

# Naturalizing Naturalization: Accounting for Naturalization in Ecology and Ecological Management

A Thesis Submitted to the Committee on Graduate Studies in Partial Fulfilment of the Requirements for the Degree of Master of Science in the Faculty of Arts and Science

TRENT UNIVERSITY

Peterborough, Ontario, Canada

Copyright by Nicholas Anthony Paul Weissflog, 2024

Environmental and Life Sciences M.Sc. Graduate Program

January 2025

## **ABSTRACT**

Naturalizing Naturalization: Accounting for Naturalization in Ecology and Ecological Management

Nicholas Anthony Paul Weissflog

This thesis presents a case of the aquatic plant species Fanwort (*Cabomba caroliniana*) significantly naturalizing in Kasshabog Lake in bays where it had been invasive. This significant naturalization presents major implications for invasive species management and invasion biology because the naturalization of invasive species is a phenomenon that has been largely omitted from study within ecology. There are several reasons for this: 1) the most used definition of the term naturalization within invasion biology categorically excluded the sense in which naturalization refers to community integration; 2) the most cited frameworks that have been created and used to describe and study biological invasions have no conception of invasive species naturalization; 3) boundary work has been conducted to exclude consideration of the naturalization of invasive species. Incorporation of an understanding of naturalization into science and management of biological invasions will make our understanding of them more complete.

Keywords: Discourse Analysis; Ecological Management; Ecological Restoration; Invasive Species; Invasive Species Management; Naturalization; The Process of Invasion; The Process of Naturalization

## Acknowledgements

With regard to acknowledgements, there are a series of people I want to thank. First and foremost I want to thank Eric for being there for me and for his love and patience, I could not have done this without you, not only in with regard to idea development, but the way you helped me get by while I did this; Coming back to a masters while actively recovering from psychosis was not easy but it was a humongous part of what healed me because it gave me the opportunity to do something that I felt was meaningful.

Next, I want to thank my co-supervisor Tom for suggesting to me to come back and for always being willing to talk about various things with me (which was essentially every day I saw you were on the campus), for always being willing to read and provide comment on my work and for being so willing to tolerate my terrible humour (which goes for Eric as well, though rarely does he go without reminding me just how bad it is ;P).

I want to thank Dave for helping me with my data and editing most particularly, thoroughness is not my strong suit in some instances, and I really appreciated you taking so much of your time to help me with it, your meticulousness gave me some structure I really appreciated and needed.

I also want to thank Philip Fry who has been my friend and mentor since I was in high school on native wildflower horticulture, ecology, ecological restoration, philosophy and art. Thank you for revising my work and being my friend. I also want to thank Rachel Everett-Fry for all of the philosophical debates and conversations that helped me flesh out the philosophical basis for my arguments. I want to thank Catherine Everett for her unconditional acceptance and her friendship and for tolerating my absolutely terrible sense of humour.

I want to thank Mark Jones for hosting me while I was doing my work on Kasshabog Lake and for taking me on a boat ride so fast I was involuntarily yelling (joyfully of course)

as well as fixing the boat numerous times, I would not have had a field season without you. I want to thank Pat Levasseur for being willing to read my work on my many unsolicited visits and for being my friend all these years since I began this process as well as helping me in the field a bit. I also want to thank Kaleigh Mooney for being such a great field partner on all the other field work in the lab that kept me afloat throughout this masters. I want to thank Shelby Walters for her help counting bugs and for coming out in the field with me. I also want to thank my brother Tom for helping me in the field. I want to thank Nick Borek for helping with a German to English translation of Holub and Jirásek 1967. I want to thank Stephen Hill for being a consistent presence in the face of being run off your feet with additional duties in the last few years. I also want to thank Stephanie Rutherford for the wonderful conversations that were greatly stimulating and a joy to have whenever it was the right time for them to occur, they really fed the humanities part of my soul and were a great form of encouragement.

I also want to thank Matt Chew for reading my work and providing critical feedback as well as just being someone to talk to about this whole thing. I want to thank David Richardson, Geerat Vermeij and Mark Davis for having conversations on the phone or on zoom, those conversations each helped me get a much clearer sense of what has been going on in Invasion Biology, particularly with regard to frameworks for the process of invasion.

Lastly, I would also like to thank the Federation of Ontario Cottage Associations (FOCA), the Kasshabog Lake Residents Association, the Township of Havelock, Belmont and Methuen and Covia Corp Canada LTD for funding support, without which I would not have been able to do this study.

## Table of Contents

Title Page .....	i
ABSTRACT .....	ii
Acknowledgements .....	iii
Table of Contents.....	v
List of Figures.....	vii
List of Tables.....	ix
Glossary .....	x
Chapter 1: Introduction .....	1
1.1 Personal Introduction .....	1
1.2 General introduction .....	3
1.2.1 Summary of the Approach/Overview of the Structure of the Thesis.....	3
1.2.2 Novelty and Importance .....	5
Chapter 2: Field Study of the Naturalization of Carolina Fanwort ( <i>Cabomba caroliniana</i> ) in Kasshabog Lake .....	7
2.1 Introduction.....	7
2.2 Materials and Methods .....	11
2.2.1 Study Area and Fanwort .....	11
2.2.2 Community Sampling.....	12
2.2.2.1 Macrophyte Sampling .....	12
2.2.2.2 Macroinvertebrate Sampling .....	13
2.2.3 Data Analysis .....	13
2.2.4 Statistical Analysis .....	14
2.3 Results .....	14
2.3.1 Criterion 1: Fanwort Dynamics in the Fanwort Sites .....	14
2.3.2 Criterion 2a: Macrophyte Community Dynamics .....	16
2.3.3 Criterion 2b: Macroinvertebrate Community Metrics .....	17
2.4 Discussion .....	18
2.4.1 Significant Naturalization of Fanwort .....	18
2.4.2 Commentary on Dominant Hypotheses for the Process of Invasion .....	19
2.4.3 Rapid-evolution.....	21
2.4.4 Rectifying Impact and Naturalization .....	25
Chapter 3: Definitions of Naturalization .....	27
3.1 Naturalization and Naturalization.....	27
3.2.1 Subargument 1: Dictionary Definitions .....	31

3.2.2 Subargument 2: Darwin’s Naturalization Hypothesis .....	32
3.3 Recent Terminological Directions and Conclusion .....	35
<b>Chapter 4: A New Proposed Unified Framework for Biological Invasions and Species Naturalization.....</b>	<b>37</b>
4.1 Introduction.....	37
4.2: Cases of Significant Naturalization.....	38
4.3 A Review of the Frameworks for the Process of Naturalization/Invasion.....	41
4.4: Terminological Review of Frameworks for the Process of Invasion .....	44
4.5: Reinterpretation of the Blackburn et al. 2011 Barrier Model.....	51
4.6: Conclusions.....	55
<b>Chapter 5: Naturalization has been the Casualty of Boundary Work in Invasion Biology .....</b>	<b>57</b>
5.1 Introduction.....	57
5.2 A brief review of accusations of invasive species denialism in invasion biology .....	59
5.2.1 Blackburn and Russell (2017) and responses .....	60
5.2.2. Ricciardi and Ryan (2018) and Munro et al. (2019).....	61
5.2.3 Boundary work in Russell and Blackburn (2017) and Ricciardi and Ryan (2018).....	63
5.3 The Excluded Work Represents a Significant Portion of the Popular and Scientific Literature that creates the Basis to Understand the Phenomenon of Naturalization .....	63
5.4 Boundary work requires Authority and the Power that comes with it.....	64
5.4 Going back to a relative beginning with how the definition of naturalization was changed by Richardson et al. 2000 .....	65
5.5 The Discourse does not have to be this way: a Comparison of the Discourse between Restoration Ecology and Invasion Biology .....	66
<b>Chapter 6: Implications and Recommendations .....</b>	<b>73</b>
6.1 Scientific Implications and Recommendations .....	74
6.2 Management Implications and Recommendations .....	75
6.2.1 Viewing Single Species Eradication Campaigns through the Lens of Ecological Restoration .....	78
6.3 Terminological Suggestions.....	81
References .....	83
Appendix 1 .....	104
Appendix 2 .....	104

## List of Figures

Figure 2.1: Map of study site locations within Kasshabog Lake.....	21
Figure 2.2: Mean and standard error for metrics pertaining to Fanwort abundance by site type and year. Fanwort (A) biomass (B) proportion of community biomass (C) occurrence in quadrats.....	24
Figure 2.3: Mean and standard error for metrics pertaining to macrophyte community structure by site type and year. (A) Quadrat Simpson's diversity (B) Quadrat Shannon's diversity (C) Quadrat species richness (D) Total community biomass.....	26
Figure 2.4: Relationship between changes in Fanwort biomass (blue line), Shannon's diversity (green line), Simpson's diversity (red line) and Fanwort ecosystem residency time.....	30
Figure 2.5: From Krebs 1972, a speculative depiction of what is meant by evolutionary time in the context of community composition equilibriums of which the process of naturalization would be a part.....	34
Figure 4.1: Literature connectivity of frameworks for the process of invasion/naturalization. Frameworks are ordered chronologically from top to bottom and arrows indicate citation by proceeding frameworks. Green boxes indicate frameworks that describe the phenomenon of naturalization and yellow boxes indicate frameworks that do not describe the phenomenon of naturalization.....	55
Figure 4.2: Reinterpretation of the framework for the process of invasion proposed by Blackburn et al. (2011). The original framework is depicted in the top box, the intermediate step making clear the changes is in the middle and the newly proposed model is at the bottom.....	62
Figure 4.3: The Invasion curve (from Cornell Cooperative Extension 2024).....	63

Figure 6.1: Adaptive decision support framework agreed on by members of the working group at the meeting in Fergus. Circles with text indicate actions, and numbered boxes indicate considerations linked to specific decision support tools devised by the working group in breakout sessions. Monitoring plays a central role in the framework, reflecting principles of adaptive management (Figure description from Robichaud et al. 2023).....89

## List of Tables

Table 2.1: Structural metrics for the macroinvertebrate community by year and site type (mean and 95% confidence interval).....	27
Table 3.1: Clauses of naturalization mentioned by interviewees.....	45
Table 4.1: Papers depicting evidence of significant species naturalization.....	50
Table 4.2: Authors that have published multiple articles depicting the process of invasion/naturalization.....	53
Table 4.3: Equivalent stages/terminology in different frameworks of the process of naturalization/invasion.....	55-57
Table 4.4: Most common terms by equivalent stage.....	58
Table 6.1: Criteria to define a significantly naturalized state.....	83
Table 6.2: Answers to the question of whether each practitioner accounts for invasive species possibly naturalizing.....	85
Table 6.3: Noted timelines for invasive species naturalization.....	85

## Glossary

**Coevolution:** an evolutionary process in which two species (or groups of species) are important agents of selection for, and respond to, each other (Vermeij 2013).

**Impact:** an impact that changes the environment in such a way as to reduce native biodiversity or alter ecosystem function to the detriment of the incumbent native species—as indicated by a change in importance or abundance following invasion.

**Invasive species:** a species which 1) has arrived in a given ecosystem relatively recently 2) is having clear negative impacts on the structure and/or function of that ecosystem relative to a reference condition prior to its arrival.

**Integration:** a process in which an introduced species becomes increasingly incorporated into a recipient community through reciprocal responses to one another evolutionarily and ecologically whereby 1) the introduced species' presence may affect the abundances of the species in the recipient community, affecting selection pressures and 2) the introduced becomes increasingly incorporated into the recipient community's food web (sensu Vermeij 1996).

**Integral:** as it refers to an introduced species, this refers to a species having become functionally important within a new ecosystem such that it functions in a similar manner to an analogous native species (Wu et al. 2004 e.g. Schilthuizen et al. 2016)

**Naturalization:** the process by which both a species becomes integrated into a new ecosystem and an ecosystem integrates a new species on a trajectory towards it becoming functionally equivalent to an analogous native species.

**Naturalize:** to become native (OED 2024)

**Naturalized:** having become native

## **Chapter 1: Introduction**

### **1.1 Personal Introduction**

This thesis goes outside the normal conventions for one in the M.Sc. ENLS program for one particular reason. That reason is that it is not strictly bound to the scientific method in the sense of looking at correlative and causal patterns in natural phenomena; it is also interested in making a commentary on the human practice known as invasive species management and the human science known as invasion biology for the purpose of suggesting changes to our approach to ecological management and ecological science as it pertains to the phenomenon described as biological invasions. A large claim no doubt for a master's thesis, but I realized that if I don't say this, I would be understating my claim; which is apart from, of course, whether it is a good claim or not. That is nonetheless the scope of this thesis.

Why did I do this? There are many reasons.

First, an interdisciplinary approach allowed me to study the strongly human reasons for the lack of study of the phenomenon of invasive species naturalization.

Second, my supervisor Eric had a recent reflection on his late father that speaks to this. His father worked on pollution in lakes and rivers in Wisconsin. Over his father's time, there was a slight decline in nutrient inputs, followed by an increase. He asked him in one of his many visits before his death; how do you think about and reflect on this; having worked so hard and seeing that not much has changed, what would you do differently? His father told him, "I would focus not just on science but poetry, to help others understand the consequences of these activities". So it is here I hope, though it is short on poetry, it does contain a significant component that draws on the philosophy and study of science that brings in a meaningful contribution via methods from the humanities (e.g. the works of Bruno Latour and Karl Popper).

The third is that this format suits me. I have always had an interest in both environmental ethics and ecology; these come together naturally in ecological management and restoration, a strong interest of mine. But this interest is not happenstance as it pertains to this and my reason for mentioning it is not passing; part of the problem I seek to address is precisely that these two have departed from one another too much, that is science and ethics, in invasive species management (Munro et al. 2019). Immanuel Kant in the book “The Critique of Pure Reason” speaks to the general problem with this separation directly:

**“Human reason has this peculiar fate that in one species of its knowledge it is burdened by questions which, as prescribed by the very nature of reason itself, it is not able to ignore, but which, as transcending all its powers, it is also not able to answer”**

Herein he means, as it is relevant here, science (in its current form and as reason), **alone**, is unable to answer questions that combine phenomenal mechanisms with moral intuitions and imperatives. But when combined with moral inquiry it can meaningfully do so, or at least attempt to do so. Kant's “*a priori*” as moral sense and the “*a posteriori*” as scientific experience, together forming wisdom for wise action as it is known and enacted by the actor/subject.

While this project began as an attempt to observe invasive species naturalization, it evolved into making a commentary on invasive species management and invasion biology in general. Inevitably whatever I have written will be imperfect however I hope it is able to make robust enough suggestions that it contributes to a fuller understanding of ecological processes and the way in which we manage all biological invasions. Nonetheless, imperfect it will be and all the better because while visiting my co-supervisor Tom Whillans, he suggested to me an article he wrote called “Historic and comparative perspectives on

rehabilitation of marshes as habitat for fish in the lower Great Lakes basin". In this article he emphasises the importance of what he calls narrative science for restoration and ecosystem management, that is, how forming a sincere, if inevitably imperfect, narrative is important and useful for informing good (in the moral sense) restoration actions (Whillans 1997).

I could not agree more, so here is mine.

## **1.2 General introduction**

### **1.2.1 Summary of the Approach/Overview of the Structure of the Thesis**

This thesis began as an attempt to observe the naturalization of an invasive species, or at least the extent to which naturalization does or does not occur over time. Initially, I had laid out a possible study design to look at differences in ecological structural metrics within lake ecosystems with a gradient of Eurasian water milfoil (*Myriophyllum spicatum*) residency times. However, given budget and logistical constraints and an amenable study design, a revisit of a study of the impact of Fanwort on Kaskabog Lake (Reid et al. 2009b) was chosen (I mention this as a form of suggestion to others, I still think a study of lakes with a gradient of invasive species residency times would be a great study design). Much of the rest of this thesis came into being after beginning my literature review whereupon, using the search terms "naturalization" and "invasive species" conjunctively, I encountered the framework created by Blackburn et al. (2011) and was subsequently confused. This thesis then became an exploration of not only why this word was defined as it was in the invasion biology and ecology literature, but also why the phenomenon which I observed in my field study and the phenomenon to which I understood naturalization to refer, had gone completely unstudied and unaccounted for in ecological management. Though, it should be noted, there are

significant exceptions to this, for instance, Anishinaabe traditional worldviews and ecological management anticipate and actively promote the naturalization of introduced and invasive species (Reo and Ogden 2018).

This thesis is an effort to comprehensively create the basis for more systematically investigating the phenomenon of naturalization within science such that it may be better accounted for in management influenced by that science. In addition, it is also an attempt to elucidate the reasons why it has not been accounted for, by and large, up to this point. Because of the broad scope of this work, I have used techniques from several different disciplines to achieve this comprehensiveness as I felt that it enabled a fuller picture to be assembled. The work within this thesis is divided as follows:

The second chapter of this thesis is a field study of Fanwort which presents a case study of an invasive species naturalizing on a relatively short timeline. It also contains new measurable criteria that define naturalization as a natural phenomenon.

The third chapter of this thesis deals with definitions of naturalization, in this chapter I put forward a new definition for naturalization in an ecological context as well as the argumentation to support that definition.

The fourth chapter of this thesis is a critical review of frameworks for the process of invasion. It analyzes them as they either do or do not describe the natural phenomenon of naturalization observed in chapter three. In this chapter I propose a new framework for the process of invasion that is a modification of the framework proposed by Blackburn et al. (2011).

The fifth chapter of this thesis is a critical review of the discourse in invasion biology in the attempt to partly answer the question of why naturalization has never been included and described within the predominant frameworks for the process of invasion.

The sixth chapter of this thesis is the general conclusion of the thesis and discusses the implications of the thesis for science, policy and management.

### **1.2.2 Novelty and Importance**

I am inclined to think (and I could be wrong) that this is, to date, the most comprehensive review of both the semantics of the word naturalization and the phenomenon I am referring to when I say or write the word naturalization as it refers to an ecological context. Richardson et al. 2000 was the most recent work, to my knowledge, that systematically approached defining and exploring this term (and phenomenon, though the reason for this as a bracketed comment will become evident in the third chapter as it pertains to a disagreement on definition). I believe that the novelty within this review can be described as:

- 1) A measurable set of criteria of what constitutes significant naturalization of an invasive species (Chapter 2)
- 2) A set of arguments advocating for a different definition of naturalization for use within ecology (Chapter 3)
- 3) A comprehensive review of frameworks for the process of invasion (Chapter 4)
- 4) Modification of Blackburn et al.'s (2011) unified framework for the process of invasion such that it includes frameworks that account for naturalization and becomes capable of explaining the phenomena observed in the field study of this thesis (Chapter 4)
- 5) A possible partial explanation as to why naturalization has not been accounted for in invasion biology and, consequently, ecology, generally (Chapter 5).

The importance of all of this is that I hope that, all together, this thesis creates the basis for naturalization of invasive species to be accounted for in invasion biology and invasive species management, as well as ecology generally. That is important because I suspect ecological management as a whole would look mildly different on a large scale if the

naturalization of invasive species were studied more comprehensively and then accounted for in management since this phenomenon is relevant to every single biological invasion.

## **Chapter 2: Field Study of the Naturalization of Carolina Fanwort (*Cabomba caroliniana*) in Kasshabog Lake**

### **2.1 Introduction**

The naturalization of non-native species by means of ecological integration into new ecosystems is a process that has occurred as long as there have been distinct ecosystems and dispersing organisms (Vermeij 1996; Burdon et al., 2013). However, it is a process that is generally unaccounted for by ecological managers and researchers. This lack of study is likely due to the urgent need for information about the impact of novel species introductions (Blackburn et al., 2011) to the extent that attention to naturalization is generally excluded (Chew 2009; Davis et al., 2011). Because of this, there is little understanding of the time needed for naturalization to occur or the factors that contribute to this process (LeBrun et al., 2022).

The globally unprecedented arrival and establishment of new species in many naïve ecosystems (Pyšek et al., 2020) provides an opportunity to study the time it takes for the ecological integration of new species to occur to a significant extent. This has the possibility of providing important insights into the prediction and management of biological invasions as well as ecological management generally.

I am defining naturalization as the process by which, simultaneously, a species becomes integrated into a new ecosystem and an ecosystem integrates a new species (e.g. Holub and Jirásek, 1967; Groves et al., 1986; Cousens and Mortimer, 1995). Significant integration becomes evident when the establishment of an increasingly stable dynamic equilibrium (*sensu* Wilson, 1969) in a species' abundance, and the ecosystem's reaction to it, is observable (e.g. Burdon et al., 2013). This occurs as a result of ecological and evolutionary

interactions such as the gradual incorporation of a new species into food webs (Carroll 2011; Burdon et al., 2013).

This definition of naturalization differs from others commonly found in the invasion biology literature (e.g. Richardson et al., 2000; Blackburn et al., 2011) because those definitions lack the connotation of community integration. I defined naturalization in this way because I think that community integration aligns with how this word is used in the English language more broadly (OED 2024; Merriam Webster 2024).

This process of invasive species becoming ecologically benign over time is known to occur (e.g. Reise et al., 2006; Lavoie 2010; Fernández 2020). However, it is rarely explicitly recognized as such, perhaps due in part to the acrimonious nature of the debates within the invasion biology literature (Guiasu and Tindale 2018) where some dominant opinions can be hostile to any evidence that departs from the paradigm of invasive species being anything but inevitably problematic (e.g. Stratton et al. 2022). For example, in the most cited frameworks describing the process of invasion, there is a general omission of a stage analogous to what I am claiming comes after a species is described as being invasive (e.g. Blackburn et al. 2011). It is my view that this later process of a species becoming ecologically unproblematic is necessarily a sign of naturalization by means of ecological integration. Studying this phenomenon, particularly the time it takes to occur to a significant extent, has the potential to inform management practices, particularly in helping define invasive species management endpoints. To be clear, the urgent need for early management and intervention to mitigate the negative ecological impacts invasive species can have is not at issue, rather I am suggesting that as species are integrated over time, continuing to use these management approaches (i.e. eradication), or to frame a species within this initial stage paradigm, is in itself problematic. Thus it becomes necessary to understand the ecological metrics and time scales involved.

This study was an attempt to observe whether significant naturalization had occurred in the submerged aquatic plant Carolina Fanwort (*Cabomba caroliniana*) within ~15-20 years of ecosystem residency time (Noel 2004; Reid et al. 2009b). Fanwort has become established in regions in at least 21 countries beyond its native range, with 7 of those countries considering it to be invasive (Roberts and Florentine 2021). Fanwort's designation as invasive in these jurisdictions (e.g. Weibert 2015) has been due to its impacts such as the shading out other submerged aquatic macrophytes resulting in reduced macrophyte species diversity, typically within a few years after introduction (Lyon and Eastman, 2006; Hogsden et al. 2007; Schooler and Julien, 2011; Vukov et al. 2013). Fanwort also interferes with recreational activities (Schooler and Julien, 2011) and has resulted in economic impacts (Schooler 2008; Wilson et al. 2007; Schooler and Julien 2011). The province of Ontario in Canada is among the jurisdictions that has listed Fanwort as invasive (Invasive Species Act 2015), and has at least one population within the Crowe River Watershed that is expanding its range towards a provincial canal system, the Trent Severn Waterway. A study done 14 years earlier assessed the impact of Fanwort on the Kasshabog Lake ecosystem (Reid et al. 2009b), and provided a suitable reference study to assess whether Fanwort has naturalized over the past 14 years within Kasshabog Lake's ecosystems.

I have four *a priori* assumptions: 1) that species naturalization occurs as a process (e.g. Groves et al. 1986; Mortimer and Cousens 1995; Reise et al. 2006; Hoffman and Courchamp 2016), 2) that naturalization entails the integration of a new species into an ecosystem over time, 3) it begins with a period of ecological instability (Strayer et al. 2017) and 4) is followed by increasing stability (e.g. Burdon et al. 2013). It is this last assumption that leads to my research question: have the other organisms adapted to Fanwort's presence in Kasshabog Lake such that Fanwort is becoming an increasingly integral part of the functioning of the Kasshabog Lake ecosystem?

### 2.1.1 Rationale behind the research question

This process of naturalization begins with a novel species being introduced into a suitable environment where it initially proliferates (Blackburn et al., 2011) through factors such as enemy release (e.g. Jeschke et al., 2012). This initial phase is often accompanied by other species becoming less abundant, either by being out-competed or through the loss of habitat (Soto et al. 2024). At this stage the new species is able to be identified as invasive by its impact on the ecosystem, with impact being defined as changes relative to a pre-invasion reference state (Blackburn et al., 2014). After this initial introduction and expansion phase, all species, including the new species, adapt through coevolution in relatively short time frames by means of natural selection (Carroll et al., 2007; Miller et al., 2020) and in some cases social learning as well (e.g. Servheen and Gunther, 2022). The newly introduced species becomes less abundant and is no longer identifiable as an invasive species based on the lack of impact to metrics of richness or diversity relative to a pre-invasion reference state. It is at this point in that the process of naturalization has reached a relative end and the species can be considered significantly naturalized.

Within this study system, I define a significantly naturalized state by two criteria:

Criterion 1: The invasive species, in this case *C. caroliniana*, is both widespread and in low to moderate abundance relative to a peak abundance following introduction.

Criterion 2: The structural metrics (e.g. richness and diversity) of the invaded community would be at levels similar to those of a pre-invasion reference community

Using these criteria I hypothesized that if significant naturalization had occurred then substantial reductions in measures of *C. caroliniana* abundance, despite it remaining widespread, would be observed in sites where *C. caroliniana* has been present for at least 14 years (hypothesis 1) and that macrophyte and macroinvertebrate community metrics such as diversity, richness and total community biomass in the sites where *C. caroliniana* has been

present for at least 14 years would be similar to pre-invasion levels measured in 2008 by Reid et al. (2009b) (hypothesis 2).

## 2.2 Materials and Methods

### 2.2.1 Study Area and Fanwort

This study looked at the introduced aquatic macrophyte species Carolina Fanwort (*Cabomba caroliniana*) in Kasshabog Lake, located in north-eastern Peterborough County, Ontario, Canada (44.63, -77.96) (Figure 2.1). This lake is oligotrophic and is situated on predominantly granite bedrock of the Precambrian Shield (Hogsden et al., 2007). Carolina Fanwort was first discovered in Kasshabog Lake in 1991 where the North River flows into Kasshabog Lake (Macdonald, 2002). There has been no management of the plant since its arrival as there were no tools deemed both allowable in Canadian waters and effective at killing Fanwort at the scale required (Macdonald, 2023, personal communication). This study resampled sites used in a previous study conducted to assess impact in 2008 (Reid et al., 2009b). In both 2008 and in this study, littoral vegetation and invertebrates were sampled from six bays in Kasshabog Lake (Figure 2.1). In 2008, three bays were found to be dominated by *C. caroliniana* and are identified as “Fanwort” bays, three bays were dominated by native plants (*Megalodonta beckkii*, *Myriophyllum heterophyllum*, *Najas flexilis* and *Vallisneria spiralis*) and are identified in this study as “Reference” bays. The 2008 Fanwort bays had a coverage area of Fanwort during the period of peak biomass ranging from 17% to 60% (overall: 30%). The bays are, on average,  $20,500 \text{ m}^2 \pm 4,100 \text{ m}^2$  in area, with little to no human shoreline development (Three cottages or fewer). As an important note, while the terminology of “reference” was used to describe the sites with no Fanwort in 2008, those sites had Fanwort arrive in the years between 2008 and 2022, as such the state of

those sites in 2022 is not seen as a reference condition, as reference would otherwise refer to a site whose community is absent of Fanwort.

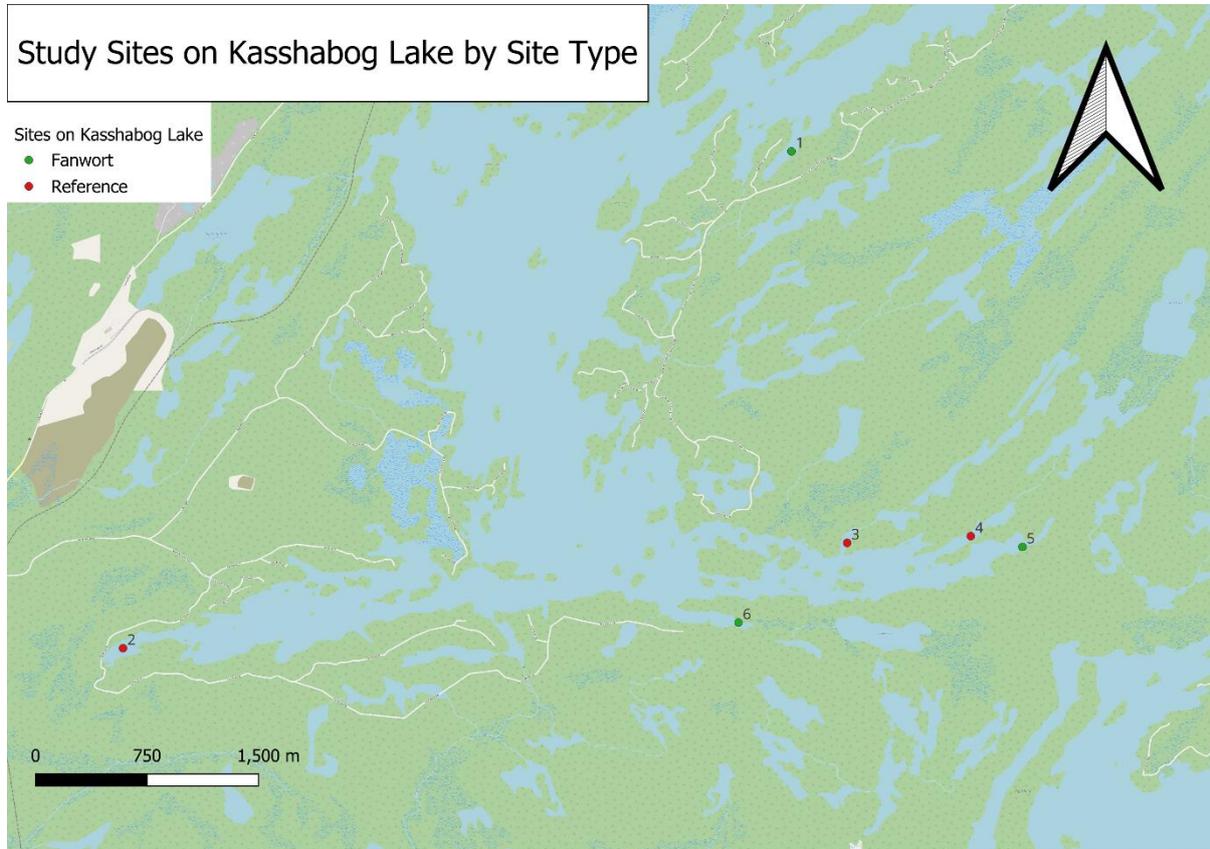


Figure 2.1: Map of study site locations within Kasshabog Lake.

## 2.2.2 Community Sampling

### 2.2.2.1 Macrophyte Sampling

The 2008 sampling took place in late summer from September 9-17. The 2022 sampling occurred in mid-summer: for macrophytes from July 29-August 25, and late summer and early fall for invertebrates from September 10 - October 2. Littoral vegetation was sampled along transects set perpendicular to the shoreline. Five transects were established in each bay and at least four 0.25 m<sup>2</sup> quadrats were sampled along each transect at 10m intervals. This repeated the methods used in the 2008 study (Reid et al. 2009b). While sample sites were the same between 2008 and 2022, quadrat and transect locations differed. Quadrat water depths

in both years ranged from 0.7 to 1.7m (mean: 1.25m). A swimmer harvested all the littoral vegetation within each quadrat.

#### **2.2.2.2 Macroinvertebrate Sampling**

I sampled the macroinvertebrates from a boat using a long handled 500  $\mu\text{m}$  mesh size D-net by sweeping the net through the vegetation and sediment below. Within each bay, I sampled at six randomly selected locations. The sampling effort was standardized as six minutes of sweeping through two approximately  $1\text{m}^2$  plots at each of the sample points. I identified the macroinvertebrates to either order or family, counting only the first 100 invertebrates from each sample, based on a method often used by the Ontario Benthic Biomonitoring Network (Jones et al. 2007).

#### **2.2.3 Data Analysis**

I quantified the Fanwort data using three methods: Fanwort biomass per  $\text{m}^2$ , the proportion of community biomass that was Fanwort, and Fanwort occurrence, where occurrence is the percentage of quadrats where Fanwort was present (Madsen et al. 2006)). The macrophyte community data was quantified in four ways: Simpson's diversity, Shannon's diversity, species richness, and total community biomass per  $\text{m}^2$ . The macroinvertebrate data was quantified in four ways: Invertebrate trophic level proportions (explained below), Bray-Curtis dissimilarity index, Simpson's, and Shannon's diversity indices.

#### **Invertebrate Trophic Levels Proportions:**

The invertebrate family and orders categories used in this study were recategorized into three general categories of feeding behaviour characteristics from Merritt and Cummins (1996):

**Primary consumers (herbivores and detritivores):** Diptera, Hemiptera, Amphipoda, Ephemeroptera, Collumbula, Turbellaria, Nematoda, Coelenterata, Oligochaeta, Isopoda, Bivalvia, Gastropoda

**Mixed/omnivores (omnivores or both primarily herbivorous and carnivorous at different points in their life cycle):** Plecoptera, Coleoptera, Trichoptera,

Hydrachnidia

**Primary carnivores:** Odonata, Decapoda, Megaloptera

## 2.2.4 Statistical Analysis

I used PAST 4 (PAST 4.10, Hammer et al., 2001) and R for all statistical analyses. Non-parametric one-way analyses was used to test differences in Fanwort metrics, macrophyte community metrics and macroinvertebrate community metrics. Non-parametric tests were used in all cases because of consistent violations of parametric assumptions. Diversity values for macrophytes were calculated with wet weight biomass rather than stem counts (Wilhm, 1968).

## 2.3 Results

### 2.3.1 Criterion 1: Fanwort Dynamics in the Fanwort Sites

As reminder, criterion 1 stated that if significant naturalization had occurred it would be expected that the invasive species, in this case *C. caroliniana*, is both widespread and in low to moderate abundance relative to a peak abundance following introduction. Fanwort biomass significantly decreased in the Fanwort sites between 2008 and 2022 (940 g/m<sup>2</sup> vs 380 g/m<sup>2</sup>, Mann-Whitney  $P > 0.001$ , Figure 2.2). Fanwort proportion of community biomass also significantly decreased in the Fanwort sites between 2008 and 2022 (38% vs 22%,  $P > 0.001$ , Figure 2.2). Between 2008 and 2022 Fanwort occurrence in the Fanwort sites was not significantly different (56% vs 44%, Tukey's Post Hoc,  $P = 0.851$ , Figure 2.2). These results indicate that Fanwort remains relatively widespread within the sites where Fanwort has resided for at least 14 years, despite significant reductions in its abundance.

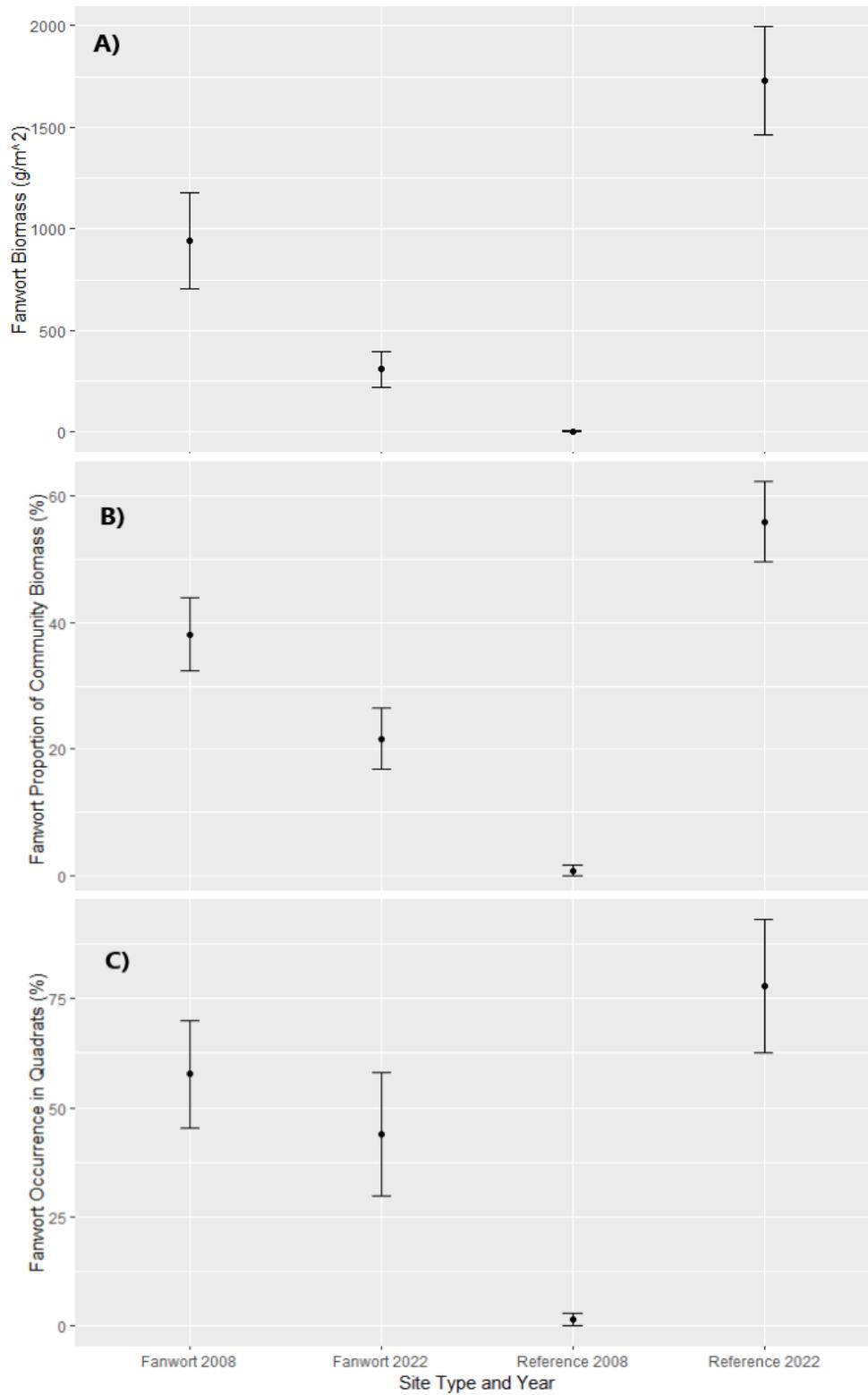


Figure 2.2: Mean and standard error for metrics pertaining to Fanwort abundance by site type and year. Fanwort (A) biomass (B) proportion of community biomass (C) occurrence in quadrats.

### 2.3.2 Criterion 2a: Macrophyte Community Dynamics

As reminder, criterion 2 stated that if significant naturalization had occurred it would be expected that the structural metrics (e.g. richness and diversity) of the invaded community would be at levels similar to those of a pre-invasion reference community. Quadrat ( $0.1\text{m}^2$ ) macrophyte diversity significantly increased in the Fanwort sites between 2008 and 2022 on both measures of Simpson's ( $0.269$  vs  $0.334$ , Mann-Whitney,  $P=0.027$ , Figure 2.3) and Shannon's diversity ( $0.447$  vs  $0.599$ , Mann-Whitney,  $P=0.045$ , Figure 2.3). Quadrat macrophyte diversity in the Fanwort sites in 2022 was not significantly different from the reference sites in 2008 on measures of either Simpson's ( $0.334$  vs  $0.342$ , Mann-Whitney,  $P=0.919$ , Figure 2.3) or Shannon's diversity indices ( $0.599$  vs  $0.572$ , Mann-Whitney,  $P=0.542$ , Figure 2.3) though quadrat macrophyte diversity in the Fanwort sites in 2008 was also not significantly different from the reference sites in 2008 on either measures of Simpson's ( $0.269$  vs  $0.342$ , Mann-Whitney,  $P=0.072$ , Figure 2.3) or Shannon's diversity indices ( $0.447$  vs  $0.572$ , Mann-Whitney,  $P=0.175$ , Figure 2.3). Quadrat species richness was significantly higher in the Fanwort 2022 sites compared to the reference 2008 sites ( $3.07$  vs.  $2.49$ , Mann-Whitney,  $P=0.0463$ , Figure 2.3) though Fanwort 2022 and Fanwort 2008 ( $3.07$  vs.  $2.66$ , Mann-Whitney,  $P=0.577$ , Figure 2.3). Total community biomass was significantly higher in the Fanwort sites in 2022 when compared to the reference sites in 2008 ( $1192\text{ g/m}^2$  vs  $569\text{ g/m}^2$ , Mann-Whitney Pairwise,  $P < 0.001$ , Figure 2.3) and there was no significant change in total community biomass in the Fanwort sites between 2008 and 2022 ( $1192\text{ g/m}^2$  vs  $1328\text{ g/m}^2$ , Mann-Whitney Pairwise,  $P=0.231$ , Figure 2.3). Notably, the reference sites in 2008 had the lowest mean quadrat species richness. Site level species richness changed from an average of  $15.3$  in the reference sites in 2008 to an average of  $11$  in 2022 and in Fanwort sites from an average of  $12$  in 2008 to an average of  $13.3$  in 2022. When the species lists from all sites in each of the site type/year groupings were pooled, species richness in the

Reference 2008 sites was highest at 21, while the Fanwort 2022 sites had a combined species richness of 19. Combined species richness was lowest (17) in the Reference 2022 sites.

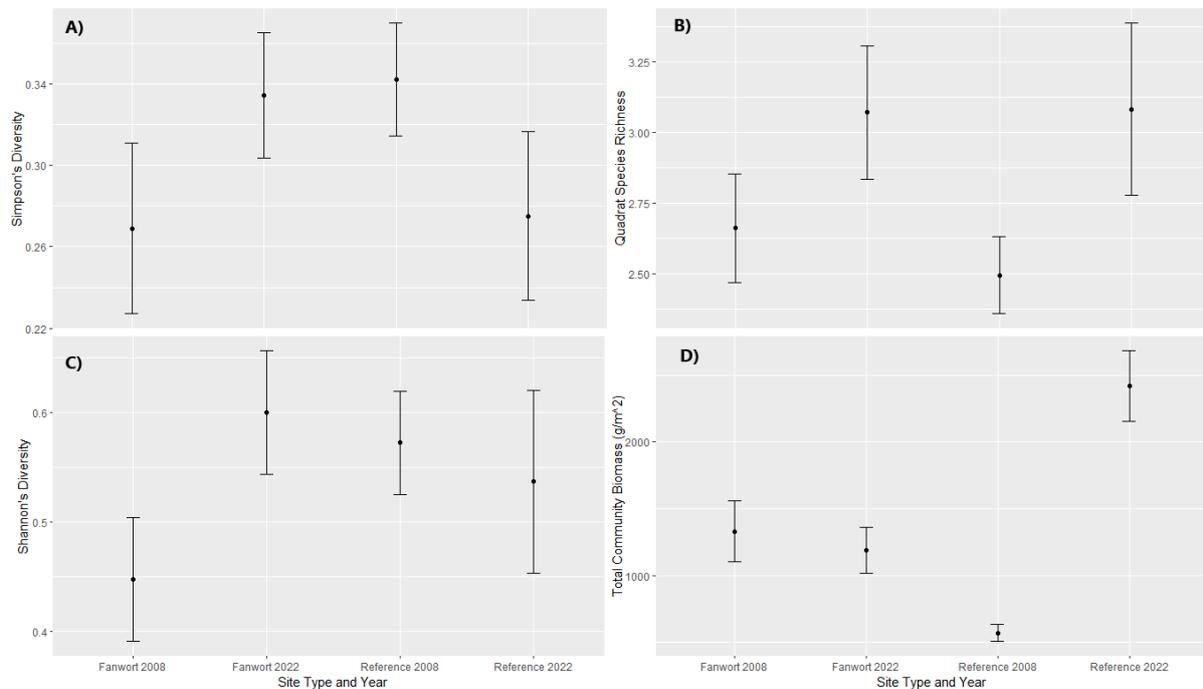


Figure 2.3: Mean and standard error for metrics pertaining to macrophyte community structure by site type and year. (A) Quadrat Simpson's diversity (B) Quadrat species richness (C) Quadrat Shannon's diversity (D) Total community biomass.

### 2.3.3 Criterion 2b: Macroinvertebrate Community Metrics

As reminder, criterion 2 stated that if significant naturalization had occurred it would be expected that the structural metrics (e.g. richness and diversity) of the invaded community would be at levels similar to those of a pre-invasion reference community. The mean proportion of both primary producers and omnivores did not significantly differ between years in sites of the same type (Table 2.1), however site types were significantly different in every case on both measures (Table 2.1). The proportion of primary carnivores was highest in the reference sites in 2008 and significantly different from all treatment type/year comparisons, the next highest proportion of primary carnivores was found in the reference 2022 sites, which seems to follow the general pattern as the proportion of primary producers

and omnivores. Richness and measures of diversity were significantly higher in 2008 compared to 2022, in every case, regardless of site type (Table 2.1), though the Fanwort 2008 sites had a significantly higher taxa richness than the reference 2008 sites.

Table 2.1: Structural metrics for the macroinvertebrate community by year and site type (mean and 95% confidence interval, asterisks indicate groupings that were not significantly different from one another)						
Site Type and Year	Mean Percentage of Primary Producers (%)	Mean Percentage of Omnivores (%)	Mean Percentage of Primary Carnivores (%)	Mean Taxa Richness	Mean Simpson's Diversity	Mean Shannon's Diversity
Fanwort 2008	36.3+/-3.77**	51.9+/-3.48**	11.7+/-2.91**	8.94+/-0.30*	0.814+/-0.008**	1.87+/-0.035*
Fanwort 2022	41.2+/-5.83**	45.5+/-5.34**	13.3+/-2.65**	4.88+/-0.48**	0.605+/-0.053***	1.17+/-0.118**
Reference 2008	53.7+/-4.79*	20.4+/-3.52*	25.9+/-3.84*	8.71+/-0.24*	0.783+/-0.011*	1.77+/-0.038*
Reference 2022	59.5+/-3.36*	22.0+/-2.08*	18.5+/-2.27**	6.67+/-0.42***	0.665+/-0.021***	1.36+/-0.050**

## 2.4 Discussion

### 2.4.1 Significant Naturalization of Fanwort

It is my view that significant naturalization has occurred within the sites where Fanwort has been present for at least 14 years. Revisiting the hypotheses from the introduction, I believe the first criterion can be considered met since Fanwort biomass and Fanwort proportion of community biomass dropped significantly in the sites where Fanwort had been present for at least 14 years, while remaining relatively widespread (44% of quadrats had Fanwort present in 2022 compared with 56% in 2008).

It is my view that criterion 2 was largely fulfilled as well. While total community biomass remains elevated relative to reference conditions, macrophyte diversity significantly increased in the Fanwort sites between 2008 and 2022 with the diversity of the Fanwort sites in 2022 being highly similar to the reference conditions on measures of both Simpson's and Shannon's diversity indices. Quadrat species richness was highest in sites with longer Fanwort residency times and lowest in the reference sites (Figure 2.3).

Variation in macroinvertebrate community structural metrics could not be explained by Fanwort residency time or the presence or absence of Fanwort (Table 2.1). Macroinvertebrate community metrics either seemed fidelous to the sites being sampled in the case of measures of taxa richness or diversity or varied based on year regardless of location in the case of proportions of various trophic positions (Table 2.1). This seems consistent with much of the rest of the literature (Tasker et al. 2022) in that no strong relationship between aquatic macrophyte abundance, either invasive or native, and macroinvertebrate diversity or community structure tends to be observed (e.g. Hogsden et al. 2007; Carniatto et al. 2020; Tasker et al. 2022).

#### **2.4.2 Commentary on Dominant Hypotheses for the Process of Invasion**

The significant naturalization of the invasive species Fanwort within ~14-20 years of ecosystem residency time observed in this study (Figure 2.4), is something that is incapable of being fully explained by the most cited hypothetical frameworks for the process of invasion, such as Blackburn et al., 2011, because no conception of naturalization, in the sense of ecological integration, has been included in the most cited frameworks for this process (Williamson and Fitter, 1996; Richardson et al., 2000; Blackburn et al., 2011). The closest explanation of the phenomenon observed in this study within the predominant understanding of the process of invasion is the "Boom and Bust" terminology included within the Blackburn et al.'s (2011) framework, particularly what is referred to as Bust (Simberloff and Gibbons,

2004; Strayer et al., 2017) since diversity recovery corresponded with a drop in the abundance of Fanwort. However the question of whether the phenomenon being referred to as Bust corresponds with some form of community integration/naturalization tends either not to be considered in those predominant frameworks (e.g. Morrison, 2002; Blackburn et al., 2011; Strayer et al., 2017). or tacitly rejected since it is expected another Boom will follow that will create a negative impact (Simberloff and Gibbons 2004). Other, less cited, frameworks for the process of invasion are capable of explaining the significant naturalization that was observed in this study (e.g. Vermeij et al., 1996, Davis et al., 2005, Reise et al., 2006; Hoffman and Courchamp 2016), since they contain a conception of ecological community integration as the final stage in their hypothetical frameworks which corresponds with a sustained decrease in the abundance of the new species.

Fanwort had an impact on the macrophyte community structure in Kasshabog Lake in the form of decreased diversity and increased total community biomass at the initial stages of invasion (Figure 2.4). This type of ecological impact is the principal concern of invasion biology (Pyšek et al. 2020) and in many respects is the reason this discipline came into being (Reichard and White 2003). Significant naturalization, and its attendant ecological impact reduction, was also observed in this study in time frames relevant to ecological management considerations (Figure 2.4).

The impact of invasive species is the organizing principle of invasive species management, whereas anticipation of invasive species naturalization has gone largely unconsidered. This study suggests that the phenomenon of invasive species naturalization needs to be better studied for the sake of management implications since I have observed it occurring on timelines relevant to management (~14-20 years) in a species widely designated as invasive (Roberts and Florentine 2021). In addition, I propose that measurable criteria, or an index derived from measurable criteria, be created that describes the relative degree of

naturalization/ecological integration of a given species within a given region of spacetime/ecosystem. This is because the larger problem with the manner by which such species are often classified is that all there is to work with currently are binaries (Karr and Chiu 1999) applied to descriptions, e.g. is it invasive or not, is it naturalized or not, etc. Developing ecological metrics that describe relative naturalization (my attempt at this here being using the descriptor, "significantly naturalization") or relative invasiveness would go a long way towards understanding this process and developing a consensus that is tied to explicit and measurable criteria.

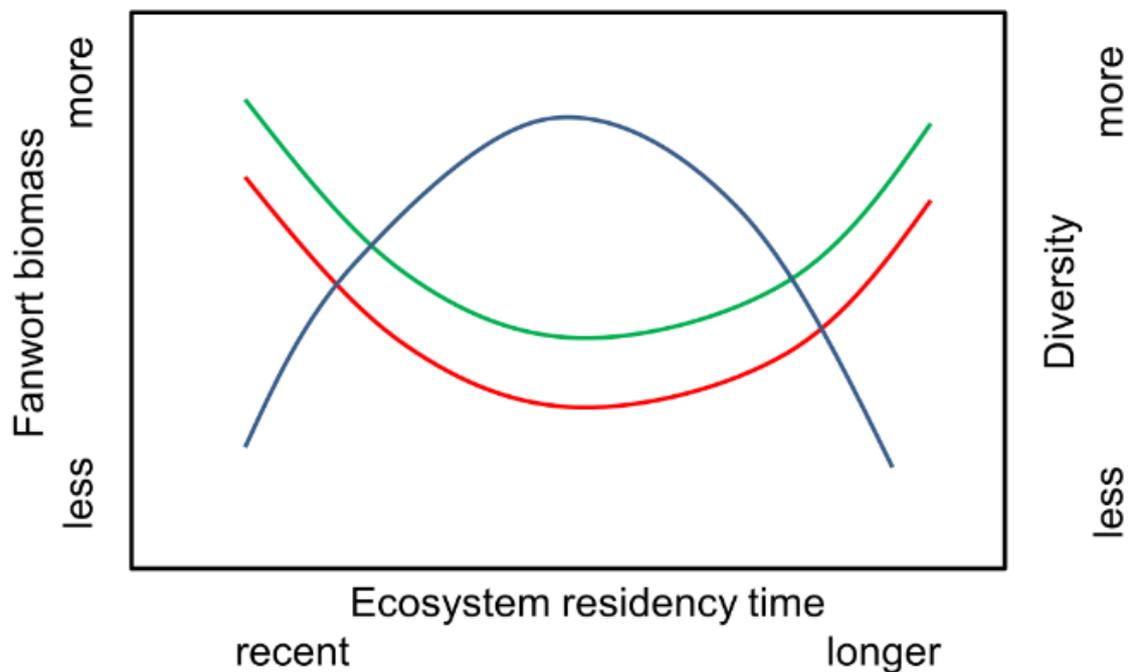


Figure 2.4: Hypothesized relationship between changes in Fanwort biomass (blue line), Shannon's diversity (green line), Simpson's diversity (red line) and Fanwort ecosystem residency time.

### 2.4.3 Rapid-evolution

The timeframe in which significant naturalization was observed within this study is of a similar scale of magnitude as those noted for significant adaptive phenotypic evolution of

invasive species across numerous different species and contexts (Carroll et al. 2007; Lankau 2012; Whitham 2020; Oduor 2022; Stuart et al. 2023). There seems to be a general consensus in the ecology and evolution literature that if significant naturalization is to occur, it would necessarily involve a meaningful evolutionary response at the community level (Vermeij 1996; Ricklefs 2005; Pyšek and Richardson 2006; Warren et al. 2006; Vellend et al. 2007; Davis 2009; Carroll 2011; Shine 2012; Trowbridge et al. 2016), i.e. it would be the ecological manifestation of what is referred to as variably as coevolution (Vermeij 1996; Ricklefs et al. 2005) or rapid-evolution (Carroll et al. 2011). What is not agreed upon is how long naturalization takes and whether this is relevant for management of ecosystems (Ricklefs et al. 2005) and, regardless of how long this takes, whether this is just another threat to native ecosystems (Pyšek and Richardson 2006; Hawkins et al. 2015; Hoff and Thum 2022) or is a beneficial addition that can help mitigate human impacts to the environment (Reise et al. 2006; Carroll et al. 2011). There have been suggestions in the literature that the timescale on which adaptive phenotypic evolution can occur is far faster (Carroll et al. 2007) than what might otherwise be thought of as an “evolutionary timescale” (Wilson 1969), which is often a colloquial shorthand for hundreds, thousands or even millions of years (Krebs 1972). There is a growing literature examining adaptive phenotypic evolution occurring on much shorter timescales as well as, more specifically, in response to the phenomenon of invasion (e.g. Lankau 2012; Whitham 2020; Oduor 2022; Stuart et al. 2023). There have been limited systematic attempts to understand the time it takes for an ecosystem to integrate a new species/a new species to naturalize, the mechanistic factors involved (Lebrun et al. 2022) and how those factors create variability in the time to integration/naturalization or measures of relative integration/naturalization as they vary within time and space (Vermeij 1996; Trowbridge et al. 2016). This lack of understanding seems to have been contributed to by the tendency in invasion biology, as well as ecological science generally, to study any given

ecological context or species for relatively short periods of time (Davis 2009), perhaps as result of funding constraints, such that there is often insufficient sustained attention to observe this process on the timescales required to observe naturalization occurring.

I would suggest that within the community being observed in this study it is likely there is such a adaptive phenotypic evolutionary response occurring, apparent or indicated through the community structures changes observed in figure 2.3, where a clear community response in the Fanwort sites between 2007 and 2022 brings the structure back in a trajectory approaching the structure of the reference sites in 2007.

With both this and the results of this work in mind I would suggest that it would be worthwhile to investigate adaptive phenotypic evolution at a community level through both genetic and phenotypic responses in species that begin interacting in a meaningful manner (i.e. food, habitat) with a newly introduced species (e.g. Lankau 2012; Vimercati et al. 2020) in tandem with an ecological community analysis that can observe food web changes (changes in the proportion of ecosystem function at different trophic levels), food web integration (e.g. comparative stable isotope studies (Kovalenko and Dibble 2014 ) and community structure (e.g. Richness and Diversity changes over time). A study such as this might provide interesting insight into the processes that facilitate naturalization and it may well be that the rapid evolution phenomenon (e.g. Carroll et al. 2007) is another way of looking at the ecological naturalization of newly introduced species given the highly similar timelines on which these process are occurring ( $\sim 10^1$ - $10^2$  years) (Table 4.1). This may provide interesting insights into the process of invasion that may help define management activity and management endpoints.

The spatial ecology of this study is also interesting, since the naturalization of Fanwort occurred in each bay individually with each bay being on average  $\sim 20,000 \text{ m}^2 \pm \sim 4000 \text{ m}^2$ . Understanding how naturalization varies in space is, to my knowledge, poorly

understood. It is largely unknown the extent to which naturalization in proximate areas may affect how it occurs with the same species when it arrives at a later time in another area nearby; whether and to what extent plant interactions such as allelopathy (Lankau 2012) change in response to a new plant community member and whether that is the most significant factor in facilitating plant naturalization; or whether it is herbivory pressure from animals, or perhaps parasitic interactions from fungi or bacteria or both. Or abiotic factors, where the proliferation of a species such as Fanwort is exploiting an unused resource and then collapses once the abundance of that resource it is able to exploit well has been depleted to a level that it cannot sustain the same population level, perhaps a reason for the boom and bust report by Simberloff and Gibbons (2004).

This discussion of rapid evolution is also highly pertinent to how I have defined naturalization with the language of "stable dynamic equilibrium". This same language is used to describe Wilson 1969's equilibrium theory. Discussing this becomes all the more important in analyzing the assumption that naturalization (in the sense I have defined it) happens on evolutionary timescales because that assumption has either come from, or been propagated by, this literature specifically the assumption that the timescale on which this happens is hundreds to thousands of years long (Wilson 1969; Krebs 1972 Figure 2.5). However, I think the view that naturalization occurs on evolutionary timescales confuses speciation for adaptive phenotypic evolution. I have no doubt that divergent speciation takes such a long time or longer (e.g. Frey 2010), but I would suggest adaptive phenotypic evolution by means of natural selection does not (Carroll 2007) and I believe these two have either been confused or that it is truly believed by some that speciation would be required for naturalization in the sense in which I have defined it here, which, if this is the case, it is this premise with which I am disagreeing.

**FIGURE 812**

*Postulated sequence of equilibria in a community of species through time. The time scale is imaginary, supplied here only to convey the notion of the vastly greater time periods required for shifts to states beyond the initial interactive equilibrium. (After Wilson 1969.)*

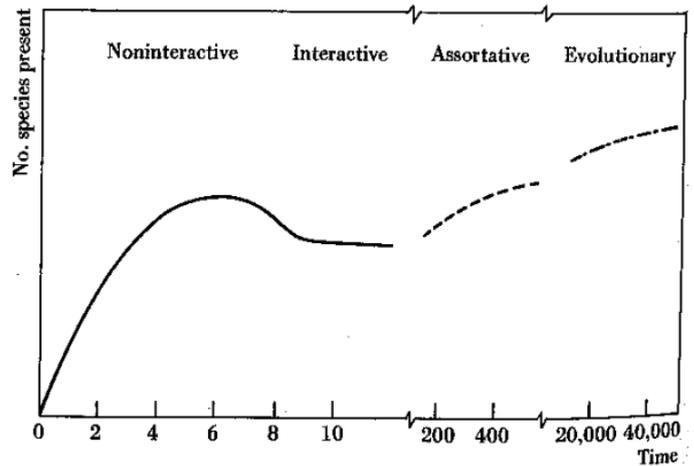


Figure 2.5: From Krebs 1972, a speculative depiction of what is meant by evolutionary time in the context of community composition equilibria of which the process of naturalization would be a part.

#### 2.4.4 Rectifying Impact and Naturalization

Fanwort had a clear impact on the macrophyte community structure in Kasshabog Lake in the form of decreased diversity (Figure 2.3) and increased total community biomass (Figure 2.2) at the initial stages of invasion. This type of ecological impact is the principal concern of invasion biology (Pyšek et al., 2020) and in many respects is the reason this discipline came into being (Reichard and White, 2003). Significant naturalization, and its attendant ecological impact reduction, was also observed in this study in time frames relevant to ecological management considerations (Figure 2.4). Similar patterns of initial impact followed relatively quickly by significant naturalization have been observed in a few other cases (e.g. Reise et al., 2006; Lavoie, 2010; Fernández, 2020), but no syntheses broadly describing this phenomenon across species currently exist.

A debate that has punctuated the invasion science literature for at least two decades has been between those who have been focused on impacts of biological invasions (e.g. Rejmánek et al., 2002; Simberloff et al., 2011; Ricciardi and Ryan, 2018) and those whose work has also studied how invasive species integrate (e.g. Davis and Thompson, 2000;

Carroll et al., 2011; Davis et al., 2011). This study may help to resolve this debate since it shows how impact and integration occur in sequence.

Anticipation of invasive species naturalization has gone largely unconsidered in invasive species management. This study suggests that the phenomenon of invasive species naturalization needs to be better studied for the sake of management implications given that the timescale on which I have observed it occurring in this study is relevant to management planning (~14-20 years). A better general understanding of this process and the factors that facilitate it would also help inform invasive species management endpoints.

## **Chapter 3: Definitions of Naturalization**

### **3.1 Naturalization and Naturalization**

The phenomenon I am using the word naturalization to describe is not the same phenomenon this word has been commonly used to describe in much of the invasion biology literature (e.g. Richardson et al. 2000; Blackburn et al. 2011), perhaps until very recently (Soto et al. 2024). This also applies to the words naturalize and naturalized as the root word and another derivation of that root word, respectively.

To the reader, I would ask you a question; based on your understanding of these words, is a species invasive before it is naturalized or naturalized before it is invasive? While conducting research for the field study for this project my naive understanding based on how I had heard these words being applied in ecological and other contexts (e.g. the word naturalize in the context of immigration) was the former, that a species is invasive and then it naturalizes. Upon encountering the invasion biology literature, I was subsequently confused by how the word naturalize, and its derivations, were being applied since in invasion biology naturalization describes a state of wild reproduction (wild in the sense of independent of human assistance) that comes before a species can be described as invasive (e.g. Richardson et al. 2000; Blackburn et al. 2011).

I am of the view that for much of the existence of the discipline of invasion biology naturalization has been defined in an etymologically strange manner relative to this word's usage in the rest of the English language (OED 2024). For that reason I want to propose another definition for naturalization in its application within the ecological sciences because I believe the invasion biology definition is largely disconnected from the manner in which this word is used in other contexts within the English language (OED 2024):

**Naturalization** is the process by which both a species becomes integrated into a new ecosystem and an ecosystem integrates a new species on a trajectory towards it becoming functionally equivalent to an analogous native species.

**Naturalize:** to become native (OED 2024)

**Naturalized:** having become native

The most used definition for naturalization within invasion biology (e.g. Blackburn et al. 2011) was substantially developed by Richardson et al. (2000) in their article “Naturalization and Invasion of Alien Plants: Concepts and Definitions”. Their article is one of the most cited scientific journal articles within the invasion biology literature and is focused on defining terminology that describes the process of invasion/naturalization as well as creating a standard framework for work studying biological invasions to better address the ecological impacts of invasive species. The major focus of their paper was to find consensus by means of a survey of the literature on the definition of the term naturalization. Their methodology in their paper was to search for and review other papers that use the term naturalization and place them into categories based on what each work uses this word to mean. The four categories they created were:

1. ‘Naturalized’ [the conventional meaning] (23% of articles analysed out of a total of 157 papers)
2. ‘Naturalized’ meaning self-sustaining populations in natural or seminatural vegetation (8%)
3. ‘Naturalized’ as a synonym for ‘alien’ [non-native] (25%)
4. ‘Naturalized’ as a synonym for ‘invasive’ (29%)

However, within the categories they create there is a clear omission; the conventional meaning of naturalization has no mention of the sense in which this means community

integration or "to become native" (OED 2024), despite the fact that they introduce their work by disagreeing with a definition that is provided by Cousens and Mortimer (1995) which is defined in precisely that way:

“To cite but one example, Cousens & Mortimer (1995; p. 21), in a chapter on ‘The dynamics of geographical range expansion’, follow Groves (1986) in advocating that the process of invasion of an unoccupied region by new taxa may be divided into the following three phases:

- “1. INTRODUCTION. As a result of dispersal, propagules ... arrive at a site beyond their previous geographical range and establish populations of adult plants.
2. COLONIZATION. The plants in the founding population reproduce and increase in number to form a colony that is self-perpetuating.
3. NATURALIZATION. The species establishes new self-perpetuating populations, undergoes widespread dispersal and **becomes incorporated within the resident flora**

In my view, this scheme confuses stages in the naturalization/invasion process. Introduction and establishment (understood as survival, not as reproduction) are clearly fundamental requirements for invasion, and I have no serious problem with lumping these under the broad heading INTRODUCTION. However, I believe that the phases COLONIZATION and NATURALIZATION in the above scheme are incorrectly defined. What is described as COLONIZATION above corresponds with what I believe is an integral part of ‘naturalization’ (see later) whereas NATURALIZATION in the above scheme conforms to our understanding of ‘invasive’.” - Richardson et al. (2000)

From that, this is how Richardson et al. (2000) define the process of invasion:

“

1. **Introduction** means that the plant (or its propagule) has been transported by humans across a major geographical barrier.
2. **Naturalization** starts when abiotic and biotic barriers to survival are surmounted and when various barriers to regular reproduction are overcome.
3. **Invasive:** further requires that introduced plants produce reproductive offspring in areas distant from sites of introduction (approximate scales: > 100 m over < 50 years for taxa spreading by seeds and other propagules; > 6 m/3 years for taxa spreading by roots, rhizomes, stolons or creeping stems).” - Richardson et al. (2000)

By categorically excluding from their analysis the sense in which naturalization refers to community integration, despite citing at least three sources that use this word or a similar word in that context (Holub and Jirásek 1967; Groves et al. 1986; Cousens and Mortimer 1995), it is my view that Richardson et al. (2000) created a definition of this word that is unintuitive relative to the other contexts in which this word is used in the English language because it lacks any sense in which an organism becomes native, which is the primary definition for the word naturalize in the two major dictionaries of the English language (Merriam Webster 2024; OED 2024), of which naturalization is a grammatical derivation. In this way, I would argue that the definition Richardson et al. (2000) have chosen is such that the term naturalization becomes an entirely different word-symbol (sensu Wittgenstein 1922) relative to its common usage, a homonym in other words. I would suggest this is so because it has a functionally different definition than the core of how this word is defined within the English Language insofar as they are referring to different phenomena (Wittgenstein 1922). In doing so it takes away from the value of the framework they have created to describe

nature because it is etymologically confusing in addition to facilitating the omission of a relevant natural phenomenon to the process they are attempting to describe. As such, I believe that the definition I have provided in, that includes the sense in which naturalization refers to becoming native (OED 2024), would increase the value of the frameworks that describe the process of invasion for two reasons, first that a relevant phenomenon that is currently unaccounted for in such frameworks would become accounted for and second that the definition of this word would become contingent with the sense in which it is used in much of the rest of the English language.

### **3.2 Additional argumentation to support the argument that naturalization was defined in an inappropriate way**

#### **3.2.1 Subargument 1: Dictionary Definitions**

The use of the noun naturalization and more specifically, naturalize, the root verb, begins in the late 15<sup>th</sup> and early 16<sup>th</sup> century from the French root verb *naturaliser*, defined as “to make native”, with reference also to the sense in which this is meant as “to acclimatize” (OED 2024). Naturalize was first used to describe the integration of human immigrants from a different society into a new society (OED 2024), with particular economic and cultural emphasis (OED 2024). The sense in which this is used to describe human immigration remains in use today within legislation governing citizenship and immigration (e.g. Citizenship Act (R.S.C., 1985, c. C-29).

The usage of this word was transposed onto non-humans and ecological phenomena at most roughly a century after its introduction into the English language, with the first usage in this manner at least as early as 1708 CE (OED 2024). Within the ecological definition of the word, the sense in which incorporation and becoming native are clear, the Merriam-Webster

Dictionary (Merriam-Webster 2024) cites a quote by John Eastman as an example of its appropriate usage:

“This phenomenon follows the typical pattern of invading plant and animal species, the gradual process of naturalization by which ecological balance tends to reassert.”

— John Eastman (Eastman and Hansen 2003)

This quote chosen by Merriam-Webster also includes the incorporation clause when Eastman says “the gradual process of naturalization by which ecological balance tends to reassert” (Eastman and Hansen 2003) i.e. the creation of a new balance through means of incorporation into the community.

The Oxford English dictionary lists nine major meanings of the word naturalize and three major meanings of the word naturalization. The first five meanings of the word naturalize in the OED, including the definitions that apply to non-human organisms specifically, all stem from the common definition “to make native”. This definition itself is the incorporation clause, and is very apparently so looking at the history of the word where its first and primary usage is to describe the integration of human immigrants into a new society as full members of that society; i.e. to incorporate as a native member or citizen (OED 2023).

### **3.2.2 Subargument 2: Darwin’s Naturalization Hypothesis**

Darwin’s naturalization hypothesis is a well-known proposition within his work “On the Origin of Species” and is often cited in the evolution, ecology and biogeography literature, including invasion biology (e.g. Ricciardi and Mottiar 2006; Diez et al. 2008; Saul et al. 2013). Noting its particular relevance to the phenomenon that the process of invasion/naturalization is attempting to describe and the general influence of this text and hypothesis on science, discussing how this word was used in Darwin’s text can be a useful

sample of its usage at the time of its publication. Darwin does not define naturalization directly in this text, but, one of his key references, Asa Gray, does (Gray 1862). Given the way in which Darwin quotes Gray (Darwin 1872 pg.) I think it reasonable to say that Darwin is using Gray's definition of naturalized or naturalization. In the book "Manual of the Flora of the Northern United States" Gray defines a naturalized plant as being this:

"I have classified our introduced plants as well as I could into two sorts, the thoroughly naturalized and the adventive; the first comprising those species which have made themselves perfectly at home in this country, propagating themselves freely by seed beyond the limits of cultivated grounds; the second, those which are only locally spontaneous, and perhaps precarious, or which are spontaneous only in cultivated fields, around dwellings, or in manured soil, and which, still dependent upon civilized man, would probably soon disappear if he were to abandon the country." - From Gray 1862, pg viii

Gray's definition relies upon a dualism involving humans, that is, that a naturalized species (in this case a plant species) no longer depends upon humans for its persistence in a new area, relative to an adventive species which does. However, there is a portion of this definition which is independent of relationship to humans; that being when Gray mentions a naturalized species being "perfectly at home". For if a naturalized species is to be "perfectly at home" in a particular country it must have integrated itself to some significant degree within the ecosystem such that its function and life are similar to that of an organism that has been there for a longer period, i.e. it has become native (OED 2024; Merriam-Webster 2024) i.e. it is naturalized.

### **3.2.3 Subargument 3: Component clauses of the term naturalization as understood by invasive species management professionals**

As part of this research, I conducted a series of semi-structured interviews with eight invasive species management professionals with at least 10 years of experience either actively managing, researching or making policy regarding invasive species. The interviews were conducted over zoom and the conversations were audio recorded. Each interview was no longer than 90 minutes. This research was vetted by the Trent Research Ethics Board and the initial focus of the interviews was as follows:

The focus of these interviews will be threefold; first to ask about their views on what they manage and whether they use eradication as a management objective; second to ask about any burnout they have witnessed in conjunction with attempts to eradicate invasive species; third to ask them about developments in the species or lands they manage that did not conform to their expectations, particularly observations which created personal acceptance of things as they are or were in the moment of recollection.

Among the questions the interviewees were asked, one of them was:

**What does it mean to you if a species is described as naturalized, how would you define that?**

Although this question was not initially designed to look at semantics of the terms naturalize/naturalization in an etymological context, it does happen to be able to. To analyze those semantics I identified then categorized the linguistic clauses within the definition for naturalization provided by each interviewee (Table 3.1). The responses to the question are listed in Appendix 2.

With regard to each of the clauses mentioned, the clauses mentioned by all interviewees were:

- 1) That a naturalized species was non-native in the sense of being from another ecosystem relatively recently, which was mentioned by all interviewees (Table 3.1).
- 2) That a naturalized species is one that is not causing negative impacts, which was mentioned by eight out of the eight interviewees (Table 3.1).

Seven out of eight interviewees stated directly or implied through their choices in examples that a naturalized species was one they would generally not expect to cause problems in the future. Three out of eight interviewees said that a species is naturalized if it has been here for a relatively long period of time (decades to 200 years). Two out of eight interviewees said that a species is naturalized if it is widespread within the new range. Two out of eight interviewees explicitly mentioned that a naturalized species is one that is established and reproducing.

Rather than just the sense in which a species is allochthonous, to borrow terminology from Soto et al. (2024), to most of those interviewed naturalization also referred to a lack of impact and a lack of expectation of future impacts i.e. ecological integration (Soto et al. 2024).

### **3.3 Recent Terminological Directions and Conclusion**

The sense in which naturalization, insofar as it derives from the root word naturalize, refers to becoming native (OED 2024) has been at least largely, if not entirely, omitted from the predominant invasion biology definitions of this term (e.g. Richardson et al. 2000; Blackburn et al. 2011) until very recently (Soto et al. 2024). In 2024 Soto et al. released a review of the terminology in invasion biology with proposed compromises to cool the debate on the subject

of terminology, including providing a definition of naturalization that is phenomenologically analogous to the one I am proposing:

“Non-native successfully established self-sustaining populations in a new environment without human intervention; non-native after being introduced successfully established self-sustaining populations in the wild; must be present long enough to be perceived as an integral [undefined] part of the resident community of organisms”

– Soto et al. 2024 referencing Wu et al. 2004

Notably, Soto et al. (2024) state that the term integral as used by Wu et al. (2004) in the definition they provide is undefined and they also recommend that term naturalization not be used in the discipline in the future. If the term integral or integration is not defined or understood within the invasion biology literature, I think this is exactly one place in which this review can be helpful if they are unwilling to or uncomfortable with defining it.

<b>Table 3.1: Clauses of naturalization mentioned by interviewees</b>	
<b>Explicitly mentioned clause</b>	<b>Proportion of interviewees that identified that clause as part of what a species being naturalized means</b>
Was introduced to the region it is inhabiting/is exotic	Eight out of eight interviewees
Not causing significant negative impacts/problems	Eight out of eight interviewees
Not expected to cause problems in the future	Seven out eight interviewees

Has been incorporated into the food web/come into an ecological equilibrium	Four out of eight interviewees
Established and reproducing	Three out of eight interviewees
Humans have accepted its presence	Three out of eight interviewees
Substantial residency time (on the order of decades or centuries)	Three out of eight interviewees
Widespread in the region to which it is described as naturalized	Two out of eight interviewees
Spreading	One out of eight interviewees
Was introduced as a consequence of human activities (intentionally or not)	One out of eight interviewees

## **Chapter 4: A New Proposed Unified Framework for Biological Invasions and Species**

### **Naturalization**

#### **4.1 Introduction**

This chapter has been included in this thesis because, while conducting a review of the literature, I was perplexed by the predominant way in which the word naturalization was being used within the ecology literature and I wanted to understand why it was being used in that way (Chapter 3). In addition, those frameworks that used this word in a manner I found strange also did not describe the phenomenon I observed in my field study i.e. an invasive species integrating into a new ecosystem (Chapter 2). I think that if a predominant scientific hypothesis does not include an observed and relevant phenomenon to the larger phenomenon

it attempts to depict systematic investigation is warranted. Given this is the case, my findings in my field study led to this review of the frameworks that describe the process of invasion to assess the landscape of theories for the process of invasion as comprehensively as possible.

The first part of this review is the compilation of cases of significant naturalization from the literature. This was done for the purpose of investigating whether others have observed similar phenomena, especially on similar timelines. The second part is a compilation and analysis of frameworks for the process of invasion/naturalization. This compilation and analysis was done for several purposes; to create a comprehensive picture of the extent published frameworks for this process, to assess whether those frameworks were capable of explaining the results in the field study (Chapter 3), to assess the degree to which those frameworks had influenced the literature, to assess the degree to which those frameworks had influenced each other and to conduct a terminological review of the way in which phenomenal states/stages were described differently or similarly using the same and different terms. The third part of this review was the creation of a new framework for the process of invasion, based upon Blackburn et al. (2011)'s model, that incorporated elements that I thought were missing based on the outcome of the review and such that the results of the field study could be suitably explained.

#### **4.2: Cases of Significant Naturalization**

Species naturalization is the relative end of the process of invasion/naturalization and there is a growing literature documenting cases of significant naturalization of invasive species in timeframes relevant to management planning (between  $10^1$ - $10^2$ ). Part of this phenomenon is what is described as “bust”, in the sense of “boom and bust” (Simberloff and Gibbons 2004; Strayer et al. 2017). This is only part of this phenomenon since the term “bust” refers only to the abundance pattern of the invasive species in question and does not implicate the

ecological community response and nor the relationship of that species with the new community in which it finds itself. Naturalization is a much better term for this since it implicates a particular relationship between the ecological community and the new species. I am using the term significant here because I do not believe that the process of naturalization ends when ecological community structural metrics approximate pre-invasion levels since there are likely many more ecological linkages that can still be established that deepen that species' integration into that new food web. For example, using herbarium records Schilthuizen et al. (2016) found that herbivory of introduced *Prunus serotina* leaves had increased from 18.8% to 40.6% over a 170 year period whereas evidence of herbivory on another native *Prunus* species, *Prunus padus* had remained stable at 35%. Nonetheless, I suggest that a species is significantly naturalized when it is no longer creating significant changes to the structural metrics of the ecosystem relative to pre-invasion levels. Specifically, the criteria I use here to define significant naturalization or a significantly naturalized state are these:

1. The structural metrics (e.g. richness, diversity, etc) of the invaded community are at levels similar to those of a pre-invasion reference community
2. The invasive species is both widespread (at the spatial scale in question) and in low to moderate abundance relative to a peak abundance following introduction.

I believe that the records from the literature shown in Table 4.1 meet both of these criteria and therefore indicate that the phenomenon I am calling naturalization has occurred to a significant degree within timeframes relevant to ecological management planning (~1-100 years).

Table 4.1: Papers depicting evidence of significant species naturalization			
Paper	Species	Location	Time to significant naturalization
Painter and McCabe (1987)	<i>Myriophyllum spicatum</i>	Kawartha Lakes, Ontario (with other cases from North America)	~10 years
Morrison (2002)	<i>Solenopsis invicta</i>	Texas	12 years
Zettler et al. (2002)	<i>Marenzelleria viridis</i>	The Netherlands	20 years
Moore et al. (2012)	<i>Potamopyrgus antipodarum</i>	California	10 years
Dostal et al. (2013)	<i>Heracleum mantegazzianum</i>	Poland	35-40 years
Schab et al. 2013	<i>Hemigrapsus sanguineus</i>	Delaware Bay	23 years
Schilthuizen et al. 2016	<i>Prunus Serotina</i>	The Netherlands	~80 years
Závorka et al. (2018)	<i>Salmo trutta</i>	global	<100 years
Fernández (2020)	<i>Sargassum muticum</i>	Coastal Spain	30 years
Llanos et al. (2021)	<i>Boccardia proboscidea</i>	Buenos Aires Province	8 years
Pintar et al. 2023	<i>Hemichromis letourneuxi</i>	Florida Everglades	18-22 years
Szydłowski et al. 2023	<i>Faxonius rusticus</i>	Wisconsin	~30 years
Chapter 3 of this thesis	<i>Cabomba caroliniana</i>	Ontario	~15-20 years

### **4.3 A Review of the Frameworks for the Process of Naturalization/Invasion**

Many frameworks to describe the process of invasion/naturalization have been made for the sake of creating workable hypotheses to coordinate the scientific study of those invasions/arrivals. In light of the findings from the second chapter, that significant species naturalization can occur on relatively short timelines, I searched the literature to identify a comprehensive list of published frameworks in the English language scientific literature that describe the process of invasion/naturalization. I did this to assess whether those frameworks did or did not anticipate species naturalization and the degree to which those frameworks have influenced the academic literature.

Frameworks were initially found through reference tracing from textbooks on invasion biology such as “Invasion Biology” by Mark Davis (2009) as well as highly cited framework articles such as Blackburn et al. 2011 and Richardson et al. 2000. Keyword searches supplemented this search, however, they rarely yielded results that systematically encompassed a significant portion of the frameworks found through reference tracing, even with search terms such as “stages of invasion” on the Web of Science. This is important to note since it may be that I have missed some relevant frameworks as a consequence of a lack of a systematic search term methodology. All frameworks were sorted into two groups according to whether a term describing a phenomenological process analogous to how naturalization was defined here was present or not. The citation number listed on the Web of Science was used as of the date of July 30<sup>th</sup> 2024. To assess the connectivity between each framework, frameworks located in the literature review were connected by their citation of one another. Total frameworks cited, type of frameworks cited and number of times cited by other frameworks were calculated for each framework.

### **4.3.1 Literature adoption**

Frameworks that did not describe the phenomenon of naturalization were cited significantly more total number of citations with that group of frameworks having 16013 total citations whereas the group of frameworks which did describe the phenomenon of naturalization had 835 total citations. This is likely one reason why naturalization as an outcome of invasion tends not to be anticipated in invasive species management, because the frameworks and hypotheses that are used most often don't anticipate it either.

### **4.3.2 Literature Connectivity**

Frameworks that did not describe the phenomenon of naturalization were highly interconnected and tended not to cite the frameworks that did describe the phenomenon of naturalization (Figure 4.1). Of the seven occasions where the authors of those frameworks did cite articles with frameworks that described the phenomenon of naturalization, two of those instances were to actively disagree with the relevance of that phenomenon (Richardson et al. (2000) disagreeing with Cousens and Mortimer (1995) and Groves (1986)) and the remaining five did not discuss it, using the articles for other content (Williamson and Brown 1986; Dicastri 1989; Duncan et al. 2003; Lodge et al. 2006; Lockwood et al. 2007). They also tended to cite more other frameworks overall, on average.

Frameworks that did describe the phenomenon of naturalization also tended to cite frameworks that did not describe the phenomenon of naturalization more often, likely as a consequence of those frameworks being more popular at the time. They also cited fewer other frameworks on average.

Three authors that have been authors of frameworks that depict the phenomenon of naturalization have published multiple framework articles; Michael Marchetti, who published two, one of which did not depict the phenomenon of naturalization (Marchetti et al. 2004;

Lockwood et al. 2007); Jan Pergl who has also published two (Davis et al. 2005; Roy et al. 2017), one of which did not depict the phenomenon of naturalization; and Petr Pyšek who has published five, only one of which depicts the phenomenon of naturalization (Davis et al. 2005). There are 13 authors of frameworks that do not depict the phenomenon of naturalization that have published multiple framework articles (Table 4.2). Most notable among these is David Richardson, who has published five articles between the years 1986 and 2011, Petr Pyšek, who has published five articles between the years 2000 and 2011, Mark Williamson who has published four articles between the years 1986 and 2007, James Carlton who has published 3 articles between the years 1985 and 2011 and David Lodge who has published 3 articles between the years 2001 and 2006. This higher number of multi-framework authorship also reflects the high level of self-citation that many of the authors who have worked on the frameworks that have no conception of the phenomenon of naturalization have had while attempting to build the discipline of invasion biology (Wilson et al. 2020). It also indicates that, compared to the group of frameworks with a conception of naturalization, that the group of frameworks without that conception were conceived of more independently from one another.

Both the heavy interconnection of frameworks with no conception of the phenomenon of naturalization and the number of authors who have published multiple frameworks with no conception of naturalization are also indicative of the a high level of cooperation and coordination on the part of a series of authors in the development of the discipline of Invasion Biology, especially between the years 1996 and 2011, when the majority of those frameworks were published (Figure 4.1).

#### **4.4: Terminological Review of Frameworks for the Process of Invasion**

Using the frameworks that were found in the literature review I created a chart to describe how the terms those frameworks use overlap in describing the same or different phenomenal states associated with the process of invasion/naturalization (Table 4.2). After the terms used in each framework were arranged according to the phenomenological states they described, the terms were aggregated by equivalent stage to assess which terms were most and least common at each stage (Table 4.3).

The result generally supports the terminological choices in the barrier model framework, with transport being the term most commonly used to describe stage 0 (18%), introduction most common for stage 1 (28.5%), Establishment most common for stages 2 and 3 (39.2% each), Spread most common for stages 4, 5 and 6 (39.2%, 37.9% and 34.4% respectively) and Integration, naturalization and persistence most common for stage 7 (20% each). This entirely parallels the barrier model framework (Blackburn et al. 2011) except on one account, that being the existence of stage 7, or naturalization. This is not a surprising result given that frameworks that described the phenomenon of naturalization (equivalent stage 7 in Table 4.2) have not been included in terminological reviews/syntheses in invasion biology previously (e.g. Colautti and MacIsaac 2004; Blackburn et al. 2011) and so I think there is great value in including them in a synthesis of frameworks for the process of invasion for that fact.

Table 4.2: Authors that have published multiple articles depicting the process of invasion/naturalization (*indicates authorship of frameworks in both groups)	
Author	Number of articles published
David Richardson	5
Petr Pysek*	5
Mark Williamson	4
David Lodge	3
James Carlton	3
Hugh MacIsaac	2
Kimberly With	2
Marcel Rejmanek	2
Richard Duncan	2
Sven Bacher	2
Tim Blackburn	2
Tina Heger	2
Michael Marchetti*	2
Jan Pergl*	2

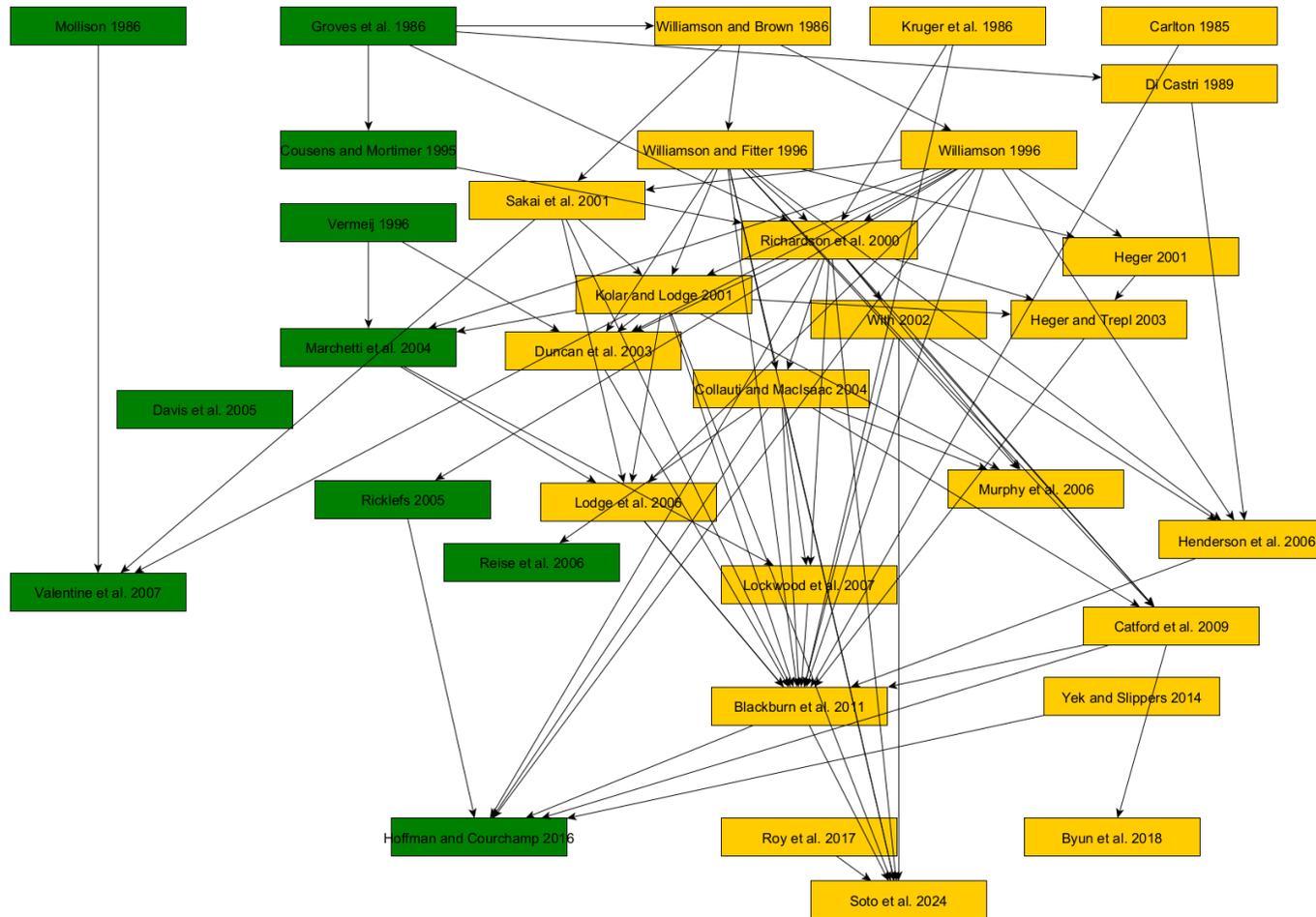


Figure 4.1: Literature connectivity of frameworks for the process of invasion/naturalization. Frameworks are ordered chronologically from top to bottom and arrows indicate citation by preceding frameworks. Green boxes indicate frameworks that describe the phenomenon of naturalization and yellow boxes indicate frameworks that do not describe the phenomenon of naturalization.

Table 4.3: Equivalent stages/terminology in different frameworks of the process of naturalization/invasion							
Framework	Equivalent stage 0	Equivalent stage 1	Equivalent stage 2	Equivalent stage 3	Equivalent stage 4	Equivalent stage 5	Equivalent stage 6
Carlton 1985	Donor Area/entrained ballast tank assemblage	assemblage upon arrival and release in the recipient region	species surviving and reproducing		established introductions		-
Groves et al. 1986	-	Introduction	Colonization				Naturalization
Kruger et al. (1986)	-	Geographic Barrier overcome		Habitat Barrier overcome		Biotic Barrier overcome	-
Mollison et al. (1986)	-	Arrival	Establishment		Spread		Persistence
Williamson et al. (1986)	-	Arrival	Establishment		Spread		-
Di Castri (1989)	-	Introduction	Colonization	Naturalization	Spread		-
Cousens and Mortimer 1995	-	Introduction	Colonization		Naturalization		
Williamson and Fitter 1996	-	Imported	introduced	established	Pest		-
Vermeij 1996	-	Arrival	Establishment				integration
Richardson et al. 2000	-	Casual		Naturalization		Invasive	-
Kolar and Lodge 2001	-	Introduction	Establishment		Spread/invasion		-
Sakai et al. 2001	Native Elsewhere	Survival in Transport	Establish in New Area	Lag Period	Spread		Ecological Impact/Human Impact

With 2002	-	Introduction	Colonization	Establishment	Dispersal/ Spatially Distributed Populations	Invasive Spread	-
Duncan et al. 2003	Transport	Introduction	Establishment		Spread	Invasive species	-
Heger and Treppl 2003	Presence in the Home Range	Presence in the new area	Spontaneous Establishment		Permanent Establishment	Spreading in the new area is completed	-
Colautti and Maclsaac 2004	Stage 0	Stage 1	Stage 2	Stage 3	Stage 4a/Stage 4b	Stage 5	-
Marchetti et al. 2004	-	Establishment			Spread		Integration
Davis et al. 2005	Community A	Colonization	Establishment	Turnover	Persistence	Spread	Community B
Ricklefs 2005	-	Colonization	Establishment		Expansion		Decline
Lodge et al. 2006	Species in Pathway	Transported and released alive	Population establishment		Spread	Ecological, human health or economic impact	-
Murphy et al. 2006	Source Population at Distant Location	Casual	Naturalized		Spreading	Invasive (Disturbed Habitats)/ Invasive (Ecological)	-
Reise et al. 2006	-	Arrival	Establishment		Expansion		Adjustment
Henderson et al. 2006	-	Introduction	establishment	Naturalization	Dispersal/Population Distribution	Invasive Spread	-
Pyšek and Richardson 2006	-	Casual	Naturalized		Invasive		-
Valentine et al. 2007	-	Establishment			Spread		Persistence

Blackburn et al. 2011	Transport	Introduction	Survival (Establishment)	Reproduction (Establishment)	Spread (Invasive)		-
Yek and Slippers 2014	Parent Populations	Arrival	Survival	Reproduction	Persistence	Spread	-
Hoffman and Courchamp 2016	Species in Current Native Range	Species Movement	Survival	Reproduction	Dispersal		Range Expansion
Roy et al. 2017	Transport	Introduction	Establishment		Spread		-
Byun et al. 2018	Transport	Introduction	Establishment/Colonization	Naturalization	Spread	Impacts	-

**Equivalent stage 0:** This stage denotes the phenomenal state prior to the arrival of the species in question into the new ecosystem in question

**Equivalent stage 1:** This stage denotes the phenomenal state at the arrival of the species in question into the new ecosystem in question

**Equivalent stage 2:** This stage denotes the phenomenal state of individuals of the species in question surviving without direct human assistance

**Equivalent stage 3:** This stage denotes the phenomenal state of individuals of the species in question reproducing without direct human assistance

**Equivalent stage 4:** This stage denotes the phenomenal state of the population of the species in question beginning localized spreading

**Equivalent stage 5:** This stage denotes the phenomenal state of the population of the species in question creating clear ecological impacts in the ecosystem in question as a result of increasing spread (impact being significant reductions of diversity, richness or other structural ecological metrics)

**Equivalent stage 6:** This stage denotes the phenomenal state of the population of the species in question becoming integrated into the ecosystem in question with significant recovery of diversity, richness or other structural ecological metrics

Table 4.4: Most common terms by equivalent stage			
Stage	Top 3 most common terms (%)		
Equivalent stage 0	Transport (30.8%)	Community A (7.7%)	Donor Area/entrained ballast tank assemblage (7.7%)
Equivalent stage 1	Introduction (33.3%)	Arrival (16.7%)	Casual (10%)
Equivalent stage 2	Establishment (41.9%)	Colonization (16.2%)	Survival (9.6%)
Equivalent stage 3	Establishment (40%)	Naturalization/Naturalized (20%)	Reproduction (10%)
Equivalent stage 4	Spread (40.6%)	Dispersal (9.4%)	Invasive (9.4%)
Equivalent stage 5	Spread (40.0%)	Invasive/invasion (22.9%)	Impact (8.6%)
Equivalent stage 6	Integration (20%)	Naturalization (20%)	Persistence (20%)

## 4.5: Reinterpretation of the Blackburn et al. 2011 Barrier Model

### Framework Unification

- In the attempt to connect and compare each framework for the purpose of creating a new unified stage-based framework for the process of naturalization/invasion, the stages described by each framework found within the literature review were placed in a table (Table 4.3), with analogous terminology/stages placed overlapping one another.
- This table (Table 4.3) was used to inform terminology choices and stages in a new framework for the process of naturalization/invasion by assessing which terms were most used to describe analogous stages (Table 4.4) to modify the Blackburn et al. 2011 barrier model framework (Figure 4.2).
- This method allows for significantly more frameworks to be incorporated than in Blackburn et al. 2011, which excludes all of the frameworks that existed at the time of its publication that included a conception of invasive species naturalization (Figure 4.1)
- Some of the terms have been rearranged in the chronosequence of how they apply, principally the term naturalized has been separated from established and now comes after invasive.
- A new stage has been added in the form of integration, a new barrier has been added in the form of niche realization.
- A new category has been added in the form of "F" which is defined as "A species which has been significantly integrated into the food web such that its ecological function has begun to significantly approach a native species with an analogous function. For example Fanwort (*Cabomba carolinianai*) could be compared

functionally with Water shield (*Brasenia schreberi*) or Alternate leaved watermilfoil (*Myriophyllum heterophyllum*)).

- The Boom and Bust off ramp has been removed and replaced with "F" and it's preceding barrier, with the argument being that while Boom and Bust describe a relevant phenomenon, these terms do not describe community dynamics and different terminology that is able to both describe patterns of abundance and community dynamics simultaneously would be better for this framework.
- Two Terminological scenarios have been created to deal with the terms naturalized and invasive. Defined according to impact, species that never cause significant ecological impacts are termed as naturalized while species that are actively causing an ecological impact are termed invasive. The first scenario deals with species that cause an impact (and are thus invasive) and become unproblematic (and are thus naturalized) while the second scenario deals with species that never cause an impact (and can be considered naturalized).
- Within the management category, eradication has been placed prior to containment, this is largely uncontroversial I think and is where the recent discourse has found itself with regard to its view on eradication as that is depicted in the invasion curve model (Figure 4.3) (e.g. Soto et al. 2024). Expecting that eradication is possible at all stages of invasion in all cases of invasion after introduction is not realistic, especially in continental contexts where there exist very few examples of successful long term eradications (eradications where the species didn't reappear later), especially when taken as a proportion of the total number of managed invasive species.
- Do Nothing has also been added in conjunction with the naturalized category in the view that with sufficient integration, there is no value in managing something that is no longer creating impact in a significant way (see chapter 2, e.g. Lavoie 2010).

- Restoration has been included at every stage in the management section in the view that 1) this is the best means we have to prevent invasion by reducing abiotic impacts and ameliorating abiotic conditions that create the causes and conditions for invasion to be possible (Elton 1958) and 2) ecological restoration is the intended purpose of invasive specie management. This echoes the framework provided by Sakai et al. (2001) in its explicit inclusion of ecological restoration.

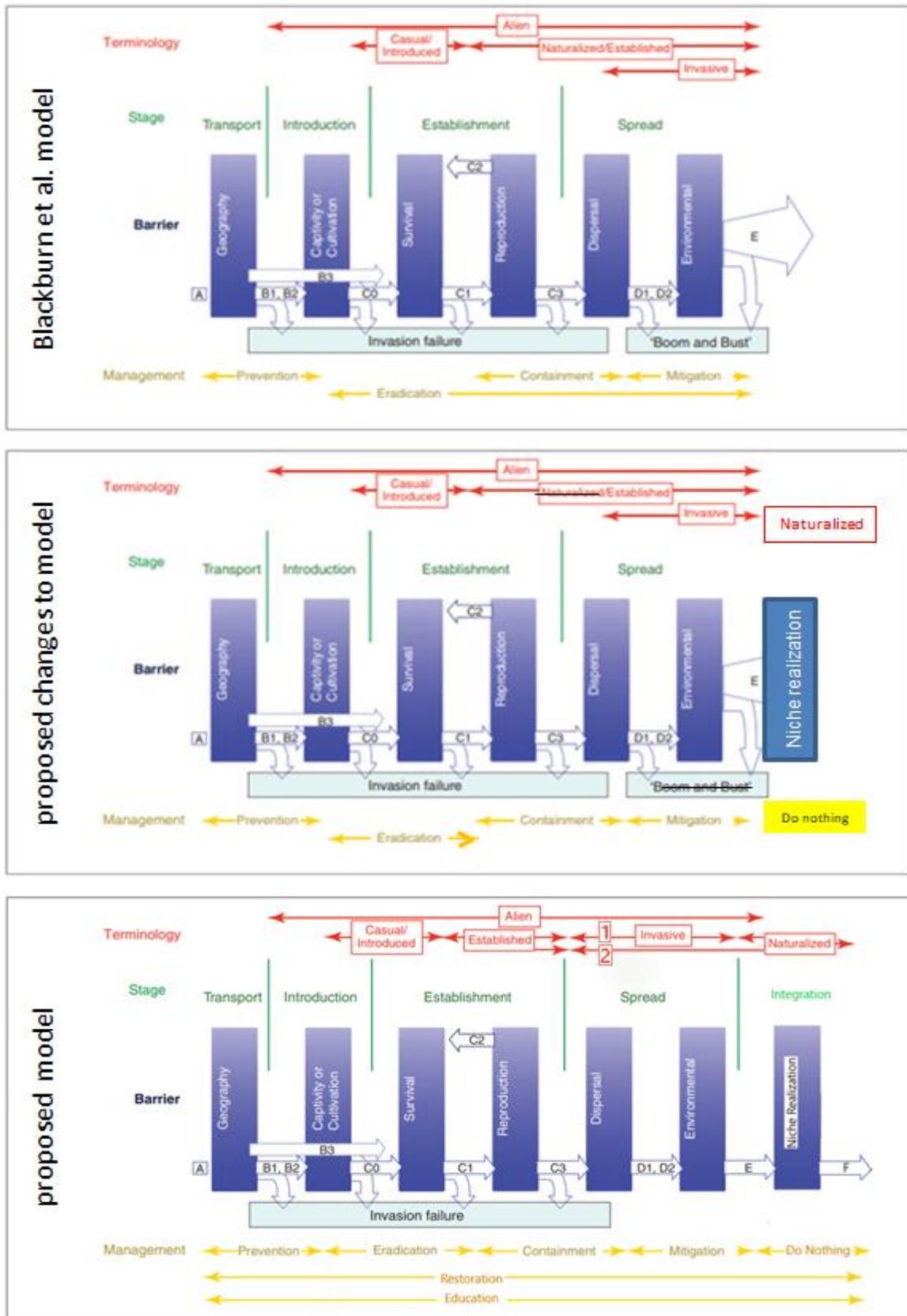


Figure 4.2: Reinterpretation of the framework for the process of invasion proposed by Blackburn et al. (2011). The original framework is depicted in the top box, the intermediate step making clear the changes is in the middle and the newly proposed model is at the bottom.

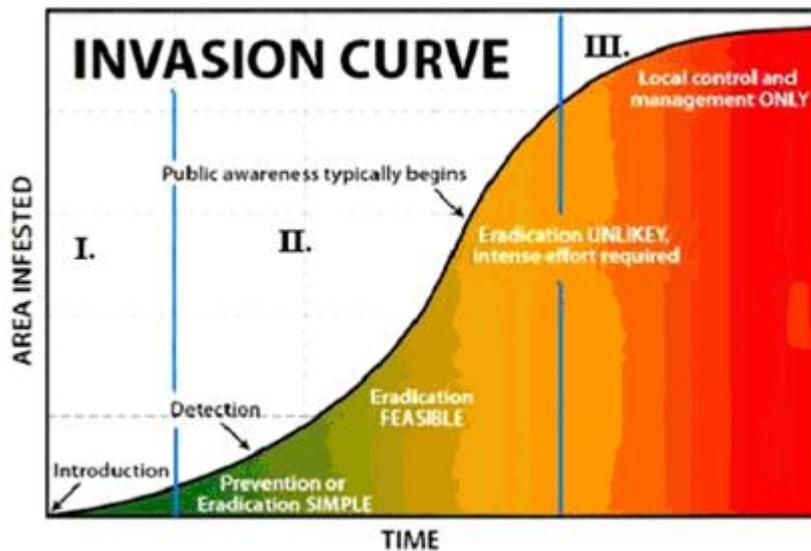


Figure 4.3: The theoretical invasion curve (from Cornell Cooperative Extension 2024)

#### 4.6: Conclusions

Invasive species management and invasion biology do not currently account for, nor anticipate, the phenomenon of invasive species naturalization as observed in my field study of Fanwort (e.g. Richardson et al. 2000; Blackburn et al. 2011; Soto et al. 20204). I suspect that part of the reason it has gone unanticipated is because the conditions to observe this phenomenon are rarely present since there is a consistent lack of long-term data on invasions (Kreps et al. 2012; Forsström et al. 2018; Fernández 2020) and research tends to focus on measurement of the abundance of invasive species without measuring the broader ecological community (Reid et al. 2009a). As a consequence there is, generally, limited ability to observe naturalization or even, arguably, ecological impact, though significant increases in abundance can likely be correlated with reductions in ecological structural metrics (e.g. mean diversity and richness). I think that the lack of accounting for naturalization is also in part because of the etymologically disconnected definition of naturalization created by Richardson et al. (2000) which omits the sense in which the conventional meaning of naturalization means community integration or "becoming native" (OED 2024). Regardless of the term applied, this is also because the phenomenon itself is not described by the most cited

frameworks for the process of invasion (e.g. Richardson et al. 2000; Sakai et al. 2001; Blackburn et al. 2011).

The natural phenomenon that I am referring to as naturalization occurs on timelines relevant to ecological management and therefore should be accounted for within the scientific frameworks used to describe invasion, insofar as those frameworks are meant to describe biological processes as they occur on timelines relevant to management and implicate management actions (e.g. Sakai et al. 2001; Blackburn et al. 2011). The lack of accounting for naturalization is important because invasive species management is one of the most common paradigms through which objectives in ecological management are conceived and decided with billions spent globally on invasive species management (e.g. Crystal-Ornelas et al. 2021). If invasion biology and invasive species management do not account for a highly relevant natural phenomenon this impedes accurate assessment of long term outcomes of species introductions. In particular, knowing the time frame within which this phenomenon tends to occur would help management agencies know when it is appropriate to stop managing (e.g. Lavoie et al. 2010). This could be quite helpful because it has often been difficult for management agencies to establish appropriate management endpoints (Robichaud et al. 2023).

## Chapter 5: Naturalization has been the Casualty of Boundary Work in Invasion Biology

### 5.1 Introduction

Why is it that the naturalization of invasive species has, largely, not been planned for within the practice of invasive species management? I think there are numerous reasons for this, not least that the naturalization of invasive species likely takes decades to occur substantially making it hard to observe except through long-term studies (e.g. Szydlowski et al. 2023). However, there are other factors that have contributed to the lack of consideration of the phenomenon of naturalization that have to do with the way suggestions that invasive species can integrate have been received by those in established positions in the invasion biology literature (e.g. Ricciardi and Ryan 2018). Just as the phenomenon of naturalization has tended to be categorically excluded from frameworks for the process of invasion created by those in established positions in the invasion biology literature (Chapter 4), boundary work (sensu Gieryn 1983) has also been conducted by those same people to keep out and prejudicially discredit work (Munro et al. 2019 e.g. Blackburn and Russell 20107; Ricciardi and Ryan 2018) that might otherwise create part of the basis for considering invasive species naturalization within those frameworks (e.g. Davis 2011; Pearce 2015). As a matter of clarity and accountability, by established position in the invasion biology literature I am referring to those who have both editorial powers in the core journals of invasion biology (e.g. *Biological Invasion, Diversity and Distributions, Neobiota*) and who have made highly cited contributions to the central epistemologies of invasion biology such that they have both a de facto ability to decide what does or does not get published as well as an authoritative voice when writing editorials. Many of the authors in Table 4.2 meet these two criteria.

The nature of boundary work is prejudicial and I believe there is sufficient evidence to show that a prejudicial approach has been taken in this case (Munro et al. 2019). I will be

using Gieryn's (1983) terminology of boundary work for this analysis because I feel it is useful in so far as I think it describes well what has transpired within the invasion biology literature as it pertains to the debates of greatest relevance to invasive species naturalization.

Gieryn (1983) defines boundary work as:

“... an ideological style found in scientists' attempts to create a public image for science by contrasting it favorably to non-scientific intellectual or technical activities”.

I should note at this stage that there are some portions of Gieryn's 1983 paper that I disagree with, specifically that he often takes a non-committal and unexplicit position on the controversies he covers, and by doing so I think he generally casts aspersions on science as a whole. In this respect I disagree with his position because I think he fundamentally misunderstands the nature of science as being about certainty and objectivity as a separate object from subjectivity. In this I think Gieryn generally misrepresents science since, rather than certainty, good science deals in relative uncertainty. This is because what makes good science is the ability to admit both what you don't know and that you may be wrong about what you do know by expounding the conditions under which you would be wrong i.e. falsifiability (Popper 1994). In addition, rather than creating some sort of unassailable objective truth, good science necessarily accounts for subjectivity because at it's best it is intersubjective comparison, through which a more objective understanding of reality is achieved by means of intersubjective verifiability (Kant 1781). With this in mind, where I think Gieryn's work is useful in this instance is in how he identifies how science can become ideology, that being that when science is presented as unassailable and unquestionable and is used to create the contrivance that is called authority, it is at this moment when science becomes ideology. There are three types of boundary work that Gieryn describes: expansion,

monopolization and protection of autonomy. In the case of the invasion biology discourse as it pertains to invasive species naturalization I think the type of boundary work being conducted is monopolization, described by Gieryn as:

“When the goal is monopolization of professional authority and resources, boundary-work excludes rivals from within by defining them as outsiders with labels such as "pseudo," "deviant," or "amateur” ”.

This is because, rather than attempting to expand into other discipline (expansion) or protect their professional autonomy from external regulating bodies (protection of autonomy), the most established authors have attempted to discredit the works of those who are critical of some aspects of invasion biology (e.g. Russell and Blackburn 2017; Cuthbert et al. 2020). Most recently, boundary work to dismiss the work of those presenting cases of invasive species providing benefit or becoming unproblematic (e.g. Davis et al. 2011; Pearce 2015) has coalesced under the terminology of Invasive Species Denialism (e.g. Blackburn and Russell 2017; Stratton et al. 2022), though boundary work has been conducted to inappropriately dismiss this type of work as unscientific prior to the invention of this terminology specifically within the discipline of invasion biology (e.g. Rejmanek et al. 2002; Richardson and Ricciardi 2013).

## **5.2 A brief review of accusations of invasive species denialism in invasion biology**

There have been at least 20 articles published referencing invasive species denialism in the period between 2017 and 2024, the majority of which were published in a period between 2017 and 2021. While this discussion has largely ended, those who have made claims of invasive species denialism occurring have not gone on record to note a change of their views. In this brief review I will cover two particular lines of discussion and exclude others for the sake of brevity. Those lines of discussion I intend to follow are the initial accusation of

invasive species denialism by Russell and Blackburn (2017) and its responses as well as the expanded claim of invasive species denialism that built upon Russell and Blackburn's article that was written by Ricciardi and Ryan (2018) as well as one of its responses written by Munro et al. (2019). My intent with this brief review is to provide an overview of the core positions and the reasoning for those positions within the debate over the terminology of invasive species denialism.

### **5.2.1 Blackburn and Russell (2017) and responses**

The first published accusation of invasive species denialism was Tim Blackburn and James Russell's 2017 article in the journal *Trends in Ecology and Evolution* titled "The Rise of Invasive Species Denialism" (Russell and Blackburn 2017). In this article they contend either that there are those that contest that invasive alien species don't have negative impacts or that they don't have quite so many negative impacts as they do and that this meets the definition of science denialism, as that is differentiated from legitimate scientific debate. They actively equate this type of science denial to climate change denial and medical science denialism. Among works they suggest are guilty of invasive species denialism are Ken Thomson's book "Where do Camels Belong?" (Thomson 2014), Scott Carroll's theory of conciliation biology (Carroll 2011), all the works previously critiqued in Richardson and Ricciardi's 2013 article "Misleading criticisms of invasion science: a field guide" as well as popular non-fiction works such as "The New Wild" by Fred Pearce (Pearce 2015) and "Beyond the war on invasive species: A Permaculture Approach to Ecosystem Restoration," by Tao Orion (Orion 2015). In addition to accusing others of denying scientific facts Russell and Blackburn also accuse those same people of having different values and disingenuous motivations, though they do not mention what those differing values and disingenuous motivations are.

This article by Russell and Blackburn (2017) elicited four direct published responses taking issue with their arguments, including from some persons they accused; Briggs (2017), Crowley et al. (2017); Davis and Chew (2017) and Tassin et al. (2017). All four responses disputed the notion that scientific facts, especially that invasive species can cause negative impacts, were being widely denied or that disingenuous motivations and rhetoric were in play. Three of the four responses also note that the approach taken by Russell and Blackburn is counter-productive to their stated value of there being “a vibrant and robust dialogue” because of how it is an attempt to shut down the valid concerns and discussion (Crowley et al. 2017; Davis and Chew 2017; Tassin et al. 2017). In response to these four responses Russell and Blackburn (2017b) maintained that invasive species denial was increasing, though they conceded that diverse values can play an important role in invasive species policy. However they did not address the argument that their approach was an attempt to shut down valid concerns, though they reiterated their commitment to dialogue. A number of other responses were also generated to the initial article and its subsequent responses including Guiaşu and Tindale 2018 and Boltovskoy 2018, these generated their own series of responses. I will not deal with these chains of discussion, however I wanted to note their existence as a matter of record.

### **5.2.2. Ricciardi and Ryan (2018) and Munro et al. (2019)**

Following this discourse the claims made by Russell and Blackburn (2017) were subsequently built upon by Anthony Ricciardi and Rachael Ryan (2018) who claimed that there is a large and increasing body of work that meets the criteria of Invasive species Denialism (ISD). Ricciardi and Ryan (2018) assert that invasive species denialism has grown at an exponential rate since the 1990's. This is work that they describe as being biased, uninformative and pseudoscientific and which lack evidence and use rhetorical arguments to disregard, misrepresent or reject evidence for the purpose of casting doubt on what they

describe as the scientific consensus on the impacts of invasive species. Examples of works they claim to be within the category of invasive species denialism include Sagoff (2005), Davis et al. (2011) in addition to all those listed by Russell and Balckburn (2017). To quantitatively establish science denial they use the criteria for science denialism provided by Diethelm and McKee (2009). Using these criteria they found that 77 works that they reviewed met the criteria for science denial, with a greater number of works in year most recent to the date of publication. The motivations they suggested that were at play for this denialism include free-market ideologues who oppose calls for increased regulation on transportation and trade in living organisms, distrust of scientific institutions radiating from a post-truth ideology, differing values and perceptions of nature, or merely using a contrarian message to get attention. The problem they identify is that this can create messages that are presented with false equivalence, distorting public debate, a phenomenon that has, most notably, occurred frequently in discussions of climate change (Boycoff and Boycoff 2004). They conclude that since they anticipate that invasive species denialism will continue to be vocalized in the mainstream media, falsely presenting scientific controversy and manufacturing doubt, that this will impede action by obfuscating the necessary consensus on invasive species management (Ricciardi and Ryan 2018).

In 2019 Munro et al. conducted their own analysis of 75 of 77 published works accused of invasive species denialism by Ricciardi and Ryan and found that none of them refuted scientific facts and that only five articles had text consistent with one of the five criteria for science denial in the framework laid out by Diethelm and McKee (2009). Munro et al. come to the conclusion that allegations of invasive species denialism are prejudicial, unfounded and lack rigour. In addition they state that:

“They threaten to stymie constructive debates in and about invasion biology. And, the name and- shame style of discourse (i.e., Ricciardi & Ryan 2017), alongside other kinds of

assaults on peoples' characters (e.g., Ricciardi & Ryan 2018), are not conducive to scientific progress in the public interest (Guiasu & Tindale 2018).”

### **5.2.3 Boundary work in Russell and Blackburn (2017) and Ricciardi and Ryan (2018)**

In addition to the material covered, one of the most consistent lines of attack used by both Russell and Blackburn (2017) and Ricciardi and Ryan (2018) is the characterization of critics as non-scientific, despite implicating a significant number of academics, as a way of discrediting arguments. This is precisely the line of approach described by Gieryn (1983) whereby invocation of the authority of science as an object, with those invoking it taking the identity of the scientist, is the vehicle to create a favourable dichotomy of legitimate and illegitimate as a means of shutting down debate. In this light I think that both Russell and Blackburn (2017) and Ricciardi and Ryan (2018) were engaged in monopolization type boundary work to discredit the work of their academic colleagues, especially in the view that their claims often lacked specific arguments or evidence of denial (Crowley et al. 2017; Munro et al. 2019).

### **5.3 The Excluded Work Represents a Significant Portion of the Popular and Scientific Literature that creates the Basis to Understand the Phenomenon of Naturalization**

Pertaining to naturalization, I wish to forward the argument that what all the work described as being guilty of invasive species denialism has in common is that all of it deals with phenomenon of the naturalization and integration of invasive species (e.g. Davis et al. 2011; Pearce 2015; Orion 2015). Since, rather than this body of work denying that invasive species can cause problems, which they generally do not (Munro et al. 2019), all of it deals with cases of species that had previously been problematic providing unexpected ecological benefits or of those species becoming unproblematic. In this way naturalization as a

phenomenon has been excluded from consideration in the central epistemologies of invasion biology through the boundary work undertaken by its most established authors.

#### **5.4 Boundary work requires Authority and the Power that comes with it**

For boundary work to be conducted it requires established authority and the use of the power that comes with that authority. This has happened in invasion biology where the most established authors have used the power that has come with their authority in their purviews over the curation of knowledge to exclude or advocate for the exclusion of work that challenges predominant understandings (Davis 2020 e.g. Cuthbert et al. 2020). Indeed, in a 2020 commentary in the journal *Conservation Biology* nineteen of some of the most prominent and established authors in invasion biology, most of whom are editors of scientific journals wrote:

“We urge journal editors to reconsider acceptance of denialist essays, despite potential boosts to impact factor” (Cuthbert et al. 2020)

Many of the authors on this comment such as David Richardson, Petr Pysek, Sven Bacher and Tim Blackburn have made numerous primary contributions to the central epistemologies of invasion biology, in particular the frameworks for the process of invasion describing the phenomenal processes that span all biological invasions (e.g. Richardson et al. 2000; Blackburn et al. 2011; Blackburn et al. 2014; Soto et al. 2024; see Table 4.2). In addition, these frameworks have strongly influenced global policy on ecological management as well as the scientific study of biological invasions (Wilson et al. 2020; Chapter 4). In the knowledge that the 19 authors of this statement are the editors of many of the core journals of invasion biology (e.g. *Biological Invasions*, *Diversity and Distributions*, *Neobiota*) this

statement by Cuthbert et al. (2020) gives good evidence to show that significant monopolizing boundary work by means of gatekeeping is likely taking place or at the very least being advocated. By contrast, most of those they accuse of science denialism do not have the same ability to curate the knowledge that is recognized as legitimate in invasion biology (see those listed as invasive species denialists in Ricciardi and Ryan 2018). For boundary work to be possible there must be power imbalances in who defines what constitutes the science and those power imbalances must be used to conduct that boundary work. It is clear there is a power imbalance within this debate and I am inclined to think that power imbalance is being leveraged to, at the very least, advocate for monopolizing boundary work. It should also be noted that, if this is the approach the advocate for journal editors, that it is likely that this is the advice they intend to follow themselves in their own capacities as journal editors i.e. to conduct monopolizing boundary work themselves.

#### **5.4 Going back to a relative beginning with how the definition of naturalization was changed by Richardson et al. 2000**

I would like to argue that the phenomenon of invasive species naturalization has been written out of community ecology in large part because of the categorical exclusion of the sense in which the word naturalization means community integration or “becoming native” by Richardson et al. (2000) when they reviewed and discussed definitions of naturalization (Chapter 2). This has been enabled by the enormous influence this article has had on the terminology used within invasion biology as well as its frameworks for the process of invasion (e.g. Blackburn et al. 2011). Indeed, in recent exchange with David Richardson he acknowledged that the term that would have better defined the phenomenon they were attempting to describe in that paper would have been “established” rather “naturalized”

because naturalized indicates being a part of a natural community which was not an ideal definitional component to him (Richardson, D. Personal Communication 2024)

This article by Richardson et al. (2000) is one the most important documents to the epistemological foundations of invasion biology for the fact that it is one of the most cited documents in invasion biology (~2500 citations) and that it is the most significant precursor to what is seen as the current consensus framework document Blackburn et al. 2011, which inherited Kruger and Richardson's barrier model (Kruger et al. 1986; Richardson et al. 2000) as well as most of their definition, including for naturalization, directly from this document. Having defined naturalization in this way in conjunction with the impact that this article has had on the central epistemologies of invasion biology I think that it has played a major role in the phenomenon of naturalization being omitted from consideration within invasion biology.

### **5.5 The Discourse does not have to be this way: a Comparison of the Discourse between Restoration Ecology and Invasion Biology**

Invasive species management and ecological restoration can be seen as two different, but non-exclusive, paradigms through which to view ecological management (Gaertner et al. 2012; Simberloff and Vitule 2014). Each of these both proceed from, and are iteratively affected by, the human cultures that contributed to their development as well as what these paradigms mean to the people that use them and develop them (Latour and Woolgar 1979; Latour 1993). We can see how shifting paradigms in ecological management are front and centre even at the global level, with the UN recently declaring this decade as the decade of Ecological Restoration (UN News 2021). At a more local level (local to myself in Ontario), this can be seen in the increasing incorporation and development of ecological restoration divisions within Conservation Authorities in Ontario starting in the late 1990's (TRCA 2016). Many of these ecological restoration divisions also conduct invasive species management,

showing that these paradigms and practice are very much non-exclusive, and are better described as deeply intertwined.

Each of these practices have a scientific discipline from which their paradigmatic development comes, in the case of ecological restoration it is restoration ecology and in the case of invasive species management it is invasion biology (also called invasion science and invasion ecology). Each of these disciplines can also be seen as human cultures with their own discourses and norms (Latour and Woolgar 1979). With regard to those human cultures of restoration ecology and invasion biology I have also noted different dynamics in their discourse, particularly in terms of how they deal with contentious topics. Whereas it is my impression that restoration ecology has had relatively civil discussions on contentious subjects I would suggest the same cannot be said about invasion biology on its own critical issues.

Examples of contentious subjects in restoration ecology have included the validity of historicity and concepts of wilderness (Katz 1992; Hiers 1995; Elliot 1997; Light 2000), socio-ecological systems (Higgs 2005; Egan et al. 2011), the definition of ecological restoration and restoration ecology (Higgs 2005), the Anthropocene (Perring et al. 2018; Lemoine and Svenning 2022), tertiary succession (Rapson 2022; Prach 2023), novel ecosystems (Hobbs et al. 2006, 2009, 2013, Seastedt et al. 2008, Hobbs 2013; Standish et al. 2013; Miller and Bestelmeyer 2016), seed sourcing and genetics (McKay et al. 2005; Pastorino 2012; Madsen et al. 2016; Dayrell et al. 2016), as well as what to do about invasive species.

By contrast, even the validity of criticism itself is questioned in invasion biology (Guiaşu and Tindale 2018; Davis 2020, e.g. Richardson and Ricciardi 2013; Simberloff and Vitule 2014; Blackburn and Russell 2017; Ricciardi and Ryan 2018) and as a result criticism of majority positions within this discipline is often met with tremendous hostility (Guiaşu and

Tindale 2018; Munro et al. 2019; Davis 2020), such that it often alienates those who want to add a productive contribution to the discourse in good faith that may differ from the most cited positions to some extent (e.g. Davis et al. 2005; Chew et al. 2009; Davis et al. 2011; White 2016). I think some well-known examples of this are Mark Davis's 2009 Book "Invasion Biology", Davis et al. (2011), "Don't judge a species by its origin" and Sagoff's 2018 critique "What is invasion biology?" as well as works by Vermeij and others which have just tended to be ignored (e.g. Vermeij 1996; Reise et al. 2006) despite offering excellent questions that remain unaddressed and unanswered. I would suggest that there are numerous instances of bad faith in the invasion biology discourse, evident in the tendency to categorically dismiss the views of others (Richardson and Ricciardi 2013; Russell and Blackburn 2017), the most extreme example of which being the charges of invasive species denialism (Russell and Blackburn 2017; Ricciardi and Ryan 2018; Cuthbert et al. 2020). I think this categorical dismissal of criticism has been done in bad faith because there is only a limited attempt to engage in intersubjective comparison (Popper 1994). This bad faith is also seen in equivalencies being drawn between conspiracy theories and advocating for integrating an understanding of naturalization into invasive species management planning and frameworks (Ricciardi and Ryan 2018; Stratton et al. 2022). This comparison, that is calling criticism "invasive species denialism", is absolutely ludicrous for the fact that it equivocates published academic work and popular science publications that contain no strong evidence of science denial (Munro et al. 2019) with malicious misinformation such as Covid vaccine conspiracy theories and climate change denial. This is deeply disingenuous conduct not only for its baselessness (Munro et al. 2019) but for the complete lack of any attempt to engage in intersubjective comparison, or in other words, trying to understand what someone else is saying in good faith. While there should be room for disagreement, allegations of science

denial go beyond a harmless hyperbole (Crowley et al. 2017; Davis and Chew 2017; Tassin et al. 2017).

Going back to a comparison of disciplines, I believe comparing the discourse in restoration ecology and invasion biology is not frivolous, many have noted that invasion biology, restoration ecology and conservation biology are sister disciplines for how they arose at the same time and similarly reify ecological theory to interact with human ecological management and moral intuitions in how we interact with other species and the environment (Simberloff and Vitule 2014). Indeed, Simberloff and Vitule (2014) make a similar comparison between restoration ecology and invasion biology, noting how there are those who call for similar ends to both disciplines (ostensibly), where in restoration ecology they say this centred around the novel ecosystem discourse and in invasion biology this is centred around discussions of incorporating a conception of integration and naturalization into frameworks of invasion. Discussing this particular article further, what I think Simberloff and Vitule (2014) get wrong about their view of the discourse in restoration ecology is that the fact of discussion is not the problem they say it is. They seemed principally concerned that just the fact of discussing novel ecosystems would undermine attempts to restore by eroding the confidence of funders and actors. In a way there is some truth to this, when we are confronted with information that creates cognitive dissonance we naturally become stressed (Cuckale-Matos and Champion 2022) because that information is not explicable within the paradigm in which we are operating. In addition, contemplating a means of integrating that information with what we have previously known can feel like dying, because our attachment to the old framework must die to give birth to a new one. Nonetheless, this is part of what the academic discourse is for and if these ideas are grounded in the truth of the world then they are worth considering. If the argument presented is “we just shouldn’t talk about it because it might confuse those working on the ground” this is not a good one, because it is ascribing

certitude; just because it might happen doesn't mean it will and even if it does happen, does not mean that it cannot lead to better approach in the future. If we walk with good intent, this discussion will help us manage, not hinder that effort because it is a discussion centred around something on which we all agree, finding ways to achieve better ecological outcomes. Indeed, if the academic literature is not a place for discussion and debate about ideas we are in bad shape; if not here then where?

The philosopher of science Karl Popper in the introduction to what was one of the last books he wrote before his death in 1994, “The Myth of the Framework: in Defence of Science and Rationality”, summarized his perspective on science and the philosophy of science in this manner:

“All, or almost all, the papers collected in this volume are written to defend rationality and rational criticism. It is a way of thinking, and even a way of living: a readiness to listen to critical arguments, to search for one's own mistakes, and to learn from them. It is, fundamentally, an attitude that I have tried to formulate (perhaps first in 1932) in the following two lines:

'I may be wrong and you may be right,  
and by an effort, we may get nearer to the truth. ' ”

- Popper 1994

An analogous approach to Popper's in these debates on the part of those in established positions within invasion biology seems to be greatly and consistently lacking (e.g. Simberloff and Vitule 2014; Russell and Blackburn 2017; Stratton et al. 2022). The approach taken categorically impugns the intent and motivations (Russell and Blackburn 2017; Ricciardi and Ryan 2018; Cuthbert et al. 2020) of those critical in such a manner that the intent inherent in “I may be wrong and you may be right” is often absent. Without just this

intent we will get no nearer to the truth and it behoves those in established positions to engage in a manner that facilitates, rather than obfuscates, this debate through good faith arguments and a willingness to be wrong under the right conditions.

I would suggest that this response is defensive, and for good reason, many of these authors and scientists likely began to do what they do because they were concerned about a world they loved disappearing around them (Elton 1958; Richardson and Pyšek 2008) and see this questioning as a threat to that work (Simberloff and Vitule 2014; Russell and Blackburn 2017b). Nevertheless, I feel this approach of impugning the motivations of others categorically is unhelpful because it will always mischaracterize their motivations since goodness does not exist in categories i.e. it is prejudice in the most literal sense (Munro et al. 2019). This takes away from a discussion of how to acknowledge where we are at such that more realistic plans can be made to do what is truly good by means of cooperation, seeing that those critical of particular positions within invasion biology are still interested in the same larger goal; looking after our world that we share. Rather than a difference in values (Russell and Blackburn 2017), these values are what we all have in common (Richardson, D. 2023 personal communication; Davis, M., 2023 personal communication; Chew, M, 2023, personal communication; Vermeij, G., 2023, personal communication).

The categorical dismissal of critical arguments (e.g. Ricciardi and Ryan 2018) by means of monopolizing boundary work does not serve the scientific purpose of invasion biology because it is the antithesis of the moral spirit of the scientific method (Popper 1994). On top of this, these positions that formulate this debate are not mutually exclusive; impact and integration are both part of the same process (Figure 4.2). There are real consequences to the manner in which discourse is conducted within invasion biology, a microcosm of which I observed when I recently attended a two day workshop run by the Great Lake Fisheries Commission, centred on invasive species (Great Lakes Panel on Aquatic Nuisance Species

2023). The first ground rule of discussion for this workshop was that discussion of whether we should or should not manage was not allowed (Great Lakes Panel on Aquatic Nuisance Species 2023), despite the fact that we were talking about expanding management efforts for purple loosestrife, for which there is excellent evidence to suggest that talking about whether we should manage it is entirely reasonable (Lavoie et al. 2010). If we are to come to more robust conclusions I think those with established positions within invasion biology must do a better job at actively facilitating plurality in the discourse and looking at the ways in which an understanding of impacts lives together with an understanding of naturalization while not compromising the spirit of work done in good faith that has gone into understanding both. Indeed, an approach that allows discussion would likely solve the problem of a lack of critical engagement with theory of invasion biology that people such as David Richardson has lamented over the course of his writings and research (e.g. Richardson et al. 2000; Wilson et al. 2020). Because, as the state of the discourse in restoration ecology illustrates, it doesn't have to be this way when it comes to contentious topics and the invasion biology discourse would be better if it looked on criticism in good faith, welcoming rather than actively attempting to control and eradicate different views of the same phenomena (Davis 2020).

## **Chapter 6: Implications and Recommendations**

Through this thesis it is my hope that I have communicated the following:

- 1) That naturalization has been defined and used in the invasion biology literature in a way that categorically excludes the sense in which it refers to integration. The definition has changed recently (Soto et al. 2024) however it has yet to be applied and even in the article that has heralded that change in definition, its use was actively discouraged for reason of imprecision despite offering no alternative to describe an integrated state (Soto et al. 2024).
- 2) A measurable set of criteria that describe naturalization as an ecological phenomenon (Table 6.1) as well as an observation of the phenomenon of naturalization in the context of Fanwort in Kashaabog Lake using those measurable criteria.
- 3) That the most cited frameworks for the process of invasion do not account for the phenomenon of naturalization.

- 4) That there are significant indications across taxa that invasive species naturalization happens on timelines relevant to management planning.
- 5) That part of the reason for why naturalization is not generally accounted in many policy and management contexts is as a consequence of boundary work conducted by the most established authors within invasion biology that has excluded the phenomenon from consideration in the central epistemologies of invasion biology.

Using these statements as premises, what I now wish to discuss is suggestions on how science, policy and management could change if they were to incorporate an understanding of naturalization.

### **6.1 Scientific Implications and Recommendations**

The phenomenon of invasive species naturalization is almost completely unstudied because it has not been conceived of within the epistemologies that are used to study and understand biological invasions. It is my hope that the framework (Figure 4.2) I have created be adopted for broad use because I believe it is a better description of nature than the framework created by Blackburn et al. (2011) which is the one which continues to be the most used for the description and study of biological invasions. Given the degree to which naturalization has been written out of the study of biological invasions I think there is a tremendous opportunity to re-examine old datasets and re-visit old studies to look at community change through the lens of the criteria that I have created to describe significant naturalization or something similar that has or may be developed by others if these criteria are unduly precise (Table 6.1). At the very least it is my hope that these criteria are a useful starting place to begin the description of and discussion about the phenomenon of naturalization.

Table 6.1: Criteria to define a significantly naturalized state
---

Criteria	Description
Criteria 1	The invasive species, in this case <i>C. caroliniana</i> , is both widespread and in low to moderate abundance relative to a peak abundance following introduction.
Criteria 2	The structural metrics (e.g. richness and diversity) of the invaded community would be at levels similar to those of a pre-invasion reference community

## 6.2 Management Implications and Recommendations

With established invasions it can often be difficult to decide when to scale back objectives such as moving from eradication to control or deciding to stop managing altogether. An understanding of invasive species naturalization can help define management endpoints and scale of management actions because it is necessarily defined by a lack of significant impact and an expectation of a low likelihood of significant future impact. This would be enabled by further study of the timescale on which naturalization occurs such that generalizations can be made about that timescale and any factors that may cause temporal variations. Knowing the timeframe on which species naturalize could be used to directly inform management endpoints, which have often been difficult for land managers to systematically determine (Robichaud et al. 2023). That there was no general sense of how long this process takes and that it was not accounted for in management was reaffirmed by the results from another question in my interviews with invasive species management professionals (Also see Appendix 2). When asked the question:

**Do you account for species that you currently manage, possibly naturalizing in the future? If so, how? If not, why not? On what time scale do you think naturalization occurs?**

All of those interviewed did not account for naturalization (Table 6.2) and had no firm ideas about how long naturalization takes, though a few expressed that it could be decades to a few centuries (Table 6.3).

Table 6.2: Answers to the question of whether each practitioner accounts for invasive species possibly naturalizing		
	yes	no
Do you account for naturalization possibly occurring?	0%	100%

Table 6.3: Noted timelines for invasive species naturalization	
Interviewee	Timeline
1	Don't know (maybe ~200 years)
2	Don't know (maybe 30+ years)
3	Don't know

4	Not relevant
5	Don't know (decades)
6	Don't know
7	Don't know (decades)
8	Don't know (150+ years)

I am going to frame the rest of this discussion of management around a recently released framework created by Robichaud et al. (2023) for helping invasive species management practitioners to understand how to proceed with established invasions. This is because it provides a useful structure through which to understand how the outcomes of this thesis can be applied. Within their framework Robichaud et al. (2023) layout three sequentially related questions to determine whether the management of an established invasion is worthwhile (Figure 6.1). Of these, the first is the most relevant to the work of this thesis, though the second question may well also be relevant in a more indirect fashion.

In many respects this thesis affirms the value of the first question (as well as the whole framework in general), that of determining whether the invader impacts are greater than the invader benefits. This is because it affirms that there may be benefits or non-impacts to the presence of the non-native species and this is well accounted for in their checklist they present in their appendices given that impacts or benefits to ecosystem structural metrics are well accounted for in that checklist for use in answering the question.

As it pertains to the second question, whether management costs outweigh the likely damage to the ecosystem and costs, I think there is only one thought I want to connect. The Fanwort populations studied in Chapter 3 were unmanaged and located in bays with low

human activity (at most 3 cottages in each bay), working on the assumption that species integration also occurs as a process of coevolution by means of natural selection (Carroll et al. 2007; Carroll et al. 2011), if this process is allowed to occur whereby the selective pressure is not influenced by massive disturbance events in the form of human management, it may be that an approach that does not seek to massively and explicitly remove may facilitate the naturalization of introduced species through non-interruption of that process of evolutionary learning. However, the information compiled within this thesis is nowhere near sufficient to offer practical recommendations to incorporate and understanding of such ecological processes and would need to be an avenue explored in a separate project.

Revisiting the proposed modifications of the unified framework for biological invasions created by Blackburn et al. (2011) created in chapter 4 (Figure 4.2), Robichaud et al. (2023) also affirms the advocacy for the consideration of doing no control, such as at a later stage of an invasion as depicted in that modified framework:

"Among the alternative actions, managers are encouraged to consider the “no control” option, thus permitting the invasion to progress. We emphasize that this decision may be, in some cases, an appropriate course of action. “No control” is not necessarily an abdication of responsibility, especially if it is a considered decision, but under the workshop framework it is crucial to recognize that a decision not to control the invasion does not mean that managers are expected to take no action. As emphasized by its centrality in Fig. 2, monitoring is expected to accompany any management action and especially the “no control” action.” (Robichaud et al. 2023)

### **6.2.1 Viewing Single Species Eradication Campaigns through the Lens of Ecological Restoration**

When single species focused invasive species management is conducted for primarily ecological objectives I would argue that its purpose is ecological restoration. Evidently other

motives and objectives can be intertwined but I think it is useful to view these projects in this way, since the goal is not to remove the invasive species but to ameliorate the ecology of the system in which that species is present. However, I have often found that this goal of amelioration gets lost and forgotten in many single species control and eradication campaigns because there is a tendency to become pre-occupied with the eradication of the species as an end in itself rather than reflecting on the overarching objective of the restoration of the environment, out of which the logic of that eradication is initially derived. This is a consequence of siloing and hyper specialization in some ways (Latour 1993) since single species eradication programs are often delegated to collectives of management agencies and non-government organizations with the tacit assumption that the eradication of that species is what is best for the restoration of the ecosystems in which they are working. While this can help create efficiencies, which is often where much of the literature and work in invasive species research is focused, it also creates a focus on those efficiencies that can tend not to encourage re-examination of the how to achieve the prime directive from which the logic of control and eradication was derived, ecological restoration. In addition, often following control efforts in single species eradication programs there are not many resources left to think about what happens to the land after control is applied (Stromberg et al. 2009) where the ecological disturbance of the control actions themselves can recreate the causes and conditions that may have allowed for those invasive species to spread and proliferate to begin with (Hobbs and Huenneke 1992). In this way, building ecological restoration into the initial planning and post-treatment plans may also help with long-term beneficial outcomes of single species invasive species management programs (Galatowitsch et al. 2016) or site based multi species invasive species management (Tang et al. 2023). What I think an understanding of naturalization encourages is an approach that is more strongly focused on goals emanating from restoration rather than control and eradication for their own sakes because I think it

suggests that restoration can occur despite the presence of species that are currently behaving invasively by building ecosystem resilience to invasion through restoration (van der Loop et al. 2022), that, perhaps, may augment the ability of the ecosystem to integrate that new species more rapidly through the greater number of possible interactions if the system is more biodiverse, allowing for regulation through food web integration and subsequent food web interactions (e.g. Elton and Nicholson 1942).

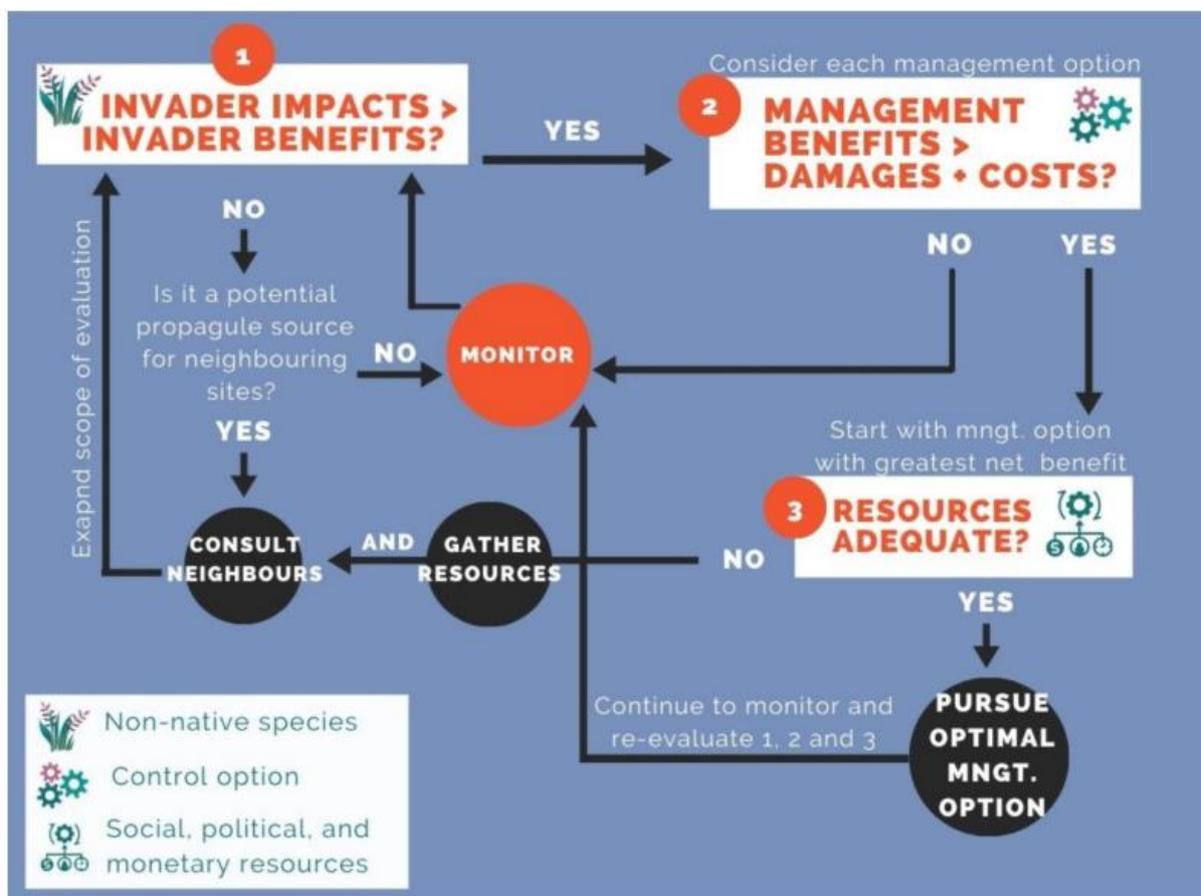


Figure 6.1: Adaptive decision support framework agreed on by members of the working group at the meeting in Fergus. Circles with text indicate actions, and numbered boxes indicate considerations linked to specific decision support tools devised by the working group in breakout sessions. Monitoring plays a central role in the framework, reflecting principles of adaptive management (Figure description from Robichaud et al. 2023).

### 6.3 Terminological Suggestions

While I have been making plenty of arguments for the use of the term naturalization to refer to the phenomenon I observed in chapter 3, what is much more important is that we plan for the phenomenon itself rather than what we call it. The term naturalization has its own problems, particularly the term's definition in relation to nativeness and the tacit implications nativeness can have as a moral category (Chew and Hamilton 2011). The incorporation of an understanding of naturalization, in some respects, solve the problem with nativeness that Chew and Hamilton (2011) propose, that being that:

“In recent discussions, human dispersal is said to render populations, and indeed any successor populations, non - native (Klein 2002; Pyšek et al. 2004; Bean 2007). **Nativeness is therefore revocable, but non -nativeness is permanent.** Being once human – dispersed accomplishes a mutagenic denaturing.”

In this way what an understanding of naturalization allows for is an understanding that non-nativeness is not permanent and nativeness is conferrable, of course, who is making the decision and how that is decision is made remains important. More than all of this, I think what Chew and Hamilton (2011) are trying to point out is that nativeness inherently creates the ability to arbitrarily dispossess species of rights in a manner that can negate an ecological reality whereby introduced species can integrate and subsequently belong. This is the ghost of historicity and I think lessons can be taken from the restoration ecology discourse here as well, where I think the general consensus is that historicity, in and of itself, is not a good basis for restoration targets (Higgs et al. 2014; Montana et al. 2024). In this way nativeness is not seen as inherently important, but as a means of identifying which species assemblages it may be useful to restore on ecological function and/or biodiversity criteria, especially in

knowing that there are many particular relationships we do not know about but can reasonably infer from our knowledge of the ecosystem residency time of the species within a given assemblage. I do not see the language of nativeness as inherently problematic, all words and terms can be misused by those determined to do unwholesome things and so I would recommend the use of the term naturalization in the description of the process of invasion/naturalization. However, what is more important than what it is called is that we account for the phenomenon to which it refers, whatever the heck you want to call it.

## References

1. Blackburn, T.M., P. Pyšek, S. Bacher, J.T. Carlton, R.P. Duncan, V. Jarošík, J.R. Wilson, and D.M. Richardson. 2011. A proposed unified framework for biological invasions. *Trends in Ecology and Evolution* 26, no. 7 333–39.  
<https://doi.org/10.1016/j.tree.2011.03.023>.
2. Blackburn, T.M., F. Essl, T. Evans, P.E. Hulme, J.M. Jeschke, I. Kühn, S. Kumschick, et al. 2014. A unified classification of alien species based on the magnitude of their environmental impacts. *PLOS Biology* 12(5): e1001850.  
<https://doi.org/10.1371/journal.pbio.1001850>.
3. Boykoff M.T. and J.M. Boykoff. 2004. Balance as bias: global warming and the US prestige press. *Global Environmental Change* 14:125–136,
4. Burdon, J.J., P.H. Thrall, and L. Ericson. 2013. Genes, communities & invasive species: understanding the ecological and evolutionary dynamics of host–pathogen interactions. *Current Opinion in Plant Biology* 16(4): 400–405.  
<https://doi.org/10.1016/j.pbi.2013.05.003>.
5. Byun, C., de Blois, S., and Brisson, J. 2017. Management of invasive plants through ecological resistance. *Biological Invasions*, 20(1), 13–27. doi:10.1007/s10530-017-1529-7
6. Carlton, J.T. 1985. Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. *Oceanography and Marine Biology - An Annual Review* 23: 313–371
7. Carniatto, N., R. Fugì, B.A. Quirino, and E. R. Cunha. 2019. An invasive and a native macrophyte species provide similar feeding habitat for fish. *Ecology of Freshwater Fish* 29(1): 112–20. <https://doi.org/10.1111/eff.12499>.

8. Carroll, S.P., A.P. Hendry, D.N. Reznick, and C. Fox. 2007. Evolution on ecological time-scales. *Functional Ecology* 21(3): 387–93. <https://doi.org/10.1111/j.1365-2435.2007.01289.x>.
9. Carroll, S.P. 2011. Conciliation Biology: The eco-evolutionary management of permanently invaded biotic systems. *Evolutionary Applications* 4(2): 184–99. <https://doi.org/10.1111/j.1752-4571.2010.00180.x>.
10. Catford, J.A., R. Jansson and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, 15(1), 22–40. doi:10.1111/j.1472-4642.2008.00521.x
11. Chew, M.K. 2009. The monsterring of tamarisk: how scientists made a plant into a problem. *Journal of the History of Biology* 42(2): 231–66. <https://doi.org/10.1007/s10739-009-9181-4>.
12. Chew, M.K. and Hamilton, A.L. 2010. The rise and fall of biotic nativeness: a historical perspective. In *Fifty Years of Invasion Ecology*, D.M. Richardson (Ed.). <https://doi.org/10.1002/9781444329988.ch4>
13. Citizenship Act (R.S.C., 1985, c. C-29).
14. Colautti, R.I. and H.J. MacIsaac. 2004. A neutral terminology to define invasive species. *Diversity and Distributions*, 10, 135–141
15. Cornell Cooperative Extension 2024. Invasion curve. URL: <https://chautauqua.cce.cornell.edu/environment/invasive-nuisance-species/invasion-curve>
16. Cousens, R. and M. Mortimer. *Dynamics of weed populations*. 1995. Cambridge University Press, Cambridge.
17. Crystal-Ornelas R, E.J. Hudgins, R.N. Cuthbert, R.J. Haubrock, J. Fantle-Lepczyk, E. Angulo, A.M. Kramer, L. Ballesteros-Mejia, B. Leroy, B. Leung, E. López-López, C. Diagne, F. Courchamp. 2021. Economic costs of biological invasions within North

- America. In: Zenni R.D., McDermott S., García-Berthou E. and Essl F. (Eds) *The Economic Costs of Biological Invasions Around the World*. *NeoBiota* 67: 485-510.  
doi:10.3897/neobiota.67.58038
18. Cuckale-Matos, S. and S.D. Champion. 2022. Exploring cognitive dissonance in the correctional nursing experience. *Public Health Nursing* 2022;39:545–552
  19. Cuthbert, R.N., Bacher, S., Blackburn, T.M., Briski, E., Diagne, C., Dick, J.T.A., Essl, F., Genovesi, P., Haubrock, P.J., Latombe, G., Lenzner, B., Meinard, Y., Pauchard, A., Pyšek, P., Ricciardi, A., Richardson, D.M., Russell, J.C., Simberloff, D. and Courchamp, F. 2020. Invasion costs, impacts, and human agency: response to Sagoff 2020. *Conservation Biology*, 34: 1579-1582. <https://doi.org/10.1111/cobi.13592>
  20. Darwin, C. 1872. *On the origin of species*. Murray, London.
  21. Davis, M. A., and K. Thompson. 2000. Eight ways to be a colonizer; two ways to be an invader. *ESA Bulletin* 81:226–230.
  22. Davis M.A. and K. Thompson. 2002. ‘Newcomers’ invade the field of invasion ecology: question the field’s future. *Bulletin of the Ecological Society of America* 83:196–197
  23. Davis M.A., J. Pergl, A. Truscott, J. Kollmann, J.P. Bakker, R. Domenech, K. Prach, A. Prieur-Richard, R.M. Veeneklaas, P. Pyšek, R. del Moral, R.J. Hobbs, S.L. Collins, S.T.A. Pickett, and P.B. Reich. 2005. Vegetation change: a reunifying concept in plant ecology. *Perspectives in Plant Ecology, Evolution and Systematics*, 7:69–76.
  24. Davis M. A. 2009. *Invasion Biology*. Oxford, UK: Oxford University Press.
  25. Davis, M.A., M.K. Chew, R.J. Hobbs, A.E. Lugo, J.J. Ewel, G.J. Vermeij, J.H. Brown, et al. 2011. Don’t judge species on their origins. *Nature* 474 (7350): 153–54.  
doi:10.1038/474153a.
  26. Davis M.A. 2020. Let’s welcome a variety of voices to Invasion Biology. *Conservation Biology* 34(6): 1329-1330. doi: 10.1111/cobi.13608

27. di Castri, F. 1989. History of Biological Invasions with a Special Emphasis on the Old World. in Drake JA, Mooney HA, Di Castri F, Goves RH, Kruger FJ, Rejmánek M, Williamson M (eds)(1989) Biological invasions: a global perspective. Wiley, Chichester.
28. Diez, J. M., J.J. Sullivan, P.E. Hulme, G. Edwards, and R.P. Duncan. 2008. Darwin's naturalization conundrum: Dissecting taxonomic patterns of species invasions. *Ecology Letters*, 11, 674–681. doi:10.1111/j.1461-0248.2008.01178.x
29. Dostal, P., J. Müllerova, P. Pyšek, J. Pergl, and T. Klinerova. 2013. The Impact of an invasive plant changes over Time. *Ecology Letters* 16: 1277–84.
30. Drake J.A., H.A. Mooney, F. Di Castri, R.H. Groves, Kruger FJ, Rejmánek M, Williamson M (eds). 1989. Biological Invasions: a Global Perspective. Wiley, Chichester
31. Duncan, R.P., et al. 2003. The Ecology of Bird Introductions. *Annual Review of Ecology, Evolution, and Systematics*, vol. 34, 2003, pp. 71–98.
32. Eastman, J. and A. Hansen. 2003. The Book of Field and Roadside: Open-Country Weeds, Trees and Wildflowers of Eastern North America. pp. 352.
33. Egan, D., E.E. Hjerpe, and J. Abrams. 2011. Human Dimensions of Ecological Restoration Integrating Science, Nature, and Culture. Island Press
34. Elliott, R. 1997. Faking Nature: the Ethics of Environmental Restoration. Routledge.
35. Elton, C., & Nicholson, M. 1942. The ten-year cycle in numbers of the lynx in Canada. *Journal of Animal Ecology*, 11(2), 215–244. <https://doi.org/10.2307/1358>
36. Elton, C. S. 1958. The ecology of invasions by animals and plants. London: Chapman & Hall.
37. Essink K, and R. Dekker. 2002. General patterns in invasion ecology tested in the Dutch Wadden Sea: the case of a brackish-marine polychaetous worm. *Biological Invasions* 4:359–368

38. Fernández, C. 2020. Boom-bust of *Sargassum muticum* in northern Spain: 30 Years of Invasion. *European Journal of Phycology* 55(3): 285–95.  
<https://doi.org/10.1080/09670262.2020.1715489>.
39. Forsström, T., O. Vesakoski, K. Riipinen et al. 2018. Post-invasion demography and persistence of a novel functional species in an estuarine system. *Biological Invasions* 20: 3331–3345. doi:10.1007/s10530-018-1777-1
40. Gaertner M., Fisher J., Sharma G. & Esler K. 2012. Insights into invasion and restoration ecology: Time to collaborate towards a holistic approach to tackle biological invasions. *NeoBiota* 12: 57-76. <https://doi.org/10.3897/neobiota.12.2123>
41. Galatowitsch, S.M., Larson, D.L. & Larson, J.L. 2016. Factors affecting post-control reinvasion by seed of an invasive species, *Phragmites australis*, in the central Platte River, Nebraska. *Biological Invasions* 18, 2505–2516. <https://doi.org/10.1007/s10530-015-1048-3>
42. Gieryn, T.F. 1983. Boundary-Work and the demarcation of science from non-science: strains and interests in professional ideologies of scientists. *American Sociological Review* 48 (6):781-795.
43. Gray, A., 1862. *A manual of the botany of the Northern United States*. James Munroe and Company, Boston and Cambridge.
44. Great Lakes Panel on Aquatic Nuisance Species 2023. Regional invasive aquatic plant control prioritization and needs assessment: January 24-25, 2023. Workshop Proceedings. URL: <https://www.glpanel.org/wp-content/uploads/2023/06/IJ-IAP-workshop-proceedings-6.19.23.pdf>
45. Groves, R.H. 1986. Invasion of mediterranean ecosystems by weeds. Resilience in Mediterranean-Type Ecosystems (ed. by B. Dell, A.J.M. Hopkins & B.B. Lamont), pp. 129–145, Junk, Dordrecht.

46. Guiaşu, Radu Cornel, and Christopher W. Tindale. 2018. Logical fallacies and invasion biology. *Biology and Philosophy* 33, no. 5–6. <https://doi.org/10.1007/s10539-018-9644-0>.
47. Hammer, Ø, Harper, D.A.T., Ryan, P.D. 2001. "PAST: Paleontological Statistics software package for education and data analysis". *Paleontologica Electronica* 4(1): 9pp.
48. Hawkins, Charlotte, Sven Bacher, Franz Essl, Philip E. Hulme, Jonathan M. Jeschke, Ingolf Kühn, Sabrina Kumschick, et al. 2015. Framework and guidelines for implementing the proposed IUCN environmental impact classification for alien taxa (EICAT). *Diversity and Distributions* 21, no. 11 (September 21, 2015): 1360–63. <https://doi.org/10.1111/ddi.12379>.
49. Heger T. 2001. A model for interpreting the process of invasion: Crucial situations favouring special characteristics of invasive species. In: Brundu G, Brock JH, Camarda I, Child LE and Wade PM (eds) *Plant Invasions. Species Ecology and Ecosystem Management*, pp 3–10. Backhuys Publishers, Leiden, The Netherlands
50. Heger, T.A. and L. Trepl 2003. Predicting biological invasions. *Biological Invasions*. 5:313–321.
51. Henderson, S. et al. 2006. Progress in invasive plants research. *Prog. Phys. Geog.* 30, 25–46
52. Hiers, K. 1995. Nature Invented: An ethical critique of preservation and restoration ecology. *Trumpeter* 12.2: 84-87.
53. Higgs, E. S. 1997. What is good ecological restoration?. *Conservation biology* 11.2: 338-348.
54. Higgs, E., D.A. Falk, A. Guerrini, M. Hall, J. Harris, R.J. Hobbs, S.T. Jackson, J.M. Rhemtulla and W. Throop 2014. The changing role of history in restoration ecology. *Frontiers in Ecology and the Environment*, 12(9), 499–506. doi:10.1890/110267

55. Hobbs, R. J., & Huenneke, L. F. 1992. Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, 6(3), 324–337. doi:10.1046/j.1523-1739.1992.06030324.x
56. Hobbs, R. J. et al. 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography* 15: 1–7.
57. Hobbs, R. J. et al. 2009. Novel ecosystems: implications for conservation and restoration. *Trends in Ecology and Evolution* 24: 599–605.
58. Hobbs, R. J. 2013. Grieving for the past and hoping for the future: balancing polarizing perspectives in conservation and restoration. *Restoration Ecology* 21: 145–148.
59. Hobbs, R. J. et al. (eds) 2013. *Novel ecosystems: intervening in the new ecological world order*. – Wiley
60. Hoff, H.K. and R.A. Thum. 2022. Hybridization and invasiveness in eurasian watermilfoil (*Myriophyllum Spicatum*): Is prioritizing hybrids in management justified? *Invasive Plant Science and Management* 15(1): 3–8. doi:10.1017/inp.2022.4.
61. Hoffmann B.D. and F. Courchamp. 2016. Biological invasions and natural colonisations: are they that different? *NeoBiota* 29: 1-14. doi:10.3897/neobiota.29.6959
62. Hogsden, K.L., E.P.S. Sager and T.C. Hutchinson. 2007. The Impacts of the Non-native macrophyte *Cabomba caroliniana* on littoral biota of Kaskashabog Lake, Ontario. *Journal of Great Lakes Research* 33(2): 497–504. doi:10.3394/0380-1330(2007)33.
63. Holub, J., and V. Jirásek. 1967. Zur vereinheitlichung der terminologie in der phytogeographie. *Folia Geobotanica Et Phytotaxonomica* 2(1): 69–113. doi:10.1007/bf02851755.
64. Hutchinson, G.E. 1975. *A treatise on limnology*. Vol. III. *Limnological botany*. Wiley, N.Y. 660 pp.
65. Invasive Species Act, 2015, S.O. 2015, c. 22

66. Jeschke, J.M., L. Gómez Aparicio, S. Haider, T. Heger, C. J. Lortie, P. Pyšek, and D.L. Strayer. 2012. Support for major hypotheses in invasion biology Is uneven and declining. *NeoBiota* 14: 1–20. doi:10.3897/neobiota.14.3435.
67. Jones, C., K.M. Somers, B. Craig, and T.B. Reynaldson. 2007. Ontario benthos biomonitoring network: protocol manual. Environment Canada.
68. Kant, I. 1781. *The critique of pure reason*. Translation by : J. M. D. Meiklejohn
69. Katz, E. 1992. The call of the wild: The struggle against domination and the technological fix of nature. *Environmental Ethics* 14.3 (1992): 265-273.
70. Kolar C.S. and Lodge D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology and Evolution*, 16: 199–204.
71. Krebs, C.J. 1973. *Ecology: the experimental analysis of distribution and abundance*. pp. 653.
72. Kreps, T.A., A.K. Baldrige, and D.M. Lodge. 2012. The impact of an invasive predator (*Orconectes rusticus*) on freshwater snail communities: Insights on habitat-specific effects from a multilake long-term study. *Canadian Journal of Fisheries and Aquatic Sciences* 69(7): 1164–73. doi:10.1139/f2012-052.
73. Kruger, F.J., D.M. Richardson and B.W. Van Wilgen 1986. Processes of invasion by alien plants. *The ecology and management of biological invasions in southern Africa* (ed. by I.A.W. Macdonald, F.J. Kruger & A.A. Ferrar), pp. 145–155. Oxford University Press, Cape Town.
74. Latour, B and S. Woolgar 1979. *Laboratory life: the construction of scientific facts*. Beverly Hills: Sage Publications. ISBN 0-8039-0993-4.
75. Latour 1993. *We have never been modern*. Translation by Catherine Porter. Harvard University Press.

76. Lavoie, C. 2010. Should we care about purple loosestrife? The history of an invasive plant in North America. *Biological Invasions*, 12(7): 1967–1999. doi:10.1007/s10530-009-9600-7
77. LeBrun, E.G., M. Jones, R.M. Plowes, and L.E. Gilbert. 2022. Pathogen-mediated natural and manipulated population collapse in an invasive social insect. *Proceedings of the National Academy of Sciences of the United States of America* 119(14). doi:10.1073/pnas.2114558119.
78. Light, A. 2000. Ecological restoration and the culture of nature: A pragmatic perspective. In Gobster, P.G and Hull R.B. *Restoring nature: Perspectives from the social sciences and humanities*. Washington, DC: Island Press.
79. Light, A. 2003. 'Faking nature' revisited. In D. Michelfelder and B. Wilcox (eds.) *The Beauty Around Us: Environmental Aesthetics in the Scenic Landscape and Beyond*. Albany, NY: SUNY Press.
80. Light, A. 2007. *Restorative relationships: from artifacts to natural systems. Healing Nature, Repairing Relationships: new perspectives on restoring ecological spaces and consciousness*.
81. Llanos, E.N., M.A. Saracho Bottero, M. L. Jaubet, G. V. Garaffo, E. Hines, G.V. Cuello, and R. Elías 2021. The Boom-Bust dynamic of the invader *Boccardia proboscidea* mediated by sewage discharge: the response of the intertidal epilithic community in the southwest Atlantic. *Marine Pollution Bulletin* 164 doi:10.1016/j.marpolbul.2021.112045.
82. Lockwood, J.L. et al. 2007. *Invasion ecology*, Blackwell Publishing
83. Lodge, D.M. et al. 2006. Biological invasions: recommendations for US policy and management. *Ecological Application*. 6, 2035–2054
84. Lyon, J., and T. Eastman 2006. Macrophyte species assemblages and distribution in a shallow, eutrophic lake. *Northeastern Naturalist* 13(3): 443–53.

85. MacDonald, F. 2002. Canada's response to the introduction of Fanwort in Ontario waters: A case study. In alien invaders in Canada's waters, wetland, and forests, R. Claudi, P. Nantel, and E. Muckle-Jeffs, eds., pp 161–167. Ottawa Ont.: Canadian Forest Service
86. Madsen, J.D., R.M. Wersal, M. Tyler, and P.D. Gerard. 2006. The distribution and abundance of aquatic macrophytes in swan lake and middle lake, Minnesota. *Journal of Freshwater Ecology* 21(3): 421–29. <https://doi.org/10.1080/02705060.2006.9665019>.
87. Madsen, M.D., Davies, K.W., Boyd, C.S., Kerby, J.D. and T.J. Svejcar 2016. Emerging seed enhancement technologies for overcoming barriers to restoration. *Restoration Ecology* 24: S77-S84. <https://doi.org/10.1111/rec.12332>
88. Marchetti, M. P., Moyle, P. B., & Levine, R. 2004. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology*, 49(5), 646–661. doi:10.1111/j.1365-2427.2004.01202.x
89. Marris, E. 2011. *The rambunctious garden: saving nature in a post-wild world*. Bloomsbury, New York.
90. McKay, J.K., C.E. Christian, S. Harrison and K.J. Rice 2005. "How Local Is Local?"—A review of practical and conceptual issues in the genetics of restoration. *Restoration Ecology*, 13: 432-440. doi:10.1111/j.1526-100X.2005.00058.x
91. McTavish, M. 2019. *Learning to live with novelty: Implications of exotic earthworms and their interactions with seeds, mulch, and wood ash for ecological restoration*. Ph.D Thesis, Waterloo University, Waterloo, Ontario.
92. Merriam-Webster.com Dictionary, s.v. "naturalize," accessed March 3, 2024, <https://www.merriam-webster.com/dictionary/naturalize>.
93. Merriam-Webster.com Dictionary, s.v. "naturalization," accessed March 3, 2024, <https://www.merriam-webster.com/dictionary/naturalization>.

94. Merritt, R.W. and K.W., Cummins 1996. An introduction to the aquatic insects of North America: Third Edition. pp. 862
95. Miller, J.R. and B.T. Bestelmeyer 2016. What's wrong with novel ecosystems, really?. *Restoration Ecology*, 24: 577-582. doi:10.1111/rec.12378
96. Miller, T.E.X., A.L. Angert, C.M. Brown, J.A. Lee-Yaw, M.A. Lewis, F. Lutscher, N.G. Marculis, et al. 2020. Eco-evolutionary dynamics of range expansion. *Ecology* 101(10). doi:10.1002/ecy.3139.
97. Mollison, D., R.M. Anderson, M.S. Bartlett and R. Southwood 1986. Modelling biological invasions: chance, explanation, prediction [and discussion]. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 314(1167): 675–693. doi:10.1098/rstb.1986.0080
98. Montana, J., T. Heger, R. Kelz , A. Bischoff , R. Buitenwerf , U. Eser , K. Kung , J. Sattler , A. H. Schweiger , A. Searle , L. H. Teixeira , B. Travassos-Britto , E. Higgs 2024. From novel ecosystems to novel natures. *GAIA - Ecological Perspectives for Science and Society*, 33 (1): 146-151. doi: 10.14512/gaia.33.1.6
99. Moore, J.W., David B. Herbst, Walter N. Heady, and Stephanie M. Carlson. 2012. Stream community and ecosystem responses to the boom and bust of an invading snail. *Biological Invasions* 14(11): 2435–46. doi:10.1007/s10530-012-0240-y.
100. Morrison, L.W. 2002. Long-term impacts of an arthropod-community invasion by the imported fire ant, *Solenopsis invicta*. *Ecology* 83(8): 2337. doi:10.2307/3072064.
101. Munro, D., J. Steer and W. Linklater 2019. On allegations of invasive species denialism. *Conservation Biology* 33 (4): 797–802. doi: 10.1111/cobi.13278
102. Murphy, H.T., J. vanDerwal, L. Lovett-Doust and J. Lovett-Doust. 2006. Invasiveness in exotic plants: immigration and naturalization in an ecological continuum. In: Cadotte,

- M. W., S.M. McMahon and T. Fukami (Eds.) 2006. Conceptual ecology and invasion biology: reciprocal approaches to nature. doi:10.1007/1-4020-4925-0
103. Noel J., 2004. Growth, reproduction and control of an invasive aquatic plant, *Cabomba caroliniana*, in Kasshabog Lake, Ontario and its potential dispersal. M.Sc. thesis, Trent University, Peterborough, Ontario
104. Nsikani, M.M., S. Geerts, S. Ruwanza and D.M. Richardson 2020. Secondary invasion and weedy native species dominance after clearing invasive alien plants in South Africa: Status quo and prognosis. South African Journal of Botany, 132, 338–345. doi:10.1016/j.sajb.2020.05.009
105. Oduor, A.M.O. 2021. Native plant species show evolutionary responses to invasion by *Parthenium hysterophorus* in an African savanna. New Phytologist 233(2): 983–94. <https://doi.org/10.1111/nph.17574>.
106. Orion, T. 2015. Beyond the war on invasive species. Chelsea Green Publishing, White River Junction, VT.
107. Oxford English Dictionary, s.v. “naturalize (v.),” December 2023, doi:10.1093/OED/9850995989.
108. Painter, D.S. and K.J. McCabe 1987. Investigation into the disappearance of Eurasian water milfoil in the Kawartha Lakes. Environment Canada.
109. Pastorino, M.J. 2012. How many seed transfer zones are necessary for the preservation of the genetic identity of *Austrocedrus chilensis* natural populations in Argentina?. Restoration Ecology, 20: 551-554. doi: 10.1111/j.1526-100X.2012.00899.x
110. Pearce F. 2015. The new wild: why invasive species will be nature’s salvation. Beacon press, Boston. pp. 288.
111. Pearce, B.K.D., A.S. Tupper, R.E. Pudritz, P.C. Higgs 2018. Constraining the time interval for the origin of life on earth. Astrobiology 18(3) doi: 10.1089/ast.2017.1674

112. Perring, M., T. Erickson and P.H. Brancalion 2018. Rocketing restoration: Enabling the upscaling of ecological restoration in the Anthropocene. *Restoration Ecology*. doi:10.1111/rec.12871
113. Pintar, M.R., Dorn, N.J., Kline, J.L. and J.C. Trexler 2023. Contrasting invasion histories and effects of three non-native fishes observed with long-term monitoring data. *Biological Invasions* 25: 3887–3903. doi:10.1007/s10530-023-03146-9
114. Popper, K. 1994. *The myth of the framework: In defence of science and rationality*. Routledge, New York.
115. Prach, K. 2023. Tertiary succession—do we really need the new term? Response to Rapson (2023). *Restoration Ecology* e13892. <https://doi.org/10.1111/rec.13892>
116. Pyšek, P. et al. 2004. Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon* 53, 131–143
117. Pyšek, P. and P. Hulme 2009. Invasion biology is a discipline that's too young to die. *Nature* 460:324 . doi:10.1038/460324b
118. Pyšek, P. and D.M. Richardson 2006. The biogeography of naturalization in alien plants. *Journal of Biogeography*. 33. 2040 - 2050. 10.1111/j.1365-2699.2006.01578.x.
119. Pyšek, P., P.E. Hulme, D. Simberloff, S. Bacher, T.M. Blackburn, J.T. Carlton, W. Dawson, et al. 2020. Scientists' warning on invasive alien species. *Biological Reviews* 95(6): 1511–34. doi:10.1111/brv.12627.
120. Rapson, G.L. 2023. Tertiary succession: a new concept to help vegetation restoration. *Restoration Ecology* 31: e13683. doi:10.1111/rec.13683
121. Reichard, S., and P.S. White 2003. Invasion biology: an emerging field of study. *Annals of the Missouri Botanical Garden* 90(1): 64. doi:10.2307/3298526.

122. Reid, A.M., L. Morin, P.O. Downey, K. French, and J.G. Virtue 2009a. Does invasive plant management aid the restoration of natural ecosystems? *Biological Conservation* 142(10): 2342–49. doi:10.1016/j.biocon.2009.05.011.
123. Reid, S., N. Mandrak, J. Barnucz, E. Sager, and K. Borrowman 2009b. Impacts of the non-native macrophyte, *Cabomba caroliniana*, on littoral biota and food web dynamics in a central Ontario lake. NALMS annual symposia 2009.
124. Reise, K., S. Olenin, and D.W. Thielges. 2006. Are aliens threatening European aquatic coastal ecosystems?. *Helgoland Marine Research* 60(2): 77–83. doi:10.1007/s10152-006-0024-9.
125. Rejmánek, M., D. M. Richardson, M. G. Barbour, M. J. Crawley, G. F. Hrusa, P. B. Moyle, J. M. Randall, D. Simberloff, and M. Williamson. 2002. Biological invasions: politics and the discontinuity of ecological terminology. *ESA Bulletin* 83:131–133
126. Reo, N.J. and L.A. Ogden. 2018. Anishnaabe Aki: an indigenous perspective on the global threat of invasive species. *Sustainability Science* 13:1443–1452. doi:10.1007/s11625-018-0571-4
127. Russell J.C. and Blackburn T.M. 2017. The rise of invasive species denialism. *Trends in Ecology and Evolution*. 32: 3–6
128. Lemoine, R.T. and J.C. Svenning. 2022. Nativeness is not binary—a graduated terminology for native and non-native species in the Anthropocene. *Restoration Ecology* 30(8): e13636.
129. Ricciardi, A. and M. Mottiar. 2006. Does Darwin’s naturalization hypothesis explain fish invasions?. *Biological Invasions*, 8: 1403–1407
130. Ricciardi, A., and R. Ryan. 2018. The exponential growth of invasive species denialism. *Biological Invasions* 20(3): 549–53. doi:10.1007/s10530-017-1561-7.

131. Richardson, D.M. and Ricciardi, A. 2013. Misleading criticisms of invasion science: a field guide. *Diversity and Distributions* 19: 1461–1467
132. Richardson, D.M., P. Pyšek, M. Rejmánek, M.G. Barbour, F. D. Panetta, and C.J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*. 6(2): 93–107. doi:10.1046/j.1472-4642.2000.00083.x.
133. Ricklefs R.E. 2005. Taxon cycles. Insight from invasive species. In: Gaines SD, Stachoweicz
134. Roberts, J., and S. Florentine. 2021. A global review of the invasive aquatic weed *Cabomba caroliniana* [a. Gray] (Carolina Fanwort): current and future management challenges, and research gaps. *Weed Research* 62(1): 75–84. doi:10.1111/wre.12518.
135. Robichaud, C.D., R.C. Rooney, B.M.H. Larson, S.E. Wolfe, Z. Nyssa, K. P. Kowalski, and H. Braun. 2023. A decision framework for the management of established biological invasions. *FACETS*. 8: 1-10. [doi:10.1139/facets-2022-0200](https://doi.org/10.1139/facets-2022-0200)
136. Roy, H. E., Rabitsch, W., Scalera, R., Stewart, A., Gallardo, B., Genovesi, P., ... Zenetos, A. 2017. Developing a framework of minimum standards for the risk assessment of alien species. *Journal of Applied Ecology*, 55(2), 526–538. doi:10.1111/1365-2664.13025
137. Sakai, Ann K., Fred W. Allendorf, Jodie S. Holt, David M. Lodge, Jane Molofsky, Kimberly A. With, Syndallas Baughman, et al. 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics* 32: 305–32. <http://www.jstor.org/stable/2678643>.
138. Sagoff, M. 2018. What is invasion biology?. *Ecological Economics* 154: 22–30. doi:10.1016/j.ecolecon.2018.07.023.
139. Saul W, J.M. Jeschke and T. Heger. 2013. The role of eco-evolutionary experience in invasion success. *NeoBiota* 17: 57-74. doi:10.3897/neobiota.17.5208

140. Sax D.F., J.J. Stachowicz and S.D. Gaines (Eds). 2005. Species invasions: insights into ecology, evolution, and biogeography. Sinauer, Sunderland, 165–199.
141. Schab, C.M., S. Park, L.A. Waidner, and C.E. Epifanio. 2013. Return of the native: historical comparison of invasive and indigenous crab populations near the mouth of Delaware bay. *Journal of Shellfish Research* 32 (3): 751–58. doi:10.2983/035.032.0318.
142. Schilthuizen, M., P. Lúcia, S. Pimenta, Y. Lammers, P.J. Steenbergen, M. Flohil, N.G.P. Beveridge, P.T. van Duijn, et al. 2016. Incorporation of an invasive plant into a native insect herbivore food web. *PeerJ* 4. doi:10.7717/peerj.1954
143. Schooler, S. 2008. Shade as a management tool for the invasive submerged macrophyte, *Cabomba caroliniana*. *Journal of Aquatic Plant Management* 46: 168-171.
144. Schooler, S., and M. Julien. 2011. Effects of depth and season on the population dynamics of *Cabomba caroliniana* in south-east Queensland. Fifteenth Australian Weeds Conference 768-771.
145. Seastedt, T. R. et al. 2008. Management of novel ecosystems: are novel approaches required? – *Frontiers in Ecology and the Environment* 6: 547–553.
146. Servheen, C. and K.A. Gunther. 2022. Conservation and management of the culture of bears. *Ecology and Evolution* 12(4). doi:10.1002/ece3.8840.
147. Shine, R. 2011. Invasive species as drivers of evolutionary change: cane toads in tropical Australia. *Evolutionary Applications* 5(2): 107–16. doi:10.1111/j.1752-4571.2011.00201.x.
148. Simberloff, D., and L.K. Gibbons. 2004. Now you see them, now you don't! – population crashes of established introduced species. *Biological Invasions* 6(2): 161–72. Doi:10.1023/b:binv.0000022133.49752.46.
149. Simberloff, D. 2011. Non-natives: 141 scientists object. *Nature* 475(7354):36. doi:10.1038/475036a.

150. Simberloff, D. and J. R. S. Vitule. 2013. A call for an end to calls for the end of invasion biology. *Oikos*, 123(4), 408–413. doi:10.1111/j.1600-0706.2013.01228.x
151. Soto, I., D.A. Ahmed, P. Balzani, R.N. Cuthbert, and P.J. Haubrock. 2023. Sigmoidal curves reflect impacts and dynamics of aquatic invasive species. *Science of The Total Environment* 872. doi:10.1016/j.scitotenv.2023.161818.
152. Standish, R.J., A. Thompson, E.S. Higgs and S.D. Murphy. 2013. Concerns about novel ecosystems. In *Novel Ecosystems* (eds R.J. Hobbs, E.S. Higgs and C.M. Hall). doi:10.1002/9781118354186.ch37
153. Stratton, N., N.E. Mandrak, and N. Klenk. 2022. From anti-science to environmental nihilism: the fata morgana of invasive species denialism. *NeoBiota* 75: 39–56. doi:10.3897/neobiota.75.90631.
154. Strayer, D.L., C.M. D'Antonio, F. Essl, M.S. Fowler, J. Geist, S. Hilt, I. Jarić, K. Jöhnk, C.G. Jones, X. Lambin, A.W. Latzka, J. Pergl, P. Pyšek, P. Robertson, M. von Schmalensee, R.A. Stefansson, J. Wright and J.M. Jeschke. 2017. Boom-bust dynamics in biological invasions: towards an improved application of the concept. *Ecology Letters* 20: 1337-1350. doi:10.1111/ele.12822
155. Stromberg, J.C., Chew, M.K., Nagler, P.L. and Glenn, E.P. 2009. Changing perceptions of change: the role of scientists in *Tamarix* and river management. *Restoration Ecology*, 17: 177-186. <https://doi.org/10.1111/j.1526-100X.2008.00514.x>
156. Stuart, K.C., N.R. Hofmeister, J.M. Zichello, and L.A. Rollins. 2023. Global invasion history and native decline of the common Starling: insights through genetics. *Biological Invasions* 25(5): 1291–1316. <https://doi.org/10.1007/s10530-022-02982-5>.
157. Szydlowski, D.K., A.K. Elgin, D.M. Lodge, J.S. Tiemann, and E.R. Larson. 2023. Long-term macrophyte and snail community responses to population declines of invasive

- rusty crayfish (*Faxonius rusticus*). *Ecological Applications* 33(3): e2818.  
doi:10.1002/eap.2818
158. Tang, J., Nolan, M., D'Antonio, C., Cooper, S.D. and Stratton, L. 2023. Reinvasion of restored California vernal pools reveals the importance of long-term restoration planning. *Restoration Ecology* 31: e13991. <https://doi.org/10.1111/rec.13991>
159. Tasker, S.J. L., A. Foggo, and D.T. Bilton. 2022. Quantifying the ecological impacts of alien aquatic macrophytes: A global meta-analysis of effects on Fish, macroinvertebrate and macrophyte assemblages. *Freshwater Biology* 67(11): 1847–60. <https://doi.org/10.1111/fwb.13985>.
160. Thompson, K. 2014. Where do camels belong?. *The Story and Science of Invasive Species*. Profile Books
161. TRCA (Toronto Regional Conservation Authority). 2016. Integrated restoration prioritization: a multiple benefit approach to restoration planning.
162. Trowbridge, C.D., C. Little, and P. Stirling. 2016. Post-proliferation population of introduced seaweed: decline of a parthenogenetic green seaweed in Irish marine reserve. *Biology and Environment* 116(2): 87. doi:10.3318/bioe.2016.10.
163. UN News 2021. UN launches decade on ecosystem restoration to counter ‘triple environmental emergency’. URL: <https://news.un.org/en/story/2021/06/1093362>
164. Valentine, J. P., R.H. Magierowski and C.R. Johnson. 2007. Mechanisms of invasion: establishment, spread and persistence of introduced seaweed populations. *Botanica Marina*, 50(5/6). doi:10.1515/bot.2007.040
165. van der Loop, J.M.M., van Kleef, H.H., van Veenhuisen, L.S., Lamers, L.L. and Leuven, R.S.E.W. 2023. The ecosystem resilience approach to control the invasive alien species Australian swamp stonecrop (*Crassula helmsii*). *Restoration Ecology* 31: e13844. <https://doi.org/10.1111/rec.13844>

166. Vellend, M., L.J. Harmon, J.L. Lockwood, M.M. Mayfield, A.J. Hughes, J.P. Wares, and D.F. Sax. 2007. Effects of exotic species on evolutionary diversification. *Trends in Ecology and Evolution* 22(9): 481–88. doi:10.1016/j.tree.2007.02.017.
167. Vermeij, G. J. 1996. An agenda for invasion biology. *Biological Conservation*, 78(1-2), 3–9. doi:10.1016/0006-3207(96)00013-4
168. Vermeij, Geerat J. 2013. On escalation. *Annual Review of Earth and Planetary Sciences* 41: 1–19. doi:10.1146/annurev-earth-050212-124123.
169. Vukov, D., T. Jurca, M.M. Rucando, R. Igić, and B. Miljanović. 2013. *Cabomba caroliniana* a. Gray 1837: A new, alien and potentially invasive species in Serbia. *Archives of Biological Sciences* 65, no. 4 (January 1, 2013): 1515–20. <https://doi.org/10.2298/abs1304515v>.
170. Warren, Philip H., Richard Law, and Anita J. Weatherby. 2006. Invasion biology as a community process: messages from microbial microcosms. In *Kluwer Academic Publishers eBooks*, 343–67. [https://doi.org/10.1007/1-4020-4925-0\\_16](https://doi.org/10.1007/1-4020-4925-0_16).
171. Weibert, C. 2015. Weed risk assessment for *Cabomba caroliniana* A. Gray (Cabombaceae) – Carolina Fanwort. Michigan Department of Agriculture and Rural Development
172. Whillans, T.H. 1997. Historic and comparative perspectives on rehabilitation of marshes as habitat for fish in the lower Great Lakes basin. *Canadian Journal of Fisheries and Aquatic Sciences*. 53(S1): 58-66. <https://doi.org/10.1139/f96-020>
173. White, R. 2016. So shoot me. *New Zealand Geographic*, Issue 141 (Nov-Dec 2016). URL: <https://www.nzgeo.com/stories/so-shoot-me/>
174. Whitham, T.G., G.J. Allan, H.F. Cooper, and S.M. Shuster. 2020. Intraspecific genetic variation and species interactions contribute to community evolution. *Annual*

- Review of Ecology, Evolution, and Systematics 51(1): 587–612. doi:10.1146/annurev-ecolsys-011720-123655.
175. Wilhm, J. 1968. Use of biomass units in Shannon's formula. *Ecology* 49(1): 153–56. doi:10.2307/1933573.
176. Williamson M, Brown K. 1986. The analysis and modelling of British invasions. *Philosophical Transactions of the Royal Society. London Ser. B* 314:505–22
177. Williamson, M. 1996. *Biological invasions*, Chapman & Hall
178. Williamson, M., and A.H. Fitter. 1996. The Varying Success of Invaders. *Ecology* 77(6): 1661–66. <https://doi.org/10.2307/2265769>.
179. Wilson, C.E., S. J. Darbyshire, and R. Jones. 2007. The biology of invasive alien plants in Canada. 7. *Cabomba caroliniana* a. Gray. *Canadian Journal of Plant Science* 87(3): 615–38. doi:10.4141/p06-068.
180. Wilson, E.O. 1969. The species equilibrium. *Brookhaven Symposium of Biology* 22:38-47.
181. Wilson J.R.U., Datta A., Hirsch H., Keet J.H., Mbobo T., Nkuna K.V., Nsikani M.M., Pyšek P., Richardson D.M., Zengeya T.A. & Kumschick S. 2020. Is invasion science moving towards agreed standards? The influence of selected frameworks. In: Wilson JR, Bacher S, Daehler CC, Groom QJ, Kumschick S, Lockwood JL, Robinson TB, Zengeya TA, Richardson DM. *NeoBiota* 62: 569-590. <https://doi.org/10.3897/neobiota.62.53243>
182. With, K.A. 2002. The landscape ecology of invasive spread. *Conservation Biology* 16, 1192–2003
183. Wittgenstein 1922. *Tractus-logico-philosophicus*. Kegan Paul, Trench, Trubner & Co., LTD, London.

184. Wu, S. H., C.F. Hsieh, S.M. Chaw and M. Rejmánek 2004. Plant invasions in Taiwan: insights from the flora of casual and naturalized alien species. *Diversity and Distributions* 10: 349–362.
185. Yek, S.H. and B. Slippers. 2014. Biocontrol opportunities to study microevolution in invasive populations. *Trends in Ecology & Evolution*, 29(8), 429–430.  
doi:10.1016/j.tree.2014.05.008
186. Závorka L., M. Buoro and J. Cucherousset. 2018. The negative ecological impacts of a globally introduced species decrease with time since introduction. *Global Change Biology* 24: 4428–4437 doi: 10.1111/gcb.14323
187. Zettler M.L., D. Daunys, J. Kotta and A. Bick. 2002. History and success of an invasion into the Baltic Sea: the polychaete *Marenzelleria cf. viridis*, development and strategies. In: Leppäkoski E, Gollasch S, Olenin S (eds) *Invasive aquatic species of Europe: distribution, impacts and management*. Kluwer Academic, The Netherlands, pp 66–75

## Appendix 1

All the raw data used in this study is available at:

Weissflog, Nicholas, 2024, "Fanwort (*Cabomba caroliniana*) in Kasshabog Lake 2008 and 2022", <https://doi.org/10.5683/SP3/NKWKZA>, Borealis, V1, UNF:6:Z3XQU3kT/If6d+gF1YUwmg== [fileUNF]

## Appendix 2

I conducted 8 semi-structured interviews with Invasive Species management practitioners with more than 10 years of involvement in aquatic invasive species management either directly (e.g. a land manager/field technician) or indirectly (e.g. policy work/project manager). The initial focus of these interviews was threefold; first to ask about their views on what they manage and whether they use eradication as a management objective; second to ask about any mental stress they have witnessed in conjunction with attempts to eradicate invasive species; third to ask them about developments in the species or lands they manage that did not conform to their expectations, particularly observations which created personal acceptance of things as they are or were in the moment of recollection.

Because of time constraints and to keep the scope of this thesis more focused I have removed all of the questions that do not deal directly with naturalization. This leaves only two questions out of the twelve that were asked. The first of those questions revisits the definitions of naturalization covered in chapter 2, whereas the second is more relevant to the management and scientific recommendations that will be presented in chapter 7. The first question was:

What does it mean to you if a species is described as naturalized, how would you define that?
---

The purpose of asking this question was for the interviewee to naively define what this word means to them insofar as that is a true reflection of how they use this word symbol to interpret their experience of the world and communicate with others. This was important because part of my motivation was to corroborate by means of inter-subjective comparison my own observation that the manner in which Richardson et al. 2000 and Blackburn et al. 2011 used this word was unintuitive to not just myself. It should be noted that these are the definitional components that were mentioned explicitly by the interviewees and that those persons may not necessarily disagree with other definitional components that they did not mention.

The Second Question was:

Do you account for species that you currently manage, possibly naturalizing in the future?  
If so, how? If not, why not? On what time scale do you think naturalization occurs?

Following being asked to define what they understand to be what this word means, they were then asked if they account for this phenomenon within the work they do. This was important, going back to the principal motivation of this component, because it set the context for understanding whether the hypothesis that we don't was true. Of course, given that others have defined this term differently, there was the potential for talking past one another because I was in fact most interested in the sense in which I meant this term, the sense of incorporation or integration. This did happen in two instances and showed one of the shortcomings of the question as formulated.

The component of this question regarding timelines was used to address the idea within the invasion biology literature that if naturalization in the sense of integration were to occur it would occur on evolutionary timelines, a common interpretation of which is that this

means hundreds to thousands of years. I wanted to understand the perspectives that those who worked in this field had, expanding upon their naive definition, to draw from their direct experience and get their sense of how long this might be based on what they know and have seen.

Interviewee	Definition
1	<p>To me when I am trying to engage with the public on that topic I usually say, you know think of a tulip, you might see a tulip bulb at the head of an urban trail, it may have found its way there, maybe its intentionally planted, perhaps it was a squirrel that moved it around, your talking about an exotic species, a species that has expanded its historical range and you are looking at it in a context that is not causing negative impacts in either biodiversity implications or environmental more broadly, socio and economic pieces too. So you are not seeing that species outcompete other species so it doesn't check the box on biodiversity or ecological impacts, you are not seeing be a costly species to manage or incur other direct financial implications and you're not seeing it have a negative impact on our social use of that natural asset, so therefore I think that is a good example to think of as naturalized. So usually there is that kind of example, there is probably other better terminology to throw around to it but I find that's more impactful and meaningful to people.</p> <p>I think baked into this topic, broadly, is this idea of time sequence and that there is some subjectivity to it, about when do you consider, at what point in time do you consider it naturalized, is it decades, hundreds, thousands of years, you know it's grey area in between and so at what point does something that has been here for more than 200 years become naturalized in a sense. If it's ubiquitous across the province? You know, I'm not sure, I see it often and I kind of wrestle with that just about the subjectivity of time, not to go too meta, but I think that's something i bump up against often, but I generally would agree with that, are you from here historically, and from here, what's your time sequence on that, I don't really know how to answer it well, are you checking the three boxes, is it having a negative impact.</p>
2	<p>If someone said a species was naturalized these are the things I would think of;</p>

	<p>1. that species is established and reproducing</p> <p>2. that its been here for a lengthy period of time (decades)</p> <p>3. I would imagine that it's distribution is also broad so if you said something was naturalized in Ontario I think that I would take that to mean that it is quite widespread as well.</p> <p>4. If it's naturalized then it's not native in that it has come from somewhere else</p> <p>5. but I also don't assume that it has negative impacts i.e. just by saying it's naturalized doesn't mean that its bad, it could be positive or they could be unknown impacts</p> <p>6. I would say as well that we have learned to live with it.</p>
3	<p>an exotic species, a species that has expanded its historical range and you are looking at it in a context that is not causing negative impacts in either biodiversity implications or environmental more broadly as well as socioeconomic impacts.</p>
4	<p>Well naturalized implies that it's a plant from somewhere else that has become established and spreading. That's a pretty simple definition, you know, naturalized can still become invasive if it creates nuisance problems. Standard US government definition of invasive is a plant from somewhere else that causes ecological, economic or aesthetic harm. Which is interestingly enough the definition of a weed with the difference being that it doesn't matter where it comes from, you could say an invasive plant is weed that came from somewhere else.</p>
5	<p>I would say that it's a species that wasn't here at one point, it was introduced and has reached some sort of equilibrium with the natural environment such that it doesn't overtake but still kind of coexist with our native species here</p>
6	<p>Naturalized to me means that it is not native but present in our landscape and has natural controls, so LDD moth or spongy moss, would be an example of that, we had a terrible year in 2021 and we saw natural controls present on the landscape in that year and then last year the population collapsed just as we predicted. So that is what naturalization means to me, some people describe common carp as naturalized, I would disagree, because they're just so invasive because we don't have any natural controls.</p>
7	<p>Naturalized is an interesting one, I'd say, naturalized, it's an exotic species that is not causing economic, environmental or social harm, it's on the landscape but is a nothing-burger in terms of impact on the landscape. That said the naturalized species could be dominant, dandelions for</p>

	<p>example, they can be the dominant species but they're not problematic. Once you have hit a threshold that humans are comfortable saying is no longer a dominant species. There's probably a threshold there where we can say there is no longer a negative impact but not all exotics are invasive and all exotics that do become invasive can become integrated into the food web and have less of an impact on other species.</p>
8	<p>...Typically we think of species that have been here since some of those early European settlers. In the aquatic world the time point is really important but I also think of its ecological impact so naturalized species can often integrate better with the existing ecosystem. Sometimes these ecosystems that these naturalized species are invading are already quite disturbed. I think of some of the roadside ditch species that like oxeye daisies, your hawkweeds, your things that again they're there, they're not native to the United States, they have been there almost 200 years now and they're growing in that area because it's a species that can adapt well, but they're not necessarily out-competing things, they're not necessarily spreading beyond these disturbed areas and so they have kind of integrated into that ecosystem since that ecosystem is changed. [Other noted examples of naturalized species; Curly Leaved Pondweed.]</p>