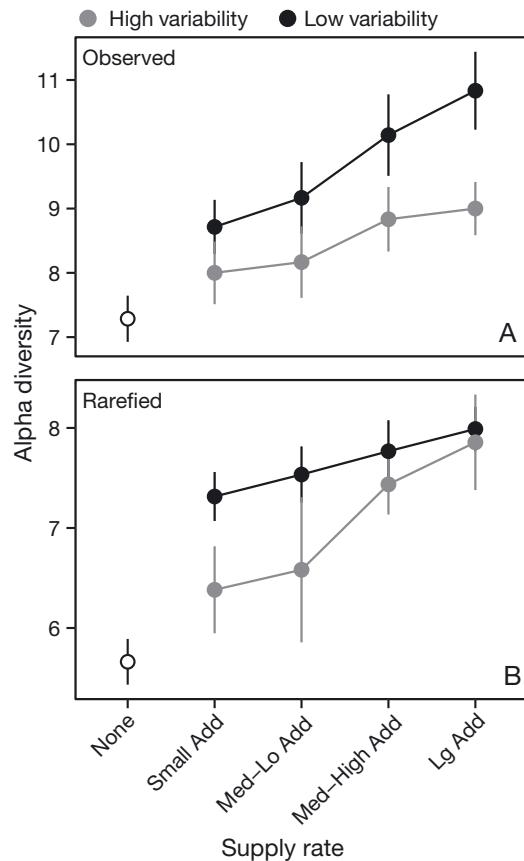


Fig. 3. Effect of (A) dispersal intensity and frequency on mean (± 1 SE) grazer alpha diversity (measured as species richness; also Fig. 1C from Lee & Bruno 2009), and (B) rarefied alpha diversity, in seagrass mesocosms. Points and lines correspond to no dispersal (white), a single pulse of propagules (high variability; grey), and a more frequent pulse of propagules (low variability; black)

was only marginally significant ($p = 0.11$; Table S2). These relatively consistent patterns of lower compositional similarity in treatments with pressed dispersal largely support the qualitative predictions from Jensen's inequality and metacommunity theory. Moreover, the modified Raup-Crick estimates suggest that community assembly is increasingly stochastic as dispersal intensity increases and that temporal variability in dispersal produces greater stochasticity in grazer community assembly at low levels of dispersal intensity, but that this effect is reversed at the highest dispersal intensity (Fig. 4C).

4. DISCUSSION

Biologists have long hypothesized that dispersal is a key factor driving the number of species shared between any 2 locations; 'barriers of any kind, or

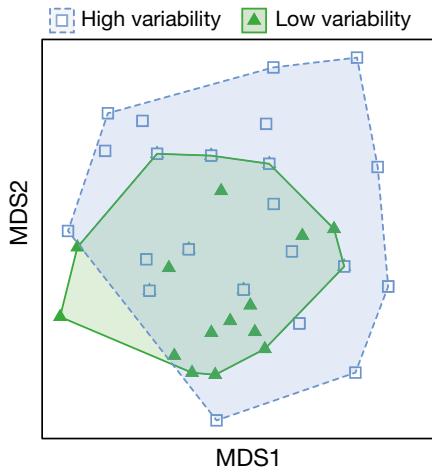


Fig. 4. Main effects of temporal variability in dispersal on beta diversity measured as Jaccard's index. Points represent the location of a replicate of a given dispersal treatment (squares: variable dispersal, triangles: pressed dispersal). Any given 2 points on the plot that are close to each other are similar in species composition, while points far apart are dissimilar. The area of convex hulls are representative of relative beta diversity between treatments. Wider hull of the press treatment indicates higher beta diversity with temporal variation in dispersal and corresponds to main effect of dispersal variability identified with PERMDISP. Stress of MDS plot is 0.22

obstacles to free migration, are related in a close and important manner to the differences between the productions [species] of various regions' (Darwin 1859, p. 345). More recently, a series of theoretical, empirical, and synthetic studies have made clear predictions for the role of dispersal in driving patterns of biodiversity and ecosystem function (e.g. Carrara et al. 2012, Matias et al. 2013, Haegeman & Loreau 2014, Marleau et al. 2014, Laroche et al. 2016, Pedersen et al. 2016, Leibold et al. 2017). Our results provide the first empirical evidence that temporal variation in dispersal can substantially modify the well-described dispersal–diversity relationship for both alpha and beta diversity.

In seagrass meadows, the demographic importance of dispersal or competition–colonization trade-offs is poorly understood. We found that compositional differences among metacommunity patches were greater for the single addition treatments (high-variability treatments) compared to the low-variability treatments. There are 2 plausible interpretations of this pattern. First, this may be a mathematical phenomenon produced by Jensen's inequality, in which temporal variability in dispersal produces a weaker decline in beta diversity with an increasing dispersal intensity (Fig. 1). There is little evidence for this nonlinearity in either treatment,

although the 4 discrete dispersal intensity treatments in the experiment make it difficult to test for nonlinearity. Therefore, we conclude that in this study, this mechanism is unlikely. An alternative explanation is that variable dispersal can allow species to persist in patches when species interactions or demographic stochasticity might otherwise exclude them. At high dispersal intensities, community similarity converges, regardless of temporal variability, suggesting that at intermediate supply rates, the

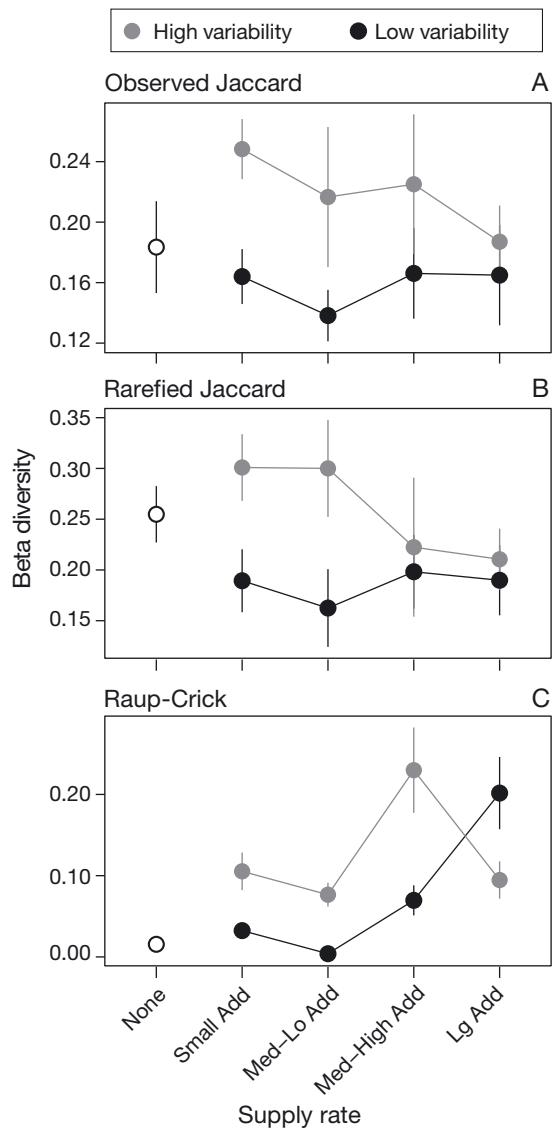


Fig. 5. Effect of dispersal intensity and frequency on beta diversity measured as (A) the observed Jaccard index, (B) the rarefied Jaccard index, and (C) the modified Raup-Crick index. Points correspond to no dispersal (white), a single pulse of propagules (high variability; grey), and a more frequent pulse of propagules (low variability; black). Points and error bars represent median \pm 1 SD

balance between local colonization and extinction is most sensitive to supply rate. Therefore, Jensen's inequality as well as the balance between dispersal and competition are likely important processes governing metacommunity dynamics in seagrass systems.

4.1. On the unique role of variance

Our study contributes to a growing ecological literature that highlights how variability around the mean effect of an ecological process can have distinct effects on patterns of species abundance and diversity that often deviate from the expected effects from changes in the mean (Ruel & Ayres 1999, Benedetti-Cecchi 2003). For example, studies factorially manipulating variability and mean effects of ecological processes suggest spatial or temporal variation in a process can modify the role of disturbance (Bishop & Kelaher 2007), predation (Butler 1989, Navarrete 1996, Stier et al. 2013), physiological stress (Miner & Vonesh 2004), and herbivory (Atalah et al. 2007) in ecological dynamics. Our findings demonstrate unique spatial biodiversity patterns among patches with identical mean dispersal intensity but different dispersal variability. Thus, we have empirically demonstrated that variability alters the effect of dispersal as a driver of metacommunity assembly.

Generalizability of our results requires further consideration of different types of variance in dispersal. For example, in models of California grassland systems, Levine & Rees (2004) showed that only certain types of temporal variability in the environment proved beneficial to the persistence of rare forbs. Similar consideration of how different types of temporal variance in dispersal alter the dispersal-diversity relationship and may interact with unique competitive dynamics and species traits in various systems is therefore critical to further generalize our findings.

4.2. Merging theoretical and empirical metacommunity ecology in seagrass ecosystems

Our findings generally support the relationship between dispersal and biodiversity predicted by Matias et al. (2013). For example, we found generally higher levels of alpha diversity and lower levels of beta diversity as dispersal intensity increased. We did not, however, find a hump-shaped relationship between dispersal intensity and alpha diversity, sug-

gesting that our experiment was restricted to the left side of the hump-shaped dispersal-alpha diversity relationship and that alpha diversity was not entirely saturated in any dispersal treatment.

Our results generally support the hypothesis that metacommunities with variable dispersal rates over time have lower alpha diversity and higher beta diversity, particularly at low-to-intermediate dispersal intensity (Matias et al. 2013). However, there are some key differences between our experimental study and the theoretical predictions. For example, Matias et al. (2013) predicts the effects of variable dispersal on the equilibrium dynamics of a metacommunity, yet little is known about the equilibrium or non-equilibrium dynamics of seagrass metacommunities. We do, however, posit that the observed diversity patterns are the product of multiple reproductive events that occurred within the study period (Lee & Bruno 2014) that were very likely to have been affected by a suite of well-documented competitive interactions within seagrass grazer communities (Edgar 1990, Duffy & Harvill 2001). This is supported by the modified Raup-Crick metric being estimated as greater than zero. However, additional research on longer temporal scales and integrating adult dispersal may be necessary to ascertain a comprehensive understanding of the role of temporal variability in altering dispersal-diversity relationships in marine metacommunities (Hanly & Mittelbach 2017). Moreover, a more mechanistic understanding of the role of temporal variation in dispersal in seagrass grazer metacommunities will emerge from additional research on grazer traits (e.g. dispersal abilities and competitive hierarchies).

4.3. Conclusions

Our experimental study on a seagrass-associated grazer metacommunity advances our empirical understanding of how dispersal drives marine metacommunity dynamics and complements recent studies that emphasize the importance of dispersal as a driver of marine metacommunity structure in temperate and tropical benthic communities (Palardy & Witman 2011, Watson et al. 2011). Ultimately, incorporating a deep understanding of how shifts in dispersal intensity and variability alter marine communities will improve our understanding of the mechanisms underlying spatial differences in community composition in marine ecosystems.

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