The responses of frogs, toads, and the aquatic community to overlapping disturbance: ecological insights and conservation and management implications

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Abstract

Disturbance is ubiquitous in nature and has been documented to affect ecological levels differently. The ecological effects and responses of biota to multiple disturbances have seldom been documented as a result of the rarity of co-occurring landscape-level disturbances. This Master's thesis aims to discern the effects of the concurrent anthropogenic and natural disturbances at Long Point, Ontario, Canada on two ecological levels: 1) to understand population-level landscape and habitat associations of frogs and toads post-disturbance, and 2) to explore differences in composition and diversity at the aquatic community-level post-disturbance. In my first chapter, I focus on the habitat associations of ranid frogs and the federally endangered Fowler's toad (*Anaxyrus fowleri*) using capture-mark-recapture, visual and acoustic surveys, and minnow traps to understand how the animals were distributed in the landscape following the disturbances. I provide evidence for apparent habitat partitioning between ranid frogs and Fowler's toads post-disturbance and link it to the presence of a dune washout disturbance in the landscape. This chapter also emphasizes the significance of maintaining the natural disturbance regime of cyclic dune washouts to maximize habitats for diverse species. In my second chapter, I further develop this idea and present the Long Point system as a case study where heterogeneous landscapes as a result of disturbances beget diverse assemblages. In this chapter, I assess the distinctions between the assemblages at sites affected by different disturbances and compare their community trajectories over the summer season. I show that the two disturbances generated different environmental conditions, and despite reducing diversity at the site level, especially in areas affected by both disturbances, when considered in conjunction across the landscape, disturbed sites exhibited higher diversity than undisturbed sites. I also identify indicator species of the disturbed habitats that may serve as appropriate study groups for future disturbance monitoring efforts. Overall, my thesis

sheds light on some of the possible effects of multiple disturbances on aquatic communities and populations, clearly demonstrating the importance of maintaining a heterogeneous landscape, which was achieved through the natural disturbance regime being allowed to affect the habitats. This research allows for recommendations for the conservation and management of biota at Long Point, but also acts as a case study of the complex and often taxon-specific responses of biota to multiple disturbances that are occurring at higher frequencies and greater severities globally in the Anthropocene.

Resumé

Les perturbations sont omniprésentes dans la nature et il a été démontré qu'elles affectent différemment les niveaux écologiques. Les effets écologiques et les réponses du biote à de multiples perturbations ont rarement été documentés en raison de la rareté des perturbations concomitantes au niveau du paysage. Cette thèse de maîtrise vise à discerner les effets des perturbations anthropiques et naturelles simultanées à Long Point, Ontario, Canada à deux niveaux écologiques : 1) comprendre les associations de paysages et d'habitats au niveau de la population des grenouilles et des crapauds après perturbation, et 2) pour explorer les différences de composition et de diversité au niveau de la communauté aquatique après une perturbation. Dans mon premier chapitre, je me concentre sur les associations d'habitats des grenouilles de la famille des Ranidae et du crapaud de Fowler (*Anaxyrus fowleri*), une espèce en voie de disparition au niveau federal. À l'aide de le méthode capture-marquage-recapture, d'enquêtes visuelles et acoustiques, et de pièges à vairons j'ai montré comment les animaux ont été répartis dans le paysage après les perturbations. Dans ce chapitre, j'ai pu fournir des indices d'une séparation apparente de l'habitat entre les grenouilles de la famille des Ranidae et les crapauds de Fowler après la perturbation et la relier à la présence d'une perturbation par emportement de dunes dans le paysage. Ce chapitre souligne également l'importance de maintenir le régime de perturbation naturelle des dunes cycliques afin de maximiser les habitats pour diverses espèces. Dans mon deuxième chapitre, je développe cette idée et présente le système Long Point comme une étude de cas où des paysages hétérogènes résultant de perturbations engendrent des assemblages divers. Dans ce chapitre, j'évalue les distinctions entre les assemblages sur des sites affectés par différentes perturbations et compare leurs trajectoires communautaires au cours de la saison estivale. Je montre que les deux perturbations ont généré des conditions environnementales différentes et,

malgré une réduction de la diversité au niveau du site, en particulier dans les zones affectées par les deux perturbations, lorsqu'ils sont considérés conjointement à l'échelle du paysage, les sites perturbés présentaient une diversité plus élevée que les sites non perturbés. J'identifie également des espèces indicatrices des habitats perturbés qui pourraient servir de groupes d'étude appropriés pour les futurs efforts de surveillance des perturbations. Dans l'ensemble, ma thèse met en lumière certains des effets possibles de multiples perturbations sur les communautés et les populations aquatiques, démontrant clairement l'importance du maintien d'un paysage hétérogène, obtenu grâce au régime de perturbations naturelles qui a pu affecter les habitats. Cette recherche permet de formuler des recommandations pour la conservation et la gestion du biote à Long Point, mais sert également d'étude de cas sur les réponses complexes et souvent spécifiques à un taxon du biote à de multiples perturbations qui se produisent à des fréquences et des sévérités plus élevées à l'échelle mondiale dans l'Anthropocène.

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Contributions of the authors

Chapter 1: Disturbance-caused landscape heterogeneity allows multiple anuran populations to persist in a dynamic wetland complex

Victoria Tawa and David M. Green designed the study; Victoria Tawa collected the data, performed data analyses, and wrote the manuscript with input from Doug Tozer and David M. Green.

Chapter 2: Responses of an aquatic community to two overlapping, multiple disturbances

Victoria Tawa and David M. Green designed the study; Victoria Tawa collected the data, performed data analyses, and wrote the manuscript with input from David M. Green.

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is indicated as the bold line across the box, and any data outside these whiskers are plotted as outlying points.

General Introduction

Disturbance

Disturbance is now recognized as an integral mechanism in creating structure in landscapes and forming ecosystems, appreciated for much more in ecology than simply its role in Clementsian climax community (Clements 1916) and successional dynamics (McIntosh 1985). Prior to the 1970s, disturbance was not a major focus of study, nor was it acknowledged for the functions and processes that we know are fundamental in structuring ecosystems (Levin and Paine, 1974), driving community structure (e.g. Connell 1978), and resulting in population-level consequences (e.g. Sousa 1984) (Turner 2010). Disturbances were most often thought of as rare and uncommon events that would prevent the attainment of the equilibrium state of natural ecosystems (With 2019). The concept of disturbance as the foundational patch-creating process as we know it today was first convincingly presented in the 1980s by White and Pickett (1985). An imminent paradigm shift away from the equilibrium theories that dominated the previous century was predicted and White and Pickett (1985) argued that natural ecosystems are more often dynamic than not (e.g. Delcourt et al., 1983). In consequence of this influential book, natural disturbances have since been recognized as major determinants of ecological community properties, drivers of patch dynamics, and overall landscape heterogeneity.

There have been many definitions of disturbance through its history of study, each claiming to improve the previously accepted definition. A definition of disturbance should consider the multifaceted processes in which it can originate and its effects, while also applying to a wide variety of systems and considering the scales on which disturbance can act. In this thesis, I will use the definition provided by White and Pickett (1985), who primarily consider the effects on biota and the abiotic responses to define disturbance, where a disturbance is “any relatively discrete event in time that disrupts ecosystem, community, or population structure, and changes resources, substrate availability, or the physical environment". Although a widely accepted definition, and useful for my purposes, using a biotic effect-centered definition such as the definition by White and Pickett (1985), limits the description and comparison of disturbances in different ecosystems. As such, the importance of characterizing disturbances by their input properties, like size, intensity, type, duration, and predictability has since been advocated (Lake 2000). Each of these input factors can vary and thus act to differentiate and describe disturbances. For example, a disturbance can be characterized by its position on a size continuum, ranging from naturally occurring instabilities to naturally sizable destructive events (White and Pickett, 1985). Disturbances can be further classified as abiotic, biotic or some mixture of both (e.g., the abiotic fire and the biotic fuel it requires). The source of disturbance can be a natural part of ecosystem dynamics, or disturbance can be anthropogenic in nature, resulting from some human-activity affecting the natural environment. Further, it is essential to note that disturbances, anthropogenic or natural, also occur at diverse spatial and temporal scales (Zelnik et al., 2018); representing important characteristics of what defines the disturbance regime of a landscape.

Disturbance regimes and heterogeneity

In a particular landscape and over time, the spatial and temporal pattern of disturbances dictates the disturbance regime (White and Pickett 1985). Thus, the disturbance regime of a given landscape comprises of the patterns in the severity, frequency, and timing of disturbance over space and time. Vegetation structure (Cheplick 2017), water cycles (Boisramé et al., 2019), biodiversity (Vanschoenwinkel et al., 2013), and community composition (Fahrig et al., 1993; Paine and Trimble, 2004) are just some of the characteristics and processes of a landscape that the disturbance regime can dictate. These processes also interact with each other, rendering disturbance regimes among the most complex and intricate factors that influence dynamics and biodiversity at the landscape-level (Keane 2017). These intricacies in natural disturbance regimes can be easily disrupted with the introduction of one or more anthropogenic disturbances, which can alter the characteristics of the regime, and can result in cascading effects. For example, the cyclic fire-regrowth dynamics are being altered as wildfires' weather seasons become longer (Jolly et al., 2015) as a consequence of climate-change. Humans are also stabilizing shorelines and natural dune barriers, disrupting the dynamic stability of the dunes (Davidson-Arnott and Fisher, 1992). As a result of their complexities, natural disturbance regimes tend to be characteristic of a particular landscape or a landscape type, defining the patterns of dynamism and landscape heterogeneity of that area and shaping numerous ecological systems.

Disturbance is both the cause and effect of heterogeneity in nature. Across space and time, heterogeneous landscapes exhibit variability in their biological, chemical, and physical characteristics (Larkin et al., 2016). While disturbance is typically thought of as a process to bring about variability and diversity in nature at all ecological levels, its effects are also influenced by these same properties. Under some conditions, disturbance can result in landscape change, decreasing or increasing landscape heterogeneity (Denslow 1985), where habitats within the landscape become more similar, or more dissimilar, respectively. In addition, landscape-level heterogeneity may prevent or augment the advancement of disturbance (Risser et al., 1984), influencing the distribution of the disturbance effects. The dual nature of heterogeneity as an effect of disturbance and a catalyst or inhibitor of disturbance further confounds its comprehension in the field of disturbance ecology.

Scale dependence and measuring the effect disturbance-mediated heterogeneity

Figure E1.

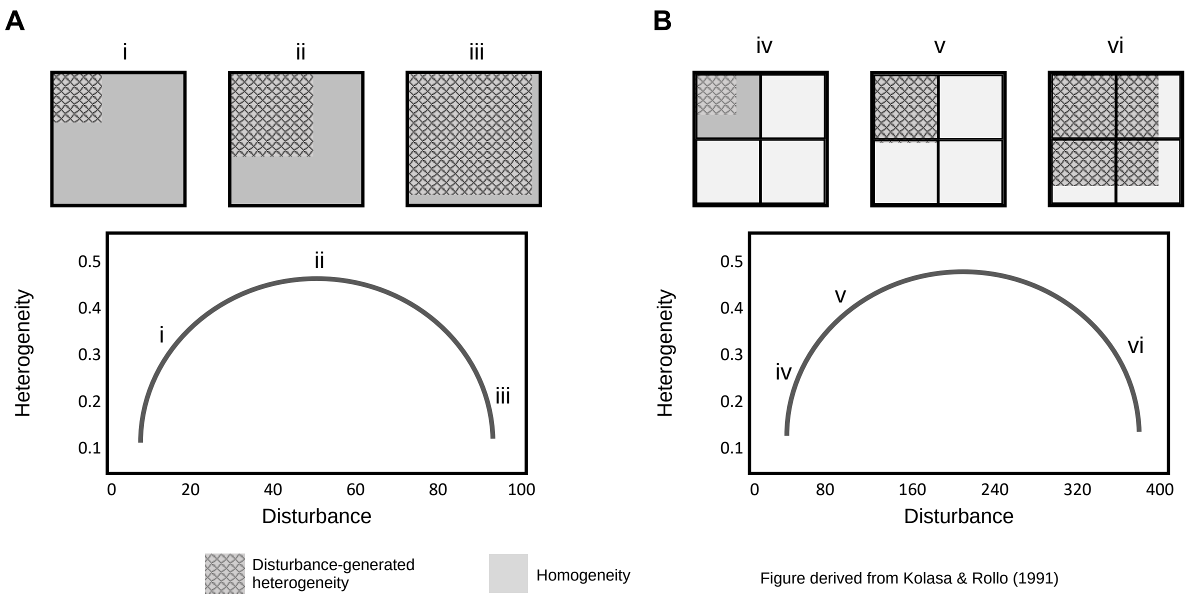

Figure E1. The scale dependence of studying disturbance-mediated heterogeneity. Cross-hatched areas in the figure represent heterogeneity brought about by disturbance, while the solid grey areas represent an initial state of homogeneity. Patch states numbered i-vi in (A) and (B) are labelled along their respective disturbance-heterogeneity curves. This figure is adapted from Kolasa and Rollo (1991).

Under the assumption of a homogenous landscape where disturbance generates heterogeneity and only one habitat patch is considered, increasing disturbance has been hypothesized to create a hump-shaped pattern of heterogeneity, where some intermediate level of disturbance generates the most heterogeneity and low and high levels of disturbance generate less heterogeneity (Fig. E1A) (Kolasa and Rollo 1991). In this case, after heterogeneity reaches approximately 50% (Fig. E1A ii), disturbance begins to homogenize the patch and reduce heterogeneity. If the same patch is considered but it is considered among one of four patches that make up a larger landscape (Fig.

E1B), we begin to see the importance of scale. Here Figure E1A ii is equivalent to Figure E1B iv and Figure E1A iii is equivalent to Figure E1B v in terms of disturbance extent. In this example, there is less heterogeneity in the landscape at point iv in Fig. E1B than in ii in Fig. E1A, and contrarily, there is more heterogeneity in the landscape at point v in Fig. E1B than at point iii in Fig E1A. This exercise clearly demonstrates the role of scale in the study of disturbance, where while a large disturbance may homogenize a landscape at a small scale, it may increase heterogeneity at a larger scale. For example, if a study is performed at a small-spatial scale, one might be more likely to find negative effects of disturbance on heterogeneity (and thus, diversity), than if one studied the same disturbance at a larger-scale. Indeed, studies on birds that considered a large-spatial scale compared to studies that considered a small-spatial scale, were more likely to discover a positive effect of disturbance on species diversity (hypothesized to be a result of increased heterogeneity) (Hill and Hamer, 2004). This positive relationship between environmental heterogeneity and species richness is well known and has been shown in enough prevalence to be considered to be a general rule (Ortega et al., 2018).

A primary goal of disturbance ecology is to measure the effects of a disturbance, usually in the form of biotic response, at a particular ecological scale, that is, the physiological-, individual-, population-, community-, or ecosystem-level. At a given disturbance magnitude, the effect a disturbance has on the biota may depend upon several factors including: the sensitivity of the ecosystem (resistance and resilience dynamics) (Nimmo et al., 2015), the sensitivity of the community (diversity and structure) (Martin-Smith et al., 1999; Micheli et al., 1999), and/or the sensitivity of the organisms involved (abundances and individual indices) (McKenna et al., 2022). However, when just one ecological level is studied, the extent to which disturbance effects can be understood is limited, as some disturbances affect only some ecological scales or affect scales differently (Simmons et al., 2021). Likewise, even within each scale, some aspects of biotic response might be altered, while others not. The effect of disturbance may be missed if its biotic effects occur at one ecological scale, but not another, or within one scale, disturbance affects one aspect of biological response but not others. For example, at the community-level, due to their habitat-preferences, some species may be pushed out of a recently disturbed habitat, altering the community composition and reducing alpha diversity at that site, but not necessarily having this same effect when the larger, landscape-scale is considered. For reasons such as this, to best understand the full biotic effects of a disturbance, research should aim to bridge ecological scales (Graham et al., 2021).

Multiple Disturbances

The fundamental role disturbance plays in ecology is now well-established, but some of its intricacies are still not well understood, such as when multiple disturbances occur in succession. In Monica Turner's (2010) perspective paper, interacting disturbances were noted as a priority for future research as projected changes in disturbance regimes occur, and in many cases, as disturbances occur at higher frequencies and higher intensities. Where multiple disturbances occur it is likely that they cause non-linear changes or "ecological surprises" (Paine et al., 1998), resulting in an outcome that is not simply the additive effect of the component disturbances (Jackson et al., 2016). The characteristics of subsequent disturbances may be altered as disturbances overlap, which can modify the natural regime and result in a chain of lingering effects across scales (Buma 2015). Compounded, overlapping disturbances, as with single disturbances, might result in alterations at all ecological levels, except that the changes as a consequence multiple disturbances are less predictable than their single components (Paine et al., 1998; Coté et al., 2016).

It is expected that as disturbance regimes change or are disrupted by anthropogenic pressures that the importance of understanding biotic responses to multiple disturbances will become augmented, especially when considering how to best conserve sensitive species and ecosystems.

Frogs, toads, and rest of the aquatic community: roles in the environment

As adults, Anura, frogs and toads, are mobile organisms and are not limited to the single freshwater system they were limited to as tadpoles. Despite this, at both parts of their lifecycle Anura are sensitive to changes in the environment due to their semi-permeable skin and their dual lifestyle as aquatic and terrestrial amphibians (Alford and Richards, 1999). As such, these animals have been acknowledged as important bioindicators of environmental changes (Storfer 2003) and are considered to serve as important model organisms for studying habitat alteration and disturbance (Foster et al., 2020; Gabrielsen et al., 2022). Anura represent 90% of amphibians (Bossuyt and Roelants, 2009) and the dual life of amphibians means they represent an important conduit for energy transfer between aquatic and terrestrial habitats (Capps et al., 2015). Although Anura can represent a large part of some ecosystems (Gibbons et al., 2006), they are also part of the greater aquatic community. Specifically, they act as predators and prey throughout their lives (Beranek et al., 2023) and link the aquatic to the terrestrial habitats through nutrient and energy input (Capps et al., 2015). Freshwater wetland communities have been noted as useful systems for studying disturbance response due to their prevalence in the landscape and their susceptibility to change (Woodward et al., 2010). Thus, like some of their component animals, anurans, freshwater wetland communities also represent effective ecological indicators of larger ecosystem changes and disturbance (De Meester et al., 2005).

This thesis

Background: Homogeneity as an initial state

In terms of biotic responses, when there is decreased landscape heterogeneity, fewer species requirements are met and there may be more competition due to an inability to partition the habitat, resulting in a less diverse assemblage maintained. An example of this can occur when a habitat-forming invasive species, a plant, becomes a dominant in a landscape. That invasive species might change the landscape, pushing out other vegetation, and homogenizing the area. This is what has occurred in Long Point, Ontario, Canada, a 35km long sandspit on the northern shore of Lake Erie. Here and in many other places in the Great Lakes, the European common reed, *Phragmites australis australis* (hereafter *Phragmites*) has redefined the landscape. *Phragmites* is a perennial wetland grass that grows in tall, dense stands, and in the previously diverse great lakes region, the establishment of the invasive reed has created large swaths of *Phragmites* monocultures. *Phragmites* outcompetes native vegetation and drastically modifies the physical environment, filling inland waterbodies and spreading to the wetland-beach interface of Lake Erie. At Long Point, the landscape alteration from *Phragmites* invasion has negative impacts on native biota (reptiles, amphibians, and birds) (Markle and Chow-Fraser, 2018; Greenberg and Green, 2013; Tozer 2016) and has resulted in extensive effort to eradicate the reed from the landscape. In 2016, Long Point was the location of the first large-scale effort in Canada to eradicate the reed directly within standing water (Robichaud and Rooney, 2021). The formula of the herbicide application was deemed unlikely to have any direct toxicity to the organisms (Robichaud and Rooney, 2021) and following the success in the Crown Marsh Region in 2016, more areas within the Long Point Provincial Park and the Thoroughfare Unit of the federal National Wildlife Area were sprayed by joint effort of federal, provincial, and non-governmental agencies in the Fall of 2020.

Background: Heterogeneity caused by disturbances

These eradication efforts, represent a landscape-modifying disturbance. The reeds were sprayed, by air or land, and rolled over with heavy machinery, aimed to push the reeds down and allow the downed *Phragmites* to decompose in the standing water of the marsh. In this case, efforts to eradicate the reed via herbicide-application and mechanical roll-over were not evenly distributed in the landscape and thus patches of disturbance were introduced in the previously homogenized landscape. This elevated landscape heterogeneity had the potential to produce diverse habitats and microhabitats, in which more species' environmental requirements may be met, reducing competition, allowing coexistence and thus more diverse species assemblages to establish. In addition to these planned efforts, there was a co-occurrence of a natural disturbance. The high lake levels of Lake Erie had been eroding the barrier sand dunes that previously protected the marsh of Long Point from the lake. This erosion is one step in the cyclic dune washover and reformation process at Long Point (Davidson and Arnott, 1992). Following the erosion of the dunes, a large storm seiche over the winter of 2020 propelled the cycle into its next step, dune washover. This part of the cycle has been prevented in much of the proximal end of the sandspit by hard barriers to protect cottages and dune stabilization to protect campsites. As a result, the landscape had not experienced such a washover in several decades. As these barriers still stand in some areas, this natural disturbance was also unevenly distributed in the landscape. In this case, whereas an established sand dune might foster homogeneity behind its banks, when it is washed over and the dune is reduced or destroyed, washover fans and wave action following the disturbance can generate heterogeneity within the landscape.

Objectives of this thesis

This thesis aims to provide evidence of multiple disturbances as a heterogeneity-creating process that can provide distinct habitats for different taxa, allowing coexistence between species and creating diverse communities. Utilizing the relatively homogenized landscape where two disturbances co-occurred, one natural dune washover and one anthropogenic herbicide application, I created a pseudo natural experiment of disturbance types. First, I wanted to assess the impacts of the disturbances on frog and toad habitat associations, given their role in the ecosystem and their environmental sensitivity. Second, I wanted to understand how the different disturbances might affect the aquatic community these frogs and toads are a part of, as each disturbance and the combination of the disturbances would likely act as distinctive stressors and affect different taxa and assemblages in various manners. The goal of this research was to bridge ecological scales by considering disturbance responses at the population-level and community-level, provide insights on the importance of each disturbance in shaping any changes observed at either scale, and to consider the consequences of multiple disturbances and the resulting implications in single-species conservation and entire ecosystem restoration efforts.

Chapter 1: Natural disturbance allows multiple anuran taxa to persist in a dynamic wetland complex

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Natural disturbance allows multiple anuran taxa to persist in a dynamic wetland complex

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ABSTRACT

The maintenance of biological diversity is frequently enhanced in a heterogenous landscape produced by some level of disturbance. Thus, when a landscape becomes stabilized and homogenized through the spread of an invasive plant species, there may be severe consequences for native biodiversity, particularly for those biotas that depend on the pre-existing, natural disturbance regime of that landscape. It is possible that only major disturbances may be consequential enough to reset such an environmental system. At Long Point, Ontario, Canada, a sandspit in Lake Erie, the community of anuran amphibians has experienced the co-incidence of two major disturbance events, one anthropogenic and one natural: an intervention to remove the invasive form of the reed, *Phragmites australis*, and a spate of extensive dune washouts caused by high water levels and storms. As a result of the unequal distribution of disturbance in the landscape, some areas within the study area were directly affected by the dune washouts alone and not the *Phragmites* treatment, while some were not affected by the washouts and only by the *Phragmites* treatment. There were also areas affected by both disturbances and some unaffected by either disturbance. With these four site types, representing four different regimes of disturbance, we explored how these disturbances affected the resident frog and toad species habitat associations using minnow traps, acoustic surveys, and visual surveys. Of the two disturbances, the dune washouts had the greater impact on resident anurans. Ranid frogs (Ranidae) tended to inhabit non-washout sites, whereas Fowler's toads (*Anaxyrus fowleri*) congregated in the newly formed, open sand flats and shallow, de-vegetated pools resulting from the washouts. Neither ranid frogs, nor Fowler's toads demonstrated avoidance of the sites affected by the herbicide-treatment and mechanical rollover of the *Phragmites*. This evidence of species-sorting, which can enable multiple species to persist in a dynamic and heterogeneous landscape, suggests that wildlife management in aid of threatened species recovery may find success by encouraging natural disturbance regimes in dynamic landscapes.

KEYWORDS

Anaxyrus fowleri, biological diversity, herbicide, landscape heterogeneity, Long Point, active management, *Phragmites australis*

Landscape heterogeneity is a principal predictor of biological diversity (Benton et al. 2003, Fahrig et al. 2011, Wiens 1997). A heterogeneous landscape consisting of a diversity of vegetation and land cover types provides environmental conditions suitable for a diversity of different species and species assemblages (Oliver et al. 2015). Such heterogeneity in environmental conditions may arise within a landscape through disturbance (Risser 1987). A disturbance can be defined as any relatively discrete disruptive incident affecting the structure of an ecosystem, community, or population, and in turn leading to changes in resources, substrate availability, or the physical environment (White and Pickett, 1985). Disturbances can be further classified by their input properties, like size, intensity, type, duration, and predictability (Lake 2000) and their severity; the effect on an organism, population, community, or ecosystem in question (White and Pickett, 1985). Many forms of disturbance are natural parts of ecosystem processes affecting the distribution and composition of natural communities (Sousa 1984) but, when severe, may have major consequences for biota (Grant et al. 2015). However, the relative rarity of major natural disturbances often limits the extent to which their effects may be studied systematically (Foster et al. 2020; Grant et al. 2015). Anthropogenic disturbances, like natural disturbances, can also range in severity and other input properties (Albuquerque et al. 2018; Seaborn et al. 2021). These human-caused disturbances, though they can take on similar attributes to natural disturbances, differ from the natural processes. Perhaps most importantly, some organisms are adapted to the changes resulting from natural disturbances and some require these disturbances (e.g. early-successional stage specialist species); but these same organisms may not be equipped to adapt to or evolve with anthropogenic disturbances (Reed et al. 2021). For example, eradication efforts to deal with an invasive species may represent one type of anthropogenic disturbance that are generally swift and often disruptive to organisms (Sievers et al. 2020; Swartz et. al. 2020).

Disturbances have been recognized as major determinants of ecological properties, such as where species occur and may coexist (Denslow 1985). Different taxonomic groups respond to changes in the landscape and their environment differently, and as a result of diverse causal factors. Generally described as species-specific responses, species have been shown to exhibit differing levels of resistance to disturbance (Walls et al., 2014) and varying recolonization rates based on the successional stage of the landscape post-disturbance, as distinct species-specific habitat requirements are met (Letnic and Fox, 1997). As such, when a landscape is disturbed, by natural or anthropogenic means, and heterogeneity introduced, there may be alterations to distribution of organisms. This is especially true for mobile species like frogs and toads that may be able to track desirable environmental conditions and distribute themselves across the landscape based on their habitat type preferences (Graeter et al. 2008).

Anuran amphibians (i.e., frogs and toads) represent 90% of amphibians (Bossuyt and Roelants, 2009) and the dual life of amphibians means they represent an important conduit for energy transfer between aquatic and terrestrial habitats (Capps et al., 2015). Anura are valuable bioindicators of the effects of disturbance and often, the subsequent success of wetland restoration projects (Mester et al. 2015). Abundances of frogs and toads tend to vary in accordance with their biotic and abiotic species-specific habitat requirements (Letnic and Fox, 1997, Walls et al. 2014). For example, in Canada, American bullfrogs (*Lithobates catesbeianus*) utilize well-established marsh habitats as their tadpoles often overwinter and require permanent water, Green frogs (*Lithobates clamitans*) inhabit a variety of wetland habitat types with emergent and submerged vegetation, and Northern leopard frogs (*Lithobates pipiens*) inhabit grassy meadows, as well as grass and marshland pools. In Canada, endangered Fowler's toads (*Anaxyrus fowleri*), require early successional habitats characterized by sand flats and beaches for foraging and shallow sandy pools for breeding (Green et al. 2011). The loss of early successional habitats to invasive *Phragmites* is thought to have contributed to the Fowler's toads' historically low abundance in Canada in recent years (Greenberg and Green, 2013). How these different anuran species, with such varying habitat requirements, respond to disturbances, alone and in combination, is unclear, but is important for improving frog and toad conservation and management in dynamic wetland ecosystems. On rare occasions in dynamic systems like coastal wetlands, a planned anthropogenic intervention, such as invasive species eradication, can coincide with a major natural disturbance process, enabling the relative effects of the disturbances to be directly compared in nature.

In Long Point, a wetland community experienced a chance overlap of two disturbance events. The invasive form of the common reed (*Phragmites australis australis*) was treated with a glyphosate-based herbicide and mechanically rolled-over, and as a result of seiches, storm surges, and Lake Erie's high-water levels, sand dune washouts occurred, resulting in dramatic landscape modifications. *Phragmites* eradication epitomizes an anthropogenic disturbance (Sullivan and Sullivan, 2003) whereas the dune washout is one step of a cyclical process of dune overwash and reformation that occurs in Long Point, and represents a natural, habitat-modifying disturbance (Davidson-Arnott and Fisher, 1992; Hesp 2002). Both disturbances have the capacity to increase vegetation and land cover heterogeneity hence altering the distribution and potentially increasing the biodiversity of the resident organisms (Edge et al. 2020; Ward 1998). Despite the documented benefits of removing the reeds for many different species, the method of *Phragmites* eradication may have non-target effects such as hypoxia due to nutrient input from the activities of decomposing aerobic and anaerobic bacteria decaying the vegetation (Polunin 1984) and to a lesser extent, the degradation of glyphosate molecules (Fugère et al. 2020, Hébert et al. 2019, Tu et al. 2001). The increased quantity of decaying vegetation may increase the surface area available for bacterial growth, which may in turn lead to higher microbial respiration resulting in a reduction in dissolved oxygen (Hall and Meyer, 1998). The depletion of dissolved oxygen as a consequence of reed bed decay has the potential to cause die-off of wetland biota (Abdel-Tawwab et al. 2019). Bufonid toads (Bufonidae) do not acquire lungs as tadpoles, whereas ranid frogs (Ranidae) develop lungs at later tadpole stages (McIntyre and McCollum, 2000), which suggests that toad tadpoles may be most sensitive to oxygen depletion (Noland and Ultsch, 1981). The washouts of the sand dunes separating the main part of the lake from the marshlands caused large amounts of sand to be washed into the marsh and form large washout fans and terraces, covering large swaths of vegetation and re-creating early successional habitats (Fig. S1.1, available in Supporting Information).

The two types of acute environmental disturbance, one natural and one anthropogenic, that affected the Long Point landscape have combined to create a mosaic of four disturbance regimes. These are: 1) sites treated with herbicide to eliminate *Phragmites*, 2) sites affected by dune washouts, 3) sites that combine these two effects, and 4) sites unaffected by either and retaining a vegetation community dominated by *Phragmites* reeds. These less recently disturbed sites constitute the equivalent of experimental controls for an examination of how the environmental conditions prevailing within each disturbance regime has affected the relative abundances of resident species of anurans. In view of their respective habitat requirements, particularly levels of oxygenation post-disturbance, Fowler's toads should be expected to increase in abundance in the newly available dune washout sites whereas the ranid frogs should remain most abundant in non-washed-out and, thus, highly vegetated sites. However, if the method used to eradicate invasive *Phragmites* reeds has resulted in oxygen-depleted waters, both Fowler's toads and ranid frogs may be expected to abandon these sites in favour of sites more conducive to the development of early-stage tadpoles. In this case, Fowler's toads should demonstrate increased habitat use in washout sites unaffected by herbicide treatment, whereas ranids should utilize sites unaffected by either disturbance. If oxygen was not depleted by the eradication of the reeds, then two other scenarios may occur dependent upon the regrowth of vegetation in washout sites. Should regrowth of *Phragmites* not occur, then no species of anurans might discriminate between herbicide-treated washout sites and un-treated washout sites. In that case, Fowler's toads should inhabit all washout-affected sites equally, whereas ranids should avoid them. Alternatively, should regrowth of *Phragmites* occur, un-treated habitat types may return to their previous states, which were more suitable for ranid species. In this case, the combined effects of the *Phragmites* eradication and washouts should be most favorable for Fowler's toads, and least favorable for the three species of ranid frogs.

STUDY AREA

Long Point, Ontario, Canada, is a 35 km long sand-spit that protrudes from the northern shore of Lake Erie in Canada (Fig. 1) and was designated a UNESCO Biosphere Reserve in 1996. This study took place from June 1st to August 23rd, 2021, in the Thoroughfare Unit of the Long Point National Wildlife Area (LPNWA) (42°34'40" N, 80°21'53" W, 174 m above sea level) and Long Point Provincial Park (LPPP) (42°34′48″N, 80°23′6″ W, 179 m above sea level). The LPNWA is federally protected and covers 350 ha and the LPPP is provincially protected, hosts a small campground, and covers 150 ha. In the temperate climate of Ontario, 2021 mean air temperatures from May to August ranged from 12.5 (May 2021) to 21.8 °C (August 2021), with a nighttime low of -1.6 °C (May 1, 2021) and a daytime high of 32.2 °C (June 22, 2021). At Long Point, Ontario, Canada, beginning in approximately 1995, the invasive form of the common reed, *Phragmites australis australis*, spread unchecked throughout the marshlands (Badzinski et al. 2008). The invasive *Phragmites* has caused changes in the vegetation community and the landscape structure which has been shown to negatively affect many wetland species, including amphibians (Greenberg and Green, 2013), reptiles (Markle and Chow-Fraser, 2018), birds (Tozer 2016), and native wetland plants (Minchinton et al. 2006). *Phragmites* has been the focus of many management projects aiming to reduce or eliminate it (Weidenhamer and Callaway, 2010) and recreate pre-existing wetland biotic communities (Tozer and Mackenzie, 2019). In the autumn of 2020, prior to our study, dense stands of *Phragmites* in the Long Point marsh were selectively treated to prioritize the large stands with the glyphosate-based herbicide, Roundup® Custom for Aquatic & Terrestrial Use (Bayer Cropscience Inc., Canadian reg. no. 32356), combined with the aquatic-safe surfactant Aquasurf® (Norac Concepts Inc., Canadian reg. no. 32152). The standing vegetation had then been rolled over during the winter of 2020 – 2021 and the dead organic matter left to decompose to promote a swift decomposition rate (Yuckin et al. 2022). The shore and the lakeside dune system is dynamic, with an extensive erosion and disposition processes actively occurring through the year (Davidson-Arnott and Fisher, 1992). Events like washouts are cyclical in Long Point, occurring on average every few decades; the most recent previous spate of extensive dune washouts occurred in 1986 (Hazen, 2000). Storms and seiches are the primary forces creating a dynamic landscape of sand-filled pools, dunes, and wetlands in the Long Point coastal region (Bedford, 1992). In addition to dunes and beaches, the study area also features small, forested areas, marshes, swamps, and savannahs (Reznicek and Catling, 1989). In the marshes, dominant flora include *Phragmites* reeds (*Phragmites austalis*), cattails (*Typha spp.),* horsetail (*Equisetum sp.)* and dogwood (*Cornus spp*.). Dominant vertebrate fauna within the marsh includes central mudminnows (*Umbra limi*), sunfish species (*Lepomis spp*.), ranid frog species (*Lithobates spp*.), northern watersnakes (*Nerodia sipedon sipedon*), eastern gartersnakes (*Thamnophis sirtalis sirtalis*), common snapping turtle (*Chelydra serpentina*), tree swallow (*Tachycineta bicolor*), red-winged blackbird (*Agelaius phoeniceus*), and muskrats (*Ondatra zibethicus*).

METHODS

Site selection for natural experiment

We could not choose sites randomly or evenly distribute our sites for the natural experiment as we were limited by the extent of the disturbances. The landscape was sprayed unequally (based on the extent of *Phragmites*), and the storm influenced the landscape in some locations but not others. As such, we chose site locations based upon historical accessibility, previous studies of Fowler's toads, and in consideration of the treatment types and disturbance status of the site (sprayed with herbicide or not, affected by dune washout or not). We applied a 2x2 factorial design of disturbance regimes with 3-replicates, for a total of 12 sites, 3 replicates at each of the four site types; herbicide-treated sites, dune washout sites, herbicide-treated + dune washout sites, and control sites. Three of the sites were located within the LPPP (sites AB, C, and M) and nine were located within the LPNWA (sites D, E, F, G, H, I, J, KL and N). Sites ranged from approximately 40m to 740m away from the next closest site (Fig. 1.1).

Minnow trap, visual, and acoustic surveys

We assessed the presence, absence, and abundances of ranid frog species inhabiting the marsh sites using minnow traps, visual surveys, and acoustic surveys. Visual and acoustic surveys were intended to improve the detection of adult life stages of anuran species. For visual and acoustic surveys, when we heard a frog calling or an animal was seen at one of the specified sites, its presence was noted. Minnow trapping surveys were meant to target juvenile life stages of anuran life stages. For the minnow trapping: five minnow traps per site were placed and surveyed. We emptied and recorded animals in the traps twice per day since minnow traps should be deployed for no more than 14 hrs at a time (Adams et al. 1997), decreasing the potential for mortality. One week of surveying consisted of two day surveys and two night surveys, such that each site was surveyed for ten trap days per site per week. Traps were emptied and reset in the same order to maintain a similar time lag between surveys at each site (Table S1.1, available in Supporting Information). This procedure was repeated 13 times through the summer of 2021.

When deployed, each of five minnow traps per site were placed among emergent vegetation in shallow water no deeper than 30 cm. Traps were not completely submerged and polyethylene foam floats were secured to the traps with zip-ties to better ensure that the air space for air-breathing animals was maintained in the event that the water rose, or a trap was displaced. When not in use, traps were disassembled and stacked at each site. Each animal caught in a trap was placed on a tray, its photo taken, and was released back into the trap location. The photo recorded the time of day and identification of the animal to species was performed post-hoc, in the months following fieldwork. When identification to species was not possible then identification was performed to the lowest possible taxon. For example, many tadpoles of Northern Leopard Frogs, American bullfrogs, and Green Frogs were recorded simply as “ranid” tadpoles due to the difficulty of distinguishing species.

Environmental variables

We measured water quality environmental parameters at each trap site following the “day” surveys when we emptied the traps using a Hanna Instruments HI 98194 multi-parameter probe

(Hanna Instruments Inc., Woonsocket, RI, USA). Measurements began at 12:00 pm at the final site and we worked backwards through all the sites, almost always finishing these measurements before 1:30pm. These included water temperature (°C), salinity (ppm), conductivity (µS/cm and µS/cm^{A}), pH, total dissolved solids (ppm), dissolved oxygen (% and ppm), oxidation-reduction potential (mV) and pressure (psi). We also measured turbidity (NTU) with a TN400 Portable Turbidity Meter Kit (Apera Instruments, Columbus, OH, USA) and monitored nitrite, nitrate, and ammonia levels using an API Freshwater MasterTest Kit (Mars Fishcare North America, Chalfont, PA, USA.). In addition, we took water samples to analyze total nitrogen (TN) (µg/L) and total phosphorus (TP) (µg/L) just below the water surface. These readings were taken five times at each site over the course of the summer (Jun. 2nd, Jun. 19th (sites C, E, F, G), Jun. 22nd (sites AB, D, H, I, J, KL, M, N), Jul. 10, Aug. 7th, and Aug, 17th). The two 125 ml Thermo Scientific™ Nalgene™ Narrow-Mouth PPCO Packaging bottles of samples were sent to and analysed by the GRIL lab (Groupe de Recherche Interuniversitaire en Limnologie) at Université de Montréal. This analysis entailed splitting each sample (one bottle) in two and performing acid digestion for TP on one and TN on the other subsample. We acquired the air temperature data from the nearby Environment Canada weather station in Delhi, ON, Canada (42°52'00" N, 80°33'00" W, 231.70 m above sea level, Climate ID: 6131983, WMO ID: 71573).

Fowler’s toad surveys

We employed an intensive survey to collect data on Fowler’s toads. Commencing after sunset on 53 evenings during the period May 2nd through Aug. 20th, 2021, teams of 2-4 surveyors walked along the approximately 5,400 m of the Lake Erie shore and adjacent marshes in search of Fowler’s toads, spotted by reflected eye-shine from the surveyors’ headlamps. During the breeding season (May and June) surveyors listened for calling male Fowler's toads to locate and capture them. Once captured, we geo-referenced a Fowler's toad's location using an EOS Arrow 100 GNSS receiver (EOS Positioning Systems Inc., Terrebonne, QC, Canada) and assigned an encounter number. We recorded the Fowler's toad as male, female, juvenile, or young-of-year. Snout-to-vent length (SVL) was measured with digital calipers to the nearest 0.1 mm. Males were discernible by their dark throats and release calls when handled in the field.

Statistical Analyses

To characterize the differences in environmental variables between the four site types, we first centred and scaled the data (created a correlation matrix) and performed a PCA using the package "FactoMineR" (Le and Husson, 2008), extracted PCA axes, and performed K-means clustering with the function *kmeans* in the "stats" package in R version 4.0.4 (R Core Team 2021). To determine the number of clusters that best fit the environmental data we used the Elbow method using the total within-cluster sum of squares with the function *fviz_nbclust* from the package "factoextra" (Kassambara and Mundt, 2020). We tested the effect of the herbicide and the dune washout disturbances on dissolved oxygen and oxidation-reduction potential to compare the water oxygenation and water's ability to break down (oxidize or reduce) other chemicals using a pairwise t-test with Bonferroni correction for multiple testing when comparing site types with the *pairwise.t.test* function from the "stats" package (R Core Team 2021). When comparing the aggregated site types (washout-affected vs not affected and herbicide-affected vs not affected) a simple t-test was used from the "stats" package was utilized (R Core Team 2021).

We obtained counts of different species by site type per trap-day by combining our ranid frog count data that was derived from twice daily surveys per site and grouped these counts according to their assigned site type. These values were then standardized by the number of trap days, as trap days varied between 110 and 150 trap days among sites. We tested the influence of the different disturbance types on the counts of ranid frogs using a generalized linear mixed model with the R package “glmmTMB” in R version 4.0.4 (Brooks et al. 2017, R Core Team 2021). We used the R package “DHARMa” (Hartig 2022) to compute the residuals of the models and test the assumptions. This simulation-based approach checks for over/under-dispersion, zero-inflation, and residual spatial and temporal autocorrelation. Using this package and Akaike information criterion (AIC) values, we determined the best-fitting data distribution for each response. We plotted the response variable (ranid counts as number of captures per trap day or survey day) as a function of one explanatory variable (site type). To prevent variation in several significant variables from masking potential differences in ranid frog association to a site type, we added blocking factors: site as a random effect, time of day (day or night), month (June, July, or August), and, when all surveys were considered, survey type (visual/acoustic or minnow trap) as fixed effects. These blocking factors were included in the model due to their importance in the study design and when appropriate, the AIC results (Table S1.3 A-D, available in Supporting Information). Pairwise comparisons were made with the function *glht* from the package “multcomp” with a Bonferroni-Holm correction for multiple comparisons (Hothorn et al. 2008).

Fowler’s toad counts and associations to the site types was determined by plotting the geo-coordinates of all Fowler’s toad encounters in QGIS Version 3.18.2-Zürich and creating a circular 40m buffer around each of the 12 sites. These data were standardized by the number of survey days as these varied between sites (between 22 and 38 survey days). We plotted the response variable (Fowler’s toad abundance) as a function of one explanatory variable (site type or washout presence/absence) using a generalized linear model with a negative binomial type II distribution, from package “glmmTMB” (Brooks et al. 2017) chosen by distribution best fit using the R package DHARMa (Hartig 2022) and AIC (Table S1.3 E-F, available in Supporting Information). We included site as a random effect and month (May, June, July, or August) as fixed factors. AIC (Table S1.3 E-F, available in Supporting Information). Pairwise comparisons were made with the function *glht* from the package “multcomp” with a Bonferroni-Holm correction for multiple comparisons (Hothorn et al. 2008). In all analyses, P-values below $\alpha=0.05$ are considered statistically significant.

RESULTS

Environmental variables

In the PCA with K-means clustering (Fig. 1.2) depicting the spread of the environmental data, the first principal component, PC1, accounted for 26.73% of total variance and was mainly comprised of total dissolved solids and conductivity (loading values greater than 0.3) (Table S1.2, available in Supporting Information). The second principal component, PC2, on the y-axis accounted for 22.84% of total variance and was mainly comprised of oxidation-reduction potential (loading value greater than 0.3) (Table S1.2, available in Supporting Information). Using the Elbow method via WSS (total within-cluster sum of squares), k=3 clusters fit the data best when applying the K-means algorithm. Dune washout sites exhibited higher values along PC2 than non-washout sites, and dune washout and herbicide-treated + dune washout sites could be distinguished along PC1, forming two clear clusters. Non-washout sites (herbicide-treated and control sites) formed a single cluster, indicating a lack of differentiation between them.

Sites that were subject to both disturbances exhibited higher percent dissolved oxygen levels than other sites (Fig. 1.3A). As such, sites affected by the herbicide-treatment (Fig. 1.3B), regardless of the dune washout status, had significantly higher dissolved oxygen than non-herbicide-treated sites ($t = -3.4626$, $p < 0.001$), and sites affected by the dune washout (Fig. 1.3C), regardless of the herbicide-treatment status, also had significantly higher dissolved oxygen than unwashed out sites ($t = -4.0038$, $p < 0.001$). Dune washout sites (Washout and Herbicide + Washout) had significantly higher oxidation-reduction potential than non-washout sites (Herbicide and Control) (Fig. 1.3D). We did not detect a difference in oxidation-reduction potential between sites affected by the herbicide treatment, irrespective of dune washout status, and non-herbicide-treated sites (Fig. 1.3E). Thus, when site types were combined according to the disturbance (washout or herbicide), only sites affected by the dune washout, regardless of herbicide status, were significantly higher in oxidation-reduction potential than unwashed out sites ($t = -12.036$, $p < 0.001$).

Surveys

The total captures in the order Anura from June through August from minnow traps were 630 captures of frogs and toads over 1,560 total trap-days (= 60 traps/day x 26 days). Of these, 318 captures were ranid tadpoles not identified to species, 125 captures were metamorphosed Green frogs, 103 captures were metamorphosed American bullfrogs, 76 captures were metamorphosed Northern leopard frogs, and 8 captures were Fowler’s toad tadpoles. Adult ranids were infrequently caught in the traps. All ranid species and life stages were captured most frequently at control site M, and no ranid captures were made at site J, an herbicide-sprayed and washed-out site. We made 1,195 captures of Fowler’s toads over the survey period, of which 197 captures were adult females, 206 captures were adult males, 495 captures were juveniles, and 297 captures were young-of-the-year toadlets. 77 of these captures were found within 40m of one of the trapping sites and are included in this study.

Distribution of anuran amphibians

When all observation types are considered (minnow trapping and visual and acoustic surveys), ranid frogs tended to use of site types unequally (Table 1.1A). Ranid frogs were less abundant at herbicide-treated + dune washout sites than control sites and herbicide-sprayed sites, ($Z = -2.595$, $p = 0.038$; $Z= -3.726$, $p = 0.001$), and at washout sites compared to herbicide-sprayed sites ($Z= -2.686$, $p = 0.036$) (Table 1.4A). Ranid frogs were also significantly less abundant at washout sites compared to non-washout sites ($Z = -3.657$, $p < 0.001$) (Table 1.1B). When considering minnow traps captures only, ranid frogs displayed a clear pattern of abundances (Fig. 1.4A); ranid frogs were less abundant at herbicide-treated + dune washout sites than control sites and herbicide-sprayed sites, ($Z = -4.580$, $p < 0.001$; $Z= -5.255$, $p < 0.001$), at washout sites compared to herbicide-sprayed sites ($Z= -1.8646$, $p = 0.0161$), and at herbicide-treated + dune washout sites compared to washout sites ($Z= -2.738$, $p = 0.0186$) (Table 1.4B). Ranid frogs were also significantly less abundant at washout sites compared to non-washout sites ($Z = -4.403$, $p < 0.001$) (Table 1.2B).

Fowler's toads also exhibited differences in site type use (Table 1.3A). There was a significant difference in abundance of Fowler's toads between dune washout sites and control sites ($Z = 2.400$, $p = 0.049$), but no difference detected between control sites and herbicide + dune washout sites, or washout sites and herbicide + dune washout sites (Table 1.4C). Juvenile and adult Fowler's toads were never within 40 m of an herbicide-treated site and thus, herbicide-sprayed sites could not be statistically compared to other site types, as there were zero Fowler's toad encounters at this site type. Fowler's toads were significantly more abundant at washout sites, regardless of herbicide treatment (combined washout and herbicide + dune washout sites) than sites not affected by the washout (combined control and herbicide-treated sites) ($Z = 3.734$, $p < 0.001$) (Table 1.3B). Fowler's toads were most commonly found within the 40 m buffer of the washout and herbicide-sprayed + dune washout sites (Fig. 1.4B).

DISCUSSION

We documented the influence of two types of acute disturbance acting at Long Point – natural dune washouts displacing sand into the marshes and anthropogenic herbicide spraying of *Phragmites* monotypic stands. Both disturbance types can increase landscape heterogeneity and allow the re-formation of early successional habitat types, characterized by open, sand-filled ponds and inland *Phragmites*-free ponds. Contrary to our hypothesis, oxygen was not found to be lower in herbicide-treated sites and our results show that ranid frog abundance in herbicide-treated ponds is not significantly different from untreated ponds. Instead, ranid frogs inhabit control sites and herbicide-treated sites at higher abundance than dune washout and herbicide-treated + dune washout sites. Fowler's toads, likewise, do not seem to avoid herbicide-treated ponds but, as expected, used sites affected by the washouts, either alone or in combination with herbicide treatments. These findings emphasize the importance of natural disturbance in the maintenance of a distinct array of habitats, generating a heterogenous landscape that provides environments for diverse species.

A main goal in many environmental restoration plans is to return ecosystem functioning to pre-disturbance levels; however, this restoration is a form of disturbance itself that may impact organisms (Mester et al. 2015). Habitat-altering, invasive species that also act as ecosystem engineers, such as the invasive form of the common reed, may generate severe impacts on the landscapes they invade (Zarnetske et al. 2010). Previous studies concerning the effect of invasive *Phragmites* eradication on biota have differed in their results, as different taxa respond differently to the environmental change. Tozer and Mackenzie (2019) demonstrated that the attempted eradication of invasive *Phragmites* increased the occurrence of breeding marsh bird species in southern Ontario, including Long Point, but were unable to demonstrate any significant difference in frog occupancy between treated and untreated sites. Similarly, the effect of herbicide-treatment of invasive *Phragmites* also produced no significant positive effects on fish and herpetofaunal communities in Michigan (Krzton-Presson et al. 2018). In our case, the predicted environmental effect of the *Phragmites* management at Long Point did not occur; oxygen was not lower at treated sites and anuran amphibians did not avoid herbicide-treated ponds. That these ponds are customarily low in oxygen, and anaerobic decomposition processes dominate, as is possible in many wetlands (Keddy 2010), may provide a likely explanation for this result. While anaerobic decomposition is less energetically favourable, many microbes can use electron-accepters other than oxygen for the decomposition of organic materials (Inglett et al. 2005). This explanation is further supported by the negative oxidation-reduction potential we found in the control sites, which is typical of permanently saturated soils and anaerobic wetlands (Inglett et al. 2005). It is likely then, as suggested by Noland and Ultsch (1981), that ranid tadpoles have adaptations to more variation in the accessibility of oxygen and utilize small microhabitats within the larger pond with more oxygen. Ranid adaptations to variable oxygen would be best tested in a controlled experimental manner, where oxygen could be controlled and tadpole space-use and the corresponding oxygen availability in that space be quantified, which is beyond the scope of this study. Fowler's toads successfully bred in sites with higher reduction-oxidation potential and sites with higher oxygen, which is also characteristic of bufonid toads (Noland and Ultsch, 1981).

The natural disturbance regime of an ecosystem is important for the maintenance of the biological diversity endemic to that landscape, in which species are distributed according to their habitat preferences and thus can coexist within the landscape (Fahrig et al. 2011). In this study, we provide an example of this generalized pattern manifest in the abundance of anuran species among site types at Long Point. Ranid frogs and Fowler's toads exhibit opposite habitat associations and inverse abundance according to the natural disturbance regime, where Fowler's toads utilize the areas affected by the washouts, while the ranid frogs utilized the unaffected areas. This species-sorting may allow taxa to increase in prevalence throughout the landscape, with reduced competition among them. The implication of this result is far-reaching, as the natural disturbance (potentially in combination with the anthropogenic intervention of the spread of the invasive reed) increased the abundance of Fowler's toads to a level that has not been seen during the decade-and-a-half prior to this study (Greenberg and Green, 2013). This suggests that the realization of conservation objectives focussing on single-species recovery may be accomplished through the promotion of natural disturbance processes in a landscape (Zarnetske et al. 2010), while ensuring the extent of the invasive *Phragmites* remains low.

The findings of this study highlight the role disturbance plays in determining the spatial distribution of amphibians within the context of significant landscape modification. As disturbance regimes are altered due to climate change and anthropogenic landscape change (Turner 2010), cyclic patterns such as the dune washout and the subsequent anuran responses seen in this study may also change. Anuran habitat associations can be context-dependant, and their assortment in the landscape has substantial implications for the relative distribution of other taxa regionally and locally, drawing attention to the multifaceted processes shaping the consequences of disturbance and landscape heterogeneity for biota.

MANAGEMENT IMPLICATIONS

Our study emphasizes the importance of targeting ecosystem function for managing focal species recovery. At Long Point, invasive *Phragmites* reeds were implicated in the loss of wetland breeding sites for Fowler's toads (Greenberg and Green 2013), and the active management to eradicate *Phragmites* did not greatly affect either Fowler's toads or ranid frogs. Instead, the dune washout disturbance allowed for the re-creation of Fowler's toads breeding sites. Conservation efforts for this species have previously included digging several ponds within the *Phragmites*-dominated wetland that were meant to provide new breeding sites (Yagi and Green, 2016) and captive breeding and headstarting of tadpoles and toadlets (Ford and Green, 2021). The ponds were not used by the toads (Green, *unpublished data*), and the headstarting and captive breeding was effective but maintained a very small population which in turn did not allow the species to recover. Fowler's toads in Canada are a federally and provincially listed species-at-risk and thus management decisions to assist in its recovery to former levels of abundance should bear in mind the result we have demonstrated here. We further advocate that for maintaining areas of dune washout in much their current state and ensuring that dune washouts occur at higher frequency than once every 35 years. This could be achieved by not preventing the washouts in some areas of the landscape, where dune stabilization is common practice but less vital than in areas where stabilization prevents flood damage to cottages or campsites. In addition, ensuring *Phragmites* eradication efforts continue to be effective would eliminate its potential role in dune stabilization (Liu et al. 2012). This could benefit not only Fowler's toads but also other at-risk animal and plant species in the region that require early successional habitats, such as Piping plover (*Charadrius melodus*), Eastern foxsnake (*Pantherophis gloydi*), Horsetail spike-rush (*Eleocharis equisetoides*), and Lake chubsucker (*Erimyzon sucetta*).

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ETHICS STATEMENT

Procedures with the animals were authorized under permits from the Ontario Ministry of Natural Resources and Environment and Climate Change Canada, and by McGill University Animal Use Protocol no. 4569.

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Tables Chapter 1

Table 1.1. (A) Generalized linear mixed model output when all anuran surveys are considered (Trap, Visual, and Acoustic surveys) for ranid abundances at site types from June to August 2021. (B) Generalized linear mixed model output when all anuran surveys are considered (Trap, Visual, and Acoustic surveys) for ranid abundances from May to August 2021 where washout was present or absent.

A.

	Generalized Linear Mixed Model: All Disturbance Treatments and All observation types			
Factor	Estimate	Standard Error	Z value	p
(Intercept)	0.21	0.34	0.612	0.541
Herbicide	0.38	0.42	0.897	0.370
Washout	-0.76	0.46	-1.637	0.102
Herbicide Washout	-1.22	0.47	-2.595	0.009
July	-0.42	0.13	-3.362	0.001
August	-0.01	0.12	-0.098	0.922
Time of Day (Day x Night)	-0.63	0.10	-6.361	<0.001
Obs. Type (Visual/Acoustic x Trap)	0.62	0.10	5.866	<0.001

B.

	Generalized Linear Mixed Model: Presence/Absence of Washout Disturbance and All observation types			
Factor	Estimate	Standard Error	Z value	p
(Intercept)	0.44	0.23	1.880	0.060
Washout Status (Yes x No)	-1.21	0.33	-3.657	<0.001
July	-0.42	0.13	-3.39	0.001
August	-0.02	0.12	-0.158	0.874
Time of Day (Day x Night)	-0.63	0.10	-6.354	<0.001
Obs. Type (Visual/Acoustic x Trap)	0.62	0.11	5.883	<0.001

Table 1.2. (A) Generalized linear mixed model output when only minnow trap surveys are considered for ranid abundances at site types from June to August 2021. (B) Generalized linear mixed model output when only minnow trap surveys are considered for ranid abundances from May to August 2021 where washout was present or absent.

A.

	Generalized Linear Mixed Model: All Disturbance Treatments and Minnow Trap Captures Only			
Factor	Estimate	Standard Error	Z value	p
(Intercept)	0.71	0.51	1.409	0.159
Herbicide	0.33	0.63	0.519	0.604
Washout	-1.54	0.71	-2.177	0.030
Herbicide Washout	-3.90	0.85	-4.58	<0.001
July	-0.55	0.22	-2.552	0.011
August	-0.06	0.21	-0.27	0.787
Time of Day (Day x Night)	-1.09	0.17	-6.337	<0.001

B.

	Generalized Linear Mixed Model: Presence/Absence of Washout Disturbance and Minnow Trap Captures Only			
Factor	Estimate	Standard Error	Z value	p
(Intercept)	0.91	0.40	2.279	0.023
Washout Status (Yes x No)	-2.75	0.63	-4.403	<0.001
July	-0.55	0.22	-2.554	0.011
August	-0.07	0.21	-0.345	0.730
Time of Day (Day x Night)	-1.09	0.17	-6.336	<0.001

Table 1.3. (A) Generalized linear model output for toad abundances at site types from May to August 2021. Note that the “Herbicide” site type was excluded as no toads were caught within 40m of a site. (B) Generalized linear model output for abundances from May to August 2021 where washout was present or absent.

A.

	Generalized Linear Model: All Disturbance Treatments and Toad Surveys			
Factor	Estimate	Standard Error	Z value	p
(Intercept)	0.13	0.63	0.206	0.837
Washout	1.73	0.72	2.400	0.016
Herbicide Washout	1.58	0.78	2.024	0.043
June	-0.54	0.79	-0.687	0.492
July	-1.09	0.85	-1.273	0.203
August	-1.25	0.82	-1.522	0.128

B.

	Generalized Linear Model: Presence/Absence of Washout Disturbance on Toad Surveys			
Factor	Estimate	Standard Error	Z value	p
(Intercept)	-0.40	0.59	-0.698	0.485
Washout Status (Yes x No)	2.41	0.64	3.734	<0.001
June	-0.80	0.80	-1.010	0.312
July	-1.33	0.83	-1.599	0.110
August	-1.51	0.85	-1.786	0.074

Table 1.4. Pairwise comparisons for all site type models with a Bonferroni-Holm correction for multiple testing. (A) considers all observations of ranid frogs observed in visual/acoustic surveys and minnow traps, (B) considers all observations of ranid frogs observed only in minnow traps, (C) considers all Fowler's toad observations, note that the "Herbicide" site type was excluded as no toads were caught within 40m of a site.

A.	Pairwise comparisons of ranid frogs in all disturbance treatments with all observation types			
Comparison	Estimate	Standard Error	Z value	p
Herbicide – Control	0.38	0.42	0.897	0.665
Washout – Control	-0.76	0.46	-1.637	0.305
Herbicide Washout – Control	-1.22	0.47	-2.595	0.038
Washout – Herbicide	-1.14	0.42	-2.686	0.036
Herbicide Washout – Herbicide	-1.59	0.43	-3.726	0.001
Herbicide Washout – Washout	-0.45	0.47	-0.969	0.665

B.	Pairwise comparisons of all disturbance treatments and minnow trap captures only			
Comparison	Estimate	Standard Error	Z value	p
Herbicide – Control	0.33	0.63	0.519	0.604
Washout – Control	-1.54	0.71	-2.177	0.059
Herbicide Washout – Control	-3.90	0.85	-4.580	<0.001
Washout – Herbicide	-1.86	0.65	-2.876	0.0161
Herbicide Washout – Herbicide	-4.23	0.80	-5.255	<0.001
Herbicide Washout – Washout	-2.36	0.86	-2.738	0.0186

C.	Pairwise comparisons of all disturbance treatments and toad surveys			
Comparison	Estimate	Standard Error	Z value	p
Herbicide – Control	NA	NA	NA	NA
Washout – Control	1.73	0.72	2.400	0.049
Herbicide Washout – Control	1.58	0.78	2.024	0.086
Washout – Herbicide	NA	NA	NA	NA
Herbicide Washout – Herbicide	NA	NA	NA	NA
Herbicide Washout – Washout	-0.14	0.67	-0.213	0.8312

Figures Chapter 1

Figure 1.1. Study site at Long Point, Ontario, Canada, showing locations used for the minnow-trapping study as a function of 4 site types and 2 landscape disturbance types, June to August 2021.

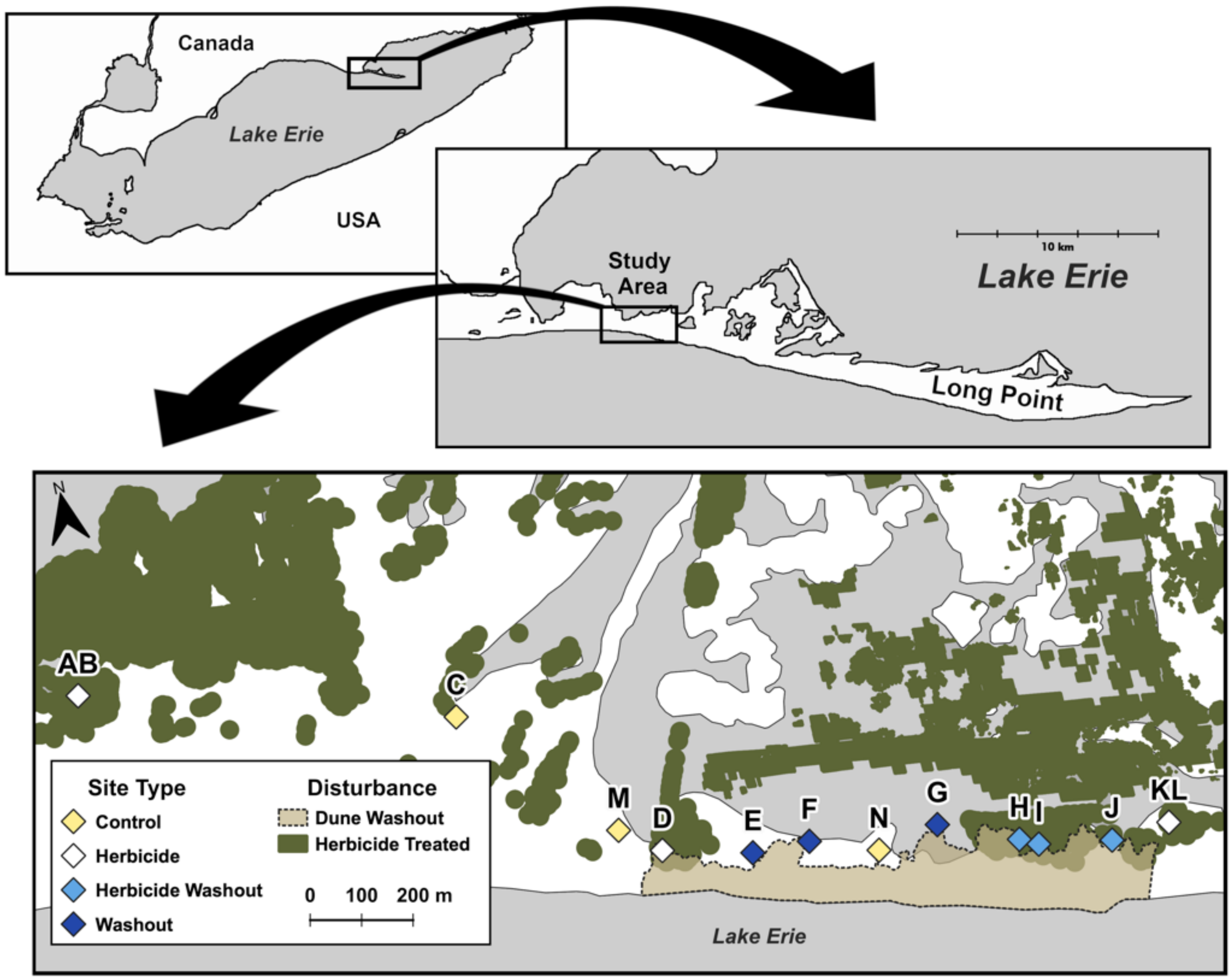


Figure 1.2. PCA of environmental variables with K-means clusters (k=3) of study ponds in the Long Point, Ontario, Canada, June to August 2021. The shape of the small points depicts the site type, the colour of the small points depicts which cluster the points belong to. The large, coloured points represent site type averages, and the black dots represent site averages and are labelled accordingly in the colour of the designated site type.

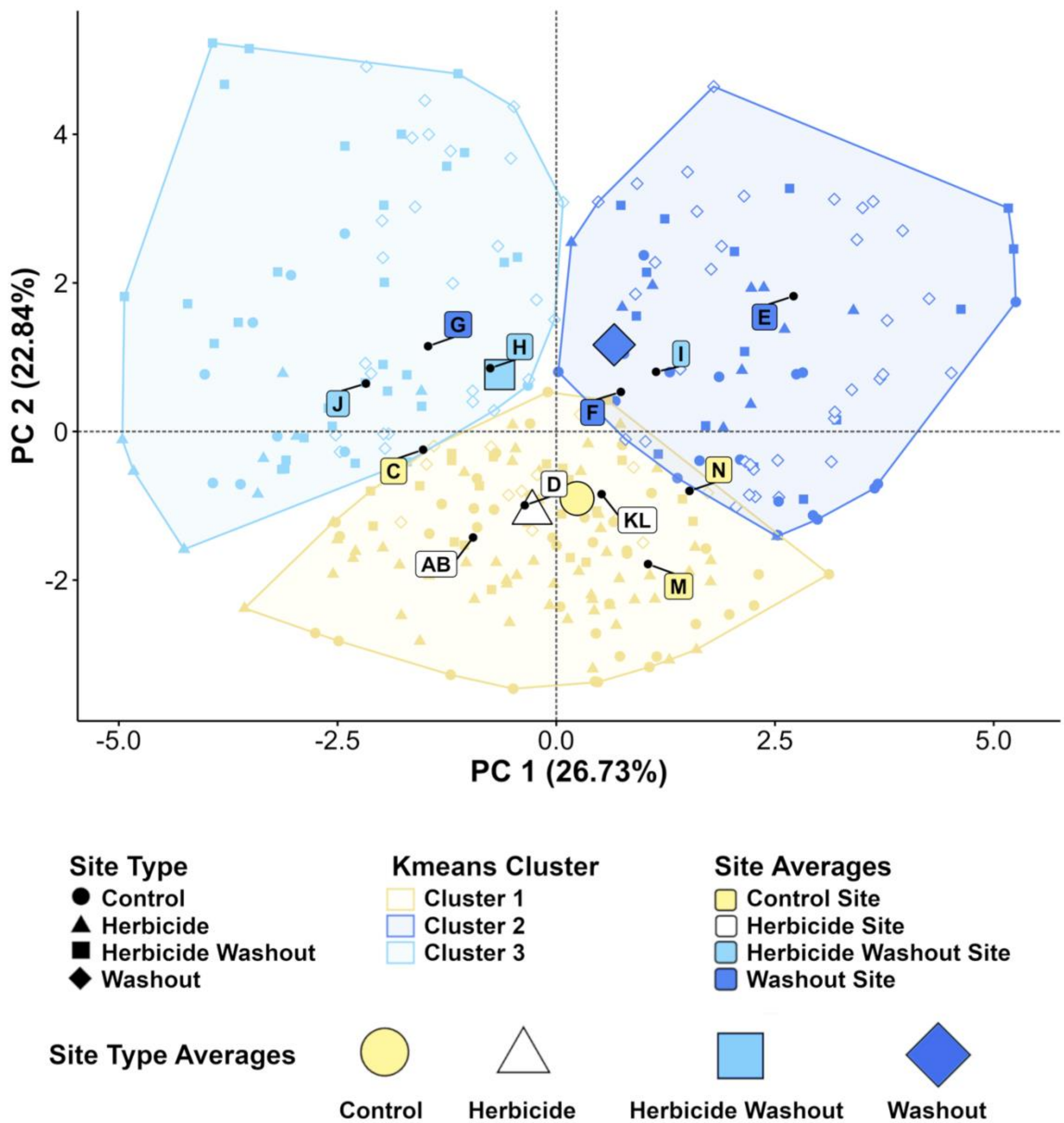


Figure 1.3. Boxplots of percent dissolved oxygen and oxidation reduction potential as a function of disturbance regimes of study ponds in the Long Point, Ontario, Canada, June to August 2021. (A) and (D): The coloured boxes represent values at the site types. Dark and light boxes (B), (C), (E), (F), represent values at aggregated sites according to the presence or absence of the given disturbance. Boxplots with the same letter above them are not significantly different, boxplots with different letters are significantly different from each other. The boxes represent the interquartile range (IQR), whiskers at the top and bottom represent the IQR multiplied by 1.5 and added to the 1st quartile, and subtracted from the 3rd quartile, the median is indicated as the bold line across the box, and any data outside these whiskers are plotted as outlying points.

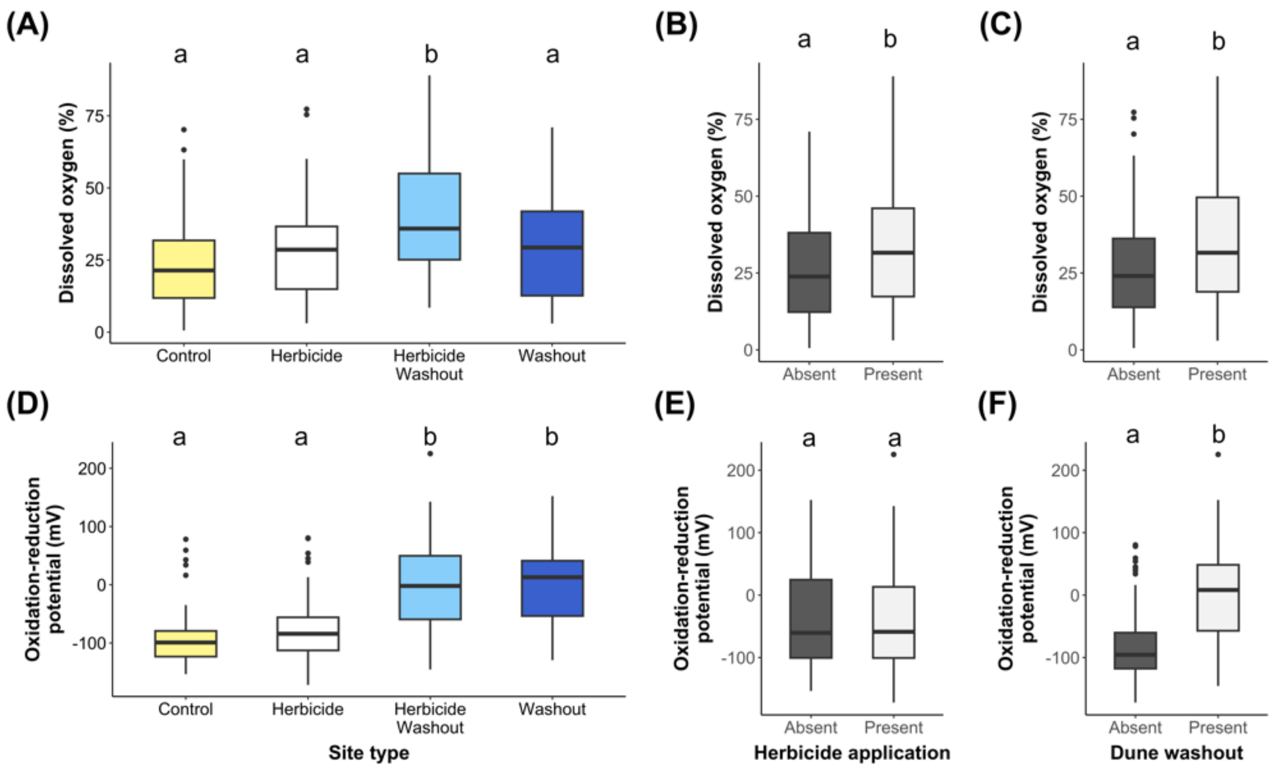
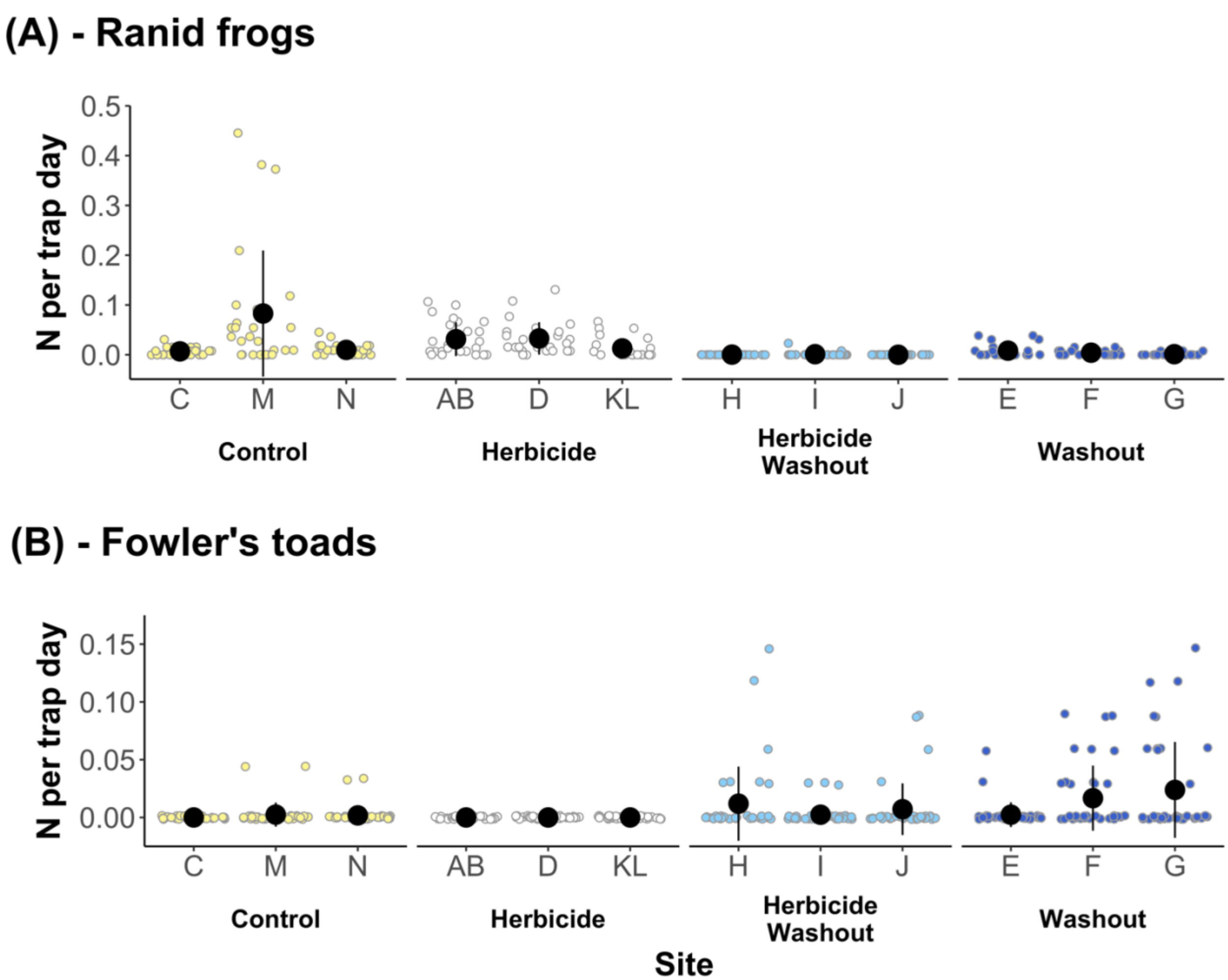


Figure 1.4. Dot plot with mean and standard deviation error bars depicting anuran site and site type abundances per survey or trap day, where on the y-axis "N" is the number of anuran encounters. (A) represents June-August ranid frog minnow trap count data per trap day and (B) represents May-August Fowler's toad count data per survey day in Long Point, Ontario, Canada in 2021. Coloured points represent separate data points, and colours or the points are representative of the site type.



Supporting Information

Tawa, V., D. C. Tozer, and D. M. Green. 2023. Natural disturbance allows multiple anuran taxa to persist in a dynamic wetland complex. Journal of Wildlife Management.

Table S1.1. Generalized itinerary for field surveys at Long Point, Ontario, Canada, where minnow traps, visual & acoustic surveys, and Fowler's toad surveys occurred from June to August 2021 to assess the responses of anurans to the site disturbances.

Day[a]	Time period			
	10:00 am - 12:00 pm	12:00 - 1:00 pm	8:30 - 10:30 pm	10:30 pm onward
Day 0			Traps Set west to east	Fowler's Toad Survey east to west
Day 1	Traps Surveyed and Reset west to east	Environmental Surveys east to west	Traps Surveyed and Reset west to east	Fowler's Toad Survey east to west
Day 2	Traps Surveyed and Reset west to east	Environmental Surveys east to west	Traps Surveyed and Removed west to east	Fowler's Toad Survey east to west

[a] Dates performed: 1-2, 7-8, 15-16, 22-23 and 27-28 of June, 3-4, 10-11, 20-21, and 27-28 of July, 2-3, 7-8, 14-15, and 22-23 of August, 2021.

Table S1.2. Environmental PCA Variable Loadings from the principal component analysis of environmental variables of sites in Long Point, Ontario, Canada, where minnow trapping occurred from June to August, 2021.

	PC1	PC2
% Explained Variance	26.7	22.8
Variable[a]		
Air Temperature (℃)	0.003	0.005
psi	0	0
Water Temperaure (℃)	-0.001	-0.003
PSU	0	0
ppmTDS	0.333	-0.033
µS/cm[A]	0.671	-0.066
µS/cm	0.652	-0.093
ppmDO	-0.001	-0.013
% DO	-0.017	-0.162
mVORP	-0.116	-0.973
pH	0	-0.002
mVpH	0.005	0.114
Turbidity (NTU)	0.004	0.021
Ammonia	0	0
Nitrate	-0.005	0.008
Nitrite	0	-0.001

[a] psi, pounds per square inch of water pressure; PSU, salinity in practical salinity units; ppmTDS, total dissolved solids in parts per million; µS/cm[A], absolute conductivity in microsiemens per centimeter; µS/cm, conductivity in microsiemens per centimeter; ppmDO, dissolved oxygen in parts per million; %DO dissolved oxygen in percent; mVORP, oxidation-reduction potential in millivolts; mVpH, pH on millivolts scale.

Table S1.3. AIC model selection for all candidate models. (A) Minnow trap and Visual/Acoustic Ranid models for all site types. (B) Minnow trap and Visual/Acoustic Ranid models where washout was present or absent. (C) Minnow trap only Ranid models for all site types. (D) Minnow trap only Ranid models where washout was present or absent. (E) Fowler's toad models for all site types (except Herbicide sites as no toads were caught at any Herbicide-only sites). (F) Fowler's toad models where washout was present or absent. ObsType is the type of observation (Minnow trap or Visual/Acoustic) and TimeOfDay denotes if it was a night observation or a day observation. As AIC is not available for quasipoisson we used the family=nb1.

(A) Trap and Observational Ranid model selection - All site types

Model	Poisson AIC	Negative Binomial I AIC	Negative Binomial II AIC
Ranid Count ~ Site.Type + Month + TimeOfDay + ObsType + (1|Site)	3979	3181	**3155**
Ranid Count ~ Site.Type + Month + TimeOfDay + (1|Site)	3985	3214	3189
Ranid Count ~ Site.Type + Month + ObsType + (1|Site)	4108	3229	3193
Ranid Count ~ Site.Type + TimeOfDay + ObsType + (1|Site)	4025	3189	3165
Ranid Count ~ Site.Type + Month + (1|Site)	4114	3264	3222
Ranid Count ~ Site.Type + TimeOfDay + (1|Site)	4032	3221	3198
Ranid Count ~ Site.Type + ObsType + (1|Site)	4154	3236	3202
Ranid Count ~ Site.Type + (1|Site)	4161	3271	3231

(B) Trap and Observational Ranid model selection - Washout presence/absence

Model	Poisson AIC	Negative Binomial I AIC	Negative Binomial II AIC
Ranid Count ~ Washout.YvsN + Month + TimeOfDay + ObsType + (1|Site)	3977	3181	**3153**
Ranid Count ~ Washout.YvsN + Month + TimeOfDay + (1|Site)	3983	3214	3187
Ranid Count ~ Washout.YvsN + Month + ObsType + (1|Site)	4105	3229	3190
Ranid Count ~ Washout.YvsN + TimeOfDay + ObsType + (1|Site)	4023	3189	3162
Ranid Count ~ Washout.YvsN + Month + (1|Site)	4112	3264	3220
Ranid Count ~ Washout.YvsN + TimeOfDay + (1|Site)	4029	3222	3196
Ranid Count ~ Washout.YvsN + ObsType + (1|Site)	4152	3236	3200
Ranid Count ~ Washout.YvsN + (1|Site)	4158	3272	3229

(C) Trap-only Ranid model selection - All site types

Model	Poisson AIC	Negative Binomial I AIC	Negative Binomial II AIC
Ranid Count ~ Site.Type + Month + TimeOfDay + (1|Site)	1681	1256	**1239**
Ranid Count ~ Site.Type + Month + (1|Site)	1798	1303	1276
Ranid Count ~ Site.Type + TimeOfDay + (1|Site)	1717	1264	1242
Ranid Count ~ Site.Type + (1|Site)	1834	1310	1278

(D) Trap-only Ranid model selection - Washout presence/absence

Model	Poisson AIC	Negative Binomial I AIC	Negative Binomial II AIC
Ranid Count ~ Washout.YvsN + Month + TimeOfDay + (1|Site)	1684	1263	**1242**
Ranid Count ~ Washout.YvsN + Month + (1|Site)	1801	1310	1279
Ranid Count ~ Washout.YvsN + TimeOfDay + (1|Site)	1720	1271	1245

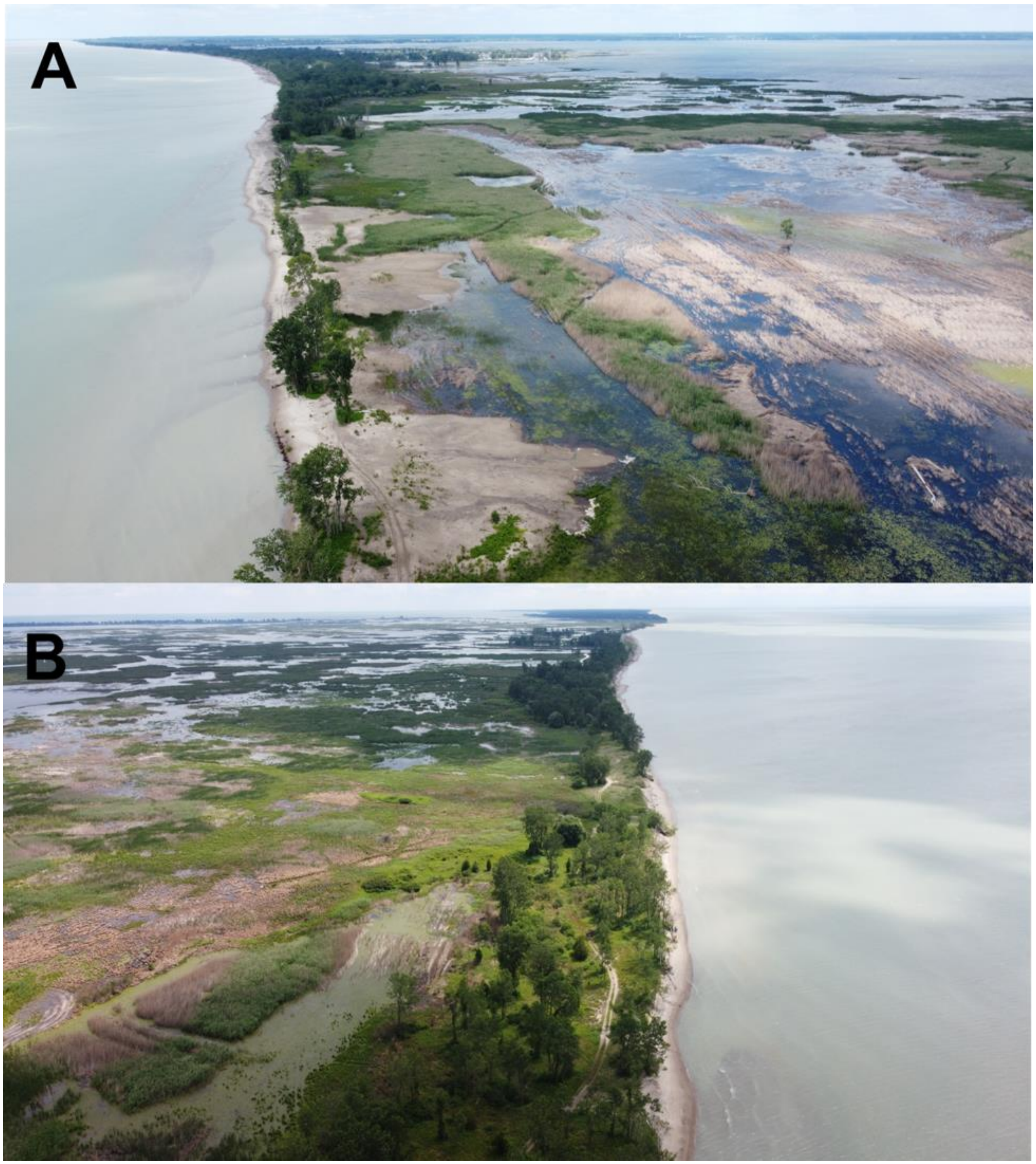
(E) Fowler's Toad model selection - All site types

Model	Poisson AIC	Negative Binomial I AIC	Negative Binomial II AIC
Fowler's Count ~ Site.Type + Month + (1|Site)	178	147	**145**

(F) Fowler's Toad model selection - Washout presence/absence

Model	Poisson AIC	Negative Binomial I AIC	Negative Binomial II AIC
Fowler's Count ~ Washout.YvsN + Month + (1|Site)	184	151	**150**

Figure S1.1. Drone shots of location of study, in Long Point, Ontario, Canada. (A) is facing West and displays a clear view of the washouts to the left middle. (B) is facing East and shows a section of marsh that has been sprayed with herbicide, towards the middle of the photo.



Linking Statement

The evidence of habitat-partitioning between the federally endangered Fowler's toad (*Anaxyrus fowleri*) and other anuran taxa, in accordance with the disturbance-type affecting the landscape seems to suggest that beyond the eradication of the invasive reed, the maintenance of the natural disturbance regime should be prioritized to best conserve the anuran species in the area. While the sensitive nature of frogs and toads to environmental change may make them an ideal group to study the effects of disturbance, their abundance in a habitat may depend on more than the state of the abiotic landscape. Anuran habitat associations can depend on the environment and/or other frog species, as seen in the previous chapter, but may also be contingent on the presence or absence of other aquatic taxa. Anura do not exist in a vacuum in nature, and as such it is probable that the aquatic community of organisms that anurans encounter plays a role in their habitat associations. This interplay likely occurs reciprocally as well, where the habitat associations of frogs and toads in this system may drive the abundances or presence of other taxa. Associations between taxa may have cascading effects for the aquatic communities they are members of. As made clear in the first chapter, there are taxonomic differences in responses to a given disturbance, and thus which taxa a community comprises of may direct the overall community trajectory post-disturbance. Importantly, if some species can no longer reside in the altered habitat, the community structure, diversity, and the relationships between taxa may change following disturbance. Changes in the community structure and diversity can scale up or down to impact other ecological levels, broadening the impacts of disturbance further. Disturbances, especially multiple and overlapping disturbances, have garnered the attention of researchers, stressing the importance of understanding interactions between disturbances and their effects on taxa. Considering the larger aquatic community in this thesis will supplement the Anura-based first chapter to provide a more complete insight on the effects of the two disturbances. Specifically, community diversity responses and identifying species other than the Fowler's toads that may be indicative of a change in the abiotic environment or the biotic community in a certain habitat, will provide guidance for the conservation of biota and the management of the landscape of Long Point.

Chapter 2: Responses of an aquatic community to two coinciding disturbances

Status: *In preparation for Journal of Applied Ecology or Freshwater Biology*

RH: Tawa and Green. • Community response to disturbance

TITLE: Responses of an aquatic community to two coinciding disturbances

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INTRODUCTION

Perturbation and disturbance are ubiquitous in nature, and when considered to be natural processes, they are often critical for the operation of many ecological systems (Connell 1978; Sousa 1984). A disturbance, defined by White and Pickett (1985) as a distinct incident that upsets one or multiple levels of ecological scale, can be biotic or abiotic, natural, or anthropogenically caused, and can occur at small or large temporal and spatial scales. While the effects of disturbance on the landscape can be imposed by the properties of the disturbance itself (ie. intensity, frequency, size, return interval), taxa tend to exhibit differential responses to disturbance (Buma and Wessman, 2012), and it is expected that communities with many species can persist because select groups can withstand different disturbances (Dornelas 2010). Thus, the initial composition of a community may dictate how the community as a whole resists change and/or responds to disturbance events (Bowker et al., 2021). As such, community-level responses to disturbance can be variable, ranging from no change to complete turnover in the community (Martin-Smith et al. 1999; Kaarlejärvi et al., 2021). As a process, disturbance has been shown to generate heterogeneity in the landscape and is dependent on the scale of study (Kolasa and Rollo, 1991; Dumbrell et al., 2008). Disturbance been attributed to creating diverse habitats and thus commonly attributed to the formation of diverse biological communities (Whittaker and Levin, 1977; Sousa 1984). Therefore, aside from composition, various other attributes of biological communities can be regulated by disturbances; including the diversity and abundances of biota, all of which contribute to the structure of communities and can scale up or down to impact other ecological levels (Smith et al., 2022).

Disturbances operating the landscape level may affect ecological community trajectories (e.g. Cimon and Cusson; 2018). Community trajectories following disturbances in a given landscape can be distinct in space and time as a function of the species present, seasonality, and biotic and abiotic environmental conditions, presenting a unique challenge for ecologists (McKenna et al., 2022; Schmitt et al., 2021; Graham et al., 2021). It is thus important to utilize effective methods to compare and visualize community-level differences. For instance, principal response curves (PRCs) use repeated measures data to reveal taxon-level compositional differences of the experimental treatments compared to controls over time and allow for the quantification of taxon-specific responses in each treatment (van der Brink et al., 1999). Indicator taxa are taxa that are characteristic of, and preferentially occur in, the specific conditions of predefined groups (e.g. sites, or disturbance-treatments). Identifying taxa that are indicators can be a useful alternative to sampling an entire community in conservation and management endeavors, particularly in follow-up or long-term monitoring efforts post-disturbance. Despite their use in ecology, classical diversity indices do not scale linearly and lack practical units, making their interpretation and their use in policy and conservation limited. On the other hand, using the effective number of species, values derived from simple algebraic manipulations of Hill's numbers, communities can be compared intuitively (Jost 2006).

Freshwater wetland communities are particularly useful for studying community dynamics following disturbances because wetlands are abundant in nature and wetlands are sensitive to environmental change (Bardecki 1991; Zedler and Kercher 2005). The communities and food webs in wetlands are relatively simple and can act as model systems to provide early indications of ecosystem change in larger systems (De Meester et al., 2005). Long Point, Ontario, Canada, a sand spit that protrudes from the northern banks of Lake Erie, is characterized by its sand dunes and freshwater wetlands beyond. This location was also the site of a chance overlap of two disturbances, an herbicide application to, and subsequent roll-over of, the invasive reed *Phragmites australis australis* and a dune washover that created large washover fans and terraces. The application of glyphosate-based herbicide, Roundup® Custom for Aquatic and Terrestrial Use (Bayer Cropscience Inc., Canadian reg. no. 32356) combined with the aquatic-safe surfactant Aquasurf® (Norac Concepts Inc., Canadian reg. no. 32152), to the invasive reed commenced in the autumn of 2020 and was followed by a mechanical roll-over of the reed. The reeds were then left partially submerged to facilitate litter decomposition. The project was undertaken by several *Phragmites* management partners (Canadian Wildlife Service (Ontario Region) Environment and Climate Change Canada 2020). Circumstantially, a dune washover occurred in late summer of

2020 as a result of high-water levels in Lake Erie that eroded the dunes until a storm seiche washed them out in some areas. These overlapping disturbances created a mosaic of landscape-level alterations in which there were areas in the landscape affected by the washover, some areas where the *Phragmites* were managed, some areas affected by both disturbances, and some areas unaffected by either disturbance.

In this study we took advantage of the opportunity to compare the effects of these two disturbances, and importantly, resolve the potentially distinctive implications for biota when these two significant disturbances occur nearly simultaneously. Here we address the following questions:

1) How did the native freshwater community (in terms of diversity and species composition) differ in response to the management of the invasive reed, the dune washover, and the coinciding disturbance of both the management and the washover?
2) How does this trend change when we consider the diversities at the landscape scale?
3) How did the two disturbances and their cooccurrence alter the environmental conditions the taxa inhabit, and how much does this explain community-level responses?

We hypothesized that 1) diversity would be decreased in habitats affected by either disturbance, as disturbance will decrease the number of species that can occupy that habitat often by simply no-longer matching their ecological needs. If the doubly disturbed habitats exhibit additive effects, diversity may be further reduced in these habitats, as even fewer species' niches may match this changed habitat. However, if the disturbances are not additive, but instead create heterogeneity where species that prefer the conditions created by the reed management and species that prefer the conditions created by the dune washover can coexist, there might be an increase in diversity. 2) We hypothesized that when considered together, the differently disturbed sites would exhibit higher diversity than control sites, where treatment and washout did not occur. It is likely that if the disturbed landscape exhibited higher heterogeneity, particularly in terms of habitat characteristics, then the landscape may have more available niche space and be able to accommodate more species. Lastly, we hypothesized that 3) environmental variables of the wetlands would differ between site types given that the disturbances act through different mechanisms. In herbicide-sprayed and mechanically rolled over sites, we hypothesized that oxygen might be decreased and turbidity be increased as leaf litter decomposed. This would select for species that are able to utilize or prefer to inhabit potentially more hypoxic and murky water habitats. We anticipated the opposite to be true in dune washover affected sites, where we expected to see increased dissolved oxygen compared to control sites and less turbid water. This, in turn, would select for species that preferentially inhabit highly oxygenated and clear water habitats.

MATERIALS AND METHODS

Study Area, Site Selection and Design

Fieldwork for our study took place in the Thoroughfare Unit of the Long Point National Wildlife Area (LPNWA) (42°34'40"N, 80°21'51"W) and Long Point Provincial Park (LPPP) (42° 34′48″N, 80°23′6″ W) from June 1st to August 23rd, 2021. Extending from the northern shore of Lake Erie, the study site is a 35-km sandspit. The shoreline is characterized by extensive erosion and deposition processes forming a Long Point's distinctive dynamic lakeside dune system (Davidson-Arnott and Fisher, 1992). Large transformations to the landscape occur with larger storms and seiches which promote a heterogenous landscape of sand-filled pools, dunes, and wetlands in the Long Point coastal region (Bedford, 1992). Beyond the dunes, the LPPP and the Thoroughfare

Unit of LPNWA host small, forested areas, marshes, swamps, and savannahs (Reznicek and Catling, 1989). Many of the aquatic habitats at Long Point have been treated with herbicide in an attempt to control the invasive *Phragmites australis australis* reed.

Sites for this study were selected to consider the disturbance status of the site (herbicide application and dune washover disturbances) to apply a 3-replicate 2x2 factorial design of disturbance regimes. This resulted in a total of 12 sites comprised of four site types: herbicide-treated sites, dune washover sites, herbicide-treated + dune washover sites, and control sites. Of these sites, three were located within the LPPP (sites AB, C, and M) and nine were located within the LPNWA (sites D, E, F, G, H, I, J, KL and N).

Aquatic Community Sampling

We assessed the presence, absence, and relative abundances of aquatic taxa inhabiting the marsh sites using metal minnow/funnel traps. With five traps placed at each site, we surveyed the sites for two days per week with traps set Jun. 1-2, 7-8, 15-16, 22-23 and 27-28, Jul. 3-4, 10-11, 20-21, and 27-28, Aug. 2-3, 7-8, 14-15, and 22-23, 2021. On each day the traps were deployed they were emptied twice, once in the morning between 10:00am and 12:00pm, and once in the evening between 8:00pm and 10:00pm to ensure the minnow traps were deployed for fewer than 14 hrs between each trap emptying (Adams et al. 1997). The traps were partially submerged in shallow water among the emergent vegetation no deeper than 30 cm with polyethylene foam floats secured to the traps. These floats were added to ensure that air-breathing animals maintained an air space if water level changed, or the trap was displaced. Captured individuals were photographed, released at location of capture, and identified to species following fieldwork. In many cases, identification to species was not possible and was performed to the lowest possible taxon.

Unidentifiable individuals were removed from the dataset and taxa were aggregated to their corresponding family taxonomic level. All individuals could be at least identified to family, apart from Odonates, Decapoda, some Hemiptera, and some Coleoptera, that were grouped together at the order level. All analyses were performed at the family level, as higher-level assemblage patterns have previously been shown to be congruent and highly correlated with species-level patterns and diversity (Heinoa and Soininenb, 2007). Prior to the analyses, abundances from one day of sampling were added together (morning and night trap emptyings).

Environmental and Topographical Surveys

Using the Hanna Instruments HI 98194 multiparameter probe (Hanna Instruments Inc., Woonsocket, RI, USA), environmental variables were taken 30cm below the water surface after each morning survey when the traps were deployed. Between 12:00pm and 1:30pm, water temperature (°C), salinity (ppm), conductivity (μS/cm and $\mu S/cm^A$), pH, total dissolved solids (ppm), dissolved oxygen (% and ppm), oxidation-reduction potential (mV) and pressure (psi) were measured. We obtained air temperature data from a proximate Environment Canada weather station in Delhi, ON, Canada (42°52'00" N, 80°33'00" W, 231.70 m above sea level, Climate ID: 6131983, WMO ID: 71573). Once each week, turbidity (NTU) from a TN400 Portable Turbidity Meter Kit (Apera Instruments, Columbus, OH, USA) was measured, and nitrite, nitrate, and ammonia levels were monitored using an API Freshwater MasterTest Kit (Mars Fishcare North America, Chalfont, PA, USA.). Additionally, on five occasions through the summer (Jun. 2nd, Jun. 19th (sites C, E, F, G), Jun. 22nd (sites AB, D, H, I, J, KL, M, N), Jul. 10, Aug. 7th, and Aug, 17th), we took water samples to analyze total nitrogen (TN) (μg/L) and total phosphorus (TP) (μg/L) just below the water surface. In each case, we used two 125ml Thermo Scientific™

Nalgene™ Narrow-Mouth PPCO Packaging bottles to take and store the sampled until they could be analyzed by the GRIL lab (Groupe de Recherche Interuniversitaire en Limnologie) at Université de Montréal. This analysis comprised of splitting each sample (one of the two bottles) into two and performing acid digestion for TP on one subsample and TN on the other subsample. The process was repeated for the second bottle and their mean values taken.

Site attributes were recorded in July and included the perimeter of the site, site elevation, distance to the shore of Lake Erie. Perimeters were collected by walking around the delineated extents of the sites with a handheld GPS (Garmin Montana 680), the site's altitude was collected from the GPS, and distances from each of the sites to the Lake Erie's edge was collected by walking with that GPS from the sites closest point to the lake, taking the most direct line possible. This was deemed the best method, as the lake's water levels, and the wetlands extents can change dramatically year to year and satellite photos were not up to date.

Statistical Analyses

<u>Redundancy Analyses</u>

We tested the influence of environmental variables, site attributes, and site type (disturbance type) on the taxonomic structure of the aquatic community using a Redundancy Analysis (RDA). Taxa counts were Hellinger transformed for all RDA analyses so that a common absence was not considered a resemblance between communities (Legendre and Gallagher 2001). Covariates were chosen using forward selection of all variables in the environmental dataset using the function 'ordiR2step', in the vegan R package (Oksanen *et al.,* 2022). We included site and week factors to reduce influences of seasonality and spatial structure, respectively. We tested for significance using a permutation test with 999 random permutations under the null model of no effect, using the function 'anova.cca' in the vegan R package (Oksanen *et al.*, 2022).

Indicator Species Analysis

To understand which taxa were most characteristic of the differently disturbed sites, we identified indicator species, species that have a strong association to a certain site type or multiple site types. We used the package *indicspecies* (Cáceres and Legendre, 2009) to identify species that occur more frequently in one or more site types compared to the other site types than randomly expected. This package uses the "IndVal" of Dufrêne and Legendre (1997) which is based on the product of (A) the specificity or the positive predictive value of the taxa and (B) fidelity or sensitivity of the taxa as an indicator for that/those site type(s). That is, the probability that a site is part of site group in which this taxon is found, and the probability that a taxon is found in a site that belongs to that site group. To consider the significance of the association between taxa and site types we used a permutation test with 999 random permutations.

Principal Response Curves (PRCs)

We used principal response curves, a special form of a redundancy analysis utilizing an adjustment where the control community trajectory is set to zero on the y-axis, to analyze the community composition over time (Van den Brink and Ter Braak, 1999). This allows for temporal trends in the baseline community to be corrected for and any deviations from this control line is considered an effect of the treatment. In this case, taxa counts were Hellinger transformed prior to analysis and canonical coefficients were generated for each week (two days, four sampling occasions) and community response to the three treatments was plotted over time, relative to the untreated control site type using the "prc" function in the R package vegan (Oksanen *et al.,* 2022). The x-axis represents time (in weeks), and the y-axis is the magnitude of effect denoted as the canonical coefficients of community response (C_{dt}). Additionally, taxon-specific weights can be extracted, where taxa with near zero weights show no response or a response unrelated to the pattern, taxa with high weights are most likely to respond similarly to the PRC pattern, and taxa with high negative weights will respond in the opposite direction. We plotted species we identified as indicators, and any species that had a regression coefficient for species *k* with respect to the sample scores (b_K) greater than |0.5|.

Effective Number of Species

We calculated the effective number of species using Hill's numbers corresponding to the species richness, exponential of Shannon entropy, and the inverse Simpson index at each site type for each week. The effective number of species or the true diversity of a community, uses the number of species as the unit and represents the number of equally abundant species required to achieve a given diversity index value, where the actual community does not have equally abundant species (Jost 2006). These values were calculated per site type and for the disturbed landscape by combining the three disturbed site types and comparing the diversities to the control site type diversities, controlling for differences in effort. Upon meeting assumptions of a parametric test, ENS values per site type were compared using an ANOVA and Tukey's Honest Significant Difference test for pairwise comparisons. When ENS values for disturbed vs control sites did not conform to parametric assumptions, a Wilcoxon rank sum test was used to compare their values.

All analyses were performed using R Statistical Software (v4.2.2; R Core Team 2022).

RESULTS

Using the minnow traps for the 13 weeks in the summer of 2021, we captured 7695 animals, of which the three most dominant taxa were Belostomatidae (1927 captures), Planorbidae (1509 captures) and Umbridae (1441 captures). In addition, we captured eight federally endangered Fowler's toad tadpoles (*Anaxyrus fowleri*) and 117 federally endangered Lake Chubsuckers (*Erimyzon sucetta*). Most animals were captured in herbicide-sprayed only sites (3037 captures), followed by control sites (2327 captures), and washover-only sites (1510 captures), and herbicide-sprayed and washover sites having the fewest captures (821 captures) (Table 2.1).

Environmental Variables and Redundancy Analysis

Despite some significant differences existing between site types in percent dissolved oxygen and turbidity, the differences were not consistent according to disturbance types. Percent dissolved oxygen was significantly higher than other site types only in the doubly-disturbed (herbicide-treated and washover sites) (Figure 2.1A). Meanwhile, turbidity was significantly lower in washout sites than control sites and doubly-disturbed sites (herbicide-treated and washover sites), but not significantly lower than herbicide-treated only sites (Figure 2.1B).

After forward selection of environmental variables, the following covariates were added to the model: oxidation-reduction potential (mV), turbidity (NTU), pressure (psi), pH, conductivity (μS/cm), and water temperature (degrees Celsius). Site variables added included site identity and week (see Table S2.1 for term effects). The first four axes were significant according to the permutation test by axis. RDA 1 accounted for 20.4% of the variance, RDA 2 for 12.9%, RDA 3 for 7.56%, and RDA 4 for 6.36%. The most influential variable along RDA 1 was oxidation-reduction potential (mV) and for RDA 2 the most influential variable was conductivity (µS/cm). In all, explanatory variables accounted for 45.8% of the variance in the community (adjusted R^2) (Figure 2.2).

Indicator Species

Upon performing the indicator species analysis, 10 indicator taxa were identified for six of the 15 different combinations of the four site types possible. Single site type associations included, Ictaluridae associated with herbicide-treated sites, and Lymnaeidae and Bufonidae associated with washover sites. Paired site type associations included Umbridae, Ranidae and Cyprinidae which were associated with undisturbed control sites and herbicide-treated sites, and Notonectidae associated with single disturbance herbicide-treated sites and washover sites. Planorbidae and Dysticidae were associated with 3 site types, all but the doubly-disturbed sites, and Catostomidae was associated with 3 sites types, all but undisturbed control sites (Table II2).

Principal Response Curves (PRCs)

In the PRC, variation was composed of differences in the community composition through the 13 weeks of study, where 19.3% of the variation is accounted for by partialling out the effect of week, and 30.3% of the variation is explained by the treatments and the interaction between treatment and time. In this model, the first canonical axis accounted for 45.59% of the explained variance. Taxon weights are indicated on a separate axis to the right of the PRC plot (Figure II3). The higher the weight of species on the right, the more a given PRC pattern matches the taxon's dynamics. Community trajectories at the disturbed site types followed a similar pattern in time but exhibited unlike levels of taxonomic response. Herbicide-treated-only sites showed fewer differences from the control site type along the PRC canonical axis, while herbicide-treated and washover sites were most similar to washover-only sites, which diverged the most from the control community trajectory. The taxa most affected by the herbicide-treated sites were Centrarchidae and Catostomidae, both with negative species weights, indicating a reduced abundance compared to the control site type. The taxa most affected by the washover sites and herbicide-treatment and washover sites were Umbridae and Ranidae, both with positive species weights and thus reduced abundance in both washover-affected site types (washover-only and herbicide-treated and washover) compared to control site types.

Effective Number of Species

The effective number of species, or the true diversity, did not significantly differ between all site types for q=0, q=1, and q=2. Control sites, herbicide-treated only sites, and dune washover only sites were not distinctive, however, for all values of q, the doubly-disturbed site type had the a significant reduction in diversity compared to the other site types (Table SII2). Despite not demonstrating a significant difference, herbicide-treated sites had increased diversity for all three values of q compared to the control. In contrast, the washover-only site type showed decreased diversity compared to control when q=0, nearly no change in diversity when q=1, and increased diversity when q=2. As q increases, it's sensitivity to rare species decreases, meaning more weight is given to more abundant species in each sample. Thus in washover sites there may be fewer species than in the control site type, but they are each more abundant (Figure II4). Disturbed sites exhibited significantly more diversity than control sites for all values of q (Table SII2).

DISCUSSION

Understanding biotic responses to disturbances and overlapping disturbances are of increasing importance as natural disturbance regimes are becoming anthropogenically modified (Turner 2010). It is particularly vital to understand community and taxon-specific responses to disturbances in threatened landscapes and for threatened species (McKenna et al., 2022). Here we establish how disturbance, in the form of a natural dune washover process and the anthropogenic intervention to eradicate an invasive reed, affects taxa in the aquatic community of Long Point, Ontario.

First, we demonstrate that the aquatic community composition differs across sites affected by the different disturbance types. Herbicide-treated only sites were most similar in composition to undisturbed control sites, where Umbridae, Ranidae, and Cyprinidae were clear indicator taxa for both site types. Umbridae (one species was captured in this family; *Umbra limi*) and Ranidae tadpoles (three species captured; *Lithobates clamitans*, *Lithobates pipiens*, and *Lithobates catesbeianus*), prefer vegetated habitats and waters with organic material at the bottom (Schilling et al., 2006; Warkentin 1992) and despite being restricted to the water, have the ability to breathe or gulp air and thus can occur in low oxygen habitats (Noland and Ultsh, 1981; Schilling et al., 2006). Cyprinidae captures, apart from a few individuals, were mostly *Cyprinus carpio*, a non-native generalist species that tends to inhabit wetlands with an abundance of aquatic vegetation and organic detritus to consume (Piczak et al., 2022).

According to the PRC and the RDA analyses, washover-only sites and the doubly-disturbed herbicide-treated and washover sites were most similar to each other. Although not exclusively sharing any indicator taxa, the two washover site types did share an indicator taxon with the herbicide-treated only site type: Catostomidae. This family comprised of a single species at these sites, *Erimyzon sucetta*, an endangered species in Canada. These fish have been shown to have very narrow habitat preferences, often showing an association with clear water, sand and silt substrates, and native aquatic vegetation (COSEWIC 2021). This specific habitat has been degraded in the fish's native range partially as a result of the spread of the *Phragmites*. *Phragmites* creates monocultures that pushes out native vegetation and reduces open water areas, which thus causes the loss or modification of these preferred habitat characteristics. Where the herbicide was sprayed and the mechanical *Phragmites* management occurred alone, sites did not seem to match the description of preferred habitat for *Erimyzon sucetta*, however its presence in this site type was primarily limited to one site that was adjacent to the washover-affected sites (Site KL; Figure SII1). It was not fully understood how the activities applied in Long Point to reduce density of *Phragmites* would affect species like the Lake Chubsuckers (COSEWIC 2021), though it was postulated that that *Phragmites* management might negatively affect this species in the short-term, but the reed's eradication would result in positive outcomes for this species in the long-term (COSEWIC 2021). Despite the reduced turbidity of dune washover-only sites compared to control sites, herbicide-treated sites did not exhibit higher turbidity, suggesting the sites did not experience an anticipated increased sedimentation (COSEWIC 2021).

We also demonstrate differences in alpha diversity at different disturbance site types. Sites affected by both disturbances, herbicide-treated and washover affected sites, were significantly lower in diversity for all values of q compared to all other site types, but this effect decreased with increasing q (as sensitivity to rare species decreased). When q=0, there is higher weight on rare species than for q=1 where weights for species in directly in proportion to their abundances, and for q=2 where more weight is given to abundant species and the effect of rare species is further reduced. The greater difference in ENS where rare species are weighted higher in the calculation of diversity suggests that there are few species, but those present are relatively more equally common in these site types. This is likely due to the deviation in the disturbance-evenness relationships from disturbance-species richness relationships, where evenness has been shown increase monotonically with increasing disturbance intensity (Svennson et al., 2012).

The larger effect on diversity of the two overlapping disturbances, may be attributed to an interaction between the disturbances. Although it is possible that the effect both disturbances combined is simply additive, we cannot assume multiple disturbances interact so simply (Ross et al., 2004), given the pervasiveness of synergies and antagonisms evidenced in the multiple disturbance literature, specifically in freshwater ecosystems (Jackson et al., 2016), and across all ecosystems (Côté et al., 2016). Despite the reduction in diversity at the site level, we also demonstrate that even when the sampling effort is corrected for, the disturbed landscape overall (the three "disturbed" site types), is significantly more diverse than the undisturbed landscape. Indeed, the effect of disturbance at one scale should not be assumed to be the effect of the same disturbance at another scale (Hamer and Hill, 2000). An increase in landscape level diversity despite a reduction in diversity at the site level has been shown to occur in intertidal systems (Paine and Levin, 1981) and in birds but not in butterflies (Hill and Hamer, 2004). This further suggests there is little agreement in disturbance response between taxa, even at similar spatial scales (Hill and Hamer, 2004) as animals such as birds and butterflies may experience habitat features and habitat heterogeneity differently. This information further impresses upon the importance of identifying multiple, diverse indicator taxa that will be representative of the ecological community when exploring the biotic responses to disturbance or general monitoring efforts for conservation and management.

As disturbances are expected to increase in frequency in response to a changing climate, it is expected that they will begin to overlap more frequently. Monitoring how biota respond to disturbances, especially overlapping disturbances, will help to provide the necessary information to mitigate their effects in future scenarios. Adaptive management frameworks will be needed when disturbances affect a landscape in order adjust how these management efforts are initiated and sustained based upon various factors. We have shown that how organisms respond to disturbance is contingent upon many factors, including but likely not limited to, spatial scale and ecological scale. Indeed, the aquatic taxa in this study exhibited taxon-specific responses to the different disturbances, likely based on their habitat preferences, which scaled up to decrease alpha diversity at the site scale and increase diversity at the landscape scale. We identified several indicator taxa that may be useful in any continued monitoring efforts in the Long Point region especially as *Phragmites* management continues in the region and throughout South-Eastern Canada. More broadly, our research draws attention to the diversity of responses of natural communities and populations, stresses the impact of the compounding effects of overlapping disturbances on community structure, and underscores the importance of promoting the natural disturbance regime in a landscape for the maintenance of diverse communities.

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Tables Chapter 2

Table 2.1. Taxon captures in minnow traps over 13 of study from June to August 2021, in total and by site type.

Taxon	*Total*	**Site Type**			
		Control	Herbicide	Washover	Herbicide-Washover
Belostomatidae	1927	544	619	482	282
Planorbidae	1509	318	829	328	34
Umbridae	1441	543	808	61	29
Centrarchidae	909	243	116	279	271
Ranidae	622	288	283	46	5
Physidae	367	200	69	65	33
Odonata	166	65	42	34	25
Esocidae	151	19	48	40	44
Nepidae	137	38	42	36	21
Catostomidae	117	0	26	24	67
Cyprinidae	81	25	46	6	4
Ictaluridae	76	1	68	6	1
Dytiscidae	75	16	14	42	3
Lymnaeidae	47	10	7	30	0
Notonectidae	12	0	4	8	0
Hydrophilidae	10	1	4	5	0
Bufonidae	8	0	0	8	0
Viviparidae	7	2	1	4	0
Coleoptera	6	1	3	2	0
Decapoda	6	5	0	0	1
unidentified	5	1	2	1	1
Amiidae	4	2	1	1	0
Corixidae	4	1	2	1	0
Colubridae	4	3	0	1	0
Araneae	2	1	1	0	0
Fundulidae	1	0	1	0	0
Hemiptera	1	0	1	0	0
Total	7695	2327	3037	1510	821

Table 2.2. Results from Indicator Species Analysis. (α=0.05, 999 permutations). Shaded-in, grey boxes indicate with which site type pattern the taxon or taxon group is associated most strongly.

Site type association(s) pattern(s)			**Taxon**	**IndVal**	**p-value**
	Untreated	Treated			
Non-washout			*Ictaluridae*	0.479	0.0002
Washout					
	Untreated	Treated			
Non-washout			*Lymnaeidae*	0.479	0.0015
Washout			*Bufonidae*	0.320	0.0145
	Untreated	Treated	*Umbridae*	0.911	0.0001
Non-washout			*Ranidae*	0.868	0.0001
Washout			*Cyprinidae*	0.424	0.0196
	Untreated	Treated			
Non-washout			*Notonectidae*	0.340	0.0169
Washout					
	Untreated	Treated			
Non-washout			*Planorbidae*	0.937	0.0001
Washout			*Dytiscidae*	0.566	0.0016
	Untreated	Treated			
Non-washout			*Catostomidae*	0.471	0.0043
Washout					

Figures Chapter 2

Figure 2.1. Boxplots across the 13 weeks of study from June to August, 2021 of (A) Percent dissolved oxygen (B) turbidity. Boxplots with the same letter above them are not significantly different, boxplots with different letters are significantly different from each other. The boxes represent the interquartile range (IQR), whiskers at the top and bottom represent the IQR multiplied by 1.5 and added to the 1st quartile, and subtracted from the 3rd quartile, the median is indicated as the bold line across the box, and any data outside these whiskers are plotted as outlying points.

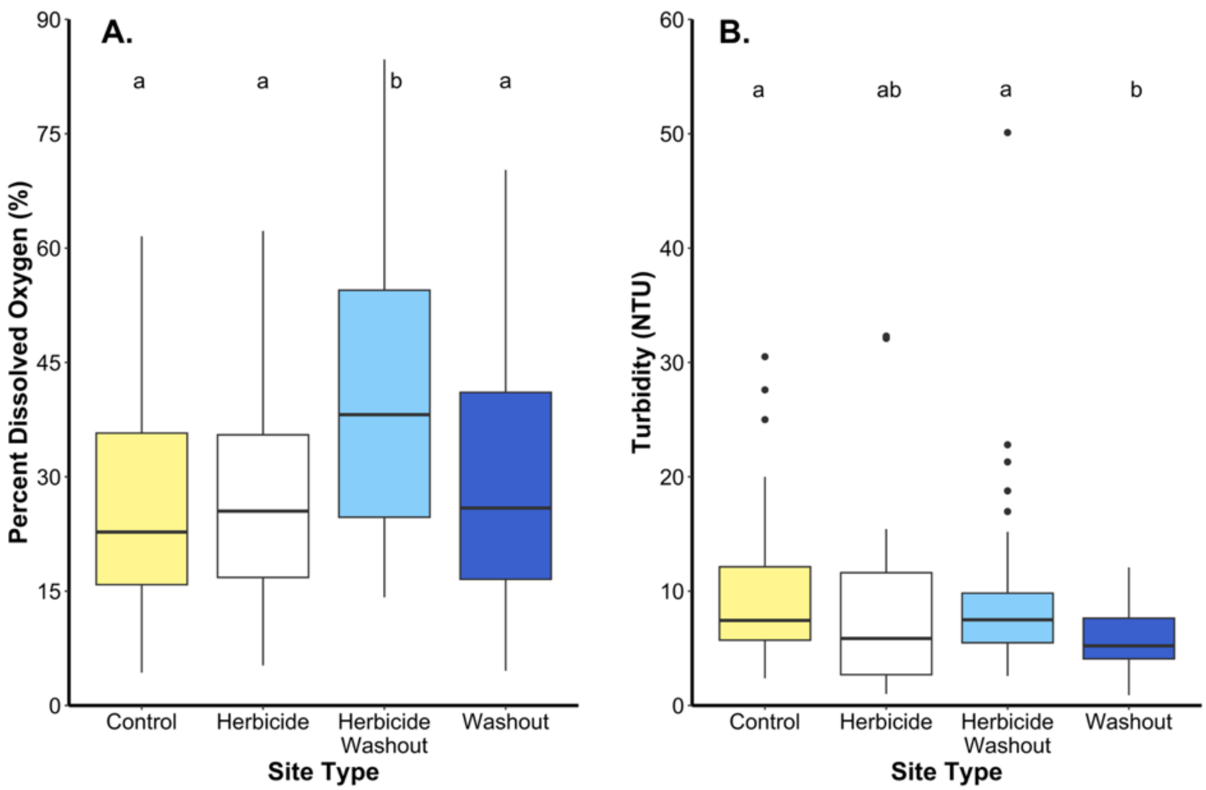


Figure 2.2. RDA of forward-selected environmental variables and aquatic community of study ponds in the Long Point, Ontario, Canada, from June to August 2021. The percentage of the total variance explained by the first two eigenvalues (RDA 1 and RDA 2) are indicated in the axes. (A) RDA plot showing the showing the relationships among sites (points); the shape and colour of the points depict the site type. Site type averages are added as black points with black box labels. (B) RDA plot showing species as red lines with points, only influential species with loadings > |0.3| along one of the RDA axes are depicted. (C) RDA plot depicting the environmental variable loadings that were selected via forward selection.

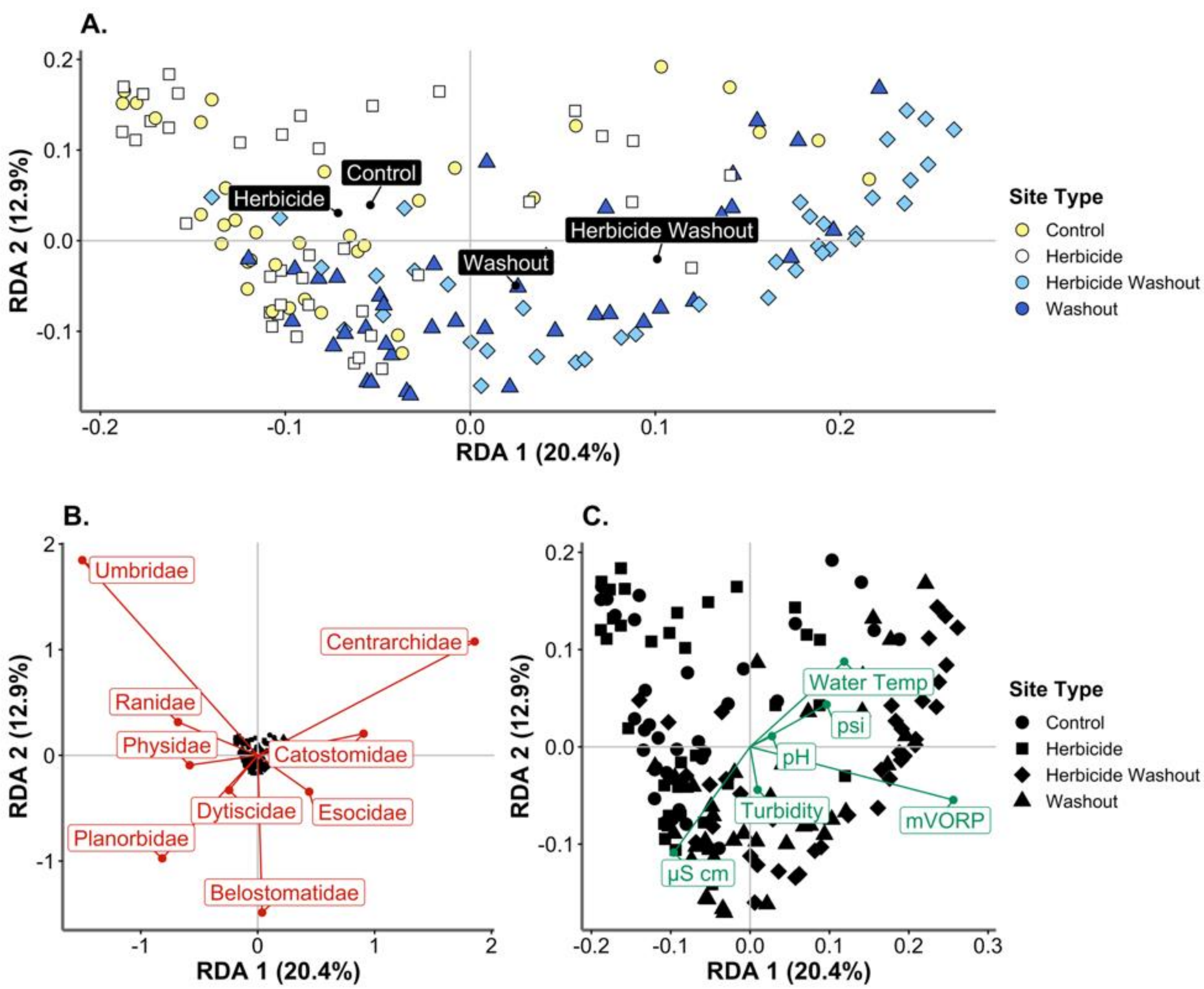


Figure 2.3. Principal Response Curve of the aquatic community. The thin black line at y=0 represents the control site type trajectory (that was set to zero). Different line colours and line type denote different site types' community trajectory deviations from the control. C_{dt} on the Y-axis represents the canonical coefficients of community response. b_K on the separate axis represents the regression coefficient. Species are listed on the separate axis, b_K, if they were identified as indicator species for one (or more) of the site types or exhibited a b_K value greater than |0.5|.

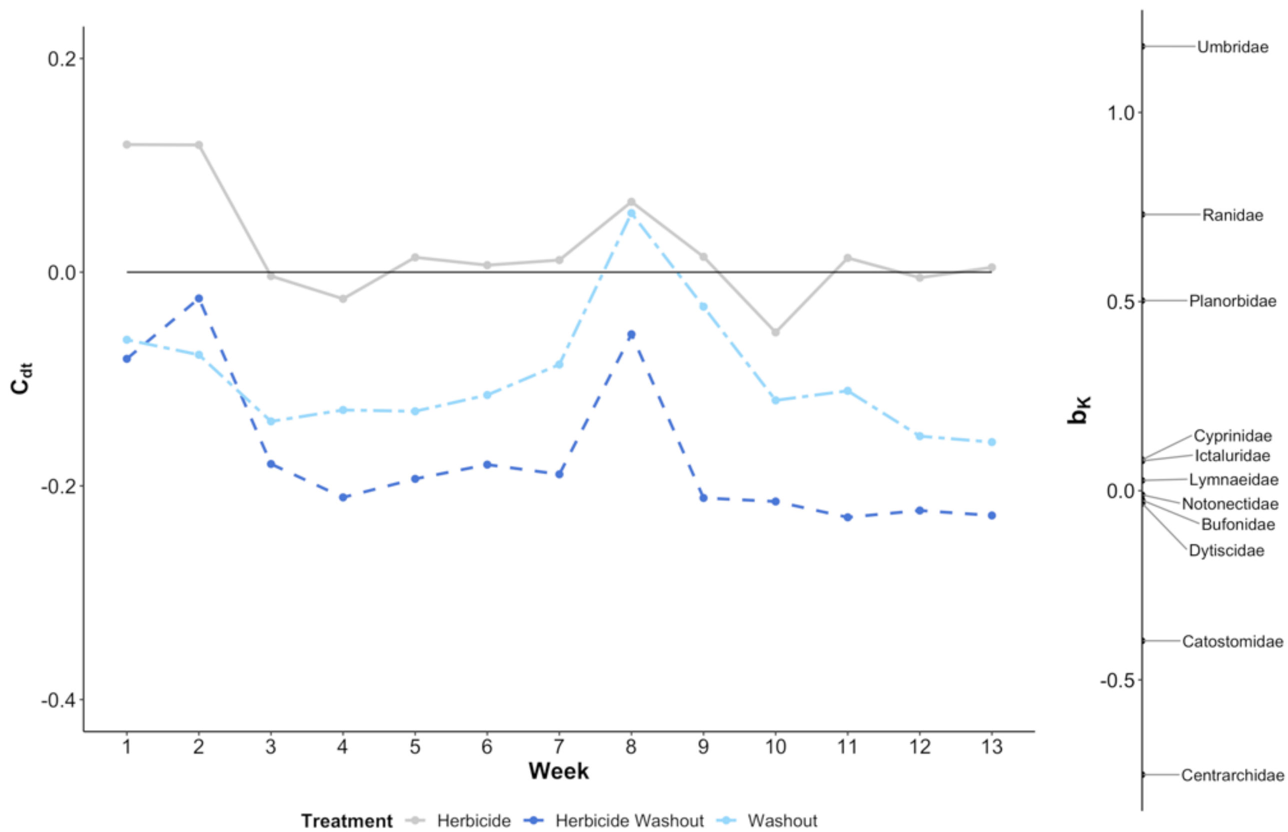
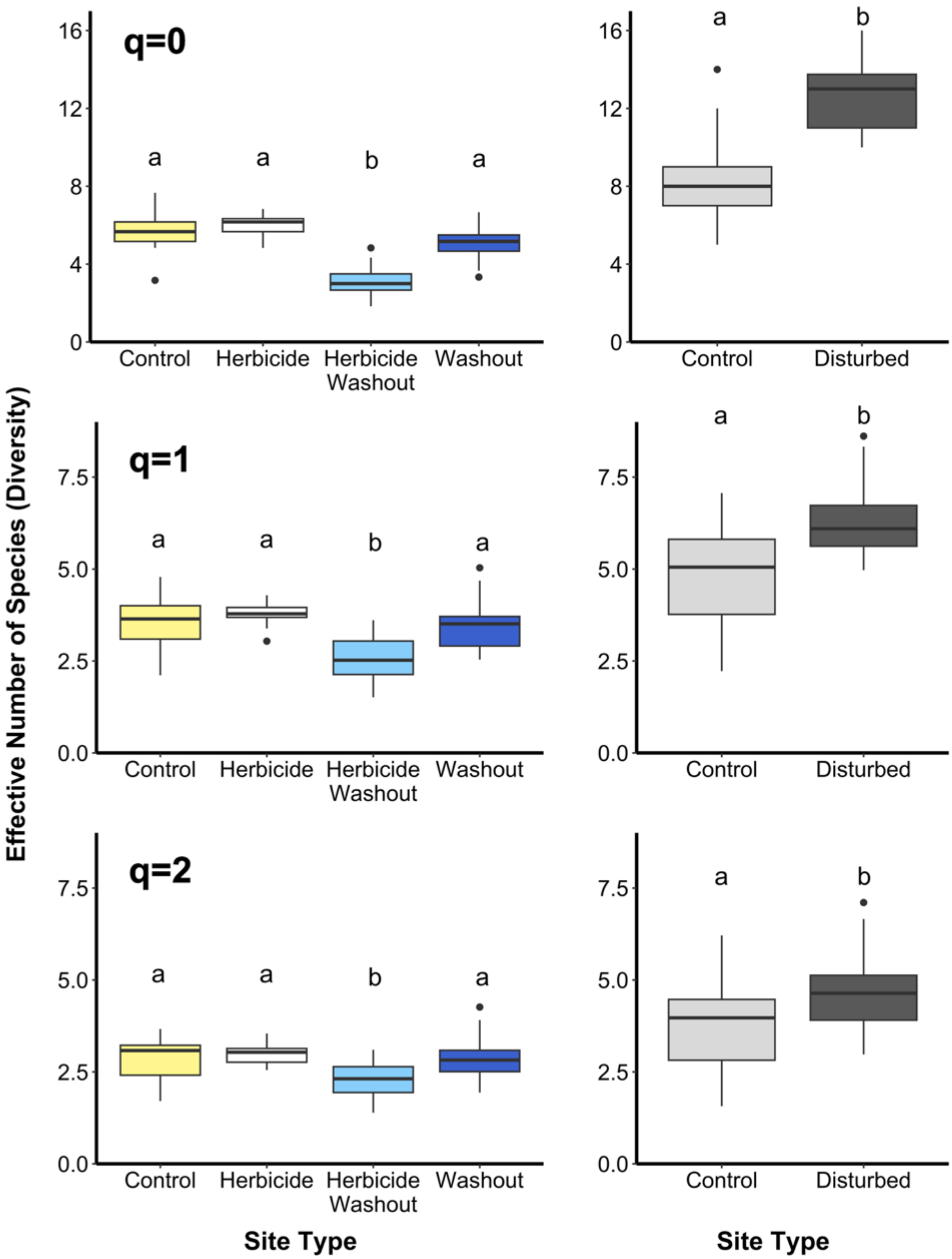


Figure 2.4. Boxplots of the effective number of species of the site types and disturbed vs undisturbed for values of q=0, q=1, and q=2. Coloured boxplots in the first column represent different site type results, the boxplots of two grey shades in the second column represent control (undisturbed) and disturbed site results. Boxplots with the same letter above them are not significantly different, boxplots with different letters are significantly different from each other. The boxes represent the interquartile range (IQR), whiskers at the top and bottom represent the IQR multiplied by 1.5 and added to the 1st quartile, and subtracted from the 3rd quartile, the median is indicated as the bold line across the box, and any data outside these whiskers are plotted as outlying points.


q=0
q=1
q=2
Effective Number of Species (Diversity)
Control
Herbicide
Herbicide Washout
Washout
Disturbed
Site Type
Site Type

Supporting Information

Table S2.1. RDA model results for effects of the treatments, environmental variables and site attributes on the aquatic community. Terms with an asterisk are significant given an α of 0.05.

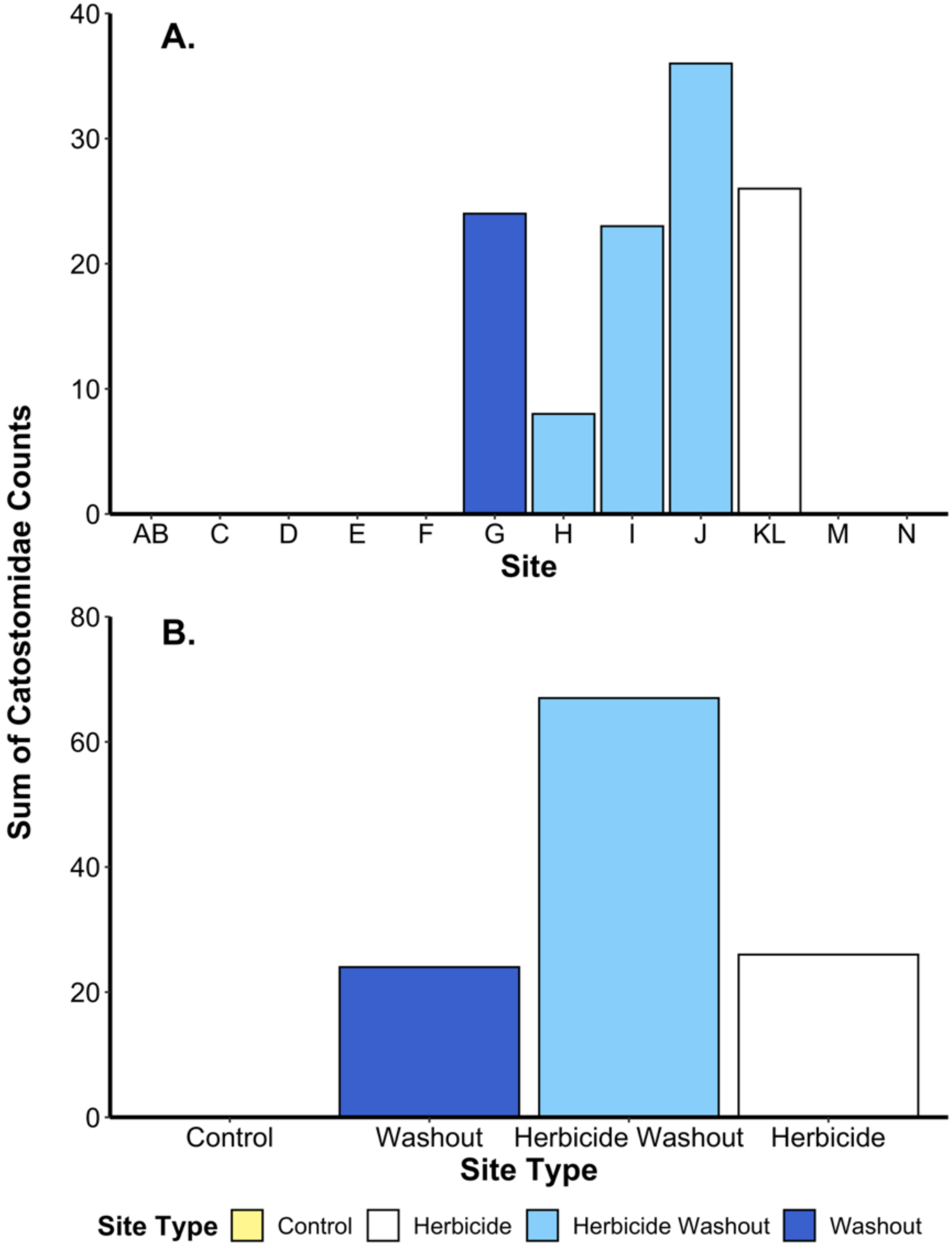
Model: sp_wk_hel ~ Treatments + Oxidation-reduction potential + Turbidity + Pressure + pH + Conductivity + Water Temp + Week + Site					
	Df	**Variance**	**F**	**P-value**	**Significance**
Model	29	0.251	5.521	0.001	*

Terms	**Df**	**Variance**	**F**	**P-value**	**Significance**
Treatments	3	0.065	13.786	<0.001	*
Oxidation-reduction potential (mV)	1	0.012	7.660	<0.001	*
Turbidity (NTU)	1	0.006	3.648	0.005	*
Pressure (psi)	1	0.010	6.322	<0.001	*
pH	1	0.018	11.431	<0.001	*
Conductivity (µS/cm)	1	0.017	11.143	<0.001	*
Water Temperature	1	0.010	6.175	<0.001	*
Week	12	0.061	3.226	<0.001	*
Site	8	0.053	4.208	<0.001	*

Table S2.2. Results for differences in the effective number of species between site types and between disturbed and control sites. Disturbed sites were compared to control sites using a Wilcoxon rank sum test, and site types were compared with an ANOVA followed by Tukey's Honestly Significant Difference test. Comparisons with an asterisk are significant given an α of 0.05.

q	Site Type Comparison	Difference in Effective Number of Species	Lower Bound	Upper Bound	Wilcoxon W	Adjusted P-value	Significant
0	Herbicide x Control	0.346	-0.586	1.279	-	0.757	
	Herbicide Washout x Control	-2.474	-3.407	-1.542	-	0.000	*
	Washout x Control	-0.487	-1.420	0.445	-	0.511	
	Herbicide Washout x Herbicide	-2.821	-3.753	-1.888	-	0.000	*
	Washout x Herbicide	-0.833	-1.766	0.099	-	0.095	
	Washout x Herbicide Washout	1.987	1.055	2.920	-	0.000	*
	Disturbed x Control	-	-	-	39.5	0.000	*
1	Herbicide x Control	0.212	-0.460	0.884	-	0.835	
	Herbicide Washout x Control	-1.030	-1.702	-0.358	-	0.001	*
	Washout x Control	0.001	-0.671	0.673	-	1.000	
	Herbicide Washout x Herbicide	-1.242	-1.914	-0.570	-	0.000	*
	Washout x Herbicide	-0.211	-0.883	0.461	-	0.837	
	Washout x Herbicide Washout	1.031	0.359	1.703	-	0.001	*
	Disturbed x Control	-	-	-	120.0	*0.000*	*
2	Herbicide x Control	0.185	-0.403	0.772	-	0.837	
	Herbicide Washout x Control	-0.605	-1.192	-0.017	-	0.041	*
	Washout x Control	0.090	-0.497	0.677	-	0.977	
	Herbicide Washout x Herbicide	-0.789	-1.377	-0.202	-	0.004	*
	Washout x Herbicide	-0.095	-0.682	0.493	-	0.973	
	Washout x Herbicide Washout	0.695	0.107	1.282	-	0.015	*
	Disturbed x Control	-	-	-	210.0	0.000	*

Figure S2.1. Sums of Catostomidae (one species: *Erimyzon sucetta*, Lake Chubsucker) counts across the 13 weeks of study from June to August, 2021, across (A) sites and (B) site types.



General Discussion

Where disturbance occurs, the ecological consequences to populations and communities can be profound, driving changes across time and space. In this thesis, the effects of disturbance at the population-level and community-level are presented. While these scales can incorporate many disturbance responses, there has been increased attention on the population consequences of disturbance (PCoD) framework, although primarily in marine animals (Pirotta et al., 2018). Since the framework's inception, many models have been developed each aiming to elucidate how behavioural and physiological changes as a result of disturbance affect population dynamics (and thus community dynamics). This framework considers disturbance responses at the individual-level, which was not considered here. Although this thesis generally demonstrates little to no effects of the reed management (herbicide application and mechanical rolling), it is possible effects were limited to behavioural changes or effects only to be seen at the individual-level. Individual-level responses that remained obscured during the summer post-disturbance might limit aspects of the animals' fitness in the year following the study, such as fecundity or overwinter survival. The effects of disturbance might have been overlooked, as they would not be captured due to the scale of study and the lack of repeat year observations; as perhaps the sites were too small for significant changes in abundances to occur and/or disturbance effects take longer than the length of this study to appear.

The importance of disturbance, especially when resulting in a change in heterogeneity can be particularly important for taxon coexistence at the population-level. Ranid frogs and Fowler's toads appeared to partition the landscape and utilized distinctive portions of the landscape; ranid frogs occupied sites unaffected by the washover, while Fowler's toad utilized sites that were washed over. This subdivision of the landscape is likely to allow these taxa to avoid competition and increase in prevalence in the landscape. Using the measure of animal habitat use for biotic response to disturbance at the population level provided an idea of the consequence of disturbances, as these animals are mobile enough to move away from undesirable conditions. Other population-level responses could include abundance, biomass, density, among others, however, generally these require identifying individual animals. While adult Fowler's toads are easily individually identifiable, it was not feasible to perform a capture-mark-recapture survey of the adult ranid frogs or tadpoles as they have no fingerprint-like pattern for mapping and given the disturbances already present in the landscape, more invasive methods like toe clipping and visible implant tags (Govindarajulu and Anholt, 2006) were avoided. This is true for all animals captured in the minnow traps; none were individually identified. While not individually identifying animals limited the metrics that could be calculated, the captures per unit effort results are sufficient to glean the effects of disturbances at a suitably fine grain.

There was no evidence that *Phragmites* management reduced oxygen in treated sites compared to control sites, but oxidation-reduction potential varied according to site type and was one of the significant environmental variables that differentiated site type communities, separating washover from non-washover sites. Indeed, in terms of environmental variables and community composition, control sites and herbicide-treated-only sites were most similar to each other, while herbicide-treated and washover sites were most similar to washover-only sites. This finding was apparent across chapters, that sites unaffected by the washover were most similar to each other, and sites affected by the washover were most similar to each other in most measures. Ranid frogs, for example, exhibited higher abundance in non-washover sites than in sites affected by the dune washover and Fowler's toads preferentially inhabited sites where the newly created sand washover fans and terraces from the natural disturbance created sandy-bottomed pools, irrespective of the site’s herbicide-treatment status. Furthermore, washover communities diverged from non-washover communities in terms of trajectories and compositions, and non-washover communities had their own set of indicator species.

The groups identified as indicator taxa in this research ranged from common groups to groups encompassing an endangered species of fish and groups encompassing an endangered species of toad. These taxa may represent ideal candidates to be utilized for future disturbance response monitoring efforts and continued management goals. Identifying indicator taxa may not be useful unless their utility in management is considered (Bal et al., 2018). For example, if a taxon is too rare, monitoring it is perhaps more arduous than sampling the whole community (Niemi et al., 1997). Thus, the groups identified as indicators here may better represent a starting point for management endeavors and the list of taxa should therefore be further filtered to meet specific management objectives and constraints (Bal et al., 2018).

Despite changes in population- or community-level metrics occurring in areas that have been disturbed, when the landscape is considered as a whole, a different trend may exist, drawing attention to the impact of the scale in disturbance ecology. In this thesis, although each disturbed site type exhibited a decrease or no change in diversity compared to control sites, when these disturbed sites were combined across the landscape, the effective number of species was significantly higher compared to the control sites. In this case, effort was controlled for when combining disturbed sites and comparison to controls. Despite what seems to be a clear and intuitive result; that disturbance begets heterogeneity and heterogeneity begets diversity; a very well-known relationship may play a role here. The species-area relationship posits that species richness increases with area, and thus where the larger combined area of “disturbed” landscape compared to “undisturbed” landscape may bias this result. While it is not entirely possible to rule out, at a coarser scale (according to the taxon's perspective), habitat heterogeneity has been shown to affect species richness more strongly than area (Kallimanis et al., 2008). Given all taxa considered in the minnow trap research are relatively small-bodied, habitat heterogeneity is likely to be more important than area at even more local scales (from the human perspective). When compared to a relatively homogeneous landscape, it is expected that disturbed sites exhibit more habitat heterogeneity; and hence this result is likely trustworthy. To ascertain beyond this, research in this area would do well to consider the impact of area and quantify heterogeneity.

Summary, Implications, and Conclusion

Summary

Using a two-by-two factorial design of site types, with control sites, herbicide-sprayed sites, sites that were washed-over, and sites affected by both the herbicide and the washover, I collected data in the dynamic landscape of Long Point, Ontario. In this thesis, I first explored the habitat associations of anurans, including an endangered species of toad, in response to two overlapping disturbances, an herbicide-application and dune washover. I demonstrate apparent habitat partitioning between ranid frogs and Fowler's toads in response to the natural dune washover. Second, I considered the wetland aquatic community responses in terms of diversity, community structure, and community trajectory, to these same disturbances. I identify several indicator taxa, reveal the intensified effects that can ensue following overlapping disturbances, and demonstrate the importance of scale in diversity responses to disturbance.

Specific Implications for the Long Point Sandspit

This thesis is the result of a need-based study where understanding the post-herbicide application responses of biota was the goal. The herbicide applications at the study site represented a unique instance that a glyphosate-based herbicide had been sprayed over aquatic habitats in Canada (Robichaud and Rooney, 2021). Despite the monitoring efforts in 2017 following this first round of treatment, the biotic responses of many more sensitive taxa were unknown. Thus, adding to the herbicide-application research done in the Long Point region of southern Ontario, Canada, I provide insights into the population-level habitat use of frogs and toads following disturbance and into the effects on the aquatic community. This method of reed management has been considered largely successful (Robichaud and Rooney, 2021) and based on the results presented here, the management causes little to no harm to the Anura or general aquatic community. However, the results reveal significant effects of the natural disturbance regime for the aquatic community and for several species at risk, that may have cascading impacts for the rest of the biological community of Long Point. The type of habitat created by the dune washover disturbance has previously been shown to be the preference of the endangered Fowler's toad in Canada (Green et al., 2011), however this habitat has been absent in the proximal end of Long Point for several years. The lack of these habitat features had likely forced the toads to inhabit ill-favoured habitats and compete for resources with other frog species. However, if the Fowler's toads were not negatively affected by the reed management, but simply used habitats affected by the washout, then it is likely that in the long run, with less *Phragmites* and existence of washover habitats, that the toads' population will continue to increase. With increases in toad populations, there may be increases in the federally threatened Eastern Hognose snakes (*Heterodon platirhinos)* that are considered toad specialists and as adults primarily feed on American and Fowler's toads in Canada (COSEWIC 2021). These types of shifts may yet cause less predictable changes in populations, which can scale up to communities and entire ecosystem function (Johnson-Bice et al., 2023) Thus, it will be important to continue to monitor the Long Point region, as results from one year are unlikely to provide the complete picture. Identifying indicator taxa has become standard in ecological monitoring, such as post-disturbance and once identified, indicator taxa can be surveyed as an alternative to studying an entire community, thereby decreasing the effort (monetary and otherwise) of monitoring programs. I would advise then that the species regarded as indicators in this research be considered future monitoring efforts of these and future disturbances.

General Implications

This thesis has implications for the "applied" aspect of ecology, the intersection of ecology, conservation, and management. There is often a lag between the research and the application, especially as it takes time to publish ecological research and it then takes time for on-the-ground conservation and management, which is informed by this ecological literature, to translate these findings into action. As a result, classical restoration and the management of landscapes have often aimed to attain a particular subset of environmental features of a reference or historical and a regularly deemed "superior" state as an endpoint or restoration goal (Perring et al., 2015). Under these conventions, a target landscape for restoration is described as one that has been reverted to a previous successional stage or to an alternate stable state that is not conducive to management goals. While the realisation of a fixed endpoint, or particular ecosystem state, is still frequently designated as an objective in many conservation efforts, this idea ignores the role of disequilibrium generating processes like disturbances and other stochastic factors in shaping communities and maintaining biodiverse ecosystems. Considered a paradigm shift (Mori 2011), ecological literature has begun to acknowledge the influence the natural disturbance regime has on the long-term patterns and general maintenance of landscapes (Perring et al., 2015). As such we have just begun to see work in these fields become well integrated with each other; where management and conservation recognize the importance of disturbance and disequilibrium in natural ecosystems.

Conclusion

Ultimately, the results of my thesis highlight the role of natural disturbance in the creating of a mosaic of different habitats, likely increasing heterogeneity in the landscape. Where two taxa exhibit differential habitat preferences, maintaining the cyclic disturbance regime that creates distinct habitats allows taxa to coexist. Where the entire aquatic community is considered, allowing the natural disturbance to occur creates patchiness in the landscape, so disturbances, despite reducing site-level diversity, increase overall landscape-level diversity. In addition, this thesis joins the body of literature that suggests that whether conservation goals be for single-species conservation or preserving ecosystem function through the maintenance of diverse ecological communities, the promotion of the natural disturbance regime may dictate the long-term success of a conservation or management endeavor. Disturbances are projected to increase in frequency and decrease in predictability with climate change, and consequently disturbance regimes will continue to be modified and new disturbances introduced. Under new pressures from these disturbances, it has never been more crucial to grasp their potential impact on our natural landscapes and the resident biota.

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