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# A Framework for Evaluating Heterogeneity and Landscape-Level Impacts of Non-native Aquatic Species

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## ABSTRACT

Non-native species are a major component of global environmental change, and aquatic systems are especially vulnerable to non-native species impacts. Much of the research on aquatic non-native species impact has occurred at the local or site level. In reality, non-native species impacts play out across multiple spatial scales on heterogeneous landscapes. How can we ‘scale up’ our understanding of site-level impacts to the broader landscape scale? To address this disconnect, we synthesize our current understanding of key components of landscape-scale non-native species impacts: geographic range, abundance, and local impacts. Most aquatic non-native species have small ranges, while a few have large ranges. However, aquatic non-native species are often far from saturated on landscapes, and occurrence records are often woefully incomplete. Aquatic non-native species are often at low

abundances where they are present, reaching high abundance in a small number of locations. Finally, local-scale impact can be estimated from abundance, but this requires knowledge of the abundance–impact relationship. Considering these multiple components enables understanding of non-native species impacts at broader spatial scales. Although the landscape-level impacts of aquatic non-native species may be high, the spatial distribution of site-level impacts is uneven, and highly impacted sites may be relatively uncommon. This heterogeneity in impacts provides an opportunity to optimize and prioritize non-native species management and prevention efforts.

**Key words:** aquatic; non-native; range; distribution; occupancy; abundance; impact; landscape; macroecology.

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## INTRODUCTION

Non-native species are an important driver of global environmental change and biodiversity loss in many of the earth's ecosystem types (Sala and others 2000). Freshwater ecosystems are particularly vulnerable to the impacts of introduced spe-

cies due to their insularity and high rate of endemism (Cox and Lima 2006; Dudgeon and others 2006; Moorhouse and Macdonald 2015). Thousands of freshwater species have been transported beyond their native range due to both unintentional and intentional introductions (Strayer 2010; Lockwood and others 2013), and many aquatic ecosystems are now dominated by non-native species (Strayer 2010; Walsh and others 2016).

Scientific and societal interest in non-native species derives not from their presence alone, but from the potential for undesirable impacts (Barney and others 2013; Ricciardi and others 2013). In this study, we define *impact* as a measurable change in an invaded system that can be attributed to the non-native species (Ricciardi and others 2013; Jeschke and others 2015). One approach to evaluating impact involves quantifying the economic damages and costs or the effects on ecosystem services (Pimentel and others 2000; Pejchar and Mooney 2009). Use of a single monetary currency allows for relatively seamless integration with policy and management decision making. Yet the economic approach may not be applicable to many ecological changes that are societally relevant, but cannot be easily expressed in economic terms (Parker and others 1999). For example, non-native species are a leading factor in freshwater species imperilment and extinctions (Dudgeon and others 2006; Jelks and others 2008; Strayer and Dudgeon 2010), which can be difficult to assign economic value. Furthermore, measuring ecological impacts poses serious challenges: Non-native species can simultaneously exert multiple impacts (Barney and others 2013) that manifest at different levels of biological organization. Furthermore, quantifying impacts is difficult for systems that lack baseline (i.e., pre-invasion) data.

Much of the research to date on aquatic non-native species impact consists of laboratory experiments or small-scale field manipulations (Dick and others 2013, 2014; Kumschick and others 2015). Such studies have provided insights about which species are most likely to be impactful, or have assessed impacts at a local spatial scale. However, an understanding of non-native species impact at a local scale must be put into a broader context in order to inform non-native species management on real and heterogeneous landscapes (Strayer 2010, 2012; Thiele and others 2010). A key goal of non-native species management is to prioritize management actions to minimize or prevent adverse impacts, and such efforts are often implemented at broad spatial scales such as counties, provinces, or states (Lodge and Shradler-Frechette 2003; Vander Zanden and Olden 2008). Factors such as non-na-

tive species abundance, as well as current and projected geographic distributions, become important considerations at these broader spatial scales. In short, there is a stark mismatch between the local-scale emphasis of much of the non-native species impact research and the broad-scale needs of environmental management. In light of this disconnect, we argue that there is a need for an improved conceptual framework that allows scaling up our local understanding of impact to broader spatial scales (Lodge and others 1998; Thiele and others 2010). The ultimate goal is to better inform the many pressing environmental management challenges caused by aquatic non-native species (Lodge and Shradler-Frechette 2003; Vander Zanden and Olden 2008).

Non-native species impact risk assessments are commonly used to inform management decisions at broad spatial scales. The majority of risk assessment research has aimed at identifying and predicting which *species* are likely to be 'high impact' based on factors such as life-history traits (Kolar and Lodge 2002; Kumschick and Richardson 2013; Blackburn and others 2014), functional responses (Dick and others 2013, 2014), and invasion history (Ricciardi 2003; Kulhanek and others 2011b). Yet managers often know which non-native species are in the region and which of these tend to be 'high impact.' Thus, there are other important dimensions for non-native species impact risk assessment beyond simply predicting which species will be high impact. For example, for a known invasive species, managers and stakeholders may be interested in knowing which sites are likely to experience high impacts. Even for a highly impactful species, local impacts may be spatially heterogeneous among sites or habitat types (Thiele and others 2010).

The need for improved frameworks for understanding non-native species impacts has been widely recognized (Pysek and Hulme 2009; Thomsen and others 2011; Ricciardi and others 2013). A useful starting point for considering landscape-level impact was provided by Parker and others (1999), which forwarded a simple mathematical formula that could be used to estimate *overall* non-native species impact:  $I_T = R \times A \times PCE$ , where  $I_T$  is the total or overall impact of the non-native species,  $R$  is the geographic area or range inhabited by the species,  $A$  is the mean abundance (per-unit-area) in the invaded range, and PCE is the per-capita effect (i.e., effect per individual) of the non-native species. The Parker framework is a useful starting point because it recognizes that landscape-level impacts are influ-

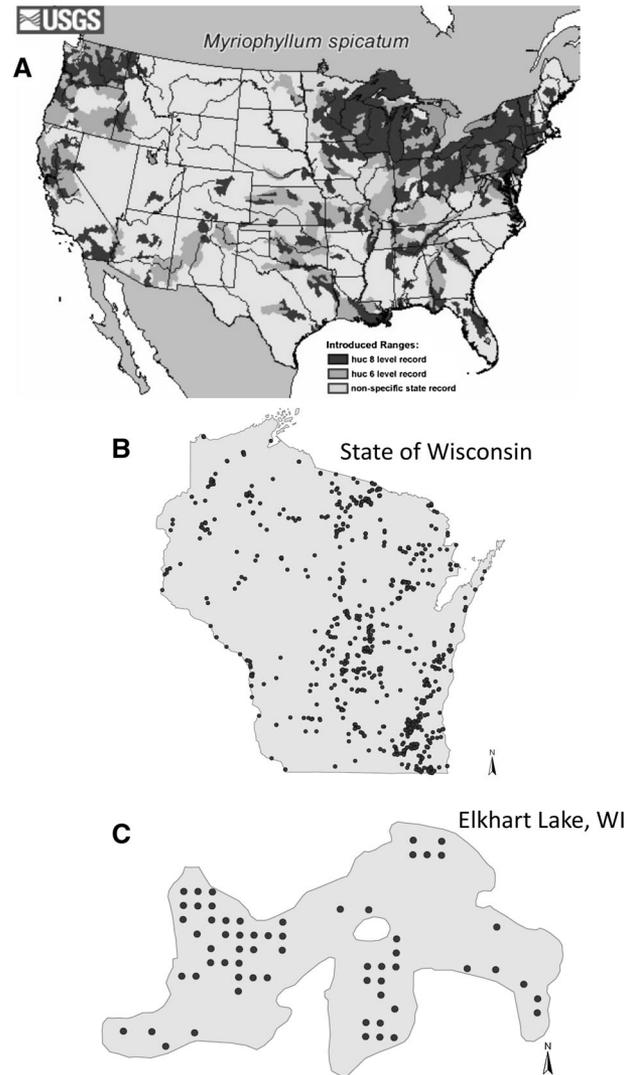
enced by this combination of factors. This paper will review our understanding of each of the three elements of the framework—geographic range, local abundance, and local impact—for aquatic non-native species. Moreover, we will examine how heterogeneity in patchy landscapes such as lakes can influence the overall assessment of a non-native species' impacts. We view aquatic non-native species as a useful example for illustrating and exploring more general principles relating to spatial aspects of non-native species impacts. Many of the ideas will be illustrated using data from lakes in the state of Wisconsin, USA, where much of our research has been based. Our synthesis will take a macroecological approach to addressing the challenges of scaling up and spatial heterogeneity in the study of aquatic non-native species impacts. Macroecology aims to understand species distribution and abundance at broad spatial scales (Brown and Maurer 1989; Brown 1995; Gaston and Blackburn 2000). Although the focus of macroecology has largely been terrestrial, a macroecological perspective may provide a useful lens for addressing the challenges of spatial heterogeneity and spatial scaling that are pertinent to understanding and predicting non-native species impacts in aquatic systems (Gido and Brown 1999). Advancing our understanding of these individual elements—range, abundance, and local impact—will ultimately provide a basis for 'scaling up' of our understanding of impact to the landscape-level (Thiele and others 2010; Barney and others 2013; Latzka and others 2016). Moreover, an understanding of spatial heterogeneity in non-native species impacts provides the foundation for prioritizing management by targeting sites most likely to be negatively affected by non-native species.

## AQUATIC NON-NATIVE SPECIES RANGE AND DISTRIBUTION

### The Importance of Spatial Scale

Understanding the overall impacts of a non-native species requires knowledge of both the species' geographic range, as well as its distribution within that range. We consider geographic range to be the broad geographic boundaries or outer limits of species occurrence (Gaston 2003). Distribution, on the other hand, refers to site occupancy within the geographic range and represents species occurrence at a finer spatial scale and at a higher spatial resolution. Concepts of species 'range' and 'distribution' are really a matter of spatial extent and grain (Kunin 1998; Gaston and Blackburn 2000). Mov-

ing from coarse to finer spatial grains, the emphasis shifts from the outer limits of species occurrence, to local-level occupancy of individual sites (i.e., lakes) within the geographic range. At even finer scales, sites themselves can consist of different sub-habitats. For example, lakes are composed of diverse habitats that themselves support different communities (Wetzel 2001).

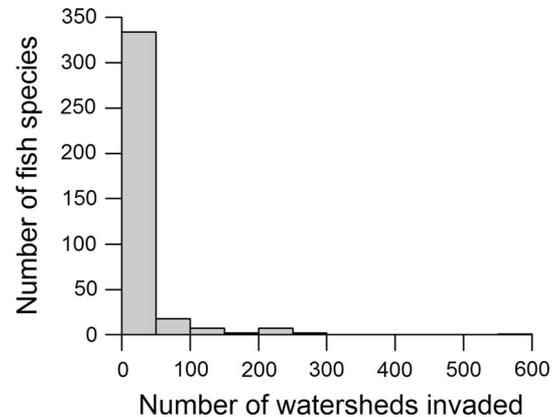


**Figure 1.** The range of the non-native aquatic plant, Eurasian watermilfoil (*Myriophyllum spicatum*) expressed at multiple spatial scales. **A** At the continental scale (USA), large watersheds (USGS HUC-6 or HUC-8) are used as the spatial unit for showing the species' range (nas.er.usgs.gov). **B** At a regional scale (state of Wisconsin), site occurrence records show the distribution of Eurasian watermilfoil (data from Wisconsin Department of Natural Resources). **C** At the within-lake scale, field survey data for Elkhart Lake, Wisconsin, show that only a portion of the lake is occupied by Eurasian watermilfoil (data from Wisconsin Department of Natural Resources).

The non-native aquatic plant, Eurasian watermilfoil (*Myriophyllum spicatum*), illustrates how our understanding and quantification of species range changes with spatial extent and grain. At the broad spatial scale of the USA (Figure 1a), the geographic range of Eurasian watermilfoil encompasses nearly the entire northeastern and midwestern USA, most of the Pacific Northwest, and several other portions of southern and central USA. At this broad spatial scale, the range of Eurasian watermilfoil includes the entire state of Wisconsin. At a finer spatial scale within the state of Wisconsin, lake-specific occupancy data (Figure 1b) reveal that just over 500 individual lakes are known to be occupied by Eurasian watermilfoil. These invaded lakes comprise a tiny fraction of the total number of lakes and of the total surface area of Wisconsin. At an even finer spatial scale, a closer look within a single invaded lake (Elkhart Lake, WI) reveals that only a portion of the lake is inhabited by Eurasian watermilfoil (Figure 1c). This comparison highlights the extent to which our description of species geographic range and distribution is scale dependent (Kunin 1998; Gaston and Blackburn 2000).

### Aquatic Non-native Species Range

Non-native species range data are often expressed using broad spatial units such as US states (Rahel 2000) or hydrologic watershed units such as USGS HUCs (Gido and Brown 1999; Leprieur and others 2008; Guo and Olden 2014). At this broad spatial scale, the invaded range of a species is the broad geographic area over which it occurs (Parker and others 1999), and does not consider within-range site occupancy. In general, the frequency distribution of species range size tends to be right-skewed (Gaston 1996); in other words, most species' ranges are small, while only a few are large. Little work has been done on patterns of aquatic non-native species range size, but two studies suggest that this broad macroecological pattern holds for aquatic non-native species. Gido and Brown (1999) evaluated spatial patterns of non-native fishes across 125 North American drainage basins and found that most introduced fish species occupied a small number of drainage basins, whereas only a few occupied a large number of basins. Similarly, an analysis for the USA using US Geological Survey 6-digit HUC watersheds revealed strongly right-skewed frequency distributions of species range size, as measured by the number of invaded watersheds (Figure 2; Guo and Olden 2014; Vander Zanden and others 2015).



**Figure 2.** Frequency distributions of the number of watersheds invaded (a measure of range size) by non-native fish species in the USA. Most non-native species inhabit a small number of watersheds, while only a few non-native species are widespread. Watersheds are USGS 6-digit HUCs (based on Vander Zanden and others 2015; Guo and Olden 2014).

### Aquatic Non-native Species Distribution

Although the outer boundaries of non-native species ranges may be reasonably well described at broad spatial scales, occupancy of individual sites within the geographic range tends to be much less well characterized. Knowledge of non-native species site occupancy within the invaded range typically derives from local site occurrence records. The availability and quality of data documenting non-native species site occurrences varies widely (Crall and others 2006). Existing records are typically of varying quality, collected for diverse reasons, and from diverse sources ranging from citizen science programs (Crall and others 2010; Gallo and Waitt 2011) to resource managers and research projects. Locally collected records are often compiled in regional, state, provincial, national, or global databases (Graham and others 2007; Fuller and Benson 2009; Simpson and others 2009). These databases are commonly used to infer non-native species distribution for a wide variety of scientific and resource management-related activities (Bobeldyk and others 2015). To what extent do non-native species records, as revealed in existing databases, reflect *actual* site occupancy? Due the diverse nature of data sources contributing to these datasets, we must consider the biases associated with these largely opportunistic observations. For example, inaccessible areas may be under-sampled and lesser-known species may have lower probabilities of detection (Dickinson and others 2010). Generally, our knowledge of site occupancy depends on a number of factors, including how many sites have

been sampled, how sites were chosen for sampling, and the probability of detecting a non-native species that is present.

For a landscape consisting of many sites, a census of all sites would be impossible. For example, the state of Wisconsin contains approximately 14,500 lakes larger than 1 ha. One approach for characterizing non-native species prevalence for a suite of lakes is to simply estimate the percentage of lakes for which non-native species presence is documented. The implicit assumption is that sites where a species has not been documented are true absences. For the state of Wisconsin, this approach indicates a prevalence of about 8% for a combined suite of six common non-native species—1189 invaded lakes/14,364 total lakes (Latzka 2015). But if non-native species occurrences have not been documented, or if certain types of lakes are less likely to be surveyed or reported, this approach would give a biased estimate of site occupancy or prevalence. To address this shortcoming, a stratified random survey combined with statistical weighting across strata can be used to more accurately estimate non-native species occupancy (Schade and Bonar 2005). Combining a targeted field survey of randomly chosen Wisconsin lakes with statistical weighting estimated non-native species prevalence to be 39%—nearly five times higher than the naïve estimate based on occurrence records (Latzka 2015). Considering that the state of Wisconsin has a relatively strong infrastructure for collecting and documenting non-native species occurrences, it is likely that this underestimation occurs elsewhere and that non-native aquatic species often have a higher rate of site occupancy than indicated by existing records, though it is not clear by how much. The degree of underestimation probably varies widely among species, and for different regions. Nevertheless, it is fair to say that we often have a limited knowledge of non-native species prevalence within their geographic range.

### Aquatic Non-native Species Detection

In a field survey for any species, non-detection of a species at a site does not necessarily mean that the species is absent, that is, the probability of detecting a species that is present is less than 1.0 (MacKenzie and others 2002). Whether aquatic non-native species are detected when present influences our understanding of both broad-scale geographic range and fine-scale distribution. How often do aquatic non-native species go undetected in a field survey when they are, in fact, present?

Delaney and Leung (2010) used occupancy modeling in a study focusing on a non-native coastal marine crab and found probabilities of detection ranging from 1.2 to 97.4%, with detection probability depending on sampling methods, search effort, and non-native species density. Harvey and others (2009) sampled the non-native zooplankton, fishhook water flea (*Cercopagis pengoi*) in Lake Ontario, and found that during times when *Cercopagis* was at low abundance, the probability of detection was never greater than 0.2. They concluded that the typical field sampling protocol (e.g., collecting no more than several zooplankton samples) for non-native species monitoring would often fail to detect this species. In part due to the diverse and opportunistic nature of many non-native species occurrence data sets, we typically have little knowledge about sampling methods, effort, or species density. As a result, unless species occurrence data are systematically collected, it is often impossible to incorporate information about detection probabilities when interpreting occurrence data and estimating species prevalence and site occupancy. This limitation is especially problematic given the highly variable and potentially low detection probabilities for non-native species.

The above discussion of detection probabilities implies that sites are sampled for non-native species in the first place. In reality, a small fraction of aquatic systems undergo non-native species field surveys. As a consequence, new aquatic non-native species records are often incidental detections by field biologists or citizen reports. For this to happen, the species needs to be abundant enough to be noticed in the absence of a targeted sampling effort. For many species, this would only be likely in the case of a population outbreak. In addition, species vary widely with regard to detectability. For example, dreissenid mussels inhabit benthic shallow-water habitats, are morphologically unique in North America, and are highly conspicuous (Vanderploeg and others 2002; Higgins and Vander Zanden 2010). In contrast, many other non-native taxa are unlikely to be recognized as non-native by lake visitors. In the absence of targeted sampling, aquatic non-native species will often elude detection, possibly until there is a population outbreak (Crooks and Soule 1999; Crooks 2005). Recent advances in the development of molecular species detection methods such as use of environmental DNA (eDNA) hold great potential for increasing the ability detect non-native species, particularly at low densities (Ficetola and others 2008; Jerde and others 2011). Such tools will ultimately provide a

better understanding of non-native species detection probabilities, occurrence, and distributions.

## Ecological Niche Modeling of Present and Future Distributions

Characterizing species distributions often involves modeling species distributions using ecological niche models. Such studies develop statistical relationships between species occurrence and local and regional environmental predictor variables. In doing so, the ecological niche of the species can be represented in environmental space and is used to project the predicted current or future distribution of the species and identify suitable habitat. A number of methods exist for modeling species distributions from environmental variables (Guisan and Thuiller 2005; Elith and Leathwick 2009; Peterson and others 2015), many of which account for biased data collection techniques and non-detection probabilities (Engler and others 2004; Papes and Gaubert 2007; Phillips and others 2009).

Ecological niche modeling studies have been carried out using two general approaches, depending largely on spatial extent and grain. At broad spatial scales, studies tend to use ecological niche modeling packages such as MAXENT to model non-native species occurrence for grid cells using climate and other gridded data as predictor variables (Elith and Leathwick 2009). This approach has been useful for predicting broad-scale species range based on climatic suitability. Ecological niche modeling studies have also been conducted at finer spatial scales, for example, developing relationships between non-native species occurrence and local site attributes, and using this as the basis for identifying suitable sites and forecasting spread (MacIsaac and others 2000; Vander Zanden and others 2004; Mercado-Silva and others 2006). In reality, these two spatial scales are complementary, whereby climate suitability determines the potential geographic range, while local site attributes determine the species' fine-grain distribution within the climatically suitable range.

Many landscapes tend to be undersaturated with regard to aquatic non-native species (Strayer 2010). For example, non-native species that originally invaded North America through the Laurentian Great Lakes, such as zebra mussel (*Dreissena polymorpha*) and spiny water flea (*Bythotrephes longimanus*), are currently undergoing 'secondary spread' to inland lakes in the Great Lakes region, largely spread by recreational boaters (Bossenbroek and others 2001; Johnson and others 2001; Kelly

and others 2013). These species are slowly 'filling in' suitable habitat patches within the invaded range (Johnson and others 2001; Vander Zanden and Olden 2008). Strayer (2010) described this phenomenon as an 'invasion debt'—highlighting that undesired impacts will continue to accumulate and unfold over decades or centuries as species spread to new sites. A subset of currently uninvaded sites can be considered *vulnerable* to future invasion based on habitat suitability and the likelihood of dispersal (Leung and Mandrak 2007) and thus indicate the scope or potential for future spread and impact (Strayer 2010). Forecasting non-native species spread and predicting future distribution provides a basis for estimating potential future impacts. To this end, there is significant research and management interest in forecasting non-native species spread and identifying sites that are vulnerable to future invasion (Vander Zanden and Olden 2008).

## AQUATIC NON-NATIVE SPECIES ABUNDANCE

Non-native species abundance is the second element related to understanding landscape-level non-native species impact (Parker and others 1999). Although data on aquatic non-native species geographic range and distribution are widely available (however imperfect), data for aquatic non-native species abundance are comparatively sparse. Non-native species databases generally do not report abundance. Although categorical (Olefin and others 2014) or quantitative (Graham and others 2007) measures of abundance are sometimes allowed to be included in these datasets, most data in these databases are simple occurrence records. Estimating aquatic non-native species abundance is laborious, and many of the common abundance measures for aquatic systems such as catch-per-unit-effort (CPUE) are best viewed as an index of relative abundance and may not be suitable for comparisons among sites. Reliable non-native species abundance data are generally only available in the case of an intensive monitoring program or from targeted research studies.

The study of species abundance distributions is an important area of macroecological research (Gaston and Blackburn 2000; Magurran 2004). These studies are carried out at the community level and generally find that at a given site, only a few species are abundant whereas most are rare, thus producing right-skewed frequency distributions of species abundance. Although species abundance distributions traditionally focus on abundances of the many species at a site or within a

community, the approach can also be used to evaluate the abundance of a single species across multiple sites (Brown and others 1995). This approach can be used to evaluate whether non-native species show right-skewed abundance distributions (among sites), and evaluate whether non-native species abundance distributions differ from that of their native counterparts. There is a general perception that invasive species tend to be more abundant than their native counterparts. A study of 104 native and 17 aquatic invasive species (species classified as invasive by relevant management authorities) from diverse freshwater habitats found that both native and invasive species show strongly right-skewed abundance distributions (Figure 3) (Hansen and others 2013c). In other words, aquatic invasive species often occur at low abundances and only rarely occur at high abundance (Hansen and others 2013c). A similar finding was reported for coastal plant communities, whereby native and non-native species did not differ notably with regard to either percent cover or site occupancy (Bruno and others 2004). Although one may be inclined to wonder why species that are considered invasive are often at low abundance, it is important to recognize that most populations of most species are at low abundance (Brown and others 1995). Regardless of native/invasive status, biotic or environmental constraints usually prevent a species from becoming abundant at a site. For non-native species, it may also be the case that the species is at low abundance because it has recently been introduced, and has not yet had the chance to become abundant. There are many examples where non-native species persist for a long period

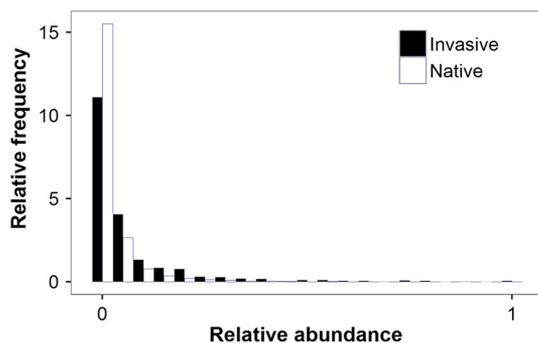


Figure 3. Probability density of species relative abundance for aquatic non-native ( $n = 17$ ) and native ( $n = 104$ ) species. Relative abundance was standardized to allow presentation on a single scale of relative abundance measured in multiple different units and is shown as the proportion of maximum abundance observed within a taxonomic group, grouped into 0.05 bins. Based on Hansen and others (2013c).

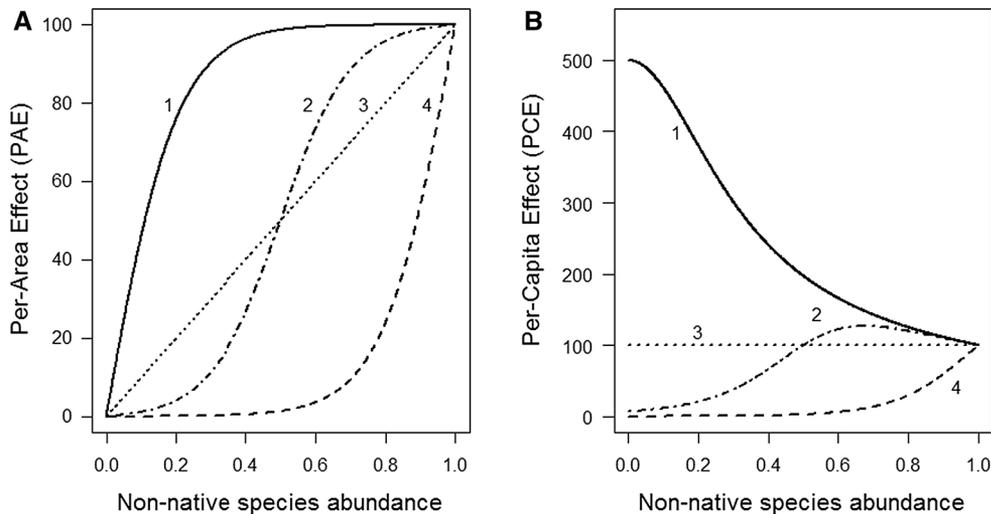
of time at low abundances. In the case where a low abundance non-native species transitions to high abundance, it is referred to as a population lag (Crooks 2005). This discussion highlights the fact that ‘species abundance’ as measured by ecologists and described here is a snapshot in time of something that is in reality temporally dynamic (Sakai and others 2001).

The above discussion illustrates that non-native species abundance is spatially heterogeneous and that, like most species, non-native species are often at low abundance. While these broad patterns are important to recognize, we know little about the factors that determine local non-native species abundance (Kulhanek and others 2011a). A few studies have taken a predictive approach to studying abundance. Naddafi and others (2011) found that lake area, total phosphorus, and dissolved calcium explained 62% of the among-lake variation zebra mussel abundance, and reinforces previous findings of a strong role for water chemistry in determining non-native zebra mussel abundance (Ramcharan and others 1992; Wilson and Sarnelle 2002). Such studies highlight the need for a more predictive understanding of the factors that determine non-native species abundance.

## AQUATIC NON-NATIVE SPECIES LOCAL EFFECTS

The final element in our consideration of landscape-level non-native species impact relates to local-scale effect. There is an impressive body of ecological research, largely field experiments and observational studies, which describe local non-native species impacts. Parker and others (1999) reviewed five different ecological levels at which non-native species impacts have been measured—effects on individuals, genetics, population dynamics, communities, and ecosystem processes. We will not summarize these different types of impacts here, but only note that non-native species can have quantifiable impacts at many levels of biological organization. Moreover, a non-native species’ impact may be characterized by multiple response metrics (Barney and others 2013).

A promising and intuitive approach for characterizing local effect of non-native species is to infer it from local abundance. The effect of a non-native species is expected to increase with abundance, and abundance–impact relationships characterize how local non-native species effect varies as a function of abundance (Figure 4a). Such relationships have recently been recognized as a useful tool for estimating or modeling non-native species impacts



**Figure 4.** Theoretical abundance–impact curves based on Yokomizo and others (2009). **A** Four hypothetical relationships between non-native species abundance and impact on a per-unit-area basis (PAE); 1 low threshold, 2 sigmoidal, 3 linear, 4 high threshold. **B** The abundance–impact curves of **A** expressed on a per-capita basis (PCE), by dividing impact by abundance.

(Yokomizo and others 2009; Thiele and others 2010; Latzka and others 2016). The simplest scenario is that the effect of a non-native species (on a per-unit-area basis, hereafter PAE) increases linearly with abundance (Figure 4a curve #3). In this case, the response metric shows a gradual response across the range of non-native species abundance. A linear relationship might be expected in the absence of complex feedbacks governing the system response to the non-native species. Yet ecosystems can undergo dramatic or catastrophic shifts in response to abiotic or biotic drivers, including non-native species (Scheffer and others 2001; Hansen and others 2013b). In such cases, the non-native species PAE would be a nonlinear function of abundance, and the abundance–impact relationship would be characterized by a threshold response, whereby at some level of non-native species abundance there is an abrupt change in the response variable of interest. This threshold could occur at low (Figure 4a curve #1), intermediate (Figure 4a curve #2), or high (Figure 4a curve #4) non-native species abundance (Yokomizo and others 2009). A nonlinear abundance–impact relationship, at the most basic level, indicates that the system response is highly sensitive to invasive species abundance at some threshold value (Scheffer 1998; Scheffer and others 2001; Scheffer and Carpenter 2003). We might expect that the non-native red swamp crayfish (*Procambarus clarkii*) effect on submerged aquatic plant biomass would exhibit a low-threshold response (Figure 4a curve #1). This non-native species is an ecosystem engineer that is capable of greatly reducing plant biomass (with dramatic effects on ecosystems) at relatively low abundances (Matsuzaki and others 2009). In contrast, we might expect that the non-

native macrophyte Eurasian watermilfoil (*Myriophyllum spicatum*) effect on native macrophyte communities to exhibit a high-threshold response (Figure 4a curve #4). This species can compete with and reduce the abundance of native macrophytes, though community-level impacts on native macrophytes generally occur at high Eurasian watermilfoil densities (Boylen and others 1999).

If the abundance–impact relationship for a species is known, it can be used to estimate local impact, given local abundance (Latzka and others 2016). Yet characterizing the non-native species abundance–impact relationship is not trivial. Several recent studies have used comparative analysis and field experiments to characterize abundance–impact relationships for aquatic non-native species. Jackson and others (2015) found the form of the abundance–impact relationship for a species could vary depending on the response variable of interest. Matsuzaki and others (2009) examined the effects of common carp (*Cyprinus carpio*) and red swamp crayfish on a range of response variables. Most responses to non-native species abundance were nonlinear, though red swamp crayfish was more likely to show linear impact responses. An experimental study of non-native Pacific red lionfish (*Pterois volitans*) on reefs in the Bahamas reported a low-threshold curve for native fish abundance and biomass (Benkwitt 2015). Kornis and others (2014) reported that impacts of non-native round gobies in streams saturated and actually declined at high densities as a result of intraspecific aggressive interactions. Overall, relatively few studies have examined how impact changes with abundance for aquatic non-native species (Matsuzaki and others 2009; Jackson and others 2015). Notably, the form of abundance–

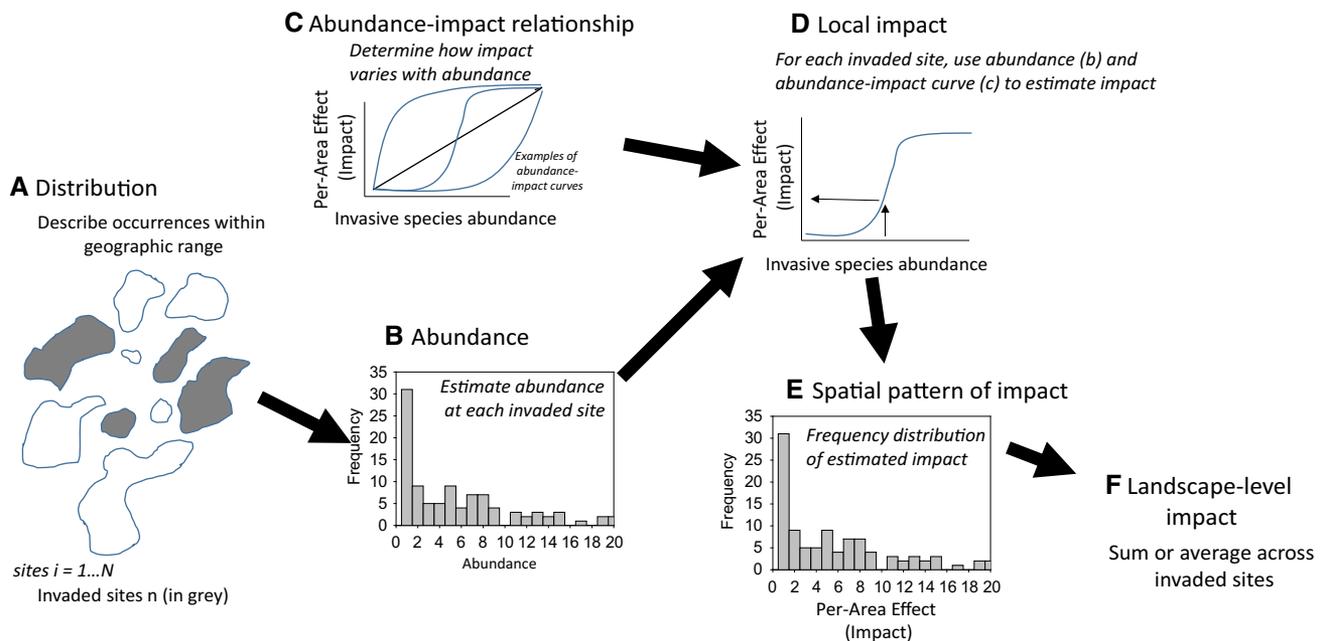
impact relationship for a single non-native species may not be consistent among response variables (Matsuzaki and others 2009; Jackson and others 2015). Although abundance–impact studies can provide the empirical foundation for making inference about non-native species impacts, more empirical work is required.

In the Parker and others (1999) impact formula, landscape-level impact is the product of species range, abundance, and per-capita effect (i.e., effect *per unit of the non-native species*). Note that in the abundance–impact relationship (Figure 4a), effect (*y*-axis variable) is expressed on a per-unit-area basis (i.e., per-area effect). Per-capita effect can be derived from abundance–impact curves (Figure 4a) by dividing per-area effect (*y*-axis in Figure 4a) by abundance or density (*x*-axis in Figure 4a). Figure 4b shows how per-capita effect varies as a function of non-native species abundance for the four abundance–impact curves in Figure 4a. In the case of a linear abundance–impact curve (Figure 4a, curve #3), the per-capita effect of the non-native species is constant across the range of abundances (Figure 4b, curve #3). In this case, the Parker framework is reasonably valid since per-capita effect can be treated as a constant. In contrast, for the nonlinear abundance–impact curves

(#1, #2, and #4), the per-capita effect is context- or density dependent. In other words, per-capita effect itself varies depending upon abundance (Figure 4b curves #1, #2, and #4). Comparison of Figure 4a, b highlights how the framework of Parker and others (1999) implies a linear abundance–impact curve since it does not allow per-capita effect (PCE) to depend on abundance (Figure 4b). Moreover, one could imagine that the abundance–impact relationship for a given non-native species could vary among habitat types (Thiele and others 2010). In sum, considering the potential for nonlinear relationships between non-native species abundance and impact is critical for scaling up and assessing landscape-level impacts of non-native species.

## FRAMEWORK FOR LANDSCAPE-LEVEL NON-NATIVE SPECIES IMPACTS

In the preceding sections, we have provided a synthetic overview of our current understanding of non-native aquatic species range, abundance, and local effects—three key factors that ultimately determine landscape-level non-native species impact (Parker and others 1999). Here, we describe a framework for estimating landscape-level non-native species impacts (Figure 5) and explicitly



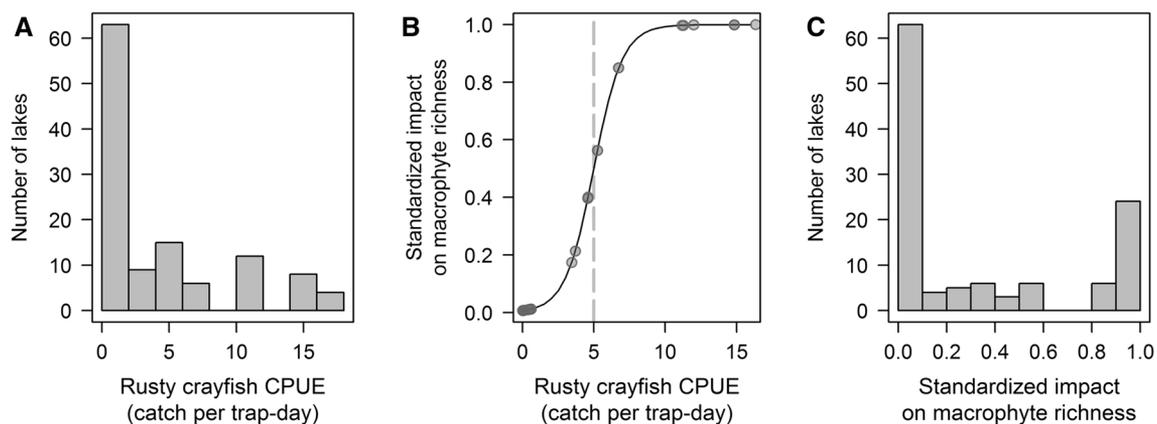
**Figure 5.** A conceptual framework for evaluating landscape-scale non-native species impacts. **A** Non-native species distribution is based on local occurrence records within known the geographic range. **B** At each site, local abundance is estimated. **C** The abundance–impact relationship is defined. **D** Given local abundance and the abundance–impact relationship, local impact is estimated for each site. **E** The spatial pattern and distribution of impact can be examined. **F** Summing local impact across all invaded sites allows estimation of total impact  $I_T$ .

incorporate several key issues including spatial scale, spatial heterogeneity, and nonlinear impact responses. Consider a spatially heterogeneous landscape comprised of several habitat patches or sites  $i$  (Figure 5a). For the purpose of this exercise, assume that all sites were sampled and species presence/absence is known at each site. The geographic distribution of the species can be mapped (Figure 5a), and there is no confounding effect of sampling intensity. At each inhabited site  $i$ , abundance ( $A_i$ ) can be estimated (Figure 5b). Across the multiple inhabited sites on the landscape, abundance varies and will often be non-normally distributed (Hansen and others 2013c). This suggests that mean abundance, which is used in the Parker and others (1999) framework, is not particularly informative and would fail to capture the spatial variation in non-native species abundance. Next, we need to know the abundance–impact relationship (Figure 5c). This relationship can be characterized using observational or experimental studies. If the abundance–impact relationship is unknown, landscape-level impacts can be assessed under a variety of abundance–impact relationship scenarios (Latzka and others 2016). If the abundance–impact relationship is nonlinear, it means that per-capita effect as used in the Parker and others (1999) framework is not constant across the range of non-native species abundances (Figure 4b). If the abundance–impact relationship is known (Figure 5c), local impact (per-area effect) for each site  $i$  can be calculated from site-level abundance ( $\text{PAE}_i = f(A_i)$ , Figure 5d). PAE will likely be spatially heterogeneous among invaded sites (Figure 5e) (Latzka and others 2016). Estimating

landscape-level impact ( $I_T$ ) involves summing impacts across all invaded sites  $i$ ;  $I_T = \sum_{i=1}^n \text{PAE}_i$ . Dividing  $I_T$  by the number of invaded sites gives average impact per site (Figure 5f).

This approach (Figure 5) explicitly recognizes that landscapes are composed of heterogeneous habitat patches, that non-native species abundance is spatially variable, and that local impact may not be a linear function of abundance. When this framework is applied to real situations, knowledge gaps may quickly become apparent. For example, the number of invaded sites or invaded area may not be well known, site-level abundance may not be known, and the form of the abundance–impact relationship may be unknown, or it may vary for different types of responses or habitat types. These uncertainties were the motivation for an analysis that simulated different plausible combinations of non-native species abundance distributions and abundance–impact relationships, as a way of exploring potential spatial patterns of non-native species impact on landscapes (Latzka and others 2016). This simulation found that many plausible scenarios result in non-native species impacts being highly heterogeneous on the landscape. Moreover, the spatial distribution of impact was strongly determined by both the non-native species abundance distribution and the type of abundance–impact relationship. Future research will need to confront these many uncertainties to increase our understanding of landscape-level non-native species impacts.

To illustrate this approach with a real-world example, we evaluate heterogeneity in impacts of non-native rusty crayfish (*Orconectes rusticus*) in



**Figure 6.** Example demonstrating the evaluation of landscape-level invasive species impacts for rusty crayfish in the northern highlands lake district of Wisconsin. **A** Frequency distribution of rusty crayfish abundance (trap CPUE) based on a stratified random field survey of 89 lakes. **B** An abundance–impact curve for macrophyte species richness with a threshold response at 5 crayfish/trap/day. **C** The resultant frequency distribution of estimated rusty crayfish impact showing low impact for most invaded lakes, but also some lakes with high impact.

lakes of northern Wisconsin (Figure 6). From 2010 to 2012, we sampled 89 lakes in the northern highlands lake district of Wisconsin using overnight sets of standard crayfish traps (Latzka 2015). Lake selection was based on a stratified random survey design. Rusty crayfish were detected in 24 of these lakes. After weighting across the nine strata (Gaeta and others 2013), our estimate of rusty crayfish prevalence was 8.5% (equating to an estimate of 117 rusty crayfish occurrences in the northern highlands lake district). Where present, rusty crayfish catch rates (crayfish/trap/day, an index of abundance) varied widely among lakes. Most lakes had relatively low catch rates, while a few had high catch rates (Figure 6a). A body of long-term and comparative studies show that rusty crayfish can have transformational ecosystem-wide effects at high abundances (Lodge and others 1998; Wilson and others 2004; Roth and others 2007; Hansen and others 2013a, b). Wilson (2002) reported an impact threshold with regard to macrophyte species richness of 5 crayfish/trap/day. We assume a simple sigmoidal relationship between abundance and relative impact (Figure 6b). For each of the 117 abundance estimates (Figure 6a), impact was estimated by plugging abundance into the abundance–impact function and solving for impact (Figure 6b). From this, we generate a frequency distribution of rusty crayfish impact for lakes in the region (Figure 6c). The resulting impact frequency distribution is right-skewed (most lakes with rusty crayfish experience low impact), though interestingly, there is a secondary peak of high impact lakes. This bimodal pattern of rusty crayfish impact is consistent with recent work highlighting feedbacks that could lead to multiple stable states of rusty crayfish impact (Roth and others 2007; Hansen and others 2013a, b).

## Summary and Implications for Management

Much of the current research on non-native species impact has focused at the local spatial scale of experimental plots or field enclosures (Kumschick and others 2015). The local-scale emphasis stands in stark contrast with the harsh environmental management reality of multiple non-native species spreading across large and heterogeneous landscapes (Vander Zanden and Olden 2008). Even with a highly refined understanding of local-scale non-native species impact, how much do we really know about landscape-scale impacts, which is more often the concern of resource management? Applying our understanding of local-level impacts

to broader scales requires efforts to ‘scale up’ our understanding (Lodge and others 1998). The Parker and others (1999) impact equation provides a useful starting point for addressing this challenge and evaluating the key information gaps. Our modifications to this framework described here address key gaps in the initial framework, such as the lack of incorporation of spatial heterogeneity, as well as simplification of abundance–impact relationships. Our hope is that this study contributes to the ‘scaling up’ of our understanding of non-native species impact. In addition to describing current impact, the modified Parker framework can also be used to forecast future impacts. For example, species distribution models can be used to predict future non-native species distribution, which can thus be used to estimate future impacts. Environmental change may also modify how an impact metric is related to non-native species abundance. Additional modifications could incorporate environmental and social changes that are known to affect aquatic non-native species spread, distribution, abundance, and impact. Risk assessments could incorporate these scenarios and potential future impacts of non-native species to better inform present-day prioritization decisions.

A key goal of this paper was to synthesize our current understanding of non-native species range, site occupancy, abundance, and abundance–impact relationships—all of which are key elements of understanding non-native species impact at broader spatial scales. In doing so, this review identified a number of key information gaps. Knowledge of non-native species site occupancy is often limited, and the existing occurrence data likely underestimate actual species prevalence. Non-native species are at low abundances surprisingly often where they are present (Hansen and others 2013c). Moreover, non-native species may often go undetected, even in cases where field surveys have been conducted. Finally, while local non-native species abundance may be a key determinant of local impact, estimating impact from abundance requires knowing the abundance–impact relationship.

The ultimate motivation for much of the research focusing on non-native species impact is to help inform non-native species management, prevention, and risk assessment. Our analysis highlights a challenging degree of heterogeneity with regard to the factors that ultimately affect landscape-level impact. For a known invader, impact is spatially heterogeneous. Yet our work also suggests that high impact may be relatively rare and that the frequency distribution of non-native species impact

may be right-skewed (Latzka and others 2016). In the case of natural disasters, it is well known that the frequency of damaging events is inversely proportional to their magnitude. The same principle may also hold true for species invasions (Ricciardi and others 2011). On the one hand, this high degree of spatial heterogeneity in impact creates management challenges. But this heterogeneity and the rarity of high impacts can also be viewed as a resource management opportunity, in that spatial variation in local impact itself underpins and motivates spatial prioritization of non-native species prevention and management efforts.

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