

Ecology, 96(10), 2015, pp. 2613–2621
© 2015 by the Ecological Society of America

A unified approach for quantifying invasibility and degree of invasion

QINFENG GUO,^{1,6} SONGLIN FEI,² JEFFREY S. DUKES,^{2,3} CHRISTOPHER M. OSWALT,⁴ BASIL V. IANNONE III,²
AND KEVIN M. POTTER⁵

¹*USDA Forest Service, Eastern Forest Environmental Threat Assessment Center, 3041 East Cornwallis Road, Research Triangle Park, North Carolina 27709 USA*

²*Department of Forestry and Natural Resources, Purdue University, 715 West State Street, West Lafayette, Indiana 47907-2061 USA*

³*Department of Biological Sciences, Purdue University, 915 West State Street, West Lafayette, Indiana 47907 USA*

⁴*USDA Forest Service, Southern Research Station, FIA, 4700 Old Kingston Pike, Knoxville, Tennessee 37919 USA*

⁵*Department of Forestry and Environmental Resources, North Carolina State University, 3041 Cornwallis Road, Research Triangle Park, North Carolina 27709 USA*

Abstract. Habitat invasibility is a central focus of invasion biology, with implications for basic ecological patterns and processes and for effective invasion management. “Invasibility” is, however, one of the most elusive metrics and misused terms in ecology. Empirical studies and meta-analyses of invasibility have produced inconsistent and even conflicting results. This lack of consistency, and subsequent difficulty in making broad cross-habitat comparisons, stem in part from (1) the indiscriminant use of a closely related, but fundamentally different concept, that of degree of invasion (DI) or level of invasion; and (2) the lack of common invasibility metrics, as illustrated by our review of all invasibility-related papers published in 2013. To facilitate both cross-habitat comparison and more robust ecological generalizations, we clarify the definitions of invasibility and DI, and for the first time propose a common metric for quantifying invasibility based on a habitat’s resource availability as inferred from relative resident species richness and biomass. We demonstrate the feasibility of our metric using empirical data collected from 2475 plots from three forest ecosystems in the eastern United States. We also propose a similar metric for DI. Our unified, resource-based metrics are scaled from 0 to 1, facilitating cross-habitat comparisons. Our proposed metrics clearly distinguish invasibility and DI from each other, which will help to (1) advance invasion ecology by allowing more robust testing of generalizations and (2) facilitate more effective invasive species control and management.

Key words: *abundance; community ecology theory; competition; invasion theory; niche availability; prediction; resources.*

INTRODUCTION

Habitat invasibility and species invasiveness are critical concepts in the field of invasion biology, not only because of their importance for invasion management, but also because of their relevance to basic ecological patterns and processes. Nonetheless, “invasibility” is among the most elusive metrics, difficult to compare across habitats, and thus, the terminology has been prone to misuse in ecology. Many hypotheses have

been proposed to describe the relationships between invasibility and various habitat features such as biodiversity (Elton 1958). However, empirical studies and meta-analyses of these relationships have produced inconsistent and even conflicting results (e.g., Jeschke et al. 2012, Catford et al. 2012).

As argued by Richardson et al. (2000), this inconsistency is in part due to the lack of precise definitions for concepts and terminology in invasion ecology (see also Pyšek 1995, Alpert et al. 2000, Richardson et al. 2000). The confusion primarily stems from the use of a closely related, but fundamentally different concept: Whereas *invasibility* represents the susceptibility of a community or region to invasion, *degree of invasion* (DI) or level of

Manuscript received 17 November 2014; revised 9 March 2015; accepted 3 April 2015. Corresponding Editor: D. C. Speirs.

⁶ E-mail: qguo@fs.fed.us

invasion measures the extent to which a community has already been invaded (e.g., based on the number of exotic species, exotic fraction; see Catford et al. 2009, Gurevitch et al. 2011). In most cases, DI increases over time. Historically, the terms invasibility and DI have frequently been used indiscriminately or interchangeably both in the literature and in communications with policy makers, land managers, and the general public. The interchangeable use of these two terms likely reflects the fact that DI is easier to quantify than invasibility. Many studies aimed at investigating invasibility actually have focused instead on DI (reviewed by Catford et al. 2012; see also Guo and Symstad 2008), likely further contributing to the contradictory findings regarding relationships between invasibility and habitat features.

The lack of commonly defined invasion metrics also makes it difficult to compare invasion ecology studies and to generalize patterns and processes in invasion ecology. For example, a review of all articles indexed by Web of Science in 2013 (119 total; Appendix A) that listed invasibility as a keyword reveals that, in general, most researchers seem to agree about what invasibility means (e.g., $69/119 = 58\%$ used susceptibility or vulnerability to either all or individual invaders; see also Elton 1958, Planty-Tabacchi et al. 1996, Lonsdale 1999, Moore et al. 2001, Fridley et al. 2004, Herben et al. 2004). However, researchers do not use a consistent unit of measure for invasibility. Of the 119 studies we reviewed, 17 (14%) quantified invasibility using the total number or proportion of exotic species. The remaining studies are hard to categorize because of the diverse and sometimes complex measures used, including cover and biomass of exotics and density, survival, growth, regeneration, establishment, and spread of selected individual invaders (see also Smith et al. 2004, Catford et al. 2012). Clearly, even within the same community and time period, using different variables to quantify invasibility such as richness, density, and biomass can generate different conclusions (e.g., Guo and Symstad 2008, Miller et al. 2014).

Of the two metrics, invasibility seems easier to define but more difficult to measure, whereas DI is easier to measure but has not been consistently defined (but see Catford et al. 2012). The combination of (1) the lack of precise definitions and indiscriminant use of these two terms and (2) the lack of common metrics continues to lead to inconsistent or even conflicting results regarding the relationships between invasibility and habitat features, hindering comparisons among otherwise comparable studies and therefore the formation of more robust generalizations. In this article, we seek to clarify the definitions of invasibility and degree of invasion (DI) and propose common metrics to quantify these two concepts that can be broadly used for comparisons across different habitats. To demonstrate the feasibility of our proposed metrics, we present an example using data collected from 2475 plots in three forest ecosystems in the United States by the Forest Inventory and

Analysis Program of the USDA Forest Service (FIA, *available online*;⁷ Bechtold and Patterson 2005, Woudenberg et al. 2010). As invasive species continue to be one of the major challenges to nearly all ecosystems (Fei et al. 2014), our proposed common metrics will help to reduce the hurdle for unifying theories in invasion ecology and to better inform future land management and policy making.

THE DIFFERENCE BETWEEN INVASIBILITY AND DEGREE OF INVASION

Invasibility can be defined as “the susceptibility of biological communities to colonization and dominance by introduced organisms” (Fridley 2011; see also Lonsdale 1999, Alpert et al. 2000). Conceptually and theoretically, “invasibility” is largely an intrinsic property of a community (Lonsdale 1999) perhaps analogous to the opposite of human “immunity.” It reflects the number of open niches within the community, and often is thought to be mainly controlled by resource availability (e.g., Davis et al. 2000), which can be strongly influenced by community features such as species composition, diversity, and biomass (Catford et al. 2012). Invasibility, by definition, is a pre-invasion, intrinsic property of a community. To estimate *future invasibility* in a community already invaded by exotic species, all species (native and exotic) need to be included as “residents” in measures of species richness and biomass (Simberloff and Von Holle 1999).

In contrast to invasibility, degree of invasion (DI) measures how much the community has already been invaded by exotic species (see Plate 1), and thus, is an outcome of previous interactions between intrinsic (invasibility) and extrinsic factors. The extrinsic factors may include invasion pressure (e.g., propagule/colonization pressure due to the combination of invader identity/traits and proximity to exotic species sources such as ports and large cities; Williamson 1996, Lockwood et al. 2009), disturbance, and time since invasion (e.g., Clark and Johnston 2011, Miller et al. 2014; see Fig. 1).

Communities with similar *invasibility* could have very different DIs, and vice versa, despite the fact that the two terms are often positively related to each other. A community with low invasibility cannot have high DI, but one with high invasibility could show either low or high DI depending on extrinsic factors (Fig. 2). A long-term increase in DI might be expected to reduce future invasibility, but high future invasibility could return, for instance if a major disturbance killed all resident species (i.e., both natives and exotics). The concept of “invasibility” is more valuable for theoretical studies and tightly controlled experimental studies (e.g., Case 1990, Robinson et al. 1995, Drake et al. 1996, Dukes 2001, Wardle 2001), whereas DI, as a measure of exotic

⁷ <http://www.fia.fs.fed.us/>

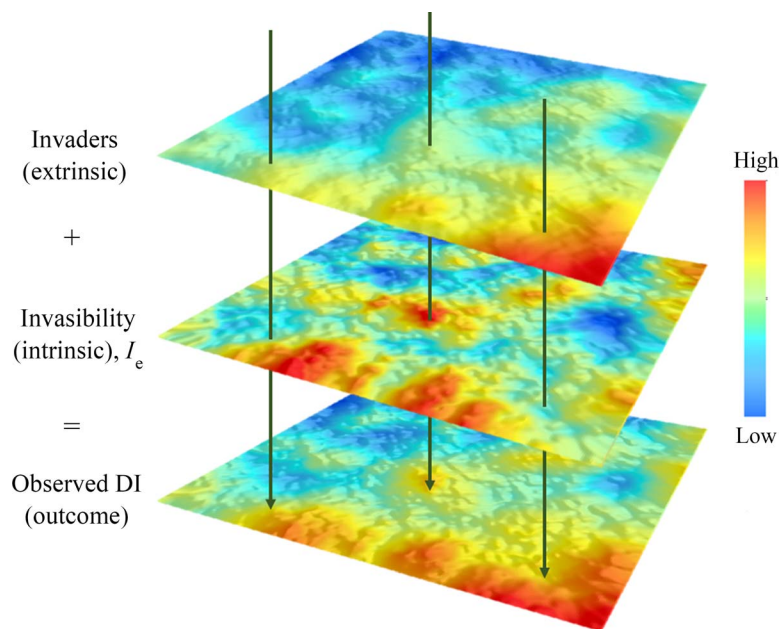


FIG. 1. The differences between invasibility (I_e) and degree of invasion (DI) in habitats across a hypothetical landscape (note that propagule pressure includes invader identity).

abundance and a potential correlate of impact, is what we measure in observational (non-manipulative) field studies and compare among empirical studies. In practice, invasibility is more difficult to measure due to its intrinsic nature and the absence of pre-invasion historical data on communities that are already invaded. Correspondingly, knowledge about invasibility is more pertinent to the prevention of future invasions, whereas knowledge of DI may help a manager prioritize the management of existing exotics species.

CRITICAL ELEMENTS OF QUANTIFYING INVASIBILITY

Contribution of species richness vs. dominance

There are several problems with using species richness or dominance alone in measuring habitat invasibility (Levine and D'Antonio 1999). First, at large scales and especially under environmental fluctuations, there is little evidence that any habitat could have stable long-term species saturation (Shurin and Srivastava 2005); that is, all habitats are likely invulnerable to some degree. In other words, short-term or transitional invasions could take place even in "saturated" habitats due to temporal population fluctuations of dominant species. Species richness is only one part of community structure, which also includes species composition, functional (or trait) diversity, evenness, abundance, and the age structure of each component species. Even if a species has a unique niche, it still needs time to fill its niche space. (Consider a community in early succession vs. a clearly less invulnerable, pure, and crowded forest stand in late succession [Clark and Johnston 2011]). Also, in a highly fluctuating environment (e.g., one experiencing frequent distur-

bances), high native species richness does not necessarily equate to high biomass and subsequent niche occupancy because, under such dynamic conditions, species will rarely have the time necessary to fully occupy niches. In other cases, richness of exotics and natives may be positively correlated; both variables accumulate with area and heterogeneity, and can respond similarly to other factors (Moore et al. 2001).

Biomass, on the other hand, can be another good indicator of controlling factors such as resource uptake (e.g., as affected by disturbance; Crawly 1987) and resource supply (Davis et al. 2000). However, using biomass of exotic species alone to quantify invasibility can also be misleading because it misses the importance of invader identity and sampling effects: Communities with higher exotic richness may contain more aggressive invaders that could penetrate even highly crowded communities (Huston 1997). Therefore, quantifying invasibility must take these two contributing factors (richness and biomass) into account, and the approach must be simple and practical for broad comparisons across communities and regions. However, within a particular community and for detailed research, quantifying invasibility with higher precision should also consider other relevant special conditions. For example, invasibility is often linked to the functional or phylogenetic traits of particular invaders vs. those of competitors or facilitators in residence (Richardson and Cowling 1992, Proches et al. 2008, Hooper and Dukes 2010). If an invader has strong mutualistic relations with certain resident species, it can successfully invade by outcompeting and/or replacing some resident species.

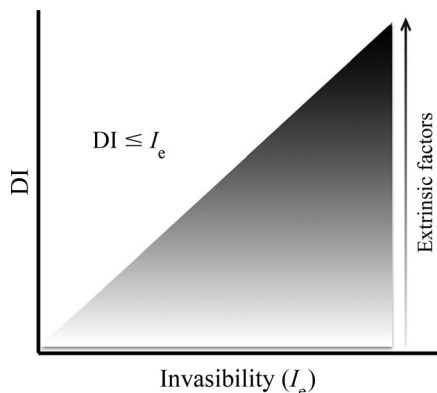


FIG. 2. Relationship between invasibility (I_e) and degree of invasion (DI). A community with low invasibility cannot have high DI, but one with high invasibility could show either low or high DI depending on the extrinsic factors time, disturbance, and propagule pressure.

Absolute vs. relative values as estimates

Using absolute or relative values (e.g., total number vs. percentages) to measure invasibility can lead to very different conclusions (Guo and Symstad 2008, Catford et al. 2012). As argued earlier, invasions depend largely on the availability of unused resources. When a habitat is still open with many niches available (e.g., in early succession), it is natural that other species (native or exotic), if not dispersal limited, will invade (Williamson 1996). Because communities are rarely saturated with species, high richness or biomass at a particular time does not necessarily indicate low invasibility; natural or human-made habitats have varying carrying capacities in total abundance or biomass and some can support higher richness and biomass of both natives and exotics than others. Thus, quantifying invasibility by using relative measures (i.e., fractions) would facilitate cross-community comparisons (Fig. 3).

Community ecology theories suggest that it is virtually impossible to measure invasibility and DI without reference to maximum possible richness and biomass in the habitat as indicators of the overall habitat capacity (Davis et al. 2000). Maximum richness and biomass are similar to the concept of carrying capacity in population biology, which is also difficult to obtain, but for which rough estimates have been widely used and have proved very helpful for studying population dynamics (e.g., the Lotka and Volterra model; Schoener 1974). In community ecology, similar terms such as species saturation, species capacity, and habitat (or island) capacity are frequently used concepts (e.g., MacArthur and Wilson 1967, Brown and Lomolino 1998, Ricklefs 2010).

Estimating the maximum richness and biomass in a habitat can be achieved through either direct field sampling or using historical records that are becoming increasingly available and assessable. In practice, for small areas, the maximum species richness and maxi-

mum biomass would be estimated with a relatively higher degree of accuracy than for larger areas, but comparisons of invasibility or DI measures can still be compared over larger scales using these estimates, especially for the same type of communities. One possible source of data is historically accumulated vegetation sampling completed during the past century. Additionally, large sampling efforts and data sets are becoming increasingly available around the world (e.g., Global Biodiversity Information Facility, Chinese Forest Biodiversity Monitoring Network, and Forestplots.net). For many of these long-term monitoring data sets, estimates of the maximum richness and biomass can be obtained for individual plots from the highest values inventoried from many years of sampling. These data may be especially relevant where they include mature communities of the relevant habitat types, which are likely to provide characteristic maximum richness and biomass values. An alternative approach is to use data from nearby similar vegetation plots or to use the space-for-time method if succession is taking place.

A UNIFIED MEASURE OF INVASIBILITY

Based on the premise that invasibility is an intrinsic property of a community, and in contrast to previous studies that often use exotic richness as a measure of invasibility or DI, we propose a generic metric for quantifying estimated invasibility (I_e) of a habitat or community based on relative resident species richness and abundance, as:

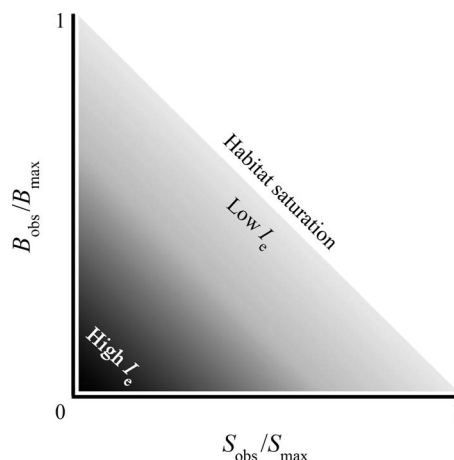


FIG. 3. The conceptual model showing the constraints of possible habitat saturation (i.e., $S_{\max}$ and $B_{\max}$) on invasibility (I_e) or degree of invasion, DI. (Note that replacing $S_{\max}$ and $B_{\max}$ with S_{tot} and B_{tot} would be for comparing DI values among plots or habitats). The relative importance of richness and biomass could switch between early and late succession and across habitat types. S_{obs} and B_{obs} are the observed plot-level richness and biomass, respectively, and $S_{\max}$ and $B_{\max}$ are maximum plot-level richness and biomass, respectively, and S_{tot} and B_{tot} are total (native plus exotic) richness and biomass in the community, respectively.

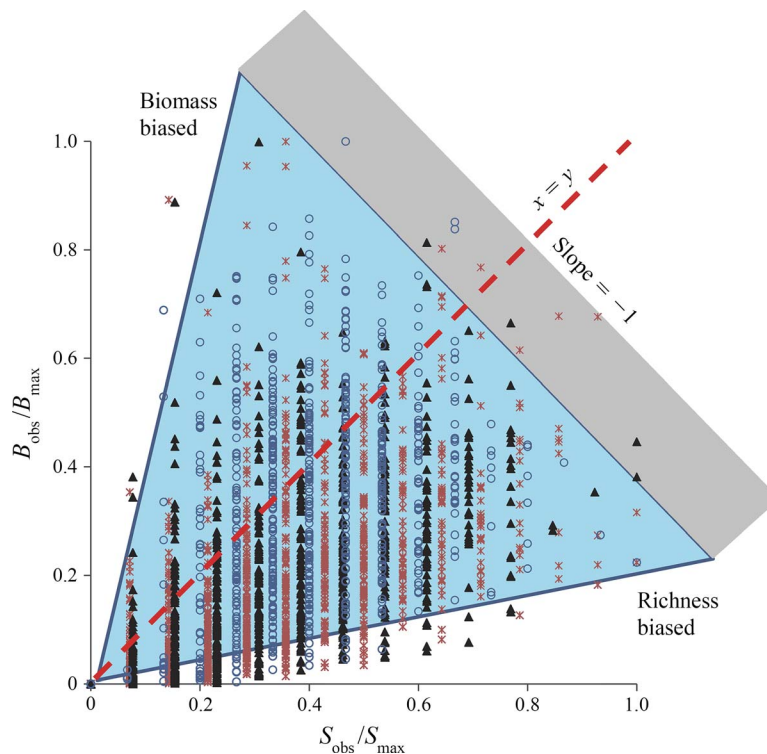


FIG. 4. An example of using the proposed definition and measure for invasibility (I_e) using the USDA Forest Service Forest Inventory and Analysis Program data (FIA; see footnote 7): Midwest Broadleaf Forest (red stars; $n = 969$), Prairie Parkland Forest (black triangles; $n = 845$), and Adirondack-New England Mixed Forest (blue circles; $n = 661$). The forest plots close to the lower left corner have a higher I_e than those in the gray rectangle in the upper right. The rectangle connects the highest values of $S_{\text{obs}}/S_{\text{max}}$ and $B_{\text{obs}}/B_{\text{max}}$ for each of the three forest ecosystems and represents possible habitat saturation levels, which vary among ecosystems. The diagonal red line ($x = y$) separates the forest plots more saturated in richness (usually in early succession; i.e., plots below the dashed line) and those more saturated in biomass (usually in late succession; i.e., plots above the dashed line).

$$I_e = 1 - \left(h \times S_{\text{obs}}/S_{\text{max}} + (1 - h) \times B_{\text{obs}}/B_{\text{max}} \right) \quad (1)$$

where S_{obs} and B_{obs} are the observed plot-level richness and biomass, respectively, and S_{max} and B_{max} are maximum plot-level richness and biomass, respectively, within the habitat type (i.e., resource-based carrying capacity); h is a habitat-specific weighting parameter that has a value between 0–1, thus accounting for variability among communities in how much biomass and species richness contribute to niche utilization, i.e., to invasibility. Both S_{max} and B_{max} can be estimated from field measurements or inferred from published literature (e.g., successional studies). The habitat-specific weighting parameter h can be derived from the slope of the blue line at top right of the triangle in Fig. 4, where plots reach saturation, which itself can be determined using data from multiple plots for each community or habitat. The values for I_e are scaled between 0 and 1, with higher values equating to higher invasibility (e.g., Terborgh and Faaborg 1980, Wilson et al. 2012). Because invasibility (I_e) defined here is both standardized and unitless, it can be used to compare different ecological communities regardless of successional stage. To estimate future invasibility in a community that has

already been invaded, existing invaders should also be included in the calculation as “resident” (native and exotic species) species. A similar approach has been presented by Blüthgen et al. (2012), who developed an index of land use intensity in responding to increased demand for studying the patterns of human land use.

To illustrate the utility of the I_e metric, we used field-based measurements from the USDA Forest Service Forest Inventory and Analysis (FIA) program (Bechtold and Patterson 2005). We first developed a relative biomass–richness space by randomly selecting three forest ecosystems, Midwest Broadleaf Forest, Prairie Parkland Forest, and Adirondack-New England Mixed Forest, from the FIA program (Fig. 4). Biomass and richness for resident tree species in each plot were calculated. Relative biomass and richness for each plot were then calculated using the observed biomass (B_{obs}) and richness (S_{obs}) divided by the observed plot-level maximum biomass (B_{max}) and richness (S_{max}) within each forest ecosystem, respectively.

The gray zone in the upper right corner of Fig. 4 encompasses the highest values of $S_{\text{obs}}/S_{\text{max}}$ and $B_{\text{obs}}/B_{\text{max}}$ for the three forest ecosystems and represents possible habitat saturation (see also Fig. 3). Within this zone, a community cannot have the highest richness and

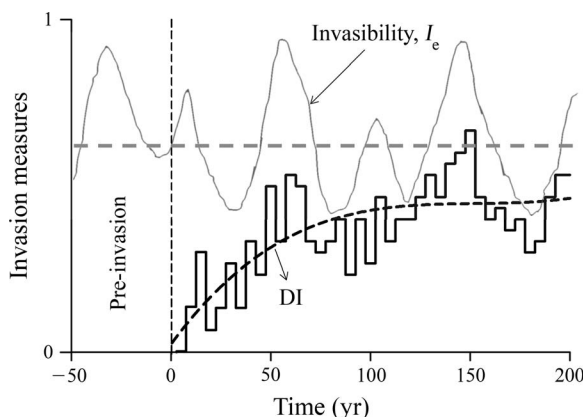


FIG. 5. Differences between invasibility (I_e , gray lines) and degree of invasion (DI, black lines) based on the hypothetical and simplified temporal trajectories in a community with varying a roughly 50-year successional cycle ($DI \leq I_e$). The gray dashed line represents the mean for I_e , and the black dashed curve is the regression for DI. The vertical dashed black line represents the starting point when invasions occur. Invasibility peaks in early succession and fluctuates around the mean during succession (short term), but may not show long-term trends. Long-term increases in DI would reduce invasibility, but every major disturbance would still increase invasibility because of the destruction of all resident species (both native and exotics). DI also increases in early succession due to high invasibility, but will show long-term increase as a consequence of continuing species introductions, especially if "invasion meltdown" takes place (Simberloff and Von Holle 1999), which may lead to extinction of native species. However, under extreme conditions such as right after total habitat destruction due to volcanic eruption, DI could briefly reach the maximum value of invasibility. Regardless of the time scale, community ecology theory predicts that increased DI would reduce invasibility.

biomass at the same time (Grime 1973), even though the two variables are often positively correlated when both values are low. The slope in this saturation zone is approximately -1 , which indicates that the biomass and richness ratios within this zone are interchangeable in measuring and controlling I_e . One unit of relative biomass is equivalent to one unit of relative richness, i.e., $h = 1 - h = 1/2$ in Eq. 1. Therefore, based on the case studies shown in Fig. 4, Eq. 1 could be potentially simplified as the following (Eq. 2), although its applicability to other habitat types need be further tested:

$$I_e = 1 - (S_{\text{obs}}/S_{\text{max}} + B_{\text{obs}}/B_{\text{max}})/2 \quad (2)$$

Moreover, for the three forest ecosystems examined here, richness generally approaches the saturation level more closely than biomass, as suggested by the majority of forest plots ($>60\%$ in all three forests) falling beneath the diagonal $x = y$ line (Fig. 4). Similarly, the many plots in the lower left corner may be highly susceptible to future invasion if propagules of exotic species become available.

The I_e index, a composite value based on richness and biomass in each plot, allows comparisons across habitat types or successional stages. For example, in our case study, there was no significant difference in the mean I_e value between Midwest Broadleaf Forest and Prairie Parkland Forest (0.72 vs. 0.73, t test, $df = 1791$, $P = 0.248$). However, the mean I_e of Midwest Broadleaf Forest and Prairie Parkland Forest was significantly higher than that of Adirondack-New England Mixed Forest (0.72 vs. 0.62, $df = 1569$, $P < 0.0001$ and 0.73 vs. 0.62, $df = 1493$, $P < 0.0001$, respectively). Although these mean I_e values represent only the current status of these forest ecosystems and may change over time, the comparative results from the analyses offer important information for management prioritization and policy making.

MEASURING DEGREE OF INVASION

The process of developing I_e led us to re-evaluate existing measures for DI. Similar to the invasibility metric (i.e., critical elements, absolute vs. relative values), we also propose a common metric to measure degree of invasion (DI). We argue that a DI metric must include both the number and dominance of exotic species. A single highly invasive species can disrupt ecosystem functioning in one community, as seen with kudzu (*Pueraria lobata*; Li et al. 2011) and reed canary grass (*Phalaris arundinacea*; Green and Galatowitsch 2002). In well-established pure stands of an invasive species such as these, it can be difficult for other species (native or exotic) to invade. In contrast, ecosystem functioning in other communities that harbor many non-invasive exotics may remain relatively unaffected (Guo and Symstad 2008). We propose to measure degree of invasion (DI) as follows:

$$DI = (S_{\text{exo}}/S_{\text{tot}} + B_{\text{exo}}/B_{\text{tot}})/2 \quad (3)$$

where S_{exo} and B_{exo} are observed exotic richness and biomass, respectively, and S_{tot} and B_{tot} are total (native plus exotic) richness and biomass in the community, respectively (see also Fig. 3 in which S_{max} and B_{max} can be replaced by S_{tot} and B_{tot} for measuring DI). In order to make comparisons of DI among communities, the value for DI is scaled between 0 and 1, with higher values equating to a higher degree of invasion. We illustrate how the DI metric can be applied to five disparate ecological communities in Supporting Information (Appendix B).

FUTURE DIRECTIONS

The factors affecting I_e and DI are inevitably interrelated (e.g., Sobrino et al. 2002; see Fig. 5). Disturbance usually reduces the ratio of existing biomass to the maximum biomass ($B/B_{\text{max}} = R_B$) in mature, stable communities, but its effects on species richness are more complex (e.g., the intermediate disturbance hypothesis or IDH; Grime 1973). Both I_e and DI would increase with decreasing R_B . High



PLATE 1. (Top) Grassland in North Dakota, USA. (Bottom) *Euonymus fortunei*. Photo credits: top, Q. Guo; bottom, S. Fei.

richness and biomass could indicate a high level of species saturation (all or most niches are occupied) and thus resistance to opportunistic invasions. Correspondingly, invasibility will not be determined solely by the number of resident species; biomass must be jointly considered as it is more directly related to competition (Bonser and Reader 1995). Based on such arguments, we recommend that (1) a habitat's invasibility, I_e , be quantified using the relative values of observed richness and biomass to community carrying capacity (or maximum values); (2) DI measures should be based on the relative values, such as the proportion or fraction of exotic richness and biomass in the community, rather than absolute values of those measures; and (3) additional and improved strategies to estimate maximum diversity and biomass should be explored. For example, Potter and Woodall (2014) recently used site productivity classes and a proxy for stand development when investigating the relationship between biomass and biodiversity on FIA plots, and through this process, the

researchers were able to obtain the highest richness and biomass values for each forest type.

It is essential to note that time plays different roles in invasibility vs. DI and that the roles vary at different temporal scales; that is, invasibility may change with the population fluctuations of dominant species (e.g., Wiser et al. 1998, Clark et al. 2013). Over a relatively short period of time such as a successional cycle, we expect a community in early stages to be more invasible than in later stages (Fig. 5). Over the longer term (e.g., across multiple successional cycles), however, as exotic species may continue to invade and some of them could persist, we expect that DI will almost always increase (Fig. 5; Heard et al. 2012), unless management activities can act to slow or even reverse this pattern. These differences will result in a long-term trend of invasibility varying around a relatively stable mean value, while DI steadily increases or stabilizes. In general, over both the short and long terms, increasing DI would reduce invasibility due to increased community saturation, at least until the

next major disturbance occurs. In addition, one must consider that successful invaders may themselves affect invasibility by altering ecological states via their impacts on important ecological and biogeomorphic processes (Simberloff et al. 2013, Fei et al. 2014).

Like many other ecological indices, our proposed metrics of invasibility and DI are sensitive to outliers. For example, if an investigated system/area had a plot with extraordinarily/abnormally high species richness and/or biomass, this skewed measure will bias estimates of maximum species richness and biomass, leading to under estimates of invasibility and DI for all other plots in that system/area. This problem could arise from inadequate sampling, causing maximum estimates to falsely appear as outliers. Increased sampling can resolve this situation by helping to fill in the gap between higher and lower values. Multiple solutions exist when a high value is a legitimate outlier (e.g., an error or nonrepresentative of the sample system/area). First, outliers could be excluded from analysis if such actions were explained and justified. Second, analyses can be done both with and without outliers to determine their impact on estimates and ecological inference. Third, one may define the maximum value using the 95th percentile instead of the potential outlying maximum value. Finally, one could average estimates across plots having the highest values (e.g., the top 1–5%). Increased sampling would lessen an outlier's effect on this average.

In short, how invasibility and DI are defined and measured can strongly influence pattern description and interpretations. In addition, clear distinction and appropriate use of habitat invasibility vs. DI are critical for comparative purposes and for informing management (Catford et al. 2012). The former is an intrinsic property of a habitat, while the latter is an outcome of species invasion controlled by both intrinsic and extrinsic factors. Because carrying capacity varies over space and time, measures of invasibility should reflect niche availability for potential invasions, and measures of DI should reflect the fractions of invaded species richness and biomass in the community. Future efforts should also incorporate other measures of niche usage in assessing invasibility and DI such as functional trait-based or phylogenetic diversity. As new ecological data sets from across the globe become available for analysis, the resource-based, unified indexes of invasibility and degree of invasion (DI) proposed here can be used to uncover basic ecological patterns across systems, and to inform land management and ecological restoration.

ACKNOWLEDGMENTS

We thank the reviewers for helpful comments. This work is supported by a NSF MacroSystems grant (DEB-1241932).

LITERATURE CITED

- Alpert, P., E. Bone, and C. Holzapfel. 2000. Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution and Systematics* 3:52–66.
- Bechtold, W. A., and P. L. Patterson. 2005. The enhanced forest inventory and analysis program—national sampling design and estimation procedures. General Technical Report SRS-80. USDA Forest Service, Southern Research Station, Asheville, North Carolina, USA.
- Blüthgen, N., et al. 2012. A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and fertilization. *Basic and Applied Ecology* 13:207–220.
- Bonsler, S. P., and R. J. Reader. 1995. Plant competition and herbivory in relation to vegetation biomass. *Ecology* 76: 2176–2183.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Sinauer, Sunderland, Massachusetts, USA.
- Case, T. J. 1990. Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA* 87: 9610–9614.
- Catford, J. A., R. Jansson, and C. Nilsson. 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15:22–40.
- Catford, J. A., P. A. Vesk, D. M. Richardson, and P. Pyšek. 2012. Quantifying levels of biological invasion: towards the objective classification of invaded and invulnerable ecosystems. *Global Change Biology* 18:44–62.
- Clark, G. F., and E. L. Johnston. 2011. Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. *Ecology Letters* 14:52–57.
- Clark, G. F., E. L. Johnston, and B. Leung. 2013. Intrinsic time dependence in the diversity–invasibility relationship. *Ecology* 94:25–31.
- Crawly, M. J. 1987. What makes a community invulnerable? *Symposia of the British Ecological Society* 26:429–453.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88:528–534.
- Drake, J. A., G. R. Huxel, and C. L. Hewitt. 1996. Microcosms as models for generating and testing community theory. *Ecology* 77:670–677.
- Dukes, J. S. 2001. Biodiversity and invasibility in grassland microcosms. *Oecologia* 126:563–568.
- Elton, C. S. 1958. *The ecology of invasions by plants and animals*. Methuen, London, UK.
- Fei, S., J. Phillips, and M. Shouse. 2014. Biogeomorphic Impacts of Invasive Species. *Annual Review of Ecology, Evolution, and Systematics* 45:69–87.
- Fridley, J. D. 2011. Invasibility of communities and ecosystems. Pages 356–360 in D. Simberloff and M. Rejmanek, editors. *Encyclopedia of biological invasions*. University of California Press, Chicago, Illinois, USA.
- Fridley, J. D., R. L. Brown, and J. F. Bruno. 2004. Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology* 85:3215–3222.
- Green, E. K., and S. M. Galatowitsch. 2002. Effects of *Phalaris arundinacea* and nitrate-N addition on the establishment of wetland plant communities. *Journal of Applied Ecology* 39: 134–144.
- Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* 242:344–347.
- Guo, Q. F., and A. Symstad. 2008. A two-part measure of degree of invasion for cross-community comparisons. *Conservation Biology* 22:666–672.
- Gurevitch, J., G. Fox, G. Wardle, and D. Taub. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters* 14:407–418.
- Heard, M. J., D. F. Sax, and J. F. Bruno. 2012. Dominance of non-native species increases over time in a historically invaded strandline community. *Diversity and Distributions* 18:1232–1242.
- Herben, T., B. Mandák, K. Bímová, and Z. Münzbergová. 2004. Invasibility and species richness of a community: a

- neutral model and a survey of published data. *Ecology* 85: 3223–3233.
- Hooper, D. U., and J. S. Dukes. 2010. Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology* 98:764–777.
- Huston, M. A. 1997. Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia* 110:449–460.
- Jeschke, J. M., L. Gómez Aparicio, S. Haider, T. Heger, C. Lortie, P. Pyšek, and D. Strayeret. 2012. Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* 14:1–20.
- Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26.
- Li, Z., Q. Dong, T. P. Albright, and Q. F. Guo. 2011. Natural and human dimensions of a quasi-wild species: the case of kudzu. *Biological Invasions* 13:2167–2179.
- Lockwood, J. L., P. Cassey, and T. M. Blackburn. 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15:904–910.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- Miller, A. L., J. M. Diez, J. J. Sullivan, S. R. Wangen, S. K. Wiser, R. Meffin, and R. P. Duncan. 2014. Quantifying invasion resistance: the use of recruitment functions to control for propagule pressure. *Ecology* 95:920–929.
- Moore, J. L., N. Mouquet, J. H. Lawton, and M. Loreau. 2001. Coexistence, saturation and invasion resistance in simulated plant assemblages. *Oikos* 94:303–314.
- Planty-Tabacchi, A. M., E. Tabacchi, R. J. Naiman, C. Deferrari, and H. Decamps. 1996. Invasibility of species rich communities in riparian zones. *Conservation Biology* 10: 598–607.
- Potter, K. M., and C. W. Woodall. 2014. Does biodiversity make a difference? Relationships between species richness, evolutionary diversity, and aboveground live tree biomass across US forests. *Forest Ecology and Management* 321:117–129.
- Proches, S., J. R. U. Wilson, D. M. Richardson, and M. Rejmánek. 2008. Searching for phylogenetic pattern in biological invasions. *Global Ecology and Biogeography* 17: 5–10.
- Pyšek, P. 1995. On the terminology used in plant invasion studies. Pages 71–81 in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. *Plant invasions: general aspects and special problems*. SPB Academic Publishing, Amsterdam, The Netherlands.
- Richardson, D. M., and R. M. Cowling. 1992. Why is mountain fynbos invulnerable and which species invade? Pages 161–181 in B. W. van Wilgen, D. M. Richardson, F. J. Kruger, and H. J. van Hensbergen, editors. *Fire in South African mountain fynbos*. Springer, Berlin, Germany.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6:93–107.
- Ricklefs, R. E. 2010. Dynamics of colonization and extinction on islands. Insights from Lesser Antillean birds. Pages 388–414 in J. B. Losos and R. E. Ricklefs, editors. *The theory of island biogeography revisited*. Princeton University Press, Princeton, New Jersey, USA.
- Robinson, G. R., J. F. Quinn, and M. L. Stanton. 1995. Invasibility of experimental habitat islands in a California winter annual grassland. *Ecology* 76:786–794.
- Schoener, T. W. 1974. Resource partitioning in ecological communities. *Science* 185:27–39.
- Shurin, J. B., and D. S. Srivastava. 2005. New perspectives on local and regional diversity: beyond saturation. Pages 399–417 in M. Holyoak, M. Leibold, and R. Holt, editors. *Metacommunities: spatial dynamics and ecological communities*. University of Chicago Press, Chicago, Illinois, USA.
- Simberloff, D., et al. 2013. Impacts of biological invasions: what's what and the way forward. *Trends in Ecology and Evolution* 28:58–66.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1:21–32.
- Sobrino, E., M. Sanz-Elorza, E. D. Dana, and A. Gonzalez-Moreno. 2002. Invasibility of a coastal strip in NE Spain by alien plants. *Journal of Vegetation Science* 13:585–594.
- Terborgh, J. W., and J. Faaborg. 1980. Saturation of bird communities in the West Indies. *American Naturalist* 116: 178–195.
- Wardle, D. A. 2001. Experimental demonstration that plant diversity reduces invasibility: evidence of a biological mechanisms or a consequence of sampling effects? *Oikos* 95:161–170.
- Williamson, M. 1996. *Biological invasions*. Chapman and Hall, London, UK.
- Wilson, J. B., R. K. Peet, J. Dengler, and M. Pärtel. 2012. Plant species richness: the world records. *Journal of Vegetation Science* 23:796–802.
- Wiser, S. K., R. B. Allen, P. W. Clinton, and K. H. Platt. 1998. Community structure and forest invasion by an exotic herb over 23 years. *Ecology* 79:2071–2081.
- Woudenberg, S. W., B. L. Conkling, B. M. O'Connell, E. B. LaPoint, J. A. Turner, and K. L. Waddell. 2010. *The forest inventory and analysis database: database description and user's manual version 4.0 for Phase 2*. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.

SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/14-2172.1.sm>