

Patterns and Mechanisms of Biodiversity in Sub-Alpine Wetlands

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Abstract:

Aquatic insect colonization dynamics were studied in an attempt to understand patterns of diversity in sub-alpine wetlands. More specifically, this study investigated three alternate hypotheses: species-level diversity in habitat patches is a function of 1) patch size, 2) patch complexity, or 3) source-community characteristics. Experimental ponds that varied in size and habitat complexity were placed around natural source ponds of varying hydroperiods. Samples of invertebrate abundance and species richness were taken after a nine days of natural colonization.

Results revealed higher species richness in more complex habitats ($F_{1,66} = 5.756$; $p = 0.0193$). Species richness also varied with respect to hydroperiod ($F_{2,66} = 12.961$, $p < 0.0001$), with highest diversity in habitat patches around vernal ponds. Species richness did not vary with respect to patch size ($F_{1,92} = 0.665$; $p = 0.417$).

Results support the hypothesis that diversity is a function of habitat heterogeneity, while they do not support the hypothesis that diversity is a function of size. Thus, the protection and/or creation of large bodies of water may not be sufficient to preserve wetland species-diversity; success may hinge on the complexity of protected/created habitat patches. Additionally, patterns of diversity in habitat patches varied with respect to source community. Thus, assessment of the biotic and abiotic characteristics of existing wetland communities may be necessary to ensure site-specific preservation of species diversity.

I. Introduction

The study of biodiversity and its effect on ecosystem resilience has become increasingly important under the precept of global climate change (Mittermeier et al. 1998, Thomas et al. 2004, Li et al. 2006, Malcolm et al. 2006). However, before we can understand how biodiversity affects ecosystem processes, we must first understand patterns of biodiversity and the how these patterns affect the stability of local and regional communities.

Historically, islands have been the focus of biodiversity studies for they present a manageable study system (Mac Arthur and Wilson 1967). Islands are discrete units; consequently, studies of species richness, evenness, immigration, emigration, and extinction are more feasible on islands than in other areas where boundaries are more difficult to decipher (Mac Arthur and Wilson 1967). Furthermore, similarities between various islands provide natural controls for comparative studies of biodiversity, while

differences (i.e. size, shape, habitat heterogeneity) provide natural variables (Mac Arthur and Wilson 1967).

Over the past forty years, studies examining insular biota have described a common pattern of diversity: larger islands that are closer to a continent have more diverse flora and fauna than smaller islands that are comparatively isolated from mainland (Mac Arthur and Wilson 1967, Gentile and Argano 2005, Triantis et al. 2005). The relationship between the proximity of an island to mainland and its level of biological diversity may be explained by physical limitations to organisms' dispersal ability. Furthermore, the probability that dispersing individuals' journeys will be thwarted by harsh weather or successful predation increases as distance increases. Alternatively, the probability that dispersing individuals will encounter and colonize a suitable habitat before they reach farther islands increases as distance from mainland increases.

While these hypotheses may explain observed patterns of diversity with respect to distance from mainland, they do not address the relationship between island size and species diversity. The equilibrium theory of island biogeography, as proposed by Mac Arthur and Wilson, suggests that $S = CA^Z$, where S is the number of species in a given taxa and A is the area of the island (Mac Arthur and Wilson, 1967). In other words, diversity is directly proportional to island size and is thus a function of probability (Mac Arthur and Wilson, 1967). In naturally occurring systems, however, larger areas generally encompass more habitat types (Hamilton et al. 1964, Russell et al. 2006). Dispersing organisms may *select* larger areas because larger areas have a higher probability of containing a suitable habitat. Alternatively, dispersing individuals may *select* larger areas for their size, rather than their habitat heterogeneity. Ambient temperature, annual rainfall, inter and intra-species interception rates, and edge effects vary with respect to patch size (Holland et al. 1991, Murcia 1995, Didham and Lawton 1999). Colonizing individuals may choose larger areas to minimize or maximize any or all of these variables. Conversely, habitat *selection* need not be involved; organisms that colonize areas with more suitable habitats may simply have higher persistence rates than organisms that colonize areas with limited niche space.

While these theories of probability, habitat choice, and persistence predict increased diversity in larger habitat patches, the mechanisms behind the theories are fundamentally

different. In an attempt to understand how the habitat-patch diversity arises, this study investigates aquatic insect colonization dynamics in sub-alpine wetlands. More specifically, this study investigates three alternate hypotheses:

Hypothesis 1: Observed diversity is a function of patch size.

Hypothesis 2: Observed diversity is a function of habitat patch heterogeneity.

In light of recent evidence that factors such as habitat permanence and predation risk may significantly influence colonization and persistence (Ebert and Balko 1987, Ward and Blaustein 1994, Spencer et al. 1999, Bilton et al. 2001), we consider a third mechanism that could influence patterns of habitat-patch diversity:

Hypothesis 3: Observed diversity is a function of source community characteristics.

II. Methods

Study Site:

Research was conducted in the Mexican Cut Nature Preserve in the Elk Mountains of Southwestern Colorado. At an elevation of 3560 m and about 10 km northwest of Gothic, CO, the study site consisted of a series of vernal (temporary), autumnal (semi-permanent), and permanent ponds dispersed over 21.6 km² of sub-alpine spruce (*Picea engelmanni*) and fir (*Abies lasiocarpa*) forest.

Experimental Design:

A. Source Ponds and Expected Colonists

Twelve natural ponds (of which four were vernal, four were autumnal, and four were permanent) were used as source communities of aquatic colonists. Four experimental ponds were placed at around each autumnal and permanent source pond, while two experimental ponds were placed around vernal ponds (Figure 1). In an attempt to minimize cross-colonization, selected source ponds were at least 6 m apart. Furthermore, the distance between the experimental ponds of one trial and the source pond of an adjacent trial was maximized (Table 1 and Figure 2).

Colonists of each experimental pond were expected to be samples of those found in their respective source ponds. Expected colonists included aquatic insects from the

orders Diptera, Coleoptera, Odonata, Trichoptera, and Cladocera (as described by Wissinger et al. 1999).

B. Experimental Ponds

Two large experimental ponds made from cattle tanks ($h = .20$ m, $d = 1.47$ m, $A = 1.696$ m², $V = .339$ m³) and two small experimental ponds made from children's wading pools ($h = .20$ cm, $d = 1.00$ m, $A = .785$ m², $V = .157$ m³) were placed 2 m from each source pond and 6 m from each other (Figure 2). The experimental ponds were randomly assigned to one of four positions around each source pond.

One experimental pond of each size class was filled with a complex habitat, while the other was filled with a simple habitat (Table 2). Simple habitats provided colonists with water, food, and minimal structure, while complex habitats mimicked the heterogeneity of natural ponds at the Mexican Cut. To compensate for the difference in size between treatments, the amounts of sedge, pinecones, and clumps of wood placed in each large experimental pond were doubled, as were the sizes of the rocks, clumps of emergent vegetation, and dried logs.

Each experimental pond was filled with filtered pond water to a depth of 20 cm. Water was filtered through ultra-fine mesh that excluded all aquatic invertebrates (adults, larvae, pupae, and eggs). The depth of experimental pond water was held constant, with water added or drained over the course of the study to prevent fluctuations in water level.

C. Control Ponds

In order to account for the accidental introduction of aquatic invertebrates during experimental set-up, two wading-pool sized control ponds (one with simple habitat and one with complex) were filled with filtered water and covered with 1 mm mesh. Both control ponds were placed two meters from source pond 9 (Figure 1).

Data Collection:

A. Duration

Experimental set-up lasted from June 18th - July 10th. Nine days after set up was completed, a comprehensive net sample was taken during the period of July 19th - July 26th.

B. Methods

Net Sample Three mini-samples were taken from each experimental and control pond for a total of 126 mini-samples per comprehensive net sample. Each mini-sample consisted of a sweep with a mesh net small enough to capture all expected colonists and their eggs. Separate nets were used at each experimental and control pond in order to prevent transfer of individuals from one pond to the next. Sub-samples in complex treatments were of the emergent vegetation, the area around the rocks, and the center area. Sub-samples in simple ponds were of the areas that corresponded to locations sampled in the complex habitats (the left and right, north and south, and center, respectively).

The contents of each sub-sample were placed in separate white, plastic sweater-boxes and filled with water from the sampled experimental or control pond. After species counts of all aquatic insects found in each mini-sample were recorded, the colonists were returned to the experimental or control pond sub-habitats from which they came.

A few individuals of most colonizing species were preserved for future laboratory analysis. However, in cases where invertebrate abundance was low enough that removal of individuals could have altered the population or community structure, no preservation took place.

Data Analysis:

Invertebrate abundance and species richness were calculated for each experimental pond. Two-way ANOVAs were used to compare the effects of size, habitat complexity, and hydroperiod on both abundance and species richness. Future analyses will incorporate abundance and richness into a single-unit measure of diversity. For the

purpose of this study, however, species richness was considered an approximate measure of species diversity.

Table 1: Distance to Nearest Neighbor

Pond	Classification	Approximate Distance to Nearest Pond	Approximate Distance From Experimental Pond to Nearest Pond
L7	Vernal	6 meters (L8)	8 meters (L8)
L13	Vernal	17 meters (L1)	19 meters (L1)
L15	Vernal	100+ meters (L5)	100+ meters (L5)
L19	Vernal	100+ meters (L5)	100+ meters (L5)
L6	Autumnal	26 meters (L7)	24 meters (L7)
L8	Autumnal	12 meters (L7)	36 meters (L9)
L10	Autumnal	6 meters (L11)	9 meters (L11)
L11	Autumnal	6 meters (L10)	25 meters (L10)
L1	Permanent	12 meters (L2)	29 meters (L12)
L5	Permanent	30 meters (L6)	38 meters (L6)
L9	Permanent	6 meters (L10)	19 meters (L10)
L12	Permanent	17 meters (L1)	15 meters (L1)

Table 2: Experimental Habitats

Simple Habitat	Complex Habitat
• Dried water sedge (<i>Carex aquatilis</i>)	• Dried water sedge (<i>Carex aquatilis</i>) • Two river rocks • Two clumps of emergent vegetation (live <i>C. aquatilis</i>) • Small clumps of rotting spruce wood (<i>Picea pugnans</i>) • Spruce cones • One dried spruce log

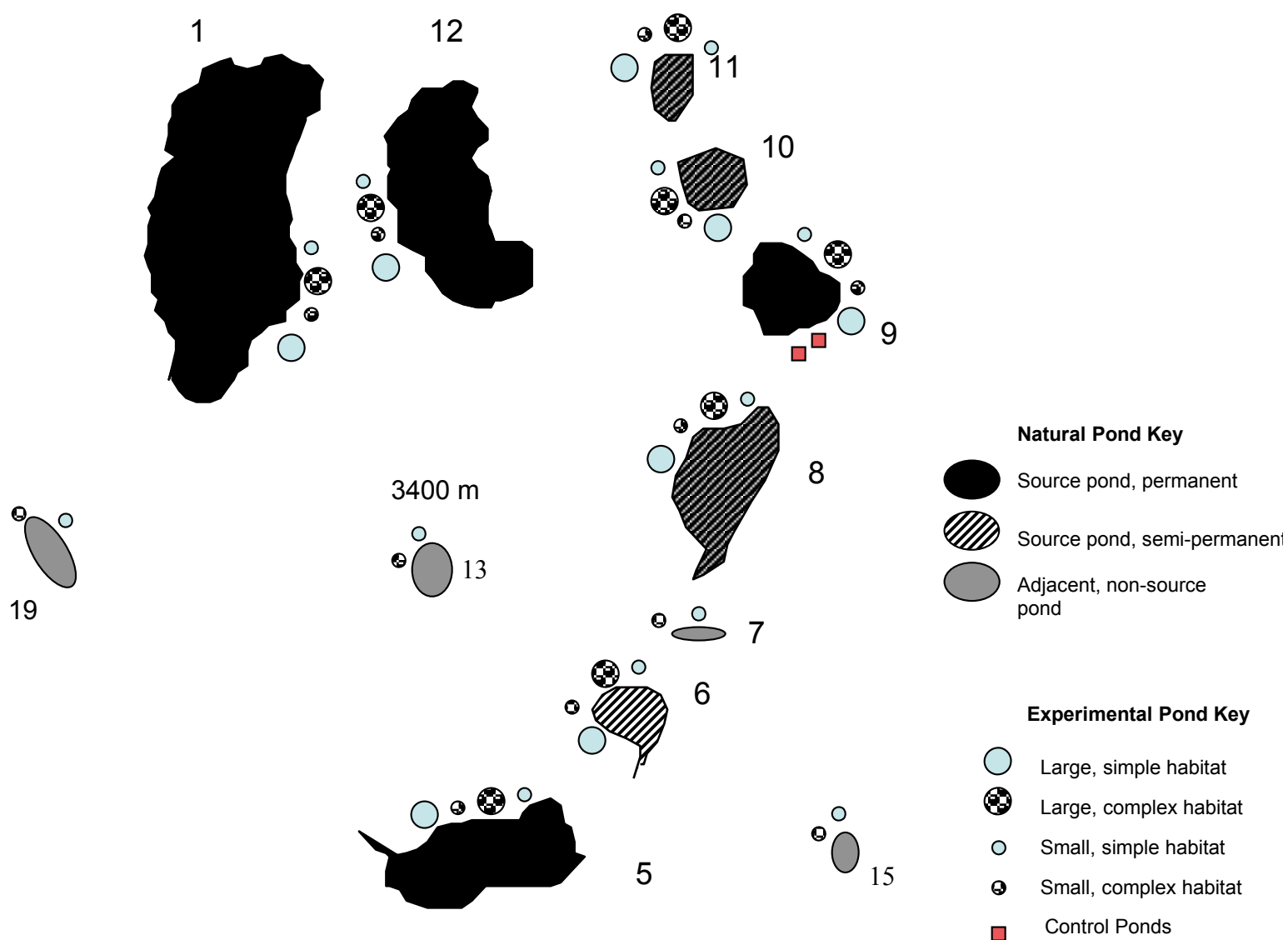


Figure 1: Natural and Experimental Ponds at the Mexican Cut Nature Preserve
(Adapted from Wissinger et al. 1999)

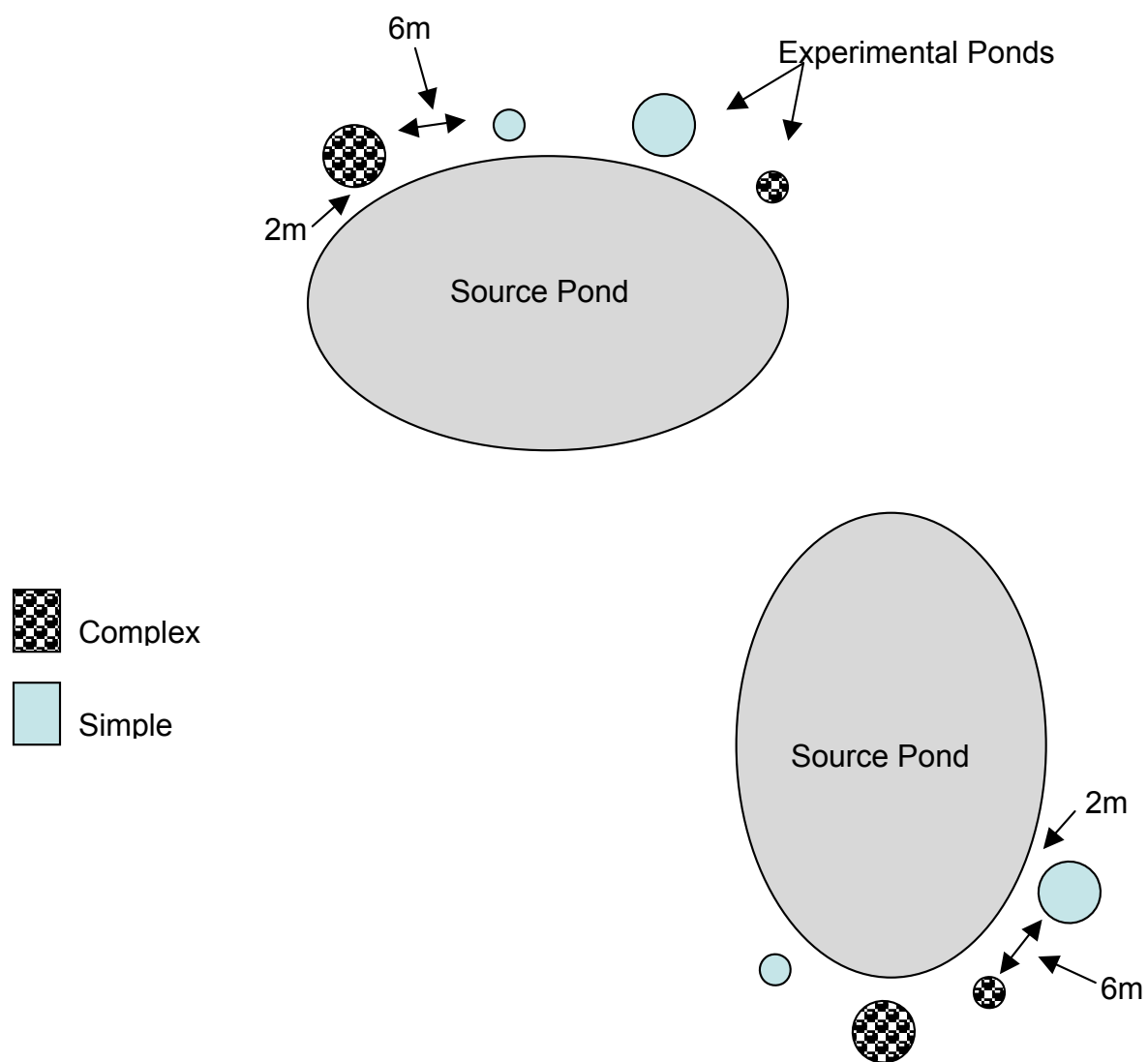


Figure 2: Distance between experimental and source

III. Results

Colonization Vs. Introduction

Over the course of nine days, 18 species were found across all experimental ponds, for a total of 8,527 aquatic colonists (Table 1). Comparatively few aquatic insects were found in control ponds (Table 1). Furthermore, 48 spiral egg masses were found across all experimental ponds, while no egg masses were found in control ponds (Table 1). Spiral egg masses were not identifiable to species; therefore, they were not incorporated into statistical analyses.

Treatment: Size

Experimental ponds around Autumnal and Permanent source ponds:

As illustrated in Figure 1, *aquatic invertebrate abundance* did not differ between large and small experimental ponds ($F_{1, 92} = 1.430$; $p = 0.235$). Similarly, Figure 2 illustrates that *species richness* did not differ between large and small experimental ponds ($F_{1, 92} = 0.665$; $p = 0.417$). Thus, neither invertebrate abundance nor species richness varied with respect to experimental pond size.

Treatment: Complexity

Experimental ponds around Autumnal and Permanent source ponds:

Figure 1 illustrates that *aquatic invertebrate abundance* was higher in complex habitat experimental ponds than it was in simple habitat experimental ponds ($F_{1, 92} = 6.644$; $p = 0.012$). Similarly, Figure 2 illustrates that *species richness* was higher in complex experimental ponds than it was in simple experimental ponds ($F_{1, 92} = 4.899$; $p = 0.029$). Thus, both invertebrate abundance and species richness varied with respect to habitat complexity in experimental ponds.

Experimental ponds around Vernal, Autumnal, and Permanent source ponds:

Figure 5 illustrates that the effect of habitat complexity on *aquatic invertebrate abundance* was lost when experimental ponds around vernal source ponds were compared to those around autumnal and permanent source ponds ($F_{1, 66} = 0.338$; $p =$

0.563). However, Figure 6 illustrates that the effect of habitat complexity on *species richness* persisted when experimental ponds around vernal source ponds were compared to those around permanent and autumnal ponds. Experimental ponds with complex habitats had higher species richness than experimental ponds with simple habitats ($F_{1, 66} = 5.756$; $p = 0.0193$).

Treatment: Hydroperiod

Experimental ponds around Vernal, Autumnal, and Permanent source ponds:

As Figure 3 illustrates, source pond hydroperiod had an effect on invertebrate abundance in surrounding experimental ponds ($F_{2, 69} = 22.969$; $p < 0.0001$). Experimental ponds around vernal source ponds had higher invertebrate abundance than experimental ponds surrounding autumnal ($p < 0.0001$) and permanent ($p < 0.0001$) source ponds. Invertebrate abundance did not vary between experimental ponds surrounding autumnal and permanent ponds ($p = 0.8593$).

Figure 4 illustrates that hydroperiod also had an effect on species richness in experimental ponds ($F_{2, 69} = 12.958$; $p < 0.0001$). Experimental ponds around vernal source ponds had higher species richness than experimental ponds around autumnal source ponds ($p < 0.0001$). Furthermore, experimental ponds around permanent source ponds had higher species richness than experimental ponds around autumnal source ponds ($p = 0.0012$). However, species richness did not vary between experimental ponds around permanent and vernal source ponds ($p = 0.1138$).

Table 1: Aquatic Insect Species List*

	Species	Experimental Ponds (n=40)	Control Ponds (n=2)
1	Purple Midge	163	0
2	Peach Midge	6914	0
3	Green Midge	568	1
4	White Midge	2	0
5	Striped Purple Midge	3	0
6	Spotted Gray Midge	7	0
7	Segmented Worm	73	1
8	Red Copepod	588	0
9	Gray Copepod	144	3
10	Green Copepod	5	1
11	Tan Copepod	21	1
12	Gray Water Flea	19	0
13	Mosquito Larvae	6	0
14	Gerridae	1	0
15	Daphnia	7	0
16	Rat-Tailed Maggot	2	0
17	Agabus Larvae	1	0
18	Midge Larvae	3	0
	Total Number of Aquatic Colonists	8527	7
	Total Species Richness	18	5
	Spiral Egg Masses	48	0

*

Laboratory analysis of preserved specimens will be used to confirm species-level classification

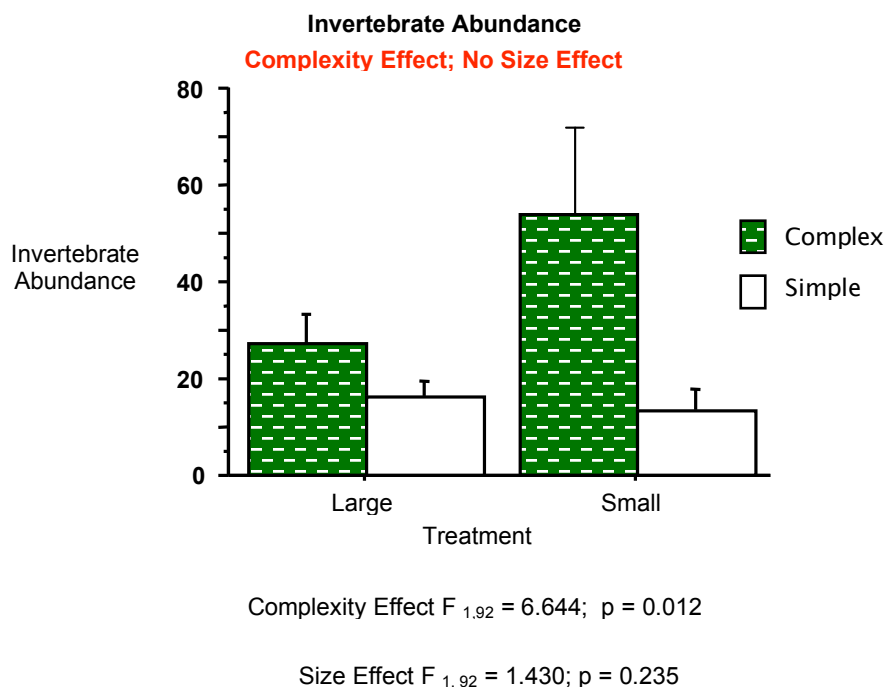


Figure 1: Effect of size and complexity on invertebrate abundance

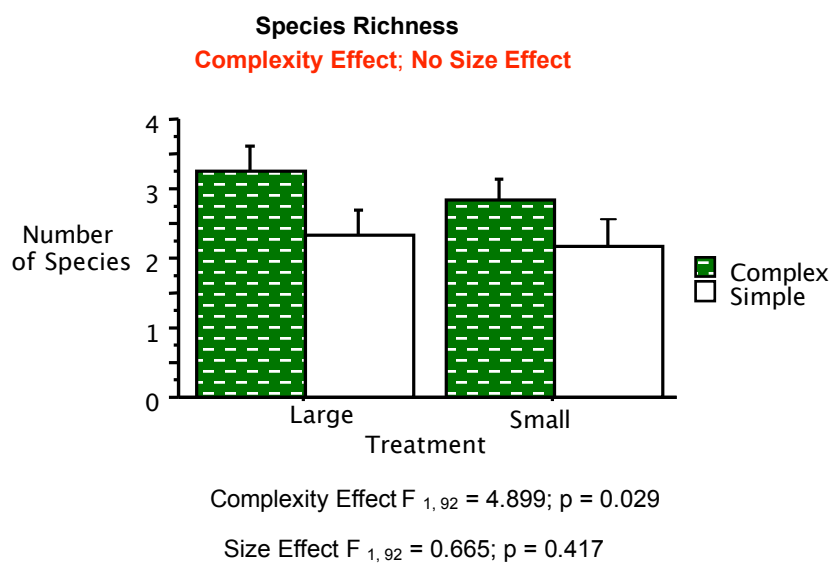


Figure 2: Effect of size and complexity on species richness

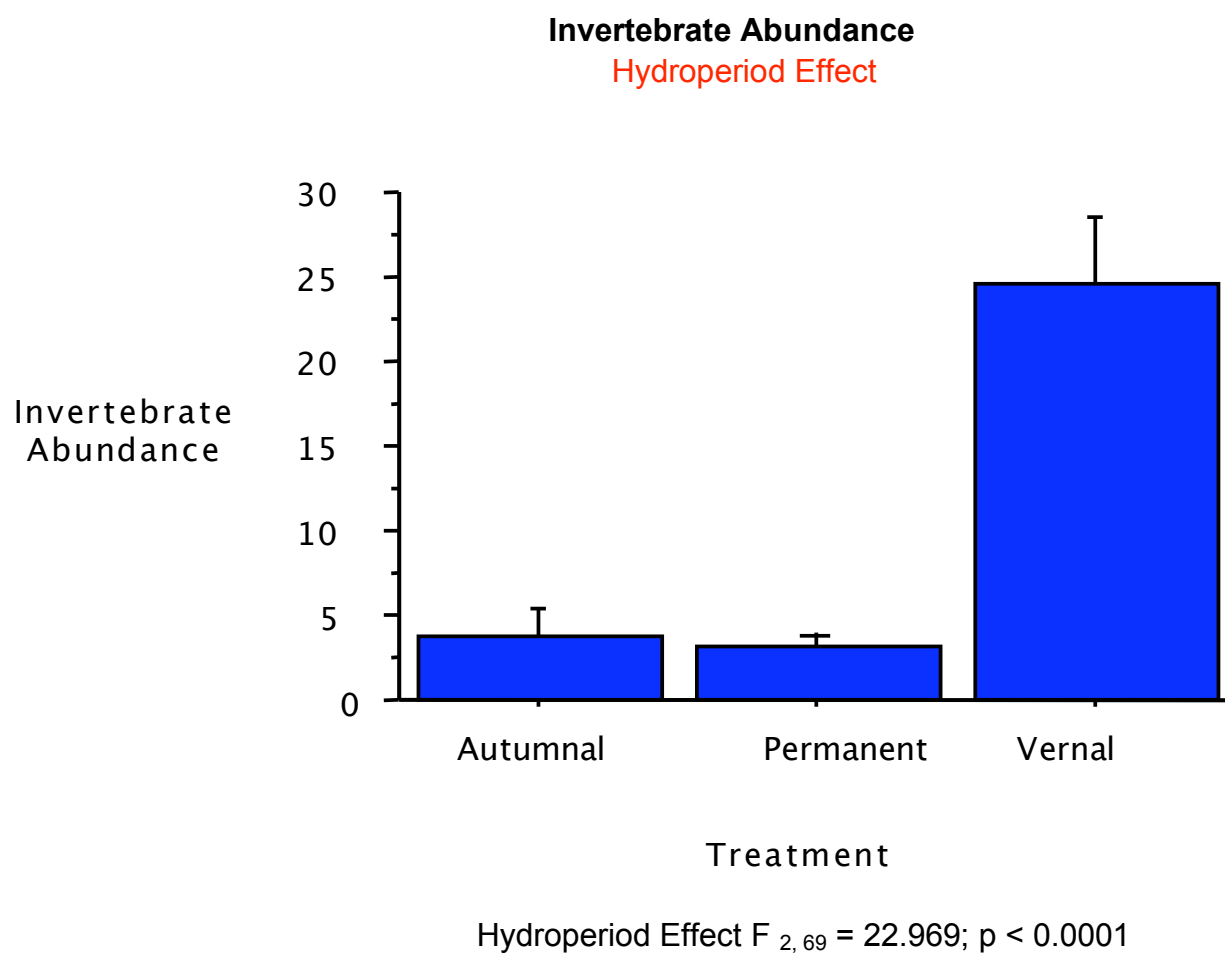


Figure 3: Effect of hydroperiod on invertebrate abundance

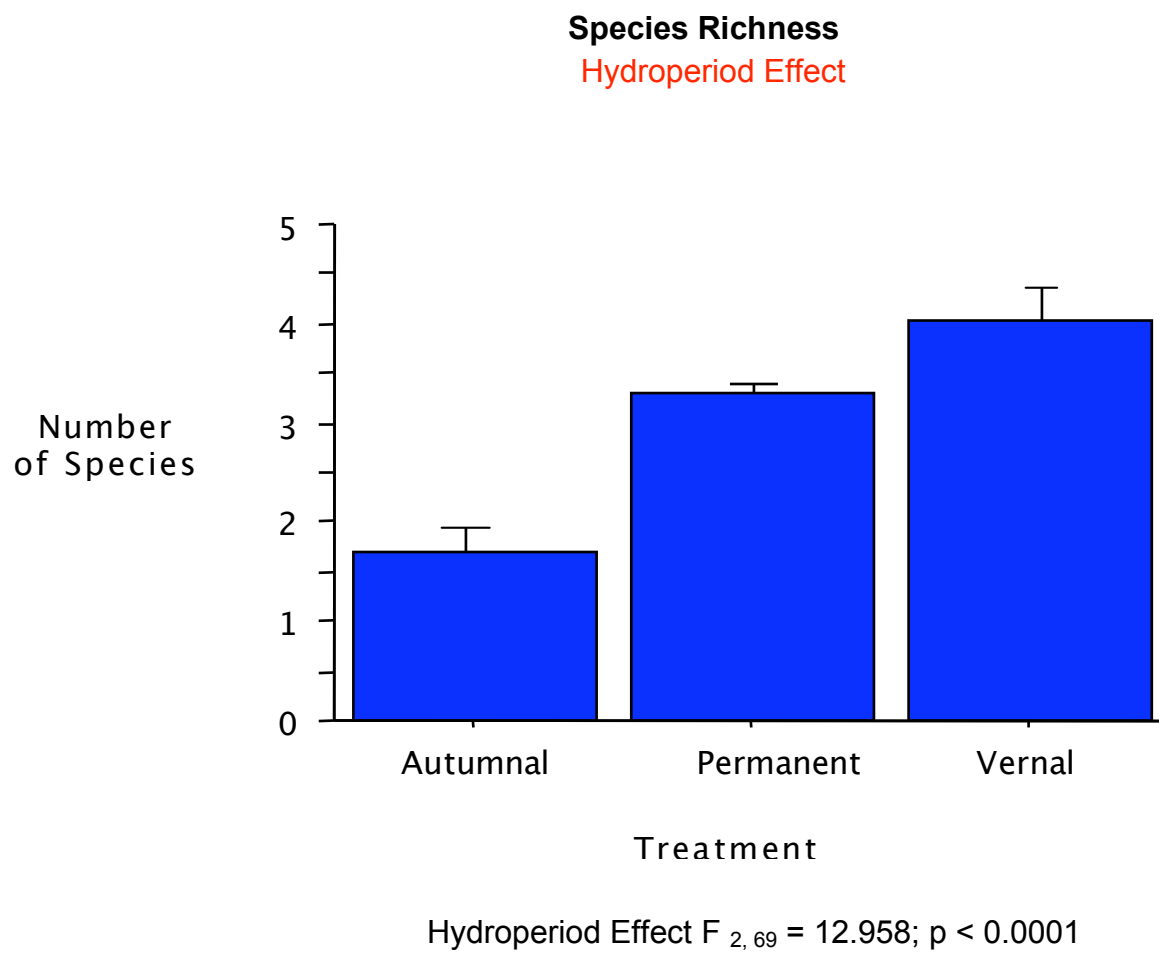


Figure 4: Effect of hydroperiod on species richness

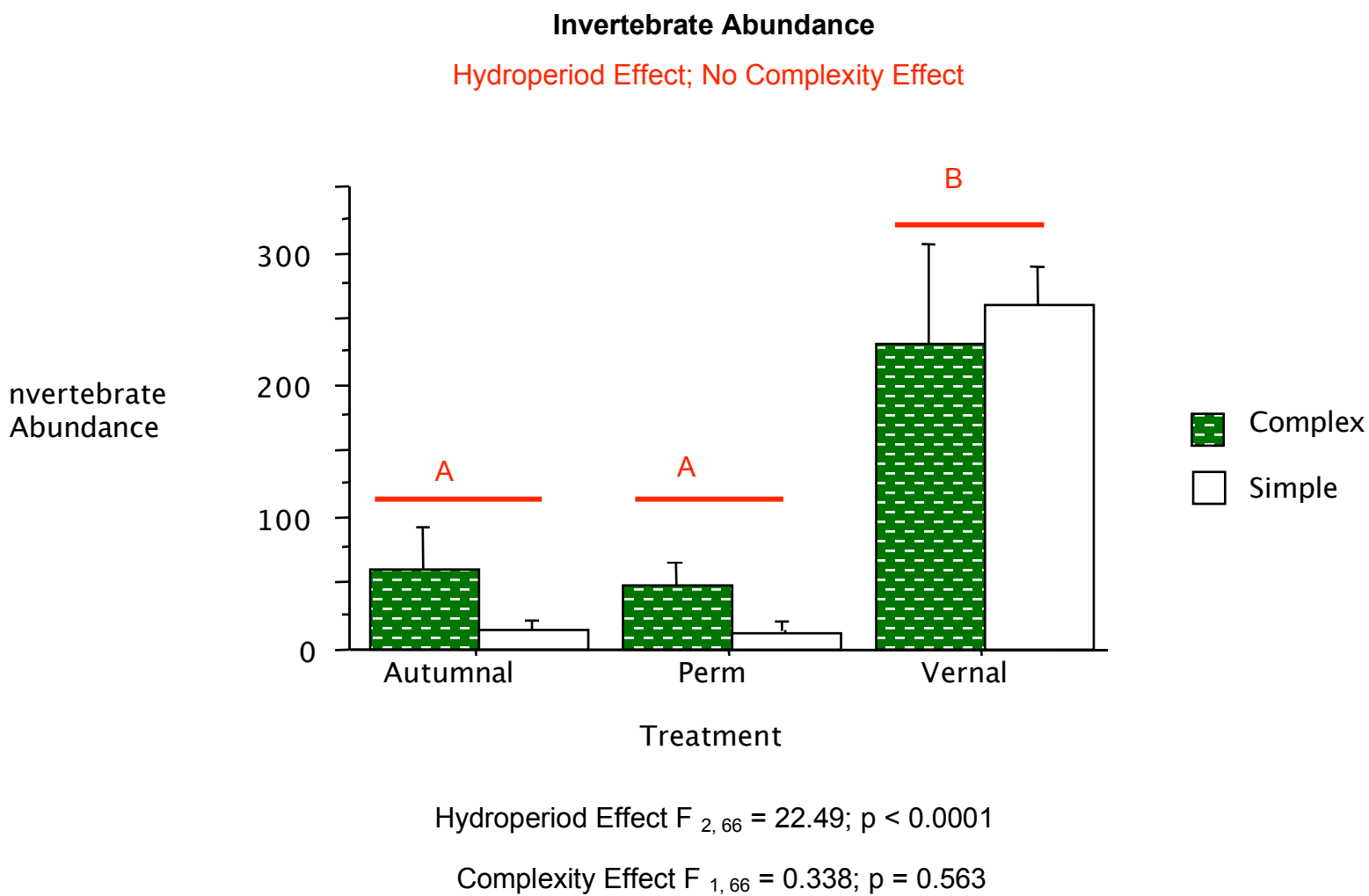


Figure 5: Effect of complexity and hydroperiod on invertebrate abundance

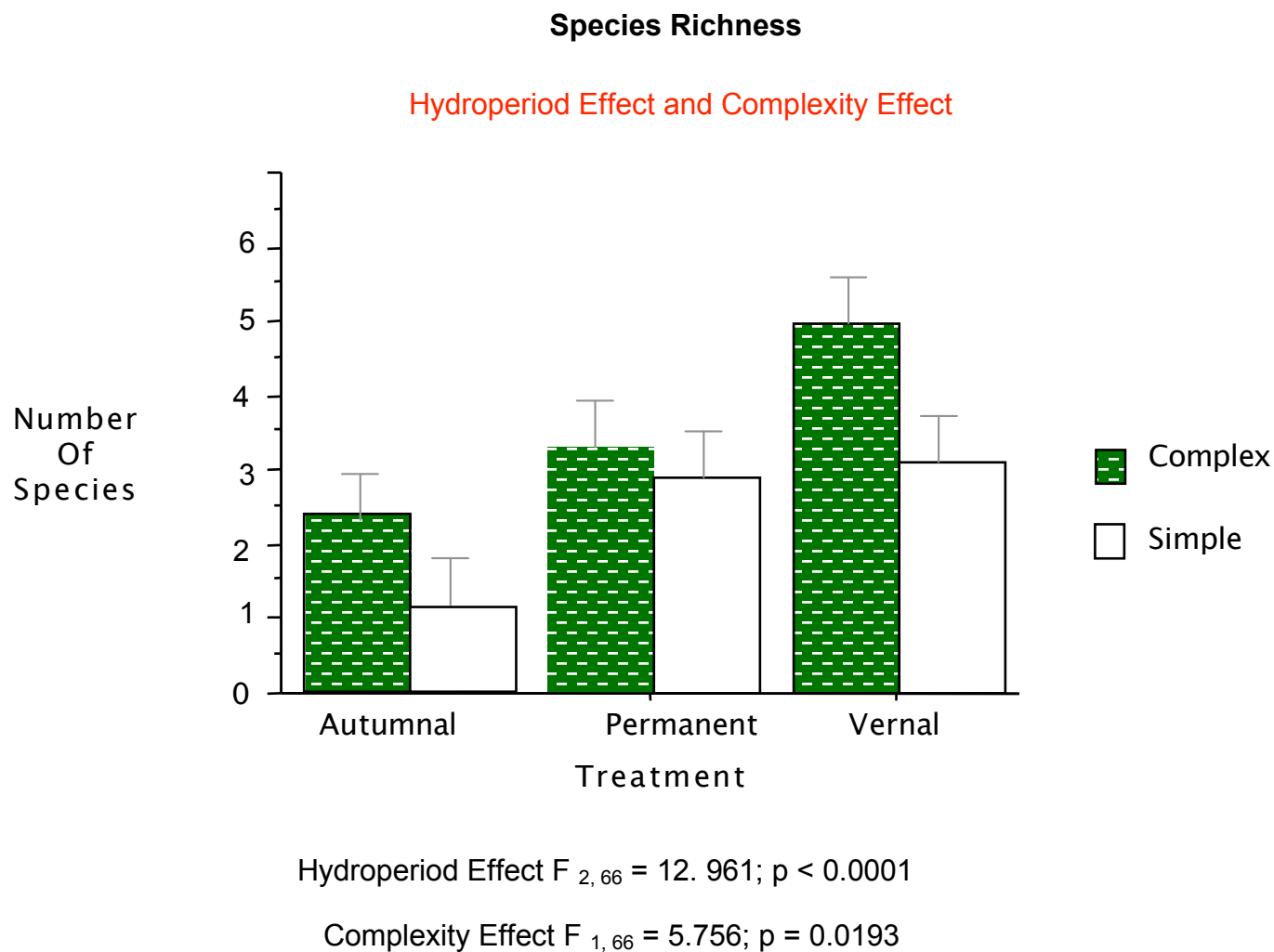


Figure 6: Effect of complexity and hydroperiod on species richness

IV. Discussion

The presence of aquatic invertebrates in experimental ponds and their relative absence in control ponds provide convincing evidence that colonization took place over the course of this experiment. Thus, the variation in patterns of diversity across experimental ponds can be attributed to variation in colonization and/or persistence rates of aquatic insects. This study provides preliminary insight into the patterns and mechanisms of metapopulation dynamics and species-level diversity in sub-alpine wetlands.

More specifically, the results of this study support the hypotheses that habitat-patch diversity is a function of habitat complexity and source community characteristics. The results fail, however, to support the hypothesis that habitat-patch diversity is a function of habitat-patch size. The following discussion not only illustrates the degree to which data support these three hypotheses but also suggests experimental design modifications that will improve the accuracy of future studies.

Hypotheses Supported:

I. Diversity is a function of habitat complexity.

Species richness and aquatic invertebrate abundance were higher in complex habitat-patches surrounding permanent and autumnal source ponds than they were in simple-habitat patches. There are two possible explanations for these results. Primarily, aquatic invertebrates may experience higher persistence and lower extinction rates in complex habitat-patches than they do in simple habitat-patches. Diversity of niche space may facilitate habitat and resource specialization and therefore lead to less inter and intra-species competition. Furthermore, aquatic insects may use rocks, logs, and emergent vegetation to avoid pursuit and capture by predators; mortality rates due to predation may be lower in complex habitats.

Alternately, species-richness and invertebrate abundance may be higher in complex habitats due to higher colonization rates. Aquatic invertebrates may actively select habitats based on the presence of emergent vegetation, submerged rocks, pinecones, and/or decaying wood. Conversely, complex habitats may be more

conspicuous to aquatic colonists due to the presence of these sub-habitats. If so, richness and abundance may be higher in complex habitat-patches due to the higher probability that dispersing insects will locate complex patches in a surrounding matrix of terrestrial habitat.

In habitat-patches around vernal source ponds, habitat complexity had an effect on species richness but no effect on invertebrate abundance. This surprising result may be due to reduced power of vernal pond analyses. Four experimental ponds were placed around each autumnal and permanent source pond, while only two experimental ponds were placed around vernal ponds. Thus, analyses comparing autumnal and permanent ponds had a larger sample size and higher power than analyses comparing autumnal, permanent, *and* vernal ponds. Aquatic invertebrate abundance in habitat-patches around vernal ponds may vary with respect to habitat complexity, and this study may not have enough power to resolve this difference.

On the other hand, environmental stress influencing aquatic invertebrate behavior may explain why abundance did not vary with respect to habitat-patch complexity. During the course of this study, vernal ponds were drying, while autumnal and permanent ponds were not. Under the threat of desiccation, aquatic insects dispersing from vernal ponds may colonize the first habitat-patch they come upon, regardless of its habitat complexity. Aquatic insects dispersing from permanent and autumnal ponds, however, may have the time to locate optimal habitat-patches. If they do not find suitable patches, dispersing individuals from permanent and autumnal ponds may return to their respective source ponds. Insects from vernal ponds, however, may not have this option.

II. *Diversity is a function of source community characteristics.*

Species richness and aquatic invertebrate abundance varied in habitat-patches across vernal, autumnal, and permanent source ponds. There are two explanations for this variation. Primarily, richness and abundance may vary due to differences in the species composition of individual source ponds. Alternatively, variation in habitat-patch diversity may be explained by variation in levels of environmental stress experienced by organisms in ponds with different hydroperiods. For example, habitat-patches around vernal ponds had higher aquatic invertebrate abundance than habitat-patches around both

autumnal and permanent ponds. As discussed above, organisms in vernal habitats faced desiccation threats during the course of this study, while organisms in autumnal and permanent ponds did not. Thus, environmental stress may drive dispersal from drying source ponds, while density-dependent factors may influence rates of aquatic insects in autumnal and permanent source ponds.

In light of earlier discussion, two findings suggest a possible mechanism behind patterns of diversity in sub-alpine wetlands. First, species richness did not vary between habitat-patches around vernal and permanent source ponds. However, richness did vary when vernal and permanent habitat-patches were compared to autumnal habitat-patches. This finding suggests that *source community species-pool* influences *species richness* in surrounding habitat patches. Future studies testing this hypothesis should compare the species-pool composition between source ponds to test the prediction that vernal and permanent communities are more similar to each other than they are to autumnal communities. Second, abundance did not vary between habitat-patches around autumnal and permanent source ponds. However, invertebrate abundance did vary when autumnal and permanent habitat-patches were compared to habitat-patches around vernal source ponds. This finding suggests that *environmental conditions* such as pond drying influence patterns of *invertebrate abundance* in habitat-patches surrounding natural source ponds. Future studies should compare environmental stresses associated with each hydroperiod to test the prediction that pressures on organisms in autumnal and permanent ponds are more similar to each other than they are to pressures on organisms in vernal ponds.

Hypothesis Not Supported:

I. Diversity is a function of size.

Aquatic invertebrate abundance and species richness did not differ between large and small experimental ponds. This result suggests that diversity is not strictly a function of probability. While area may affect competition rates, degree of environmental fluctuations, and magnitude of edge effects, it does not influence colonization and/or persistence rates enough to alter patterns of aquatic invertebrate diversity.

Proposed Improvements:

The scope of this study should be expanded in order to increase the power of statistical analyses. More specifically, large-simple and large-complex experimental ponds should be placed around vernal ponds. Furthermore, sampling should take place multiple times throughout the year, not only to increase sample size but also to determine if patterns of diversity vary over time.

In order to ensure the detection of a size effect, the difference between large and small experimental ponds should be increased. While this study found no effect of area on species richness or abundance, one could argue that a two-fold difference in treatments size was not enough to mimic natural size variation between habitat-patches. Increasing the distance between source ponds would also increase the accuracy of this study by minimizing the potential for cross colonization between ponds of varying hydroperiods. Additionally, increasing experimental pond depth would facilitate thermal stratification in experimental ponds, thereby providing aquatic insects with micro-habitats similar to those found in natural ponds.

The placement of sticky nets around experimental ponds would facilitate the estimation of dispersal to colonization ratios. This information could be used compare the metapopulation dynamics of ponds with varying hydroperiods. Furthermore, estimates of species/ species-pool relationships should be incorporated into future analyses, as should calculations of diversity that take into account both species richness and species evenness. Finally, replication of this study in other areas would be useful to determine whether or not the patterns observed in sub-alpine wetlands of the Elk Mountains are indicative of more general patterns in aquatic invertebrate richness and abundance.

Implications and Applications of Results:

Urbanization, deforestation, and rural development threaten wetland ecosystems across the globe. Increased temperatures and altered rainfall rates associated with global climate change also pose a serious threat to wetlands, many of which depend upon specific hydrological regimes. Thus, for those concerned about the future of wetlands and the diversity of life therein, the results of this study become increasingly important. For example, results suggest that the success of wetland conservation efforts may depend

less on the area and more on the complexity of protected habitats. Furthermore, this study suggests that habitat-complexity may be the primary factor influencing aquatic invertebrate diversity in habitat-patches around autumnal and vernal source ponds, while it may be of secondary importance in patches around vernal source ponds.

More generally, this study suggests that effective preserve design involves more than the simple preservation of large bodies of water. The effects that area, habitat complexity, and source community characteristics have on patterns of diversity vary from pond to pond. Thus, the success of wetland conservation efforts may depend upon a solid understanding of the unique biotic and abiotic characteristics of each endangered source pond.

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