The Role of Habitat Type and Nutrient Quality on Invertebrate Dispersal and Diversity

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The presence of invertebrates in a given area is governed by a variety of factors including competition, predation, habitat selection, and resource availability. Manipulating one or more of these factors could affect invertebrate survival, based on differences in the ability to detect habitat quality. A field experiment was conducted to test the relationship between food quality and environmental type on invertebrate dispersal and diversity. Containers filled with lake water were treated with algae cultured on varying amounts of phosphorus and were placed within an experimental plot with varying vegetation to allow for insect oviposition. Nutrient quality was found to have an effect on (1) number of invertebrate egg clusters, (2) number of chironomid larvae, and (3) overall invertebrate diversity. Additionally, there was a positive relationship between the amount of chlorophyll *a* and the measured variables; however, habitat type was found to have no effect. These results stress the importance of nutrient availability in oviposition decisions made by adult invertebrates. Furthermore, they hint at the sensitive balance of ecosystems and the role that phosphorus-loaded fertilizers, pollution and human land use in general plays in the stability of these systems. © *2007 Oklahoma Academy of Science*

INTRODUCTION

Identifying factors influencing invertebrate dispersal are essential to understanding ecosystem interactions. The distribution of resources within an ecosystem, for example, often dictates the dispersal and ultimate distribution of individuals (Lancaster et al 2003). Co-dependent relationships involving competition, predation, habitat selection and resource availability are key factors and the manipulation of one or more of these factors may affect the diversity of organisms in a given area (Palmer et al 1996). Resource availability can be defined in many ways including quantity (e.g. habitat density) and quality (e.g nutrient composition), both of which are crucial to the survival and success of invertebrates.

Habitat density facilitates survival by providing shelter from predation and minimizing the impact from disturbances. Many studies have highlighted the benefit of habitat quantity by demonstrating a positive relationship between host plant density and insect abundance (e.g., Gunnarsson 1990; Haddad et al 2001; Cook and Holt 2006). The underlying mechanism for this may be that habitat density influences habitat heterogeneity by providing different structures, and differences in resource availability and quality.

Differences in food quality can influence invertebrate larval development and therefore life-history decisions (Ward and Cummins 1979). In herbivorous insects, plant host quality can have an effect on egg size, condition, and the allocation of resources to eggs (Awmack and Leather 2002). Therefore, releasing offspring into specific environments may be affected by an adult's ability to determine nutrient availability within a habitat. For example, insects have been shown to discriminate among algal species by sampling the water with their abdomen to determine habitat quality before ovipositing (Brittain 1982). Food quality limitations are related to the availability of certain elements such as nitrogen, phosphorus, and iron (Stiling 1996; Schesinger 1997). Phosphorus, in particular, has been considered to be an important dietary subsidy with respect to larval growth rates (Hiltner and Hershey 1992; Jeyasingh and Weider 2005; Jeyasingh 2007). For example, experimental reduction or supplementation of phosphorus content reduces or increases invertebrate growth rates and reproduction (Elser et al 2001; Urabe and Sterner 2001; Perkins et al 2004).

Midges (family: *Chironomidae)* are one of the most ubiquitous groups in freshwater ecosystems. Females lay egg clusters encompassed by a gelatinous matrix at the edge of the water (Halpern et al 2006). Due to winged dispersal, midges are highly mobile and have the ability to move between habitat patches. Given their mobility and ability to discriminate between habitats of differing quality (Gresens and Lowe 1994), we would expect them to preferentially oviposit at sites with highest food quality (i.e. highest phosphorus levels). Here, we used a field experiment to manipulate habitat heterogeneity and food quality to determine the role of habitat characteristics on invertebrate oviposition preference and species diversity (i.e. taxonomic richness).

STUDY AREA

This experiment was performed over the course of eight days in the Southern midwest United States in Kingston, Oklahoma near Lake Texoma at the University of Oklahoma Biological Station. The chosen habitat was an un-grazed pasture at the edge of a hardwood forest located at 33º52′50.33″N & 96º48′00.62″W.

METHODS

We defined *a priori* that the pasture in its original state was of high vegetation density and created low vegetation density by mowing randomly chosen plots within the pasture with a weed-eater. The 6m x 4m experimental grid was measured with meter tape and meter sticks to constitute 24 plots of 1 m^2 each. In addition, each plot was marked with wire flags and the cut grass was raked to remove any excess vegetation.

A 1.47L Rubbermaid® (top diameter of 180mm) container was filled with 1L of lake water and placed at the center of each plot. A cultured algae (*Scenedesmus* spp.) was devised using COMBO, which is an effective artificial medium capable of supporting freshwater algal growth and can readily be manipulated to contain different nutrient levels (Kilham et al 1998). To meet the two different nutrient regimes, algae were cultured under either a high (N:P ratio=5:1) or low phosphorus ratio (N:P ratio =50:1). Each container was then treated with 20 mL of either high-P algae, low-P algae, or additional lake water (serving as the control). Thus, each plot contained high- or low-density vegetation and lake water samples treated with either high-P, low-P, or no supplemental P (lake water only). This was replicated four times, allowing 12 high-density and 12 low-density plots with differing levels of phosphorus.

After eight days, chlorophyll *a* concentration was measured in each container using a Hydrolab® DataSonde 4 (Hach Environmental). All organisms were collected by filtering the water of each container through a plankton net (mesh width: 153 microns). Using tap water, organisms were then washed off the plankton net into a Petri dish and examined under a dissecting microscope. To contrast organisms from organic debris, each dish was stained with Rose Bengal solution. For each sample, the number of different organisms was recorded and organisms ware identified according to morphotype (see results section).

Prior to analysis, abundance and diversity data were log-transformed to meet the assumptions of variance homogeneity. We performed a two-way ANOVA using habitat (high, or low vegetation density) and nutrient quality (high-P algae, low-P algae, or lake water control) as independent variables. Dependent variables included the number of egg clusters, the number of chironomids, and taxonomic richness. The number of egg clusters was used as an index of oviposition preference, and chironomid abundance was used as an index of colonization preference. The number of morphotypes was used as an index of taxonomic richness. A Pearson correlation analysis was employed to determine if there was a relationship between container chlorophyll *a* (i.e. algal abundance) and the aforementioned dependent variables. All analyses were performed using SPSS version 15.0.

RESULTS

The containers were colonized by a variety of morphotypes: chironomids, copepods, dipteran larvae, egg clusters, mites, nematodes, ostracods, and rotifers. In addition, several terrestrial organisms including ants, beetles, spiders, and unidentified insects were recorded. Taxonomic richness in each container ranged from 0 to 10 morphotypes.

There were no significant effects of habitat structure (high density vs. low density) on the number of egg clusters ($F_{(1,24)} = 0.108$, $p= 0.746$), chironomids ($F_{(1,24)} = 1.151$, $p= 0.298$), or taxonomic richness ($F_{(1,24)} = 0.437$, $p= 0.517$; Figure 1); however, significant effects of nutrient levels (high P, low P, or lake water control) on number of egg clusters ($F_{(2,24)}=4.831$, $p=0.021$) and chironomids ($F_{(2,24)}=6.844$, $p=0.006$) were discovered (Figure 1). Additionally, there was a marginally significant effect on taxonomic richness ($F_{(2,24)}=3.364$, $p=0.057$; Figure 1), but there was no significant interaction between the two main effects on the number of egg clusters ($F_{(2,24)}= 0.551$, $p=0.586$), chironomids ($F_{(2,24)}= 0.388$, $p= 0.684$), and taxonomic richness ($F_{(2,24)}= 0.023$, $p= 0.977$; Figure 1).

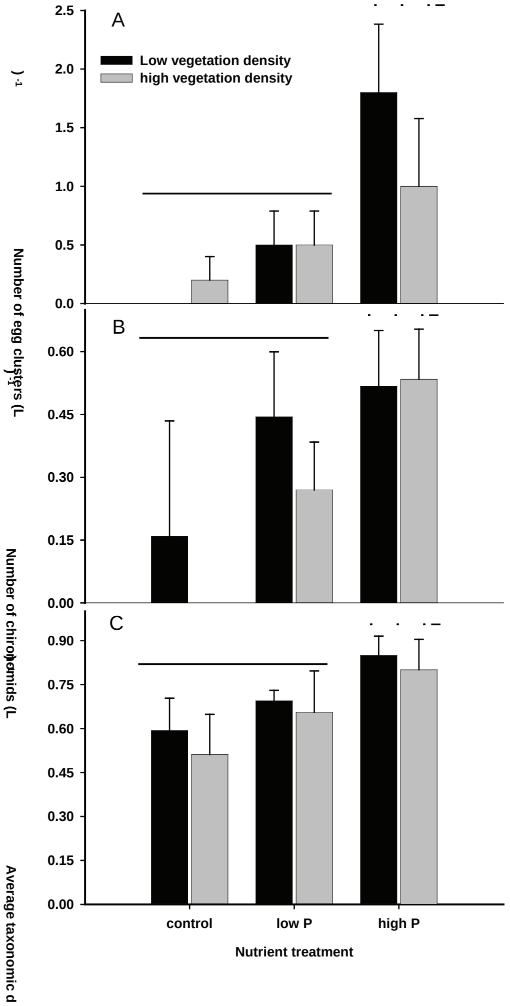

Figure 1. Two-way Anova results depicting the effect of habitat density (low vegetation density, grey bar; and high vegetation density, dark bar) and resource quality (lake water control, low P, and high P) on dependent variables: (A) number of egg clusters, (B) number of chironomids, and (C) taxonomic diversity. Differences in solid versus dashed lines denote significant main effects at p < 0.05.

Finally, there was a positive relationship between the amount of chlorophyll *a* in the containers and the number of egg clusters (r = 0.391, p= 0.059), chironomids (r= 0.592, p= 0.002), and taxonomic richness (r= 0.487, p= 0.016).

DISCUSSION

The results of this experiment demonstrate that food quality (nutrient content) is an important determinant of habitat preference (presence of egg clusters, chironomid abundance) and community composition (taxonomic richness). The number of egg clusters and chironomids were greatest in the high nutrient treatment suggesting that invertebrates prefer to place their offspring in high-quality environments. In addition, high phosphorus treatments also attracted the greatest diversity of invertebrates. Given the small experimental area (6m x 4m), and equal access to all treatments, the results indicate that invertebrates can distinguish and preferentially select habitat quality, even on a small spatial scale. However, we speculate that the invertebrates were cuing in on food quality, as the habitat manipulation had no detectable effect on colonization rates. This may be interpreted as an invertebrate's inability to select between vegetation density or a design flaw in our experimental setup.

Furthermore, we found a positive correlation between container chlorophyll *a* and all dependent variables (numbers of egg clusters, chironomid number, and taxonomic diversity). Hence, although phosphorus content was experimentally manipulated, the invertebrates may have simply responded to algal abundance. It is known that algae are an important energy source for insects: *Glossosoma* caddisflies larvae, for example, appear to feed selectively on algae, while mayfly nymphs consume algae if available (McNeely et al 2006). The influence of phosphorus availability on algal growth has been intensively studied in freshwater systems, and phosphorus is considered to be an important limiting nutrient at the base of food webs (Elser et al 2001; Perkins at al 2004). Higher phosphorus levels may create a larger resource base to allow more organisms to co-exist with each other, promoting increased diversity.

By choosing to oviposit in high phosphorus environments, adults select a habitat that maximizes food abundance for their offspring. The ability to detect quality habitats has ecological and evolutionary consequences with direct and indirect fitness benefits (e.g. McMillan 2000; Peckarsky 2000). Placing offspring in food-rich environments maximizes the survival, development, and subsequent reproduction of future generations. For example, Peck and Walton (2005) demonstrated that low food density decreased survivorship, and delayed larval development in mosquitos (*Culex* spp.).

This experiment was designed and executed over the course of two weeks by an undergraduate level class. Ideally, the experiment would have been performed over an extended period of time to ensure maximum larval development and colonization. This was not a problem for the nutrient manipulation as we were able to detect significant differences among treatments; however, colonization due to vegetation density may occur over longer temporal and spatial scales. Further, we performed the experiment in a densely vegetated habitat, which may have biased our results by masking our manipulated low vegetation plots. Also, a considerable amount of precipitation caused container overflow, but all treatments experienced the same amount of rain.

Additionally, lake water was used as the medium for all treatments. It is highly likely that at least copepods and ostracods were therefore already present in our treatments and did not subsequently colonize the containers. This assumption is strengthened by the fact that we did not find any significant influence of nutrient level or habitat density on either copepod or ostracod abundance; however, since we cannot completely rule out any subsequent colonization, we included both in our count of taxonomic richness.

Our results highlight the importance of habitat type and nutrient quality on invertebrate dispersal and diversity. This is a relevant issue concerning the conservation of freshwater ecosystems. Disturbances, associated with shifts in land use and degradation of water quality, are threatening the nature of habitat quality and nutrient availability. For each species, the ability to travel from one suitable habitat to another may vary greatly, and ultimately influences dispersal success (Malmqvist 2002). A recent study by Gibb and Hochuli (2002), for example, could show that larger habitat fragments (due to urban fragmentation of arthropod habitats) cannot support any more species than small habitats; however, smaller habitat fragments have been shown to have different arthropod assemblages (e.g. more generalist species) than larger fragments.

Another factor influencing invertebrate life histories is pollution. Studies of macroinvertebrate diversity in the Nile River have shown that lower biodiversity was found in sites with known inputs of pollution (Fishar and Williams 2006); while Hardy and Dennis (1999) proposed that the development of urban communities and resulting pollution is expected to have a negative impact on butterflies and butterfly dispersal. In accordance with the existing literature, our results suggest that changes in the nutrient regime (e.g. caused by phosphorus-loaded fertilizers, habitat fragmentation, or pollution) may influence the structure of communities and life history decisions made by terrestrial insects.

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