Spatial heterogeneity in invasive species impacts at the landscape scale

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Abstract. Invasive species have substantial impacts across the globe. While management efforts should aim to minimize undesirable impacts, we have a poor understanding of how impacts of a given invasive species vary spatially. Here, we develop a framework for considering heterogeneity of invasive species impacts that allows us to explore the range of possible spatial patterns of impact. This framework incorporates two factors—how invasive species abundance varies among sites (i.e., abundance distributions) and how invasive species impact varies as a function of abundance (i.e., abundance–impact curves). Combining these two factors allows for the creation of probability distributions that represent how invasive species impacts may vary spatially among sites. We used published abundance distributions and inferred abundance–impact curves to generate impact distributions for two problematic invasive species—zebra mussel and Eurasian watermilfoil—across lakes in Wisconsin, USA. Impact distributions of these species tended to be right-skewed (i.e., the majority of sites had low impacts), although the tail thickness varied. We also simulated how a broader range of combinations of invasive species abundance distributions and abundance–impact curves produce different patterns of invasive species impact. These simulations illustrate a remarkable diversity of invasive species spatial impact patterns—probability distributions of impact were left-skewed, right-skewed, bimodal, and normal. Total landscape-level impacts, estimated by summing site-level impacts, were similarly variable depending on the distribution of site-level impacts. Our results indicate that invasive species abundance and abundance–impact curves ultimately affect how invasive species impacts are distributed across the landscape, which has important implications for invasive species management.

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INTRODUCTION

Invasive species are among the leading drivers of global change (Sala et al. 2000), causing substantial ecological (Ricciardi et al. 2013) and economic impacts (Pimentel et al. 2005). Minimizing the undesirable impacts of invasions is a major goal of environmental agencies (Byers et al. 2002), but achieving this goal is nontrivial given the problem's scope and continued

growth. The large number of invasive species to consider, vast landscapes with many invaded or vulnerable sites, heterogeneity of impacts among sites, and the suite of management options (prevention, containment, control, eradication) all contribute to the complexity of invasive species management (Byers et al. 2002).

Funding for invasive species management pales in comparison to the scale and complexity of the problem (Simberloff et al. 2005), and thus understanding patterns of impact is necessary to use resources cost-effectively. Resource management is often confronted with this inequality between a problem's magnitude and available management resources, necessitating action plans that achieve the largest benefit per unit cost. Global biodiversity conservation, for instance, maps biodiversity hotspots to help maximize species protection given limited funding for land acquisition (Myers et al. 2000, Brooks et al. 2006, Game et al. 2013). An analogous approach for invasive species management may be to identify and target sites on the landscape where impact is likely to be highest in order to maximize the impact reduction per dollar spent (Epanchin-Niell and Hastings 2010). Unfortunately, current understanding of the spatial patterns of invasive species impacts is inadequate to inform this sort of prioritization. Although several impact assessment frameworks have been developed to estimate and compare species' total impacts (Parker et al. 1999, Thomsen et al. 2011 and citations therein), few have incorporated spatial heterogeneity of impacts among sites (but see Thiele et al. 2010, Barney et al. 2013).

Heterogeneity of invasive species impacts among sites encompasses two critical components: spatial heterogeneity in invasive species abundance, which is a universal driver of impact (Thomsen et al. 2011), and the relationship between a species' abundance and its impact (Fig. 1). Neither of these components is well-described empirically for the majority of invasive species. Variation in invasive species abundance across the landscape may take many possible forms (Fig. 1a). Native species generally occur at low abundance at most sites where they occur (Brown 1984), and a number of aquatic invasive species (AIS) follow similar patterns, producing right-skewed frequency distributions of abundance (hereafter "abundance distribution") (Hansen

et al. 2013). In contrast, invasive species are sometimes characterized by their tendency to dominate a community, as demonstrated empirically for some monotype-forming wetland plants (Zedler and Kercher 2004, Frieswyk et al. 2007) and anecdotally for some terrestrial plants such as kudzu, producing left-skewed abundance distributions. Furthermore, understanding spatial variability in impacts requires knowledge of the relationship between abundance and impact (hereafter "abundance–impact curve"). Although this relationship is likely to be positive in most cases (but see Kornis et al. 2014), the shape of this curve may take different forms for different species (Fig. 1b; Yokomizo et al. 2009). However, abundance–impact curves have not been quantified for most invasive species (Kulhanek et al. 2011b), hindering estimates of impact from abundance data.

Here, we combine empirical analyses and theoretical simulations to evaluate heterogeneity in invasive species impacts. Our objective is to gauge the extent of possible invasive species impact distributions, and how those patterns are influenced by abundance–impact curves and patterns in abundance. We use published abundance data for zebra mussels and Eurasian watermilfoil, and likely abundance–impact curves to examine potential patterns in their impacts. To explore a broader range of patterns that may be possible for species and regions with little currently available empirical data, we simulated impacts using a range of possible abundance distributions and abundance–impact curves (Fig. 1). For both analyses, we also explore how different patterns in impacts may influence an invasive species' cumulative impacts.

METHODS

Invasive species impacts on a heterogeneous landscape—a conceptual framework

In order to characterize heterogeneity in impacts across invaded landscapes, we first need to break the landscape into components of interest—lakes, habitat patches, pixels, etc.—which we refer to generally as sites ($s = 1… n$). A subset of these sites ($\leq s_n$), determined by environmental characteristics matching species' ecological requirements and dispersal abilities, are inhabited by an invasive species. Across
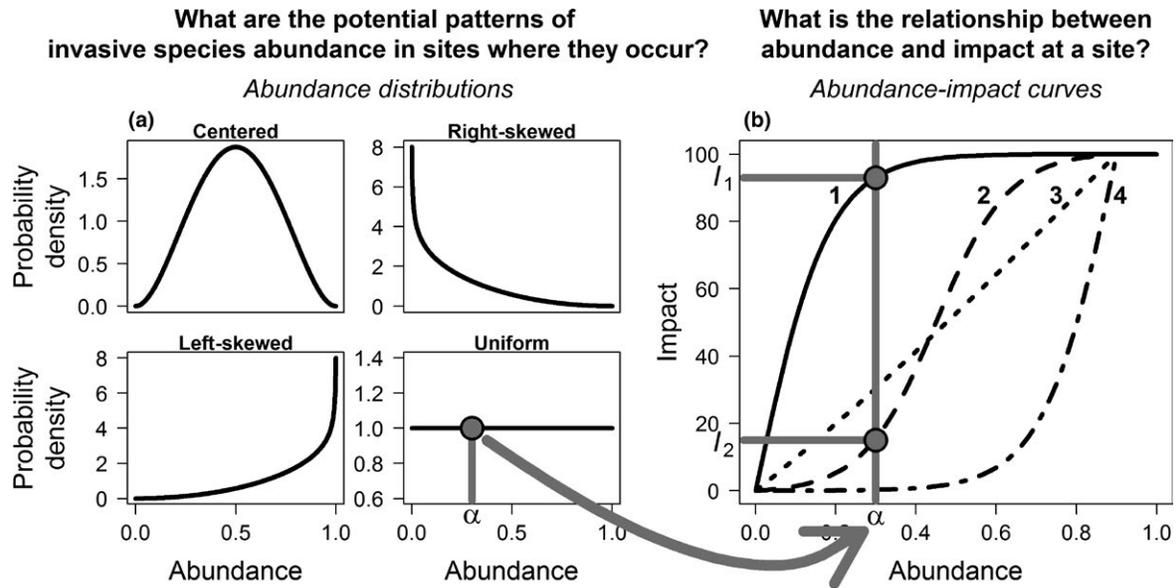
Fig. 1. The process and inputs we used to simulate probability distributions of the site-level invasive species impacts across a landscape. All abundance values are standardized on a 0–1 scale. (a) Potential frequency distributions of a species' site-level abundance, where each site is characterized by a single value for the species' abundance. Centered and skewed distributions are beta distributions, and the uniform distribution represents an equal probability of occurrence for any value of abundance. (b) The four types of relationships between abundance and impact (i.e., abundance–impact curves) used in our simulations (modified from Yokomizo et al. 2009). Impact is standardized on a 0–100 scale. To generate distributions of impact, we randomly draw an abundance value (α) from an abundance distribution and plug it into an abundance–impact curve to calculate impact for that site (I_1 or I_2 depending on curve used, although any curve could be used), as shown in gray. For each unique combination of these abundance distributions and abundance–impact curves, we repeated the process 1000 times to calculate impact for 1000 sites and sum all values of I to calculate total landscape-level impacts.

these inhabited sites, the species' abundance (a_s) will vary, and how it varies will differ among species. We can use probability distributions of abundance to characterize this variation ($P(a_s)$) (Fig. 1a), which may be theoretical or empirical if average or snapshot estimates of site-level abundance are available. Next, we need to describe the relationship between impact and abundance. Impacts at a site are likely to be positively related to species abundance, but the shape of this relationship will vary among species and among types of impact (Fig. 1b). We can thus use various abundance–impact curves, which also can be empirical or theoretical depending on data availability, to calculate a site-level impact (I_s) for any value of abundance drawn from an abundance distribution: $I_s = f_{AI}(\alpha_s)$ (Fig. 1). The frequency

distribution of site-level impacts (hereafter "impact distribution") can be used to visualize patterns in impact heterogeneity. At the landscape scale, we can then sum all site-level impacts to determine the species' total impact: $I_T = \Sigma_{s=1}^{n}(I_s) = \Sigma_{s=1}^{n}(f_{AI}(a_s))$, where I_T is analogous to impact estimates in previous formalizations (e.g., Parker et al. 1999). Note that this landscape scale may be considered the entire range of the species, or a subset of that range that is relevant to a given regional manager, such as a state.

Methods for empirical analyses

We used the above framework to compare site- and species-specific impacts of two problematic invasive species in Wisconsin lakes: zebra mussels (*Dreissena polymorpha*) and

Eurasian watermilfoil (*Myriophyllum spicatum*; hereafter "milfoil"). Wisconsin has many lakes that provide crucial ecosystem services (Peterson et al. 2003), where invasive species are a major threat (Peterson et al. 2003), and where the leading goal of management is to minimize the impacts of invasive species in cost-effective ways (Wisconsin Invasive Species Council 2013). We used invasive species occurrence records from the Wisconsin Department of Natural Resources (Wisconsin Department of Natural Resources 2012) to determine the number of sites invaded. For each site, we randomly sampled with replacement a value from a published abundance distribution (data in Hansen et al. 2013). We estimated the impact using relationships between abundance and impact that have been demonstrated in the literature, or which fit our understanding of how these species affect

lakes (specifics for each species detailed below). This process generated a frequency distribution of impacts for invaded lakes, which we summed to estimate total state-level impact. We repeated this randomization process 1000 times to simulate variability in the impact distribution and total impact estimates.

Zebra mussels.—Zebra mussels are present in 117 Wisconsin lakes (Wisconsin Department of Natural Resources 2012), so we estimated abundance and impact for each. Globally, zebra mussels have right-skewed abundance distributions in invaded sites (Hansen et al. 2013) (Fig. 2a). Thus, we randomly drew 117 abundance values, with replacement, from this distribution. Relationships between abundance and impact may vary depending on the response variable of interest, of which we chose two to
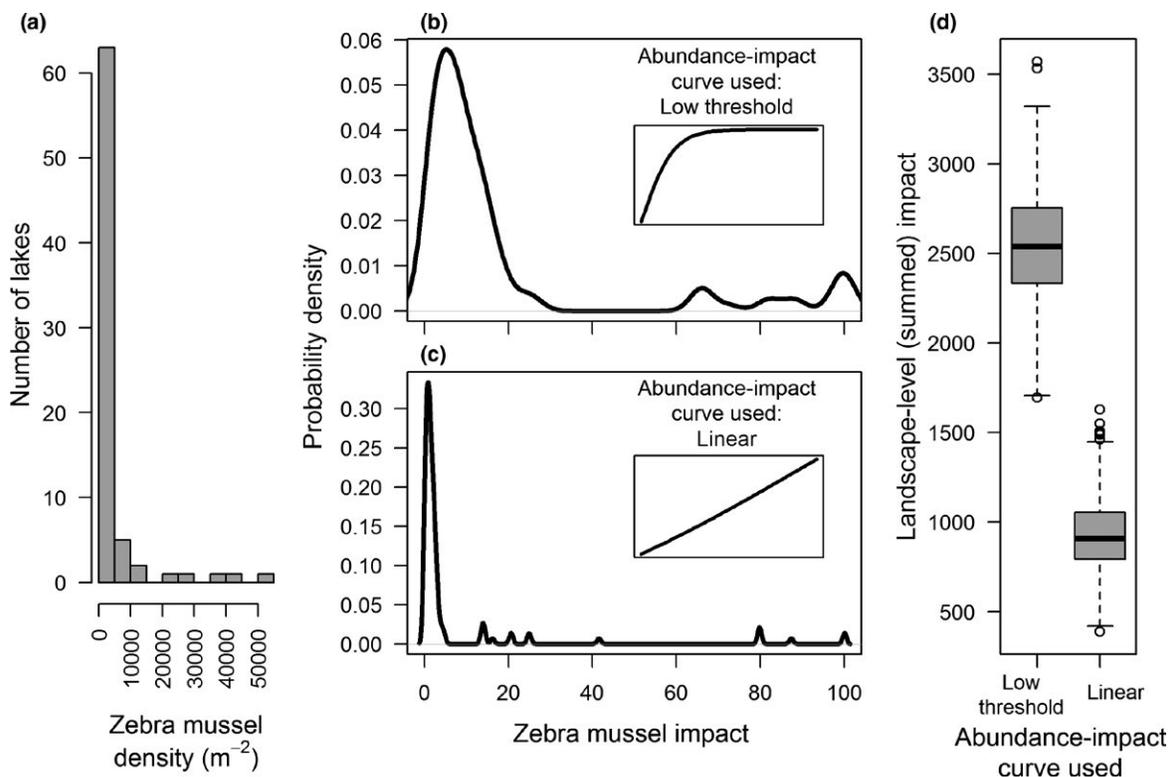

Fig. 2. (a) Histogram of site-level densities for zebra mussels (from Hansen et al. 2013). (b, c) Abundance values are sampled with replacement for all invaded lakes in Wisconsin (n = 117) and combined with a low threshold abundance–impact curve (b: inset) and a linear abundance–impact curve (c: inset) to calculate two potential distributions of zebra mussel impacts. (d) Boxplots of landscape-level summed impacts across all lakes, where each box displays the quartiles of 1000 impact estimates from repeated resampling of abundance data.

demonstrate. Zebra mussel impacts on native mussels asymptote at relatively low zebra mussel abundance (Ricciardi 2003), which aligns with their status as a keystone species (Karatayev et al. 2002). In contrast, Ricciardi (2003) also found native gammarid density to be linearly related with zebra mussel abundance. Thus, we used two abundance–impact curves to calculate impacts for each randomly selected abundance value: one in which abundance increases rapidly at low abundance and then asymptotes (Fig. 2b), and the other in which impact increases linearly with abundance (Fig. 2c). Equations for each curve were taken from Yokomizo et al. 2009 and are described Appendix S1.

Eurasian watermilfoil.—Milfoil is present in 527 lakes (Wisconsin Department of Natural Resources 2012). Thus, we randomly drew 527

abundance values from a published distribution, which is also right-skewed, but exhibits a thicker tail than that of the abundance distribution for zebra mussels (Hansen et al. 2013) (Fig. 3a). Milfoil abundance is likely to have different relationships with impact than zebra mussels, but may still have different forms for different impacts. Milfoil's impacts on boaters may be modeled as a linear relationship, since rates of propeller entanglement are likely to be directly related to abundance, while milfoil's impacts on adjacent property values are more severe at high abundance (Zhang and Boyle 2010). Thus, we used two abundance–impact curves to calculate impacts for each randomly selected abundance value: a linear curve (Fig. 3b), and a curve in which impacts remain low until high abundance values are reached, at which point impacts increase rapidly (Fig. 3c). As for the zebra mussel
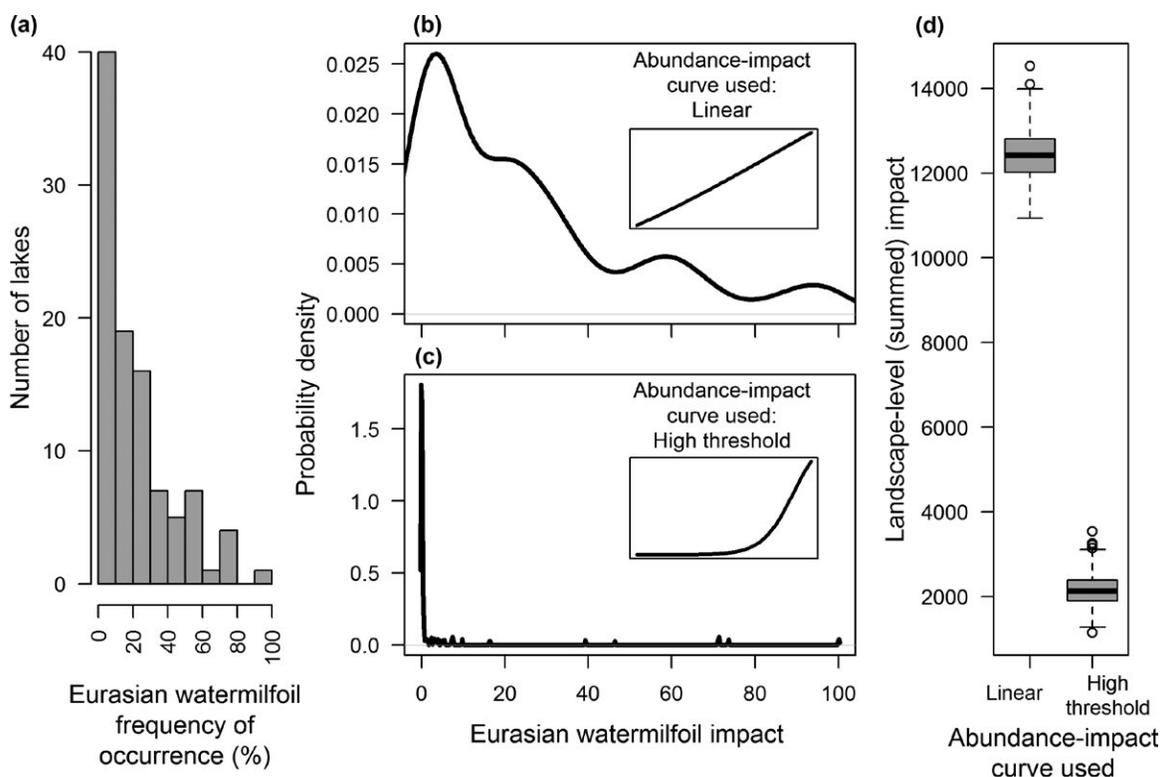

Fig 3. (a) Histogram of site-level frequency of occurrence for Eurasian watermilfoil (from Hansen et al. 2013). (b, c) Abundance values are sampled with replacement for all invaded lakes in Wisconsin ($n = 527$) and combined with a linear abundance–impact curve (b: inset) and a high threshold abundance–impact curve (c: inset) to calculate two potential distributions of Eurasian watermilfoil impacts. (d) Boxplots of landscape-level summed impacts across all lakes, where each box displays the quartiles of 1000 impact estimates from repeated resampling of abundance data.

abundance–impact curves, equations for each of these curves were taken from Yokomizo et al. 2009 and are described Appendix S1.

Simulating site-level and landscape-level impacts

While the empirical examples above demonstrate our framework's applicability to the likely scenario in which abundance data may exist and abundance–impact curves are deduced from the literature, we explored additional, theoretical possibilities for the many species with poorer empirical information to draw from that may follow different abundance distributions and abundance–impact curves. To do so, we used four hypothetical probability distributions to represent a broad range of species abundance patterns (Fig. 1a). In all distributions, abundance was expressed on a standardized scale ranging from 0 to 1. We used three Beta distributions with varying shape parameters α and β to represent centered (α = 3, β = 3), right-skewed (α = 0.8, β = 3), and left-skewed (α = 3, β = 0.8) distributions. We also used a uniform distribution (ranging from 0 to 1) to represent equal probability of invasive species occurring at any abundance.

We modeled the possible relationships between species' abundance and impact using four curves described by Yokomizo et al. (2009). These curves include a low abundance threshold where high impacts occur at all but the lowest abundances ("Low threshold", Type 1), a sigmoidal curve where impacts start low then increase rapidly at moderate abundance and asymptote at high abundance ("Sigmoidal", Type 2), a linear response ("Linear", Type 3), and a high abundance threshold in which high impacts only occur at high abundances ("High threshold", Type 4) (Fig. 1b). We standardized abundance values to range from 0 to 1 and scaled impact on a percentage scale (i.e., 0 = no impact, 100 = maximum possible impact). Since the asymptotic curves never reach their maximum potential impact, we assumed that abundances greater than 0.9 produced the maximum impact (results were not sensitive to variations in this threshold).

To quantify the distributions of site-level impacts, we randomly drew 1000 values from each of the four abundance distributions (Fig. 1a) to represent site-level abundances across an invaded range. For each value, we determined its associated impact using each of the four abundance–impact curves (Fig. 1b; described in Yokomizo et al. 2009 and Appendix S1), resulting in 16 unique combinations of abundance distributions and abundance–impact curves. We recognize that a single species may have multiple impacts, and that each impact may follow a different abundance–impact curve. For the purposes of this simulation, impact can be considered any measurable impact, such as a specific ecological impact on another taxa or an economic effect, or an index that integrates multiple types of impact.

We calculated landscape-level total impacts by summing all site-level impacts. In this analysis, we kept the number of sites constant at 1000 in order to isolate the effects of abundance distributions and abundance–impact curves on total impacts, but changes in the number of sites invaded would cause proportional changes in total impacts.

RESULTS

Empirical results

The modeled frequency distributions of impacts of zebra mussels were right-skewed for each response variable (Fig. 2b,c), although skewness was greater for impacts on gammarids. Summed landscape-level impacts on native mussels were nearly three times higher than those associated with gammarids (Fig. 2d).

The modeled frequency distributions of impacts of milfoil were right-skewed (Fig. 3b,c), with greater skewness when the linear abundance–impact curve associated with boat propeller entanglement was used. Summed landscape-level impacts were six times higher for linear abundance–impact curves than high-threshold curves, which may incur only small impacts at low to moderate abundance levels (Fig. 3d).

Simulation results

Simulated impacts were highly variable among sites (Fig. 4). For most scenarios, the frequency distributions of site-level impacts were highly skewed: six with left skew and five with right, although some of these also display bimodality. When site-level abundances were left-skewed (row 2 in Fig. 4), three of the four scenarios produced left-skewed impact
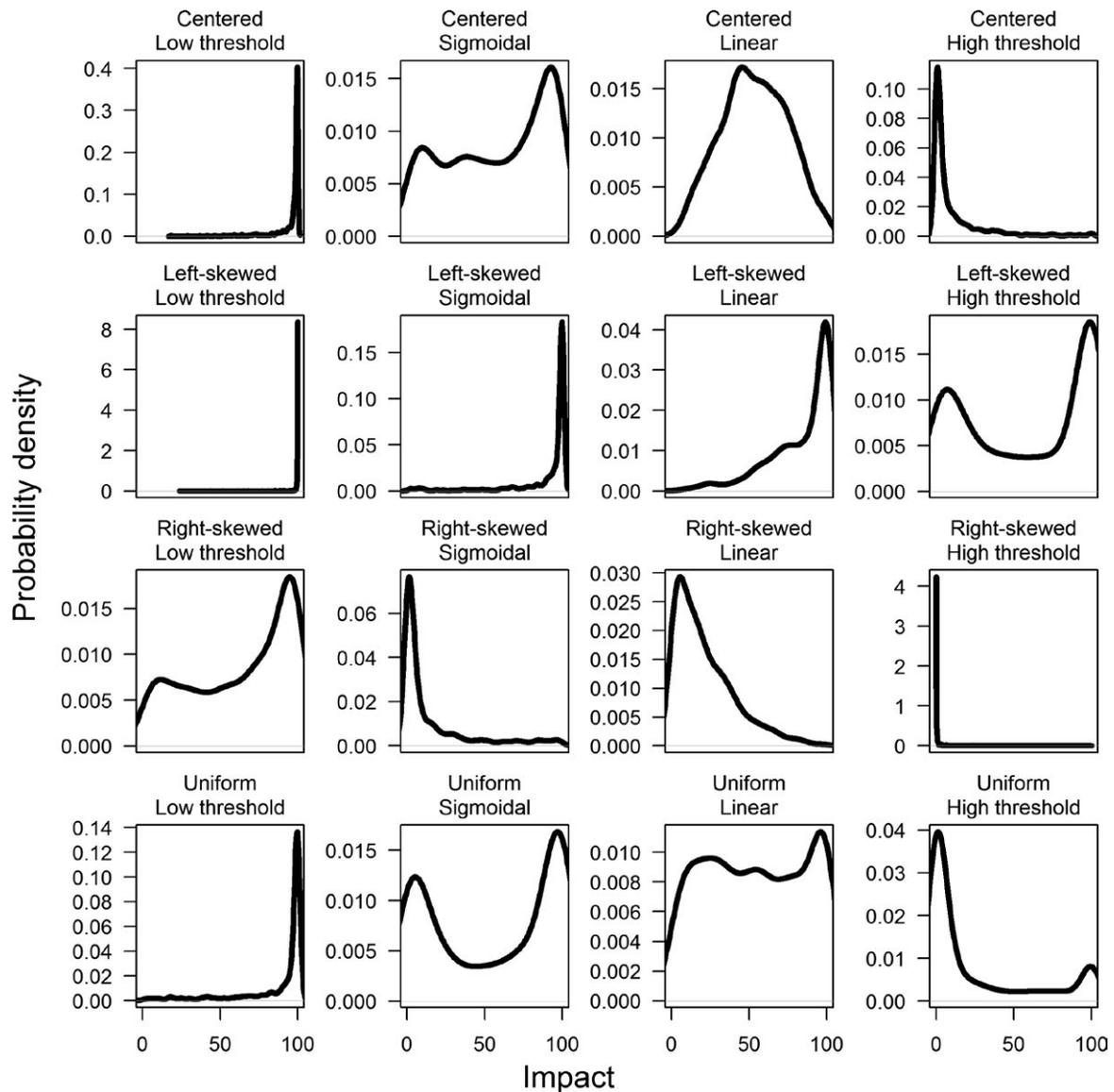
Fig. 4. Probability distributions of impacts for each combination of abundance distribution (rows) and abundance–impact curve (columns), which correspond to those shown in Fig. 1, simulated by randomly drawing 1000 values from each abundance distribution and calculating impact using each abundance–impact curve. Impacts are standardized so that 0 = no impact and 100 = maximum possible impact.

distributions. The exception, which paired a left-skewed abundance distribution with a high-abundance impact threshold, produced a slightly left-skewed bimodal impact distribution. When the abundance distribution was right-skewed (row 3 in Fig. 4), three of the four scenarios produced right-skewed impact distributions. The exception, which paired a right-skewed abundance distribution with a low-abundance impact threshold, produced a slightly left-skewed bimodal impact distribution. Impact distributions created by low- and high-abundance impact thresholds (columns 1 and 4 in Fig. 4) were similar to those created by left-skewed and right-skewed abundance distributions, respectively.
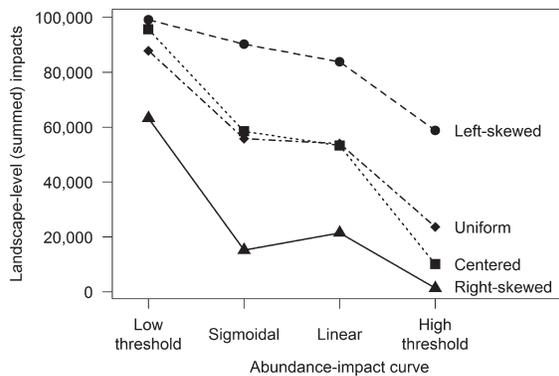
Fig. 5. Landscape-level (summed) impacts for each combination of abundance distribution (by shape and line type) and abundance–impact curve (on *x*-axis), which correspond to those shown in Fig. 1. Units for impacts are the same as Figs. 1 and 4, such that maximum impacts at a site equal 100, and thus maximum possible landscape-level impacts across 1000 sites sum to 100,000.

Landscape-level impacts were sensitive to both the abundance distribution and the abundance–impact curve (Fig. 5). Values ranged from 1884 to 99,500, where a value of 100,000 would indicate that a species achieved its maximum possible impact of 100 at each of the 1000 sites in the landscape. When abundance distributions were left-skewed, landscape-level impacts were always high, with three of four species exhibiting impacts greater than 85% of the maximum (i.e., >85,000) and all with impacts above 60% of the maximum. In contrast, when abundance distributions were right-skewed, three of the four scenarios had landscape-level impacts below 25% of the maximum observed total impact, and all had total impacts below 65% of the maximum. Similarly, abundance–impact curves that produced high impacts at low abundances tended to produce high landscape-level impacts, while those that only exhibit impacts at high abundances were less impactful.

DISCUSSION

Impact distributions

Our results highlight how abundance distributions and abundance–impact relationships of invasive species affect patterns of heterogeneity in impacts across sites. The empirical right-skewed abundance distributions of both zebra mussels and Eurasian watermilfoil led to impact distributions that were also right-skewed, although the shapes of these distributions varied depending on the abundance–impact curve used. Each species had one impact distribution that was thick-tailed and another that was thin-tailed. For zebra mussels, the thick tail was generated by a low threshold in the abundance–impact curve. For milfoil, the thick tail occurred with a linear abundance–impact curve, so the relatively high frequency of high impacts was caused by the thick tail in milfoil's abundance distribution. Thus, although high levels of impact for both of these species are likely to be rare relative to low impacts for metrics we assessed, the frequency of occurrence of these highly impacted sites still can still vary.

Additionally, our simulations, which we conducted to evaluate possible impact distributions for species with abundance distributions or abundance–impact curves that differed from those used in the empirical examples, demonstrated substantial variability in the shapes of potential impact distributions. Some scenarios produced a high relative probability of high site-level impacts, others a high probability of low impacts, and others normal, bimodal, or uniform distributions of impacts across sites (Fig. 4). Such variability is a crucial consideration for management. Species invasions are often managed in a binary way—they are either deemed invasive or not (Kolar and Lodge 2001). Given that their abundance is variable among sites (Hansen et al. 2013), and using the simple assumption that abundance is related to impact, we have shown that impacts are highly heterogeneous within a landscape, and that patterns in such heterogeneity vary among species. Such variation can create opportunities for management to focus on high-impact sites or leave unimpacted sites alone when resources are scarce. These facts necessitate a better consideration of the spatial variability in invasive species impacts in research and management decisions. In particular, measurement or prediction of impact distributions may be able to inform management. Notably, our results showed that knowledge of just one of the attributes—the abundance distribution or abundance–impact curve—was enough to approximate the shape of potential

impact distributions in some cases. This possibility could make predicting a species' pattern of heterogeneity in its impacts possible, even if its abundance distribution or abundance–impact curve is unknown. Such a case may be likely for a manager tasked with reducing the state- or county-wide impacts of a particular invasive species, for which abundances have been measured but impacts have not. Invasive species with left-skewed abundance distributions or low-abundance impact thresholds will almost always exhibit left-skewed impact distributions, where high impact sites are common. In these cases, targeted management that prioritizes some sites over others may be relatively inefficient because all sites have similarly high impacts. In contrast, species with right-skewed abundance distributions, including zebra mussels and milfoil, or high-abundance impact thresholds almost always exhibit right-skewed impact distributions, where high-impact sites are relatively rare. In these cases, prioritized approaches to management could be promising because reducing or eliminating impacts at a small number of highly impacted sites may significantly reduce total impacts.

Landscape-level impacts

Landscape-level impacts were sensitive to both the abundance distribution and the abundance–impact curve of the species, as well as to differences in the tail thickness of similarly shaped impact distributions. Specifically, species with simulated left-skewed abundance distributions, where sites experiencing high impacts are common, and low threshold abundance–impact curves, where high impacts are achieved even at low abundances, exhibited the highest total impacts (Fig. 5). Species with these attributes could have total impacts much higher than those with right-skewed abundance distributions or high threshold abundance-impact curves, respectively (assuming equal number of occupied sites). For species with right-skewed distributions of impact—that is, where sites experiencing high impacts are relatively rare—including zebra mussels and milfoil, thicker tails in these distributions caused landscape-scale estimates of impact that were three to six times higher than those associated with thin-tailed impact distributions. Note that such

a comparison assumes that the maximum site-level impacts of species are equal. As with the impact distributions, knowledge of just one attribute—the abundance distribution or abundance–impact curve—can greatly improve predictions of total impacts. For example, invasive species with left-skewed abundance distributions or low-abundance impact thresholds will almost always achieve relatively high total impacts, all else being equal.

Without an objective weighting scheme to compare impacts of milfoil and mussels, we cannot definitively say which species generates higher landscape-level impacts from this analysis. Nonetheless, managers tasked with prioritizing which species should be targeted for management to reduce landscape-wide impacts may be reasonably expected to make such valuations; so, it is useful to address some illustrative examples. First, if we determined that the maximum site-level impacts of each species are the same, such that the worst-case scenario of high abundance and high per capita effects for milfoil is comparable to that of zebra mussels, milfoil's landscape-level impacts would be higher, given their presence in nearly five times as many lakes and by the thick tail in their abundance distribution. On the other hand, if we determined that there is a low threshold causing high impacts of mussels at low abundance, which may be the most realistic given their role as a keystone species, and a high threshold for milfoil (which we used to model their effects on housing values), then landscape-level impacts of mussels would actually be greater, despite their presence in many fewer lakes. Finally, if we judged the maximum impacts of mussels to be higher than those of milfoil, thus requiring a differential weighting scheme, then mussel impacts may easily outweigh milfoil impacts.

Abundance distributions and abundance–impact curves

Despite their importance in determining landscape-level impacts and the heterogeneity therein, abundance distributions have rarely been quantified for invasive species. Hansen et al. (2013) reported right-skewed abundance distributions for several high-impact aquatic invasive species from a wide range of taxonomic groups and geographic locations. For these

species, time since invasion and effects of invasive species control efforts were both ruled out as drivers of such distributions, suggesting that species' and environmental traits that create right-skewed abundance distributions of native species may be similar for invasive species (Hansen et al. 2013). Nonetheless, invasive species may not always follow right-skewed abundance distributions. Invasive terrestrial plants seem to have great potential for centered, uniform or left-skewed distributions, the last of which may align with anecdotal evidence of invasive species "dominance". For example, several invasive plants are known for forming monotypes where the invader has high abundance with few co-occurring species (Frieswyk et al. 2007). Zedler and Kercher (2004) examined 21 commonly occurring invasive wetland plants, and note that 15 of these species (71%) form monotypes in invaded regions. Monotype-forming invaders may be best described by left-skewed distributions—when present, these species are usually found at high abundance. While these examples indicate that left-skewed abundance distributions may be possible for invasive species, future work should focus on quantifying abundance distributions for a broad range of taxa, and identifying the traits that lead to their abundance distributions. Existing site-level abundance data may be available in public databases, enabling quantification of abundance–impact curves for other taxa.

Similar to abundance distributions, abundance–impact curves are not yet described for even the most harmful invasive species (Kulhanek et al. 2011b), despite their substantial effect on landscape-level impacts and their heterogeneity. Nonetheless, there are empirical examples supporting the abundance–impact relationships used here (initially proposed by Yokomizo et al. 2009). Linear responses frequently occur in nature for processes such as litter decomposition (Elgersma and Ehrenfeld 2011) and filter feeding or grazing (Holling 1965). For example, filter feeding by zebra mussels (*Dreissena polymorpha*) reduces phytoplankton biomass, which in turn has a linear effect on zooplankton biomass (Higgins and Vander Zanden 2010). Elgersma and Ehrenfeld (2011) documented a high-abundance threshold response of the ratio of soil bacteria to fungi across abundances of invasive Japanese

barberry (*Berberis thunbergii*). High-abundance thresholds may be common for impacts that are met with a certain amount of resistance at low abundance, such as the decline/extirpation of native species that would otherwise be impacted by predation or competition at high invasive species abundance. Low-abundance impact thresholds may occur for invasive species that function as ecosystem engineers (Crooks 2002) or keystone species, which have effects disproportionate to their density (Paine 1969, Power et al. 1996). Sigmoidal response curves are the least supported by examples from the literature. However, invasive species often serve as prey in invaded ecosystems (Kitchell et al. 2000, King et al. 2006). Predators of invasive species may switch from native prey following invasion if the invasive species' density is sufficient for detection and learning by predators. Such predator/prey relationships are best modeled by a sigmoidal curve (or Type-III functional response) (Holling 1965). It should be noted that these four abundance–impact curves are not exhaustive of all possible relationships—thresholds may occur anywhere along the abundance axis, for instance. Additionally, fundamentally different curves may occur for some species. For example, experimental evidence suggests that the negative effects of an invasive fish, round goby (*Neogobius melanostomus*), on the growth rates of native competitors peaks at moderate densities (Kornis et al. 2014). At high densities, increased intraspecific interactions among round gobies appeared to result in diminished impacts on native species (Kornis et al. 2014). Such alternative abundance–impact curves would potentially lead to different impact distributions, but could easily be incorporated into our conceptual framework.

Management implications—single species on a landscape

In order to determine the best approaches to managing invasive species across landscapes, it is crucial to understand how impacts may be spread among sites. Our results demonstrate the possibility for strikingly different patterns of such impacts, and such different patterns may have contrasting management implications. Growing efforts to predict which sites may become invaded (Karatayev et al. 2015) and where abundance will be high (Kulhanek et al.

2011a, Guo et al. 2015) inform risk assessments that create management priorities (Stohlgren and Schnase 2006). However, when the goal of management is to minimize impacts across a landscape, prioritizing sites for protection from invasion or for eradication may provide an improved design only when the impact distributions are right-skewed, as was the case for milfoil and mussels and for most simulations that used either a right-skewed abundance distribution or high threshold in the abundance–impact curve. More generally, the number of sites that ought to be managed intensively to achieve the greatest reduction in an invasive species' overall impact is inversely related to the degree of right-skewedness in the impact distribution. On the other hand, if highly impacted sites are common (left-skewed) or if almost all sites are moderately impacted (unimodal or uniform), prioritizing a small number of sites based on their impacts may be no better than a randomized selection of sites and may only cause a small reduction in the total impact of an invasive species. In these cases, it may be relatively more beneficial to invest in more pervasive management techniques, such as education and outreach to organize a widespread volunteer network to participate in control efforts and reduce further spread. Volunteer-based control efforts have the potential to achieve massive amounts of manpower that would traditionally be rejected as unfeasible (Simberloff 2008). The decision of whether management should be pervasive or prioritized at a small number of sites should depend on either strategy's potential benefits, which in turn depend on the distribution of impacts. Thus, when deciding how to reduce the impacts of an invasive species across a landscape, some knowledge about the species' impact distribution across that landscape may be beneficial.

In addition, specific knowledge about the species' abundance distribution and/or abundance–impact curve can also inform management decisions, especially in cases where a particular impact distribution could be occurring due to different combination of abundance distributions and abundance–impact curves. For instance, consider the impact distributions created by a right-skewed abundance distribution and a sigmoidal abundance–impact curve

and by a uniform abundance distribution with a high threshold in the abundance–impact curve. Both distributions are right-skewed with similar tail thickness. In the former scenario, high impacts occur when the species abundance surpasses the moderate threshold in the abundance curve, which happens rarely. In the latter, high impacts occur only at the highest abundances—even though the species reaches moderate abundances more often in this scenario, those are not enough for it to have high impacts. Thus, even though in both cases a prioritization approach should target a similar number of sites, the former scenario may target any site with moderate to high abundances, while the second would target only those sites with highest abundances. In this comparison, knowing the combination of inputs that created the resulting impact distribution may help to inform which sites should be targeted. Lack of knowledge of the inputs may cause a manager to expend more effort than is needed differentiating moderate from high abundances even though both have similar impacts, in the first case, or allocating moderate-abundance sites for management even though they have relatively low impacts in the second case. Nonetheless, the simple knowledge that both impact distributions are right-skewed and that a prioritization approach to management is worthwhile is still better than nonprioritization approaches. In addition, given that the vast majority of abundance–impact curves are likely to be positive (but see Kornis et al. 2014), a simple rule of thumb for prioritizations is to target sites with the highest abundances (assuming costs of management are equal).

Management implications—multiple species

Assessments of species' total impacts exist, and were emphasized in inaugural issue of Biological Invasions, in which Parker et al. (1999) postulated that a species' total impact is the product of its range size, average abundance, and per capita effect. Several additional models have been adapted to incorporate various characteristics such as species and habitat attributes (Thomsen et al. 2011). Other risk assessments have either been qualitative or binary in nature or have not directly addressed site-to-site heterogeneity for a given species. For example, Kolar and Lodge (2002) identified five potential

problematic invaders from a list of 66 fish species that could invade the U.S. Great Lakes from the Ponto–Caspian region. Our results indicate that the impacts of these high-risk species are likely to be spatially heterogeneous. The pattern of heterogeneity, which we illustrate with impact distributions, depends on the shapes of the species' abundance distributions and abundance–impact curves, and can affect estimates of their total, landscape-wide impacts. Thus, knowledge of the attributes that could drive spatial variation in their impacts could enable total impact estimates and ranking of the five species for prioritization. This spatial texture underlying invasive species impacts is not widely acknowledged or understood—only recently have impact assessments begun to incorporate spatial heterogeneity (Thiele et al. 2010, Barney et al. 2013). Characterizing heterogeneity in impacts, as we have done here, simultaneously allowed us to estimate landscape-level impacts by summing across sites, helping to inform both species-specific management plans detailed above, and prioritizations among species.

For management agencies tasked with allocating resources among many different invasive species, an implicit goal of estimating and ranking species total impacts is to inform risk assessments and prioritizations among species. Summing impacts estimated for all sites in which an invasive species is present on a landscape from its abundance distribution and abundance–impact curve is one method of estimating total impacts, and would produce estimates equivalent to those based on Parker et al. (1999). However, we recognize that simple addition across sites may not always be appropriate—in some cases, managers may be particularly concerned with highly impacted sites, so that one site with maximum impact is judged to be worse than 10 sites with 10% of maximum impact. In other cases, managers may be concerned with the number of invasions, so that the 10 invaded sites with low impact are worse than one site with high impact. Such a weighting scheme would have to be implemented by a manager to incorporate his or her own goals into this framework. In any case, incorporation of the underlying spatial heterogeneity in impacts will enable better landscape-wide estimates, for instance by indicating the number of high impact sites to weight more strongly in the calculation.

Conclusion

Our results highlight the potential value of describing heterogeneity in impacts for managers tasked with minimizing the impacts of a species across a landscape or the impacts of multiple species. Because heterogeneity in impacts is driven by heterogeneity in abundance and its relationship with impact, it will be helpful to begin describing these attributes for a wide range of invasive species whose impacts are rarely measured. However, abundance is relatively easily measured or indexed for many taxa, and existing data sets with such information likely exist for many problematic invasive species. Similarly, we have shown how potential abundance–impact curves can be inferred from the literature. Additional experiments isolating the effects of incremental changes of abundance on measured impacts would also be helpful. When existing information or new studies are unfeasible to make conclusions about a species' abundance–impact curve or abundance distribution, it may become necessary to predict impact distributions from other information. While our results highlight some characteristics, such as a left-skewed abundance distribution (where species frequently achieve high abundances), a low threshold in the abundance–impact curve (where they have high impacts regardless of abundance), or keystone species traits, that may independently provide insight into heterogeneity of impacts, we have not explicitly attempted to predict impacts. Therefore, we strongly urge future trait-based research to consider how species traits may affect abundance distributions and abundance–impact curves, given their importance in determining landscape-scale patterns of impact. To date, most trait-based analyses of invasive species focus on predicting invasion success at the colonization, establishment, and spread stages (Marchetti et al. 2004, Theoharides and Dukes 2007). Future work could simply address abundance and impact as additional stages in this framework and determine the traits associated with various outcomes. One important consideration in these studies will be the traits of invasive species relative to those

present in the resident community, as functional differences between the two may lead to higher impacts (Levine et al. 2003). Such studies would help to make the crucial next step of predicting heterogeneity in invasive species impacts.

The framework presented in this article allows for simultaneous characterization of impact heterogeneity and estimation of landscape-level impacts. This information can then inform resource allocation to reduce impacts of single or multiple invasive species across a landscape. With presently available data and literature, managers, specifically those managing invasive species across large landscapes, may be able to make more informed decisions on their management strategies. However, our results show that the potential patterns of heterogeneity in impacts are diverse. Without quantifying abundance distributions and abundance–impact curves for more invasive species, our knowledge of the heterogeneity in invasive species impacts and ability to inform management is limited.

Acknowledgments

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