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Disturbance regime alters the impact of dispersal on alpha and beta diversity in a natural metacommunity

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Abstract. Disturbance and dispersal are two fundamental ecological processes that shape diversity patterns, yet their interaction and the underlying mechanisms are still poorly understood, and evidence from natural systems is particularly lacking. Using an invertebrate rock pool metacommunity in South Africa as a natural model system, we studied potential interactive effects of disturbance regime and patch isolation on diversity patterns of species with contrasting dispersal modes (passive vs. active dispersal).

Isolation and disturbance regime had negative synergistic effects on alpha diversity: both directly, by excluding late-successional species from isolated patches; and indirectly, by modulating establishment success of generalist predators in well-connected patches. Unimodal relationships between isolation and alpha diversity, as predicted by mass effects, were only detected for passive dispersers in frequently disturbed patches and not in active dispersers. For passive dispersers, indications for a positive effect of isolation and a negative effect of disturbance on beta diversity were found, presumably due to differences in deterministic succession and stochastic colonization–extinction dynamics among different patch types. Our findings illustrate that interactions between dispersal rates and disturbance regime are important when explaining species diversity patterns in metacommunities and support the idea that diversity in frequently disturbed habitats is more sensitive to effects of dispersal-based processes.

Key words: active dispersal; dispersal limitation; dispersal mode; mass effects; metacommunity dynamics; passive dispersal; species coexistence; temporary pools.

INTRODUCTION

Dispersal and disturbance are two key ecological processes that shape local and regional diversity patterns. Both processes are also closely linked since dispersal may determine the recovery rate of communities after disturbances (Reed et al. 2000, Dodd et al. 2006). On the other hand, disturbance may promote establishment success of incoming dispersers by freeing resources (Sousa 1984) or removing establishment constraints based on biological barriers (Shurin 2000, Moles et al. 2012); i.e., the restricted establishment of immigrating species due to biotic interactions with resident species that benefit from priority effects and local adaptation (De Meester et al. 2002).

Interestingly, both dispersal and disturbance have been conceptually linked to variation in local richness patterns (hereafter referred to as alpha diversity) in a similar way by theoretical models predicting unimodal responses (Connell 1978, Petraitis et al. 1989, Mouquet and Loreau 2002, Shea et al. 2004). Unimodal disturbance–diversity patterns, however, are quite uncommon (Mackey and Currie 2001, Svensson et al. 2009) and historical explanations for this pattern in terms of the intermediate disturbance hypothesis (IDH; Connell 1978) have recently been refuted based on empirical and theoretical grounds (Fox 2013). Instead, stable disturbance mediated coexistence is thought to rely on colonization–competition trade-offs preventing the extinction of early-successional species at regional scales (Cadotte 2007) and/or nonlinear or nonadditive responses of species to environmental fluctuations (Chesson and Huntly 1997, Angert et al. 2009). In contrast, predictions of dispersal–diversity patterns are of relatively recent origin with metacommunity models predicting upper and lower boundaries on dispersal rates under which coexistence of interacting species is possible (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, 2003, Cadotte 2006). Given low dispersal rates and/or a high degree of patch isolation, a combination of dispersal limitation (i.e., the absence of species from suitable patches) and priority effects (Levins and Culver 1971) may lead to communities dominated by few species and result in lower local richness. In turn, increased dispersal in these patches can promote local richness by lifting the constraint of dispersal limitation and facilitating more efficient species sorting (Leibold et al. 2004). When dispersal is high enough to sustain populations in suboptimal habitat patches, mass effects can come into play and maintain local diversity (Shmida and Wilson 1985, Leibold et al. 2004). However, mass

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effects models also predict that high dispersal rates can reduce both local and regional diversity by facilitating establishment of regionally (sub)dominant competitors or generalist predators (Amarasekare and Nisbet 2001, Mouquet and Loreau 2002, 2003, Urban 2006). Overall, these processes may result in a hump-shaped relationship between average dispersal rates and average alpha diversity in metacommunities (Mouquet and Loreau 2002, 2003). Empirical data supporting this predicted dispersal-based pattern are still scarce (but see Kneitel and Miller 2003, Matthiessen and Hillebrand 2006, Venail et al. 2008). Furthermore, the extent to which within-metacommunity variation contributes to a similar hump shaped relationship with alpha diversity of individual patches remains to be tested and the potential impact of disturbance regime on this relationship has received relatively little attention (but see Warren 1996, Östman et al. 2006).

Physical and biological barriers largely determine the possibility of an organism dispersing, establishing, and reproducing in a new patch (Jenkins and Buikema 1998, Shurin 2000). Since disturbance can break down biological barriers, it is likely that the translation of dispersal into species establishment will depend on patch disturbance regime. Moreover, in frequently disturbed habitats, extinction rates can exceed immigration rates resulting in unsaturated communities dependent on continuous recolonization (patch dynamics perspective; Leibold et al. 2004).

Besides effects on alpha diversity, the interplay between dispersal and local or regional disturbance (Limberger and Wickham 2012) is also likely to influence community structure including evenness and dominance structure (Hillebrand et al. 2008, Svensson et al. 2012) as well as beta diversity. Frequent disturbance may reduce beta diversity by imposing more stringent environmental filters (Chase 2007) and decrease both local and regional evenness by favoring a small group of disturbance tolerant specialists (Kimbro and Grosholz 2006). In turn, disturbance can also promote evenness by preventing dominant competitors from reaching high population densities (Petraitis et al. 1989, Svensson et al. 2012) both at the scale of the individual patch and the metacommunity. Paradoxically, low dispersal rates can result in both low and high beta diversity. The former effect can be attributed to the predominance of a few good dispersers in isolated patches whereas the latter may be the consequence of stochastic colonization and priority effects (De Meester et al. 2002). Both outcomes, however, are generally accompanied by low evenness because patches will be dominated by either efficient dispersers or early colonizers. High dispersal rates, on the other hand, can reduce beta diversity and increase evenness, due to dispersal-driven homogenization or the continuous colonization of regionally sub-dominant competitors (Amarasekare and Nisbet 2001, Mouquet and Loreau 2003). It is probable that the expected responses at the community level, will depend on the frequency of species traits associated with trade-offs between disturbance tolerance and dispersal ability.

Thus far, the effects of disturbance regime in a metacommunity context have almost exclusively been studied using modeling (Elkin and Possingham 2008, Altermatt et al. 2011*a*) or simplified experimental conditions (Östman et al. 2006, Altermatt et al. 2011*a*, *b*) meaning that information from natural ecosystems is particularly scarce. The main reason for this scarcity is that both dispersal rates and disturbance regimes in natural metacommunities are notoriously difficult to quantify (Altermatt et al. 2009, Jacobson and Peres-Neto 2010). More specifically, the effect of disturbance regimes, as opposed to responses to a single disturbance event or a limited number of experimentally induced disturbances, is generally not considered (Miller et al. 2011).

Here, we use aquatic invertebrate communities from a cluster of temporary rock pools on an isolated mountaintop to investigate the effects of natural variation in patch isolation and disturbance regime on diversity patterns (alpha diversity, beta diversity, evenness). A main advantage of the model system is the simple hydrology of the pools, which simplified the reconstruction of the hydrological disturbance regime of each patch based on basin properties and 85 years of historic climate data and field validation (Vanschoenwinkel et al. 2009). Additionally, direct measurements of passive dispersal in this metacommunity confirm that pool isolation is a good proxy for passive dispersal rates mediated by wind and water (Vanschoenwinkel et al. 2008). Invertebrates inhabiting this pool cluster can be subdivided into two main groups that differ fundamentally in the way they disperse and cope with disturbances. A first group consists of passively dispersed resident species that produce dormant propagules to survive dry phases. The second comprises actively dispersing colonists that do not produce dormant propagules and have to recolonize patches from elsewhere during each inundation by means of active flight.

We hypothesize that (1) the effects of disturbance regime on diversity patterns would be more pronounced in isolated pools due to less efficient spatial rescue effects. As such, the effect of dispersal limitation on alpha diversity patterns would be more pronounced in more frequently disturbed patches. Additionally, we expect that (2) in less isolated patches there is a greater chance of species exclusion by dominant competitors or generalist predators via mass effects. However, the effects of a dominant species may be more pronounced in frequently disturbed patches, especially in cases where the establishment of a dominant species is facilitated by disturbance. Following hypotheses 1and 2, a hump-shaped relationship between dispersal rates and alpha diversity can emerge, which, we expect, will be more pronounced in frequently disturbed patches and more prominent for passive dispersers. Furthermore, late-successional species are expected to be absent in frequently disturbed patches since these species typically require more time to reproduce than species that appear earlier after inundation.

Finally, we hypothesize that (3) beta diversity will be promoted by patch isolation as a result of more stochastic colonization processes and, additionally, that selection for a limited set of disturbance tolerant specialists will reduce beta diversity in frequently disturbed habitats (Chase 2007, Lepori and Malmqvist 2009).

METHODS

Study system

The study was performed in the eastern Free State Province of South Africa. This semiarid region has an average annual precipitation between 600 and 800 mm with a clear summer rainfall period typified by the first rains arriving between October and December. The study system consists of an isolated cluster of 36 temporary rock pools situated on a flat sandstone rock ledge (9000 m^2) at the summit of the Korannaberg Mountain (28°51′13″ S, 27°13′51″ E; summit at 1700 m above sea level). Pool basins periodically hold water after rains (i.e., inundations) for lengths (i.e., hydroperiods) varying between a few hours and 200 days depending on precipitation, evaporation and the morphometry of the impermeable pool basins (Vanschoenwinkel et al. 2009). A map of the study system showing its location in South Africa, descriptions of the basins and a detailed list of their fauna are provided in Appendix A.

Sampling procedure

A community data set was assembled based on four quantitative samplings of invertebrate communities (meio- and macroinvertebrates) in the 1993–1994 rainy season over a period of 32 weeks (12, 37, 96, and 140 days after initial inundation) to integrate seasonal variation. A detailed account of the sampling procedure, identification of taxa, and measurements of physical, abiotic, and biotic variables is provided in Appendix A. Based on a previous study that described community assembly in this system and designated successional phases (Vanschoenwinkel et al. 2010), species can be subdivided in early and late-successional species based on the time of appearance and the timing of the peak in population density. Early-successional species are present in the first week after inundation, reach maximum population densities during the first weeks and generally decline in numbers afterward. Late-successional species are typically absent or present in extremely low population sizes (<1% of the community) during the first weeks after inundation and steadily increase in numbers until the habitat dries out.

Defining natural dispersal and disturbance gradients

Dispersal of the actively dispersing insects that colonize rock pools at the start of each inundation from other habitats in the region would not be limited at the scale of this study because inter-pool distances varied between 15 cm and 350 m. Experimental interception of dispersing propagules in this study system, however, revealed that the influx of passive dispersers significantly decreased with pool isolation (Vanschoenwinkel et al. 2008). Dispersal rates were higher in pools that were closer together because wind dispersal is more effective over shorter distances and temporary water connections (eroded channels transporting water among pools during heavy downpours) that mediate dispersal only occur between adjacent pools (Vanschoenwinkel et al. 2008). As a result, isolation can be interpreted as a proxy for the influx of passively dispersing propagules, which was estimated as the average distance to other pools in the cluster (sum of all nearest edge to edge distances to all other pools divided by the number of other pools [Vanschoenwinkel et al. 2007]).

Pools experience disturbances as a recurring dry phase that kills all aquatic organisms other than those that persist in the propagule bank as drought-resistant resting stages or those that actively migrate to other habitats. Although partial hatching of dormant propagules enables populations to survive inundations with unsuccessful reproduction (Brendonck et al. 1998), field observations support that sequences of inundations that are too short for species to mature and reproduce, regularly lead to propagule bank depletion and population extinctions (B. Vanschoenwinkel, *unpublished data*). Consequently, rather than individual dryings, it is the disturbance history of the patch (the disturbance regime) that determines the persistence of populations. To accurately quantify variation in patch-disturbance regime, the long-term (85 years) inundation history of each of the 36 rock pool basins was previously quantified using a field-validated hydrological model (Vanschoenwinkel et al. 2009). The model, which is recapitulated in Appendix B, can construct a water level time series at a daily resolution based on pool morphometry (depth and surface area) and daily rainfall and evaporation records. Model outputs were validated using water levels measured in the field and had an average accuracy of 96% (predicted vs. observed water levels). Based on model reconstructed time series of daily water levels in each of the 36 rock pool habitats, a total of eight disturbance-related hydrological variables were simulated. In addition to mean hydroperiod (days) and desiccation frequency (dryings/year), the median, maximum, and standard deviation of both variables were also considered to characterize pool disturbance regimes. Although the hydrological model was based on 85 years of climate data (the full availability of weather station data), two additional characterizations were performed on water levels for the 25 and 5 years preceding to sampling of communities. These characterizations resulted in highly consistent patterns (results not shown) so our hydroregime simulations were robust across various temporal scales. As outlined in Appendix

B, hierarchical cluster analysis revealed that pools clustered in two natural groups with contrasting disturbance regimes. A first group contained rock pools that frequently dry up and are characterized by short hydroperiods resulting in a "high-disturbance" regime. The second cluster groups pool basins that experience longer hydroperiods and dry up less frequently giving rise to a "low-disturbance" regime. Due to this natural dichotomy, it was decided to consider disturbance as a categorical variable in our analyses, which was more suitable for our main hypothesis and permitted us to better visualize contrasting patterns. All analyses were repeated using disturbance as a continuous variable from principal-components analysis (Appendix B) and are shown in Appendix C.

Data analysis

All analyses were performed in R (R Development Core Team 2012 version 2.14.2 using packages VEGAN (Diversity, Betadisper, MOS test, PCA; version 2.0-3) and BETAREG (beta regression; version 2.4-1)

Alpha diversity and evenness.—To reduce potential bias associated with variation in sample sizes, richness estimates were rarefied (diversity function). For passive and active dispersers, local richness estimates were scaled down equivalent to samples of 200 and 20 individuals, respectively, to correspond with the approximate minimum number of individuals from each functional group found within individual patches. Two indices were used to capture evenness of rock pool communities. Pielou's evenness (J; Pielou 1966), a general evenness measure of the community, reflects how evenly abundances are distributed among species while Berger-Parker dominance (Berger and Parker 1970), a cruder evenness index, is equivalent to the relative abundance of the most abundant species.

The interactive effects of disturbance regime and patch isolation on alpha diversity and evenness were analyzed using linear models (lm function). Since it was anticipated that late-successional species would be more sensitive to disturbance than early-successional species, an analogous beta regression model was constructed with the proportion of late-successional species ($\mathrm{Pl}_i =$ [number of late-successional species in patch i]/[total species richness of patch i]) as a response variable. Beta regression (betareg function) shares properties with linear models but is more suitable for modeling non-normal proportional data restricted between 0 and 1 (Ferrari and Cribari-Neto 2004). Predictor variables included isolation (continuous: linear and quadratic term), disturbance (categorical: high vs. low) and the interactions between these variables. To confirm the robustness of this analysis an alternative model including disturbance as a continuous variable is provided in the electronic supplementary material (Appendix C).

To account for effects of patch size, log-transformed pool area (from here on referred to as patch size), and the interactions between patch size, disturbance regime, and patch isolation (e.g., larger patches can be better dispersal targets) were included as additional predictor variables in the models. Since pool basins have vertical sides there is little variation in the area of a given patch throughout the duration of an inundation; it is, therefore, assumed to be constant. Interaction terms and quadratic isolation terms that were not statistically significant at a significance level of 5% were stepwise removed from the models. To explicitly test whether quadratic relationships represent unimodal relationships with an intermediate maximum, we performed additional Mitchell-Old Shaw tests (MOStest function). Preliminary analyses showed that the inclusion of other connectivity measures besides isolation (number of incoming connections, total number of connecting elements) did not significantly explain additional variation (pools with low isolation tend to have temporary connecting elements to other pools) and were therefore discarded.

Since there are fundamental differences in the way active and passive dispersers are affected by disturbance and isolation, dispersal mode (active-passive) was included as an additional categorical predictor variable in these analyses. Due to a less efficient dispersal strategy, we expected that effects of isolation within this metacommunity would be much more pronounced in passive- than in active dispersers, as suggested by a previous study documenting metacommunity structure in this system (Vanschoenwinkel et al. 2007). Additionally, because active dispersers generally survive dry periods ex situ by migrating to permanent aquatic habitats in the region and passive dispersers survive disturbance in situ as dormant eggs, we expected that habitat selection cues such as patch size (Resetarits et al. 2005) rather than disturbance regime will be the main determinant of species distributions in this former group.

Beta diversity.—Beta diversity was calculated based on pairwise resemblances among communities as the average distance to category centroids in the space defined by the resemblance measure (Anderson et al. 2006). Potential effects of isolation and disturbance on beta diversity in active and passive dispersers, respectively, were tested using a permutation-based multivariate analogue of the Levene's test (999 permutations) for homogeneity of variances (betadisper function). For these analyses, which require categorical predictors, pool basins were subdivided in low isolation ($n = 24$, isolation $= 44 \pm 9$ m [mean ± SD]) and high isolation ($n = 12$, isolation $= 88 \pm 8$ m) habitats, This cut-off value of 70 was based on the natural bimodal distribution of this variable (Appendix D). Analyses used two common dissimilarity indices: the abundance-based Bray Curtis Index and the incidence-based Jaccard Index in addition to a third index that is independent of differences in alpha diversity: a modified version of the Raup-Crick index (Raup and

Crick 1979), as recommended by Chase and co-workers (2011), which was standardized using 10 000 randomizations of a null model. Variation in beta diversity within different patch types is further illustrated using multidimensional scaling (MDS) plots provided in the electronic supplementary material (Appendix E).

Finally, the mass effects paradigm predicts that generalist predators or dominant competitors may be more abundant in patches with low isolation compared to more isolated patches, enabling them to reduce local diversity. To test this prediction we used PCA biplots based on Hellinger transformed relative species abundance data (Legendre and Gallagher 2001) to visualize variation in abundances of individual species while including "low isolation" and "high isolation" categories as supplementary dummy variables.

RESULTS

A total of 20 passively and 14 actively dispersing species were identified. In general, rarefied alpha diversity was higher in larger patches and lower in isolated patches and there was also a significant quadratic isolation term. Additional Mitchell-Olds and Shaw tests confirmed that this quadratic relationship between isolation and alpha diversity represents a unimodal relationship with an intermediate maximum for passive dispersers (pseudo $F = 7.36$, $P = 0.01$) but not for active dispersers (pseudo $F = 1.14$, $P = 0.29$). A significant dispersal mode × isolation interaction indicated that the effect of isolation depended on dispersal mode. Additionally, a significant three way interaction supports our main hypothesis that disturbance regime modulates the effect of isolation on alpha diversity and that this effect depends on dispersal mode. The hump-shaped pattern was only present in passive dispersers (Fig. 1A, Table 1).

There was a marginally significant trend of lower Pielou's evenness in isolated patches (Fig. 1B). Consistently, Berger-Parker dominance significantly increased with isolation (Fig. 1C). A higher proportion of typical late succession species was found in larger patches (Fig. 1D, Table 1).There was also a trend of a lower proportion of late-successional species in more disturbed habitats but this effect was marginally significant ($P = 0.05$). Additional analyses considering disturbance as a continuous gradient supported these conclusions (Appendix C).

Conforming to our hypothesis of mass effects reducing alpha diversity in isolated patches, several generalist predators were positively associated with patches with a low degree of isolation compared to patches with a higher degree of isolation. These included cyclopoid copepods (Cyclopoida), predatory flatworms (Turbellaria A, B), diving beetle larvae (Dytiscidae), backswimmers (Notonectidae), dragonfly larvae (Libullulidae), and larval stages of the biting midge *Dasyhelea* sp. However, since a reduced local richness in less-isolated and thus better-connected patches was only detected in frequently disturbed habitats, this analysis was restricted to the pools that experience a high disturbance regime ($n = 14$, Appendix D).

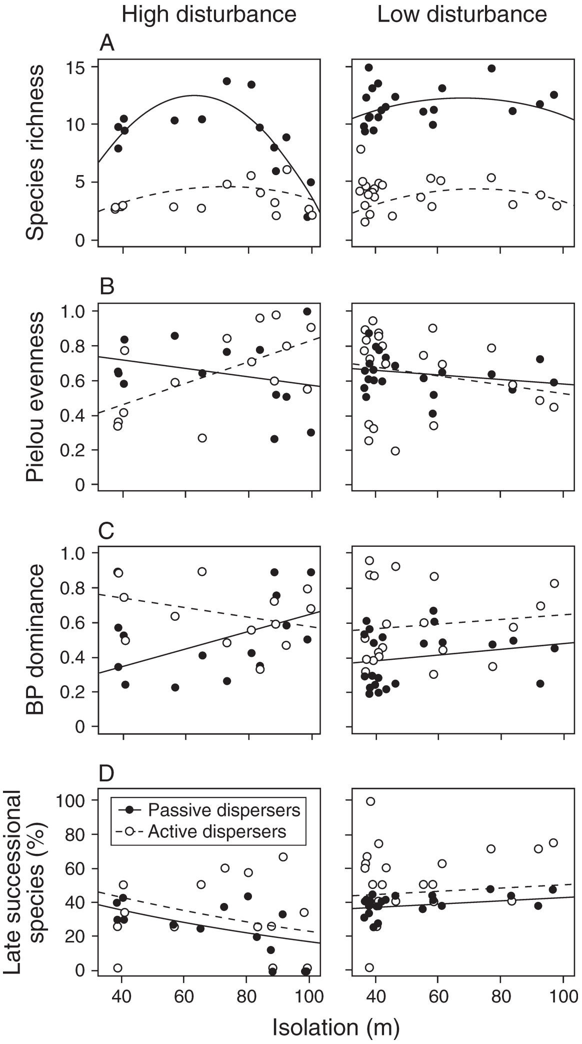

FIG. 1. Relationships between pool isolation and (A) local richness, (B) Pielou evenness, (C) Berger-Parker dominance, and (D) the percentage of late-successional species in pools experiencing contrasting disturbance regimes. Symbols are data points, lines are regression lines. Solid circles and solid lines represent passively dispersing taxa; open circles and dashed lines represent actively dispersing taxa.

Analyses of beta diversity based on multivariate dispersions calculated using Jaccard and Bray Curtis dissimilarities revealed significant effects of disturbance regime and isolation only for passive dispersers (Table 2, Fig. 2). Disturbance increased beta diversity and this effect was most pronounced in isolated patches. For active dispersers beta diversity was lower in smaller patches. These patterns, however, were not confirmed in analyses based on the modified Raup-Crick dissimilarity index.

TABLE 1. Linear models of taxon richness, Pielou's evenness, Berger Parker dominance, and beta regression model of the proportion of late-successional species.

	Richness†				Pielou evenness‡				Berger-Parker dominance§			
Parameter	Est.	SD	*t*	*P*	Est.	SD	*t*	*P*	Est.	SD	*t*	*P*
Intercept	−4.41	2.88	−1.5	0.13	0.9	0.07	12.4	<0.0001	0.46	0.09	5.17	<0.0001
Dispersal mode	10.47	2.01	5.21	<0.0001	−0.07	0.04	−1.95	0.056	−0.1	0.04	−2.34	0.022
Disturbance	−2.33	1.78	1.31	0.19	0.022	0.047	−0.46	0.65	0.02	0.06	−0.36	0.72
Patch size	0.57	0.18	3.14	0.003	−0.017	0.017	−0.96	0.34	−0.01	0.02	−0.64	0.52
Isolation	0.22	0.09	2.51	0.01	−0.002	0.001	−2.67	0.009	0.003	0.001	2.5	0.015
Isolation^2	−0.001	0.0006	−2.4	0.019								
Isol. × Disp. mode	−0.068	0.027	−2.52	0.014								
Dist. × Isol.	−0.037	0.027	−1.38	0.17								
Dist. × Disp. mode	−4.06	2.47	−1.65	0.1								
Dist. × Isol. × Disp. mode	0.09	0.038	2.45	0.017								

Notes: Nonsignificant interaction terms and quadratic isolation terms were removed from the models. Abbreviations are: Est., estimate; Isol. isolation; Disp. mode, dispersal mode; Dist., disturbance.

† $F_{9,62} = 42.6$, $P < 0.0001$, $r^2 = 0.84$.

‡ $F_{4,67} = 3.14$, $P = 0.02$, $r^2 = 0.11$.

§ $F_{4,67} = 3.94$, $P = 0.006$, $r^2 = 0.14$.

¶ $P < 0.001$, pseudo $r^2 = 0.32$.

DISCUSSION

Results support our main hypothesis that disturbance regime alters the effect of dispersal on alpha diversity and beta diversity. In the passively dispersing community component, we found empirical support for the predicted hump-shaped relationship between dispersal and local richness. Although both models and experimental data suggest a unimodal relationship between average alpha diversity and dispersal rates among metacommunities that differ in (homogeneous) dispersal rates (Mouquet and Loreau 2002, 2003, Matthiesen and Hillebrand 2006, Altermatt et al. 2011*a*, *b*), this pattern has not been previously demonstrated within a natural metacommunity with heterogeneous dispersal. Current evidence for nonlinear dispersal–diversity relationships remain largely restricted to results from laboratory experiments with microorganisms (Venail et al. 2008, Matthiessen et al. 2010) and evidence from natural systems remains largely deficient. One, possibly the only, exception is a short term field experiment with microorganisms inhabiting phytotelmata performed by Kneitel and Miller (2003). In that experiment, a hump-shaped relationship between manipulated dispersal rates and alpha diversity was uncovered, but only in the absence of predators. Several studies report that dispersal may have differential effects on communities when they are dominantly structured by a single driving agent, such as the presence of a generalist predator (Shurin and Allen 2001, Kneitel and Miller 2003, Cadotte 2006). As demonstrated in our study, disturbance regime may perform a similar role by mediating the impact of dispersal on communities.

Dispersal limitation and reduced alpha diversity in isolated patches

Consistent with results from other empirical studies (Gilbert et al. 1998, Gonzalez et al. 1998), isolation reduced alpha diversity for both active and passive

TABLE 2. Multivariate dispersions calculated as average distance to centroids ($\overline{d_{\text{cen}}}$) of rock pool communities in habitats that differ in their disturbance regime (high vs. low) and isolation (high vs. low), including results of permutation tests to compare differences among habitat categories.

	High disturbance		Low disturbance				
Index	Low isolation (HL)	High isolation (HH)	Low isolation (LL)	High isolation (LH)	*F*	*P*	Pairwise test results
Passive dispersers							
Bray Curtis	0.463	0.578	0.386	0.276	8.41	0.001	HH > HL > (LH, LL)
Jaccard	0.537	0.611	0.487	0.383	6.47	0.0015	HH > (HL, LH, LL)
Raup-Crick	0.311	0.066	0.061	0.0007	30.33	<0.001	HL > (HH, LL, LH)
Active dispersers							
Bray Curtis	0.387	0.5356	0.429	0.434	1.86	0.156	n.s.
Jaccard	0.470	0.5834	0.516	0.508	1.84	0.159	n.s.
Raup-Crick	0.0002	0.1667	0.159	0.253	3.81	0.0228	LH > (HH, LL) > HL

Notes: Pairwise inequalities indicate statistically significant differences in dispersions between groups ($P < 0.05$). In all cases, df = 3, 32. The abbreviation "n.s." stands for not significant.

TABLE 1. Extended.

Late-successional species¶			
Est.	SD	Z	P
−0.42	0.61	−0.69	0.49
−0.29	0.22	−1.3	0.19
−0.71	0.72	−0.98	0.33
0.39	0.1	3.79	0.0001
−0.02	0.008	−1.95	0.05
0.02	0.01	1.78	0.075

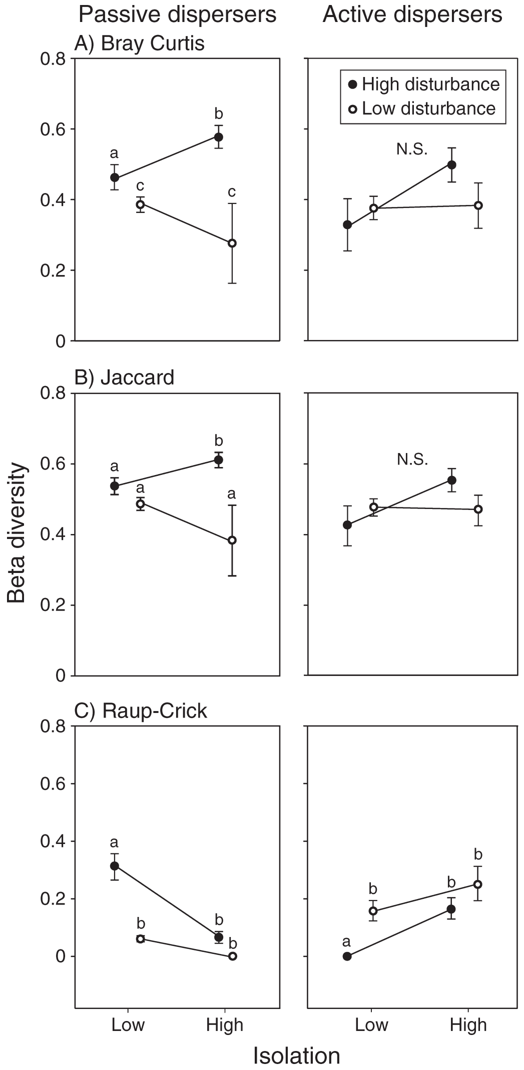

FIG. 2. Relationships between patch disturbance regime, patch isolation, and beta diversity, calculated as multivariate dispersions (distances to centroid) based on three different dissimilarity indices (Bray Curtis, Jaccard, and Raup-Crick). Results are shown for passive and active dispersers. Statistically significant differences ($P < 0.05$) in dispersions among groups are indicated by different lowercase letters.

dispersers. However, this effect was most pronounced in passive dispersers and in frequently disturbed patches and was mainly due to a decrease in the number of late-successional species. Since the latter typically require more time to complete their life cycle, they are more sensitive to premature pool drying and may require high dispersal rates to persist in pools that frequently dry out (Gonzalez and Chaneton 2002, Hoyle and Gilbert 2004, Östman et al. 2006). Results indicate that, although they may persist in frequently disturbed patches when dispersal is high enough to sustain populations (spatial rescue effects; Brown and Kodric-Brown 1977), these late-successional specialist species are deficient in isolated patches with a high disturbance regime. Consequently, dispersal limitation should be considered a relative concept in this context, which not only depends on species dispersal ability and patch isolation, but also on the disturbance regime of the target patch.

Similar patterns of dispersal rates compensating for the negative effects of disturbance, as observed for the passive dispersers in this study, were obtained using short term experimental microcosm experiments with micro-zooplankton (Warren 1996, Altermatt et al. 2011*a*) and benthic microalgae (Matthiessen et al. 2010), albeit at an inter-metacommunity scale rather than at the intra-metacommunity scale considered in this study. Conversely, Östman and co-workers (2006) did not find a significant interaction between disturbance and dispersal explaining local richness in a petri-dish experiment with microzooplankton. Their study, however, only investigated two dispersal and two disturbance treatments so its conclusions might not be robust across a broader range of dispersal and disturbance treatments.

Surprisingly, passive dispersal rates measured on the site by intercepting wind and water dispersed propagules revealed no indications of dispersal limitation (Vanschoenwinkel et al. 2010). Instead, over a period of one month, nearly all species were shown to be dispersed frequently by wind and most species were able to reach the most distant parts of the studied pool cluster with different species showing highly similar dispersal kernels (Vanschoenwinkel et al. 2008, 2010). The patterns of dispersal limitation observed in the current study, therefore, only make sense in the light of disturbance; illustrating that frequently disturbed patches rely on high dispersal rates to maintain local diversity.

Due to the superior dispersal capacity of active dispersers, lower alpha diversity in isolated patches was initially not anticipated. As in passive dispersers, the existence of source-sink dynamics is a possible reason. This explanation is consistent with field observations of active dispersers (e.g., beetle larvae), dispersing through overflow connections that temporarily establish between

PLATE 1. Temporary rain-filled rock pools at the summit of sandstone mountains in the Free State Province of South Africa house diverse communities of freshwater invertebrates. The picture shows a vegetated rock pool which is part of a cluster of pools on Korannaberg Mountain. In the background, a neighboring inselberg (Vegkop Mountain) is visible, which holds a comparable rock pool cluster. Photo credit: B. Vanschoenwinkel.

certain pool pairs during heavy rains (Vanschoenwinkel et al. 2008). Alternatively, the same pattern can also emerge when the proximity of suitable neighboring patches is used as a cue for active habitat selection (contagion effect) as suggested by Resetarits and coworkers (2005). Finally, since several active dispersers in our study, such as water boatmen (Notonectidae) and diving beetles (Dytiscidae), are important predators, it is also plausible that they track the distributions of their mostly passively dispersing prey to some extent (Lima 2002), resulting in a pattern of apparent dispersal limitation.

Mass effects and reduced alpha diversity in less isolated patches

Besides dispersal limitation in isolated patches, the significant unimodal pattern found for passive dispersers also implies a reduced alpha diversity in less isolated (and thus better connected) patches. In these patches, several important generalist predators were shown to be relatively more abundant, suggesting that dispersal might also mitigate negative effects of disturbances. Dispersal may permit these species to maintain larger populations and enable them to exclude certain prey species. This explanation is supported by dispersal measurements in the field since flatworms, beetle larvae, cyclopoid copepods and biting midge larvae have been shown to frequently disperse passively, by wind and/or via overflow connections, in this metacommunity (Vanschoenwinkel et al. 2008; B. Vanschoenwinkel, *unpublished data*). These species are important generalist predators in temporary rock pools (McLachlan and Cantrell 1980) that are able to prey on animals much larger than themselves. Turbellarian flatworms, cyclopoid copepods and biting midge larvae are also quite disturbance tolerant because they produce drought-resistant resting stages. Results, thus, suggest a negative synergistic effect of disturbance and dispersal (mass effects) on alpha diversity and evenness presumably mediated by generalist predation. In combination with observations of reduced richness in isolated patches, this shows that both mass effects and dispersal limitation can operate simultaneously in the same metacommunity.

Effects on beta diversity

Beta diversity analyses based on Bray Curtis and Jaccard indices suggest that common assumptions about the relationship between disturbance and beta diversity may not be as general as previously assumed, although we cannot exclude the possibility that patterns were affected by differences in species richness (Chase et al.

2011). While we hypothesized that beta diversity would decrease in more frequently disturbed patches as a result of more stringent habitat filters selecting for disturbance-tolerant species consistent with results from other empirical studies (Chase 2007, Lepori and Malmqvist 2009), this is contradicted by our results. Beta diversity was higher in patches with a high disturbance regime than in patches experiencing a low disturbance regime and higher in isolated patches than in less-isolated patches. At least three factors could contribute to this pattern. First of all, in our system, there does not seem to be a clear group of disturbance tolerant specialists. Instead, a large group of generalists is complemented by a smaller number of specialists of late-successional phases (Appendix F). Typical early-successional species, such as fairy shrimp and clam shrimp, occur in both highly disturbed as well as in less-disturbed patches (Vanschoenwinkel et al. 2010); although in the latter, they are restricted to early-successional phases. The fact that late-successional species, such as certain water fleas, are predictably found in patches that experience longer inundations (Vanschoenwinkel et al. 2010) can explain a reduction in beta diversity in these habitats. A second explanation might be that, since most species do not seem to differ much in terms of their disturbance tolerance, disturbance-mediated extinction rates may not be predominantly deterministic (i.e., species have similar probabilities of going extinct). Under these circumstances, disturbance may promote beta diversity. Finally, the higher beta diversity in isolated habitats observed in this study may point to the importance of stochastic colonization and priority effects (De Meester et al. 2002, Urban and De Meester 2009). However, it must be noted that parallel analyses performed using Raup Crick dissimilarities calculated using null models did not support these patterns. While this index is less sensitive to a potential confounding effect of alpha diversity, it has the disadvantage of lower power to detect deviation from the null expectation when alpha diversity is low (Chase et al. 2011). As such, it is less suitable to analyze patterns of beta diversity for patches with low alpha diversity, as is generally the case for the frequently disturbed and isolated patches in our study.

Conclusions

We believe that in addition to input from simplified experimental settings, natural and seminatural model systems, such as ponds, moss patches, and grassland plots, will continue to play an important role in testing the assumptions and predictions of metacommunity models (Logue et al. 2011). However, care must be taken before generalizations are to be made to larger macro ecosystems, as the peculiarities of the model systems should be taken in to account (Srivastava et al. 2004). For instance, rock pool fauna have evolved to tolerate highly variable environments so the patterns shown in this study might not occur in less volatile systems.

Nonetheless, our study further extends and helps to generalize patterns found in previous experimental studies to natural systems. First, it illustrates that patterns of dispersal limitation are more likely to occur in disturbed patches and, second, that connectivity and disturbance may have negative synergistic effects on local diversity by determining establishment success of generalist predators. This has important consequences for metacommunity dynamics as both mass effects and dispersal limitation could have a greater impact in disturbed habitats than in stable ones. This mechanism may also have conservation implications. Several invasive species have, for instance, been shown to establish more easily in disturbed habitats (Fausch et al. 2001, Lake and Leishman 2004) and, in particular, changes in disturbance regime increase the likelihood of successful invasions (Moles et al. 2012). Similarly, increased climatic fluctuations associated with ongoing environmental change are likely to make communities more reliant on dispersal to maintain diversity. In combination with increased habitat fragmentation, and reduced spatial rescue effects, this may result in unwanted synergies which lead to local species extinctions.

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SUPPLEMENTAL MATERIAL

Appendix A

Study site description, sampling methodology, and species identification (*Ecological Archives* E094-234-A1).

Appendix B

Hydrological model: summary statistics, cluster analysis, and principal-component analysis of reconstructed disturbance variables (*Ecological Archives* E094-234-A2).

Appendix C

Linear models of taxon richness, Pielou's evenness, Berger-Parker dominance, and beta regression model of the proportion of late-successional species (*Ecological Archives* E094-234-A3).

Appendix D

Associations of generalist predators with isolated, frequently disturbed patches (*Ecological Archives* E094-234-A4).

Appendix E

Multi-dimensional scaling (MDS) ordinations illustrating effects of patch isolation and disturbance regime on beta diversity (*Ecological Archives* E094-234-A5).

Appendix F

Link between successional niche and nested species rank along a gradient of patch disturbance regime (*Ecological Archives* E094-234-A6).