Title: Top predator introduction changes the effects of spatial isolation on freshwater community structure

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Abstract

Introducing top predators in a community can produce cascading effects due to predation upon larger, frequently intermediate predatory taxa, and indirectly benefit consumers. Similarly, spatial isolation can limit predator's dispersal rates more strongly than that of their prey, thus generating similar trophic cascades. We tested the effects of spatial isolation on the outcome and strength of the cascading effects caused by fish, as our top predator, on macroinvertebrate community structure. Overall results show that fish did reduce the abundance of predatory insects but had no effect on herbivores and detritivores. Spatial isolation caused trophic cascades, but only in the absence of fish. A potential explanation to this is because fish also preyed upon consumers when they increased in abundance. In contrast with traditional theoretical expectations for metacommunities, we found that the difference between communities with and without fish increased with isolation, because fish dampened the cascading effects of spatial isolation.

Introduction

Dispersal is a key driver of community and metacommunity structure (Mouquet & Loreau 2003; Leibold *et al.* 2004; Vellend 2010; Leibold & Chase 2018). Classic metacommunity theory recognizes that the frequency and intensity of dispersal can determine the relative importance of ecological drift (*i.e.* stochasticity) and niche selection in structuring metacommunities (Leibold *et al.* 2004). When species dispersal rates are low for all species involved, or patches are isolated, stochastic events are likely to cause communities to drift towards multiple different compositions that aren't necessarily related to local environmental conditions (Leibold & Chase 2018). In contrast, if species dispersal rates are sufficiently high for all species involved or patches are highly connected, the constant arrival of migrants should override the effects of drift or niche selection making communities more similar to each other irrespective of local environmental variation (Mouquet & Loreau 2003; Leibold & Chase 2018). Thus, niche selection processes are more likely to shape community structure at intermediate levels of dispersal rates or connectivity (Fig. 1A). However, these predictions may not be fully realized if there is also interspecific variation in dispersal rates among species (Vellend *et al.* 2014; Guzman *et al.* 2019). Variation in dispersal rates can reduce the effect of stochasticity in community structure because species with higher dispersal rates will predictably colonize a patch, increasing the predictability of the subsequent community assembly process (Vellend *et al.* 2014). Additionally, interspecific variation in dispersal rates can actually intensify the consequences of niche selection if traits that confer higher fitness within a set of local environmental conditions are positively correlated with traits that confer higher dispersal frequency or ability (Vellend *et al.* 2014; Fig. 1B).

Freshwater pond species can vary substantially in dispersal and colonization rates (Bilton *et al.* 2001; Shulman & Chase 2007; Chase & Shulman 2009; Shurin *et al.* 2009; Guzman *et al.*

2019) and such variation is often correlated with trophic level. For example, predatory insects tend to have larger body sizes their prey, and thus higher locomotory ability (McCann *et al.* 2005). However, predatory insects also tend to have smaller population sizes (Cohen *et al.* 2003) and longer generation times than their prey, possibly making colonization events in spatially isolated ponds rarer (Chase & Shulman 2009). Predators can also be indirectly disfavored by habitat isolation if their prey is dispersal-limited or unable to reach high population sizes (Hein & Gillooly 2011). Non-predatory insects, by contrast, have shorter generation times and larger population sizes, which can increase the number of dispersal events (Poff *et al.* 2006). Moreover, the smaller body sizes of non-predatory insects may greatly expand their dispersal range by wind transport (Muehlbauer *et al.* 2014). An important outcome of this negative correlation between dispersal rate and trophic level is that spatial isolation can lead to trophic cascades, causing herbivores and detritivores, hereafter referred to as consumers, to be more abundant in more isolated habitats (Shulman & Chase 2007; Chase & Shulman 2009).

Freshwater community structure is also strongly influenced by the presence of predatory fish (Hrbáček 1962; Brooks & Dodson 1965; Wellborn *et al.* 1996). In the absence of fish, predatory invertebrates such as aquatic beetles and dragonfly larvae are often the top predators. Compared to fish they are usually less efficient, gape-limited sit-and-wait predators that consume smaller prey (Wellborn *et al.* 1996). However, when present, fish, which are generally large visually oriented predators, tend to preferentially consume large prey, which frequently happens to be predatory insects (Wellborn *et al.* 1996; McCauley 2008). This can lead to trophic cascades like those caused by spatial isolation, leading to an increase in the abundance of small herbivores and detritivores (Diehl 1992; Goyke & Hershey 1992). Therefore, the consequences of the

presence of fish for aquatic macroinvertebrate communities could be even stronger in more isolated habitats.

Our study aimed at experimentally assessing whether and how spatial isolation can change the effects of the introduction of a generalized fish predator on freshwater community structure. We designed our study to test the following hypotheses with special attention to the role of interspecific variation in dispersal: First, the presence of predatory fish would promote a cascading effect by preferentially preying upon larger predatory insects, causing the abundance of consumers (*i.e.* herbivores and detritivores) to increase. Second, spatial isolation would promote a similar cascading effect by reducing the abundance of predatory insects, which frequently have lower dispersal rates, also increasing the abundance of consumers. Finally and third, increasing isolation should intensify the effect of fish on community structure because the ecological traits that promote trophic cascades in both cases are positively correlated (Fig. 1B). We show that the effect of fish not only inceases as ponds become more isolated, it actually change. We show that because generalist fish also pray upon consumers, it can inhibit the trophic cascade promoted by spatial isolation, causing communities with and without fish to diverge in structure as spatial isolation increase.

Methods

We conducted our field experiment at the Estação Ecológica de Santa Bárbara (EESB) in Águas de Santa Bárbara, São Paulo, Brazil (22º48’59” S, 49º14’12” W). The EESB is a 2,712-ha protected area predominantly covered with open savanna habitats, with smaller portions of seasonal semideciduous forests, *Pinus* sp., and *Eucalyptus* sp plantations (Melo & Durigan

2011). Soils are sandy and climate is Koeppen´s Cwa, i.e., warm temperate with dry winters and hot summers (Kottek *et al.* 2006). Mean annual rainfall is ~1250mm with a distinct rainy season from October to March (January being the wettest month with ~200mm rainfall) and a dry season from April to September (July being the driest month with ~25mm rainfall; (Hijmans *et al.* 2005). In the EESB the experiment was implemented in an area covered by second-growth cerrado *sensu stricto*, a moderately dense, open-canopy savanna habitat (Melo & Durigan 2011).

Experimental units consisted of ~1,200L artificial ponds dug into the ground and lined with a 0.5 mm thick, high-density polyethylene geomembrane to retain water. Each pond was 4 m long, 1m wide and 40 cm deep. Walls were vertical along the length of the pond; 1 m-long ramps terminating at ground level at each short side of the pond provided shallow microhabitats for freshwater organisms and escape for terrestrial fauna that eventually fell into the water. Two roof tiles were placed at the waterline in each of the short sides to provide shelter and/or oviposition habitat. Three 30 cm-long, 10 cm-wide PVC pipes were placed in the water to provide shelter for fishes.

Experimental design

The experiment followed a fully factorial design crossing fish presence (presence/absence) with spatial isolation (three levels of isolation). The isolation treatment was achieved by establishing 8 artificial ponds along each of three parallel transects 30m, 120m, and 480m from a source wetland consisting of a stream (Riacho Passarinho) and its floodplain (Fig. 2). Within each transect, the distance between adjacent artificial ponds was 30 m (see Appendix S1 in Supporting Information) for possible implications of our spatial design). The artificial ponds were naturally colonized by organisms dispersing in the landscape including phytoplankton,

zooplankton, and macroinvertebrates. The chosen distances from the source habitat and their spacing intervals represent a steep spatial isolation gradient for most aquatic insects (Wilcox 2001; Trekels *et al.* 2011); see Appendix S2). The well-drained sandy soils ensured that no other ponds and puddles formed during the rainy season at our study site, making the near stream and its floodplain the main source of aquatic insects colonizing the artificial ponds. Each fish-by-distance treatment was replicated four times for a total of 24 artificial ponds.

The experiment ran from 18-Jan-2017 to 24-Apr-2017. Between 18 and 25-Jan-2017 mesocosms were filled with well water, which is unlikely to contain already established plankton or macroinvertebrate communities. On 28-Jan-2017 we added to each mesocosm 1000g (wet mass) of leaf litter composed of equal amounts of grass and tree leaf litter to provide structural complexity for benthic organisms. On 29-Jan-2017 we added to each mesocosm 15g of dog chow to provide an initial pulse of nutrients. The same day we added one Redbreast Tilapia (*Coptodon rendalli*, standard length 99.2 mm ± 5.9 mm, wet mass 40.2 g ± 8.8 g, mean ± SD, N=12) per predator treatment pond, collected in a small reservoir outside the EESB. Over the course of the experiment, we monitored ponds for fish survival; dead fish were replaced as soon as noticed (see Appendix S3).

We selected Redbreast Tilapia for three reasons. First, tilapias are generalized omnivorous predators that, even though many times described as having a preference for feeding upon macrophytes (Rao *et al.* 2015) and zooplankton (Lazzaro 1991), can also prey upon macroinvertebrates when they are available (Chimbari *et al.* 1997); also confirmed in a pilot laboratory experiment we conducted, see Appendix S4). Second, they are hardy species capable of surviving in a wide range of environmental conditions including low oxygen levels and a broad range of temperature (Caulton 1977; Tran-Duy *et al.* 2008), conditions likely to be found

in our shallow artificial ponds. Third, the Redbreast Tilapia is, along with the Nile Tilapia (*Oreochromis niloticus*), one of the most widely introduced fishes in the world for aquaculture and recreational fisheries (Britton & Orsi 2012). These African species represented ~11% (6.1 million tons) of the entire freshwater fish production in the world and ~40% (0.6 million tons) in the Americas in 2017 (FAO 2019). In Brazil, Redbreast and Nile Tilapias are found in reservoirs and lakes in most river basins, and their spread to new river basins may be a matter of time considering that their stocking is still encouraged by public policies (Zambrano *et al.* 2006; Britton & Orsi 2012; Pelicice *et al.* 2014; Daga *et al.* 2016). Indeed, a very common land management practice in rural Brazil is the construction of dugout or impounded lakes, where the Tilapia is usually the first choice of fish species for stocking.

Freshwater community sampling surveys

To assess the influence of fish presence, spatial isolation, and their interaction on community assembly we conducted three sampling surveys of the artifitial ponds after ~3 weeks (18 to 23-Feb-2017), ~8 weeks (23 to 27-Mar-2017) and ~12 weeks (20 to 24-Abr-2017) of the experiment. Freshwater communities were dominated by insects, which were sampled by sweeping half of the pond twice, including both pelagic and benthic habitats, with a hand net (mesh size 1.5 mm). Samples were cleaned of debris and stored in 70% ethanol. We identified and counted all aquatic macroinvertebrates to the lowest reliable taxonomical level using taxonomic keys for South American freshwater insects (Costa *et al.* 2004; Pereira *et al.* 2007; Segura *et al.* 2011; Hamada *et al.* 2014).

Data analysis

To test the hypothesis that community structure is influenced by fish presence, distance to the source, and their interaction, we used a model-based approach for multivariate data where the matrix of site-by-raw species abundance data represents community structures (Warton *et al.* 2015b). The main advantages of model-based approaches are the possibility of accounting for the mean-variance relationship of abundance data, and the better interpretability of data. Specifically, we can assess which and how species in a community are being influenced by treatments and test for the effect of traits in their responses (Warton *et al.* 2015a). Prior to this analysis, we removed species that occurred in less than three ponds considering each sampling survey (*i.e.* singletons and doubletons) both because they are uninformative to general community patterns and because they complicate model parameter estimation (Warton *et al.* 2015a).

To test for differences in the effect of treatments on species abundances across different sampling surveys, we performed likelihood ratio tests to test if the progressive addition of terms to the model provided a statistically better fit based on values of deviance. We modeled abundances using a negative binomial distribution because of overdispersion (Appendix S5). First, we tested if we had any effect of time in species abundances, then we tested if progressively adding the effect of fish, isolation, and their interaction provided a significantly better fit to the data. Those tests were always assessed by comparing the best model so far against the next more complex model. After that, we tested if the effect of treatments were different across different sampling surveys by adding an interaction between the effect of time and the interaction between fish and isolation treatments. Because we found significantly different effects of fish and isolation treatments across different sampling surveys, we repeated

the analysis in each sampling surveys separately. To account for correlations in species abundances when computing p-values we shuffled entire rows of the incidence matrix (ponds), keeping species abundances in the same ponds always together. To account for lack of independence between the same ponds sampled across time, ponds were considered blocks, so in each permutation step we shuffled ponds freely within blocks (*i.e.* only across time), then we shuffled the entire bocks freely (*i.e.* across fish and isolation treatments). P-values were computed using the PIT-trap bootstrap resample procedure, which operates on probability integral transform residuals (Warton *et al.* 2017). P-values were obtained from 10,000 bootstraps resamples.

To assess how individual taxa respond to the different treatments we looked at 95% confidence intervals of estimated parameters for each taxon in each treatment. To see if the trophic level (*i.e.* strict predator VS consumer) is a good predictor of the changes in community structure, we further tested if the inclusion of the categorical trait predator/consumer increases the fit of the models also performing likelihood ratio tests. We considered strict predators only the predators that were prone to prey upon other sampled macroinvertebrates. Insects that are not predators at all, that prey mostly upon zooplankton, or that have only a small portion of their diet based on predation were considered consumers (see Appendix S6). This trait-based approach is called the model-based fourth corner solution (Brown *et al.* 2014).

A significant interaction between fish and isolation means that there is either or both a difference in direction (*i.e.* positive or negative effect) or magnitude of the effect of fish in different isolation treatments. To specifically test for differences in the size of the effect of fish, regardless of direction, we performed a model-based unconstrained ordination via generalized linear latent variable models (GLLVM; Niku *et al.* 2017) with a negative binomial distribution

using two latent variables for each of the sampling surveys (Hui *et al.* 2015). The latent variables were estimated via variational approximation (Hui *et al.* 2017). After performing the ordination, we computed the centroids of each treatment group, and the distance between the centroids of fish and fishless treatments in each isolation treatment as a measure of the size of the effect of fish. Then we tested whether this distance is significantly different across all the isolation treatments. To test for that we designed a permutation procedure to only permute ponds across isolation treatments, keeping the fish treatment constant. This represented a null scenario where the effect of fish is the same in all isolation treatments. We corrected p-values for multiple comparisons using the false discovery rate (FDR). We also used those ordinations to visualize the effect of treatments on community structure.

All analyses were implemented in software R version 3.6.1 (R Core Team 2019), using packages 'mvabund' version 4.0.1 (Wang *et al.* 2012) and 'gllvm' version 1.1.7 (Niku *et al.* 2019). Code and data to reproduce the analysis and figures are available on github in the following repository: RodolfoPelinson/Pelinson_et_al_Top_predator_isolation.

Results

Mesocosms were colonized by aquatic and semiaquatic insects comprising five orders and 17 families (Odonata: Libellulidae, Coenagrionidae; Coleoptera: Dytiscidae, Hydrophilidae, Noteridae; Diptera: Ceratopogonidae, Chaoboridae, Chironomidae, Culicidae; Ephemeroptera: Baetidae, Caenidae, Polymitarcyidae; Hemiptera: Corixidae, Gerridae, Naucoridae, Notonectidae, Veliidae). The most abundant families, with more than 200 individuals sampled in the entire experiment, were chironomids (total abundance of 11,558 individuals), veliids (1,097 individuals), libellulid dragonflies (901 individuals) and culicid mosquitoes (707 individuals).

The rarest families, with less than 10 individuals sampled in the entire experiment, were Gerridae, Naucoridae, Corixidae, Coenagrionidae, Ceratopogonidae, and Hydrophilidae. More detailed information is available in Appendix S6.

Effects of treatments on community structure became clearer and stronger over time. We therefore will only show the results of the last (third) survey for clarity. Results for all surveys are available in Appendix S7. The inclusion of the fish treatment significantly increased the fit of the explanatory statistical model to community data (Difference of degrees of freedom: 1; Deviance: 49.09; p: 0.018). The subsequent inclusion of the distance treatment only marginally improved its fit (Difference of degrees of freedom: 2; Deviance: 72.96; p: 0.056), however, the inclusion the interactive effect of distance treatments and the fish treatments highly improved the fit of the model with only the fish treatment (Difference of degrees of freedom: 4; Deviance: 164.1; p: 0.009). More importantly, this interactive effect of treatments was significantly explained by trophic level (Difference of degrees of freedom: 5; Deviance: 33.71; p: 0.028; Fig. 3).

Presence of fish had a negative impact on the abundance of predators only at 120 and 480 m (Fig. 4A). The general lack of this negative effect on predators at 30 m was mostly because *Pantala* dragonflies suffered no effect of fish and *Orthemis* dragonflies were positively affected by it at this distance (Fig. 5A). Different from what we expected, consumers were not generally positively affected by fish at the end of the experiment (Fig. 4A).

Spatial isolation negatively affected predators from 30 to 120 and 480 m distances, but only in ponds with fish (Fig. 4B and C). In fishless ponds, some predators were negatively affected by isolation, while others, such as *Pantala* and *Orthemis* dragonflies, were positively

affected (Fig. 5A). Consumers, on the other hand, were, as expected, positively affected by isolation from 30 m to 120 m and 480 m of isolation, but only in fishless ponds (Fig. 4C).

When we tested for differences in the size of the effect of fish on community structure, we found that the effect of fish at 480 m was larger than at 30 m (Difference in distance between centroids: 1.63; adj. p: 0.038; Fig. 3) meaning that, as we expected, fish and fishless ponds are more different from each other in more isolated ponds. The size of the effect of fish at 120 m was not significantly different from 30 m (Difference in distance between centroids: 1.25; adj. p: 0.098; Fig. 3) or 480 m (Difference in distance between centroids: 0.38; adj. p: 0.601; Fig. 3).

Discussion

Generally, both the presence of fish and spatial isolation had important effects on freshwater community structure and responses to treatments were different for different trophic levels. More importantly, our results, as expected, diverged from classic metacommunity models, which predicts that the effect of environmental filtering and local interactions on community structure should be stronger at intermediate levels of isolation (Mouquet & Loreau 2003; Leibold *et al.* 2004; Leibold & Chase 2018). However, even though we show that the difference between ponds with and without fish only increases with isolation (Fig. 3), it does not happen because of a positive correlation in the responses of predatory insects and consumers to the presence of fish and isolation.

We found that the presence of fish indeed shifts species composition through a reduction of predatory insects. The most negatively affected taxa were dytiscids beetles, notonectids, and dragonfly larvae, all of them relatively large taxa (see Appendixes S6). However, contrary to our

expectations and previous work (*e.g.* Goyke & Hershey 1992), consumers were not positively affected by the presence of fish. We believe that this lack of positive effect of fish on consumers comes from the fact that tilapias are generalist omnivores that might prey not only upon most conspicuous prey (*i.e.* predatory insects), but also any available prey, including herbivores and detritivores. In a pilot experiment (Appendix S4), tilapias readily ate not only large conspicuous prey such as *Scinax* tadpoles, guppies, belostomatids, nepids and dragonflies, but also much smaller ones, such as damselflies and mosquito larvae, the latter having about 5 orders of magnitude less wet mass than the manipulated tilapias. Similar results were observed by (Diehl 1992) when the presence of juvenile perch, a generalist benthic predator, caused biomass of invertebrate predators to decrease, but did not affect the biomass of consumers, because it was also preying upon them. Therefore, the same process might have occurred in our experiment where consumer abundances might suffer the net effects of direct negative effects of predation by fish, and indirect positive effects caused by the reduction of predatory insects also by fish (*i.e.* trophic cascade; Fig. 6B).

Orthemis dragonflies were the only exception for the expected negative effects of fish on predatory insects. They consistently had higher abundance in ponds with fish, but only in low isolation treatments. Some dragonfly species are known to exhibit different vulnerability to predation depending on body size and flexible antipredatory behavior, allowing them to coexist with fish (Johnson 1991; McPeek 1998; Johansson 2000; Hopper 2001; McCauley 2008). Indeed, *Orthemis* larvae were one of the smallest benthic predators we had in our experiment (around 20 times smaller than *Pantala*; see Appendix S6) and it has been reported to occur in high abundance in aquaculture ponds with no vegetation, usually buried into the sediment (de Marco *et al.* 1999). It is thus possible that higher availability of more suitable prey (*i.e.* other

predatory insects) in low isolation decreased predation rate on *Orthemis*, allowing it to have a greater abundance in ponds with fish.

We initially hypothesized that the abundance of dispersal-limited predatory insects should decrease as spatial isolation increases, and the abundance of consumers should increase in response, as a cascading effect. We partially found support for this hypothesis. Most of the substantial changes in community structure that we observed because of spatial isolation were from low (30 m) to higher levels of isolation (120 m and 480 m). Spatial isolation only generally reduced predatory insect abundance when fish was present, and the positive effect of isolation on consumer abundance was only observed when it was absent. The lack of a negative effect of isolation on predatory insects in fishless ponds might be explained by two clear exceptions to the expected patterns for predatory insects: *Pantala* and *Orthemis* dragonflies. While other predators, such as diving beetles (*i.e. Rhantus*) and water striders (*i.e. Microvelia*), exhibited a strong decrease in abundance in both fish and fishless ponds with spatial isolation, both of these dragonflies were positively affected by isolation in fishless ponds. Dragonflies are known to be good dispersers, thus it is not surprising that at the scale of our experiment they would suffer small or no negative effects at all of the isolation distances (McCauley 2006). We believe that the positive effects observed might be a consequence of the absence of other predatory insects in more isolated ponds, which could have released those dragonflies from competition or made these ponds more attractive for adults to lay their eggs (Fig. 6A). Such effect did not happen in ponds where fish was present, likely because fish increased predation pressure upon dragonflies as other suitable prey became scarce. Similarly to these dragonflies, if fish indeed prey upon both consumers and predatory insects, predation pressure upon consumers would be expected to increase with increasing isolation, explaining why we do not observe the cascading effect upon

consumers when fish is present. Indeed, if we consider predatory insect biomass as an estimate of food availability for fishes, we observe that average insect biomass per fishless pond decreases about 17% from low to intermediate and high isolation (19.2 g in low isolation to 15.9 g in intermediate and high isolation; see Appendix S8).

Finally, we found that more isolated communities have a greater difference in community structure between fish and fishless ponds then less isolated ones. However, we initially predicted this pattern would be due to correlated responses of predators and consumers to both presence of fish and spatial isolation (Vellend *et al.* 2014; Guzman *et al.* 2019), which was not what we observed. We did not find fish to have a stronger similar effect on more spatially isolated communities, instead, we argue that the presence of fish changed the effects of spatial isolation, making communities with and without fish to diverge with increasing isolation. We observed that because fish preys upon both predatory insects and consumers, it can dampen the cascading effect of spatial isolation on insect consumers by increasing predation pressure upon them in the absence of more suitable prey (Fig. 6). Also, the presence of fish can dampen any further indirect positive effects that spatial isolation might have on predatory insects that are less dispersal limited (Fig. 6). Our results could be due to either consumptive (*i.e.* direct predation upon available prey) or non-consumptive effects of predators upon preys (*i.e.* avoidance of ponds with fish or high density of predatory insects through habitat selection; see Binckley & Resetarits 2005; Blaustein *et al.* 2005; Resetarits 2005), which does not change the general conclusions of this work, as both processes represent a negative selective pressure of predators upon preys.

Conclusion

Our results diverged from those expected for more simplistic metacommunity models (Mouquet & Loreau 2003; Leibold *et al.* 2004; Leibold & Chase 2018; Fig. 1). We argue that the higher complexity of our study system, both in terms of interspecific variability in dispersal rates and responses to the local selective pressure are the main causes of such divergence. Nonetheless, we were able to show that the presence of a generalist top predator can dampen the trophic cascades caused by spatial isolation when consumers have higher dispersal rates than predators (Fig. 6). Our results also highlight the importance of considering interspecific variation in dispersal rates and multiple trophic levels to better understand the processes generating community and metacommunity structures in spatially structured landscapes (see van de Meutter *et al.* 2007; Vellend *et al.* 2014; Hill *et al.* 2017; Guzman *et al.* 2019).

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Figure Legends

Figure 1. Prediction of experimental effects: Right-hand panels show the importance of niche selection and ecological drift on community structure along a gradient of dispersal limitation with (A) and without (B) interspecific variation in dispersal. If species have no variation in dispersal rates, the importance of niche selection processes on community structure is predicted to be the highest in intermediate dispersal limitation. However, if species vary in dispersal rates and good dispersers are also favored by local conditions, they will be disproportionally favored in more isolated habitats, making the importance of niche selection to increase with dispersal limitation. Left hand panels show ordination plots with the predicted difference among macroinvertebrate communities with and without fish along a gradient of spatial isolation. Each symbol represents a hypothetical community and similar symbols communities from the same hypothetical treatment. In this case, the greater importance of niche selection causes a larger difference between fish and fishless communities (black bars) in a given level of isolation.

Figure 2. A. Diagram of the experimental layout. B. Representative photo of one of our experimental units.

Figure 3. Model-based unconstrained ordination showing pond communities (symbols) and species (filled circles) for the third sampling survey. Yellow filled circles represent predatory insects and green filled circles represent consumers. The sizes of the circles are proportional to maximum body size (the volume of the largest individual of each species in a log-scale). Abbreviations of names of taxa are provided in Appendix S6. Symbols close to each other have

more similar community structures than those that are further apart. Species are positioned closer to symbols (*i.e.* communities) where their abundance are higher. Note that consumers are more strongly associated with high distance treatments, especially fishless ponds, whereas predatory insects are associated with low distance treatments, especially fishless ponds. Note also that *Pantala* and *Orthemis* dragonflies (Pan and Ort) are detached from the other predatory insects.

Figure 4. 95% Confidence intervals for the maximum likelihood estimates (MLE) of the effect of fish and isolation on the abundance of predators and consumers when comparing pairs of treatments for the last survey. Confidence intervals not crossing the zero hatched line were considered significant effects and colored; blue bars represent an increase and red bars a decrease in abundance from the reference treatment. Note that both predators and consumers were negatively affected by fish (A). Consumers were positively affected by isolation only in fishless ponds (B) and predators were negatively affected by isolation only in ponds with fish (C).

Figure 5. Maximum likelihood estimates (MLE) of abundance and their 95% confidence interval of abundance for the six most abundant predatory taxa (A), and six most abundant consumer taxa (B). Gray symbols indicate the absence of a taxon in a treatment. Blue triangles are MLEs for fish treatments and orange balls are MLEs for fishless treatments. The actual estimated differences are provided in Appendix S9. Note in A that *Pantala* and *Orthemis* dragonflies are the only exception to the tendency of decreasing abundance of predatory insects along the isolation gradient in fishless ponds.

Figure 6. Hypothesized processes generating the observed patterns. Black arrows represent the flow of energy. Red solid arrows represent direct negative effects of predators on lower trophic levels and blue dashed arrows represent indirect positive effects on lower trophic levels. The thickness of the arrows represents the proportional amount of energy flowing or the intensity of the effect. In fishless habitats (A) the increase in spatial isolation causes an increase in the abundance of predatory insects with higher dispersal ability, but a reduction in the abundance of those with lower dispersal ability, which results in a cascading effect increasing the abundance of consumers. The presence of fish (B) however, generally reduces the abundance of predatory insects, but it also keeps the abundance of consumers unchanged since fish also preys upon them. As spatial isolation increases, fish prevents the increase in abundance of both consumers and predatory insects with higher dispersal ability by increasing predation pressure upon them.

Figure 1

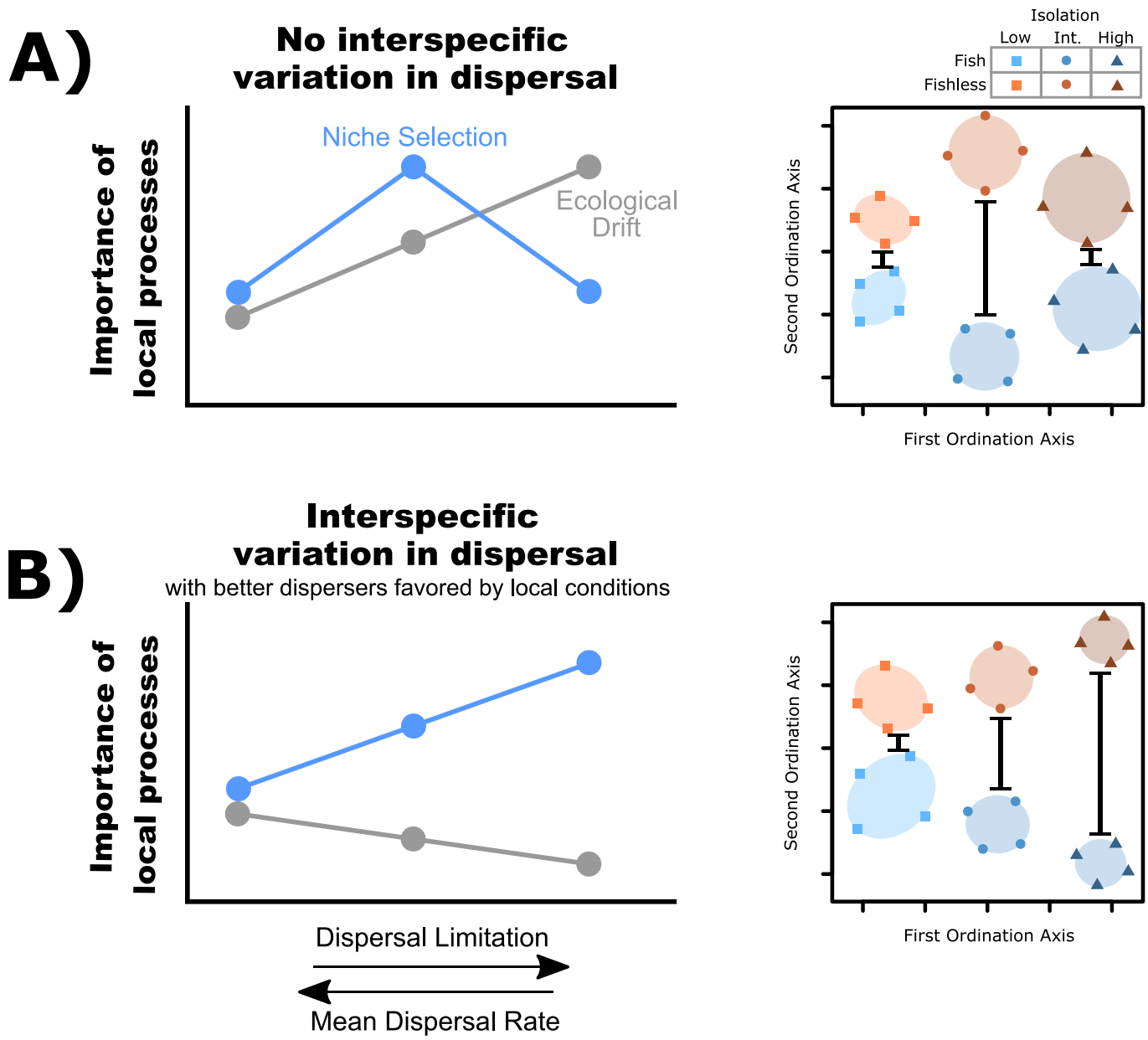

A)
No interspecific variation in dispersal
Importance of local processes
Niche Selection
Ecological Drift
Isolation
Low
Int.
High
Fish
Fishless
Second Ordination Axis
First Ordination Axis
B)
Interspecific variation in dispersal
with better dispersers favored by local conditions
Importance of local processes
Dispersal Limitation
Mean Dispersal Rate
Second Ordination Axis
First Ordination Axis

Figure 2

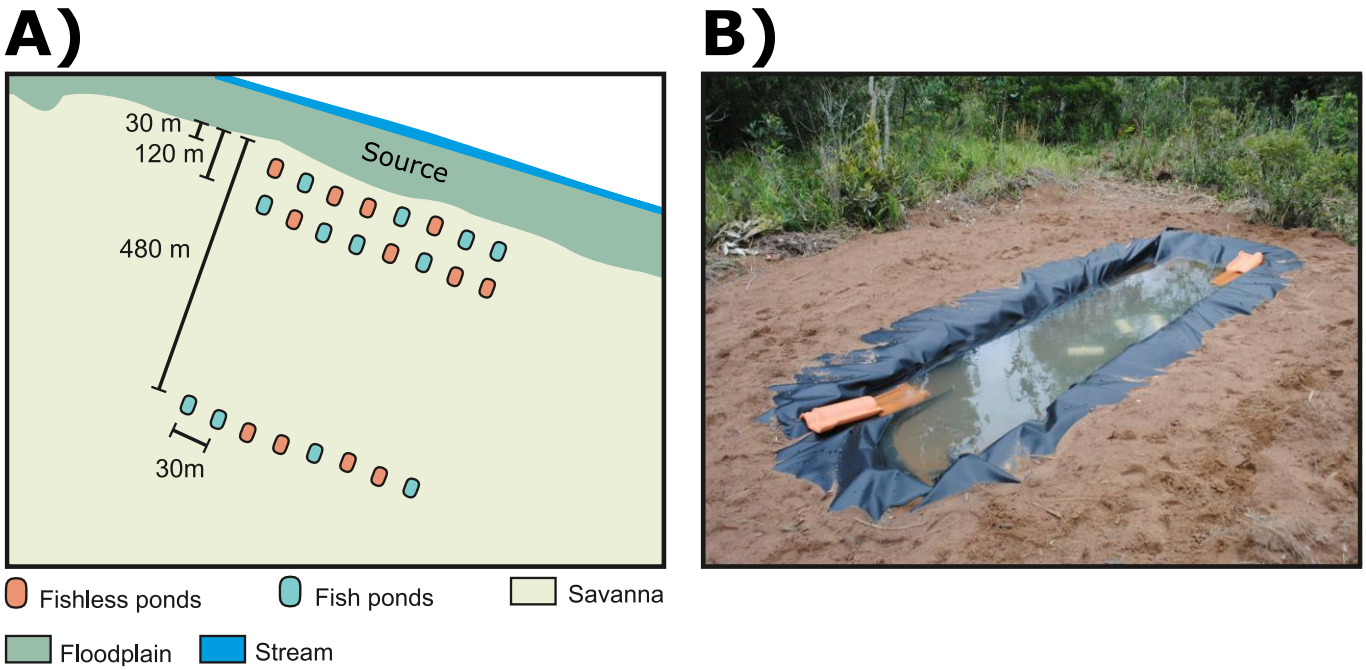

A)
B)
30 m
120 m
Source
480 m
30m
Fishless ponds
Fish ponds
Savanna
Floodplain
Stream

Figure 3

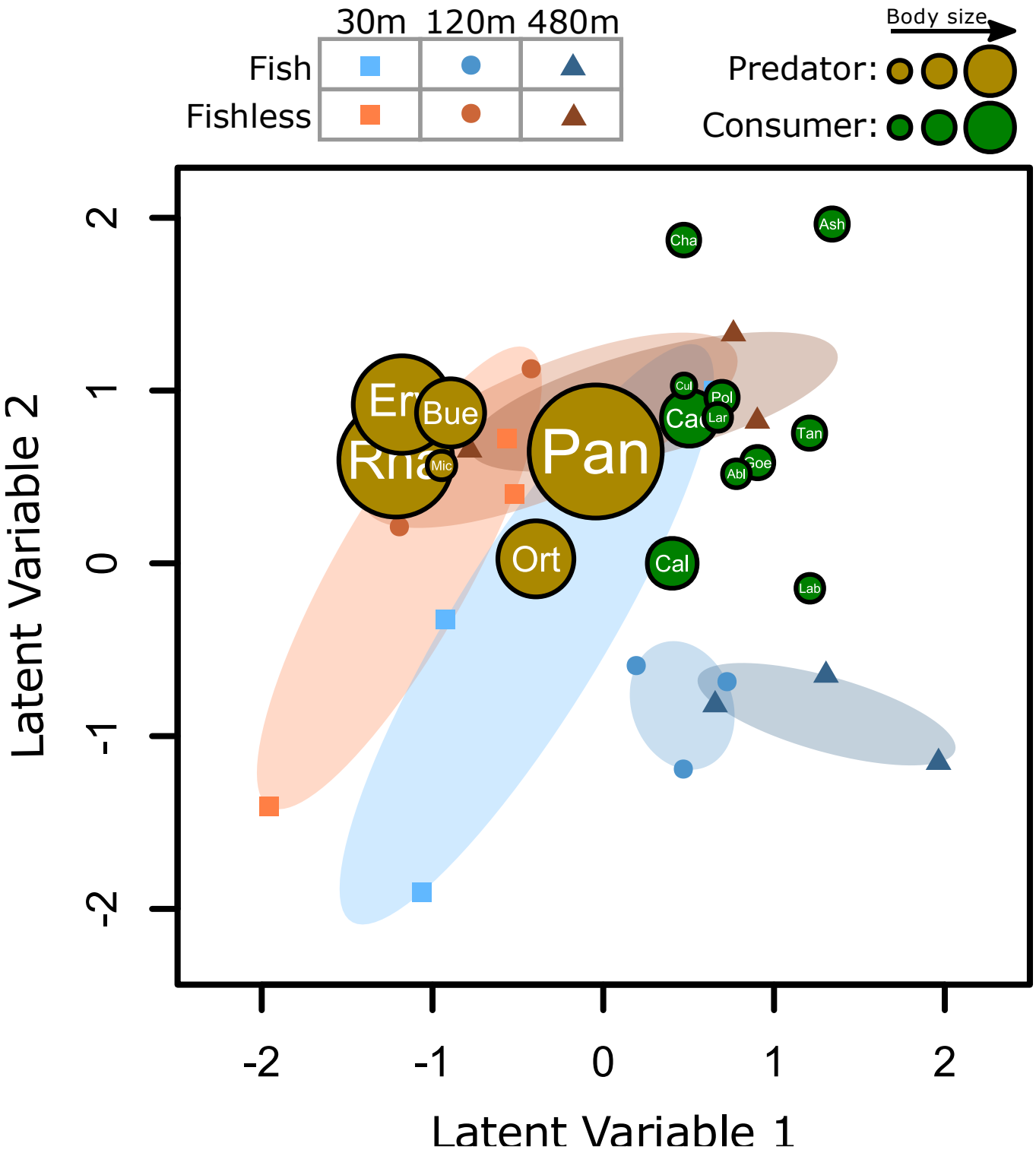

30m
120m
480m
Fish
Fishless
Body size
Predator:
Consumer:
Cha
Ash
Cul
Pol
Lar
Tan
Bue
Mic
Pan
Abl
Goe
Ort
Cal
Lab
Latent Variable 2
Latent Variable 1
-2
-1
0
1
2

Figure 4

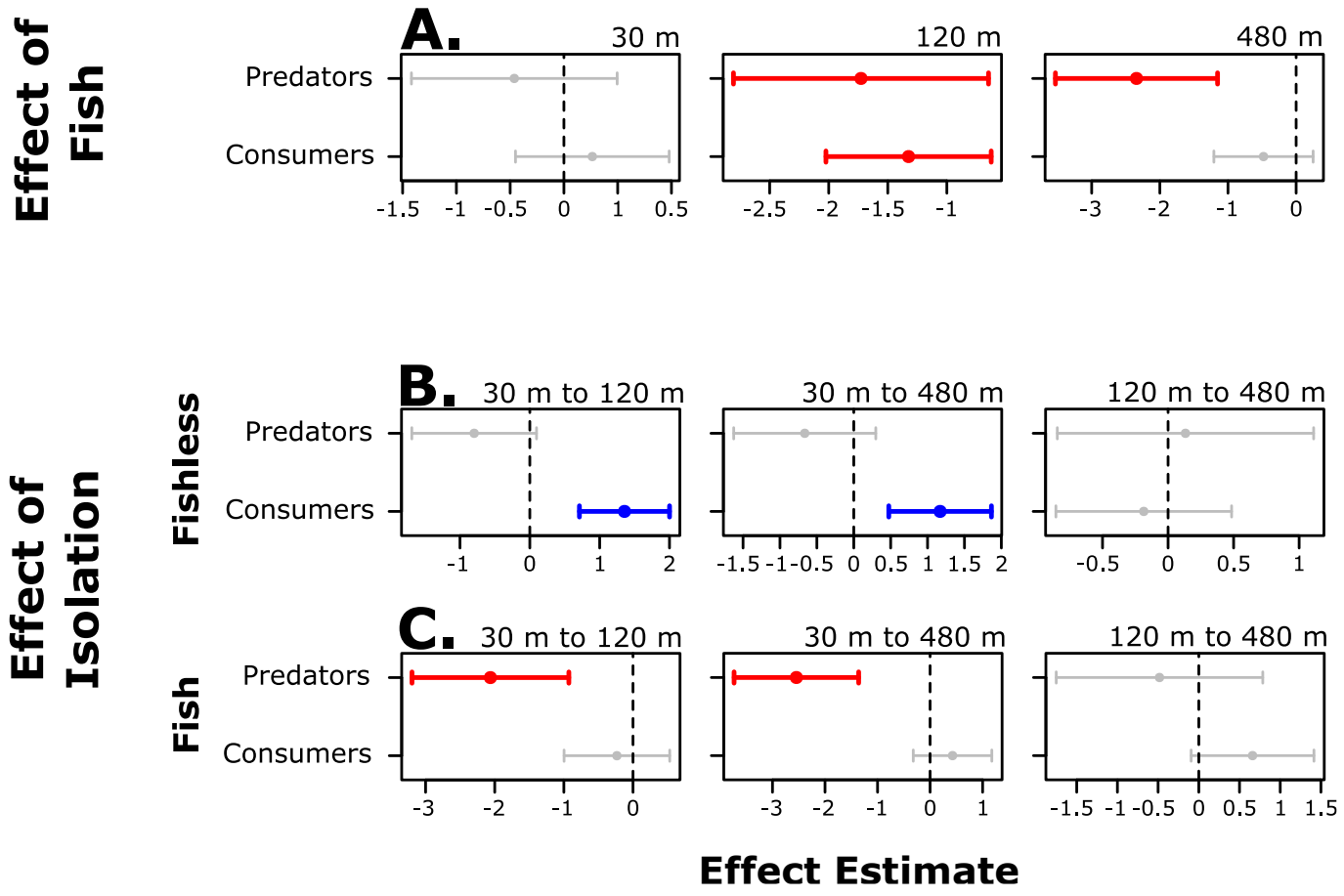

Effect of Fish
A.
30 m
120 m
480 m
Predators
Consumers
-1.5 -1 -0.5 0 1 0.5
-2.5 -2 -1.5 -1
-3 -2 -1 0
Effect of Isolation
Fishless
B.
30 m to 120 m
30 m to 480 m
120 m to 480 m
Predators
Consumers
-1 0 1 2
-1.5 -1 -0.5 0 0.5 1 1.5 2
-0.5 0 0.5 1
Fish
C.
30 m to 120 m
30 m to 480 m
120 m to 480 m
Predators
Consumers
-3 -2 -1 0
-3 -2 -1 0 1
-1.5 -1 -0.5 0 0.5 1 1.5
Effect Estimate

Figure 5

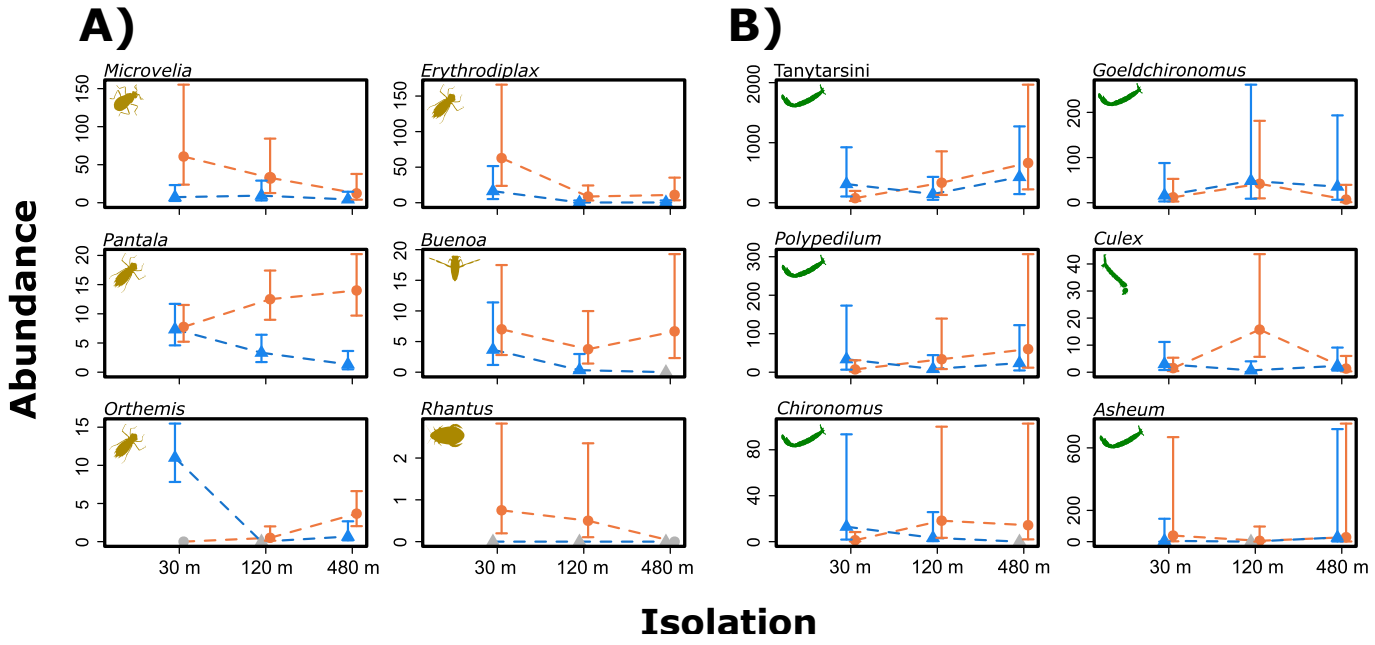
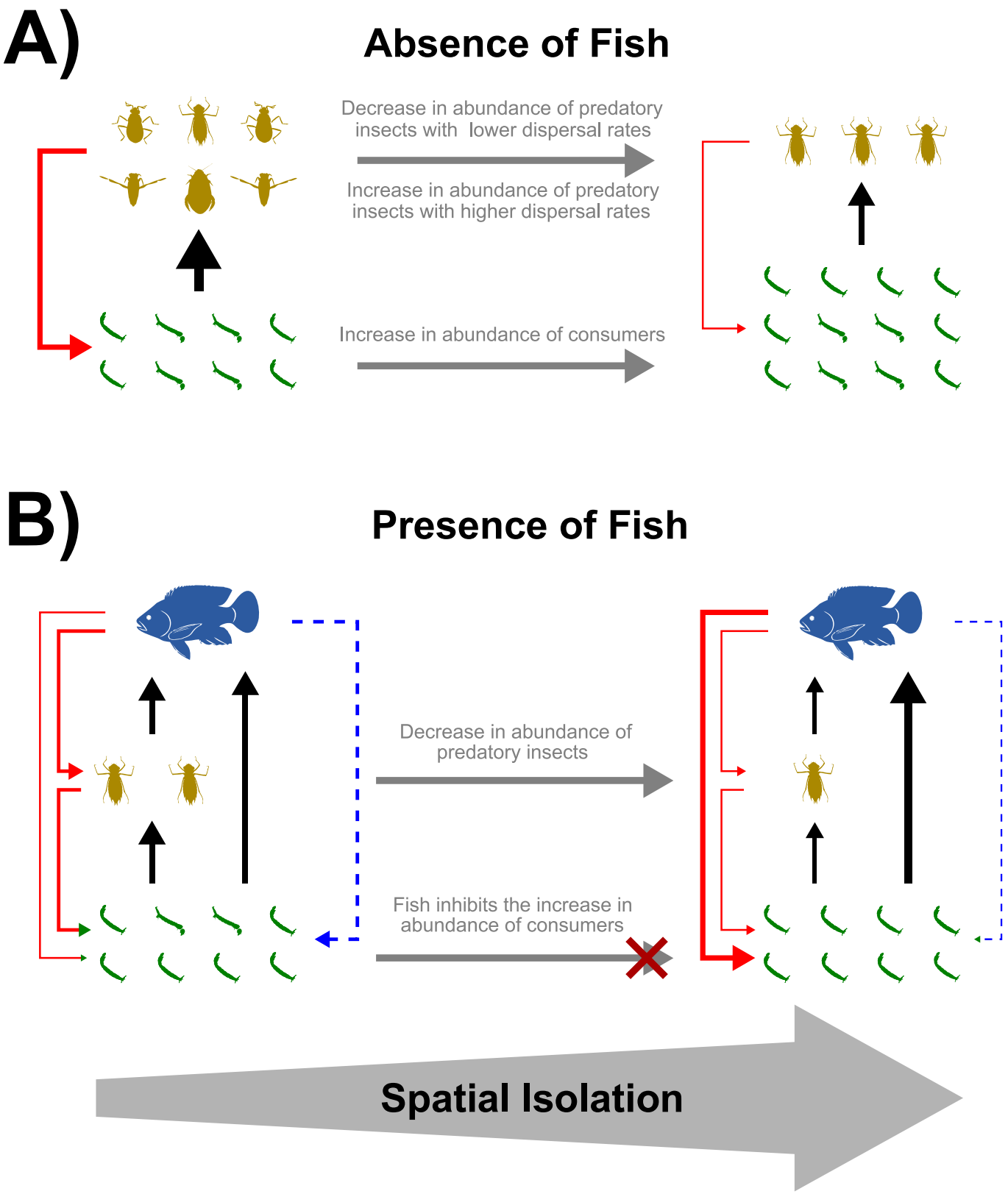

A)
B)
Microvelia
Erythrodiplax
Pantala
Buenoa
Orthemis
Rhantus
Tanytarsini
Goeldchironomus
Polypedilum
Culex
Chironomus
Asheum
Abundance
Isolation
30 m
120 m
480 m

Figure 6


A)
Absence of Fish
Decrease in abundance of predatory insects with lower dispersal rates
Increase in abundance of predatory insects with higher dispersal rates
Increase in abundance of consumers
B)
Presence of Fish
Decrease in abundance of predatory insects
Fish inhibits the increase in abundance of consumers
Spatial Isolation