

1 **A unified approach to quantify invasibility and degree of invasion**

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16
17 *Abstract.* Habitat invasibility is a central focus in invasion biology due to its importance for
18 understanding basic ecological patterns and processes and for effective invasion management.
19 “Invasibility” is, however, one of the most elusive metrics and misused terminologies in ecology.
20 Empirical studies and meta-analyses regarding invasibility to date have produced inconsistent
21 and even conflicting results. This inconsistency and subsequent difficulty in making broad
22 cross-habitat comparisons stem in part from: (1) the indiscriminant use of a closely related but
23 fundamentally different concept - degree of invasion (*DI*) or level of invasion, and (2) the lack of

24 common metrics, as illustrated by our review of all invasibility papers published in 2013. To
25 facilitate both cross-habitat comparison and more robust ecological generalizations, we clarify
26 the definitions of invasibility and *DI*, and for the first time propose a common metric for
27 predicting invasibility based on a habitat's resource availability as inferred from relative resident
28 species richness and abundance. We demonstrate the feasibility of our metric using empirical
29 data collected from 2,475 plots from three forest ecosystems in the eastern United States. We
30 also propose a similar metric for *DI*. Our unified, resource-based metrics are scaled from 0 to 1,
31 enabling cross-habitat comparison. Our proposed metrics clearly distinguish invasibility and *DI*
32 from each other, which will help to (1) advance invasion ecology by allowing for the formation
33 of more robust generalizations and (2) facilitate more effective invasive species control and
34 management.

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36 *Key words: abundance; competition; index; invasion theory; niche availability;*
37 *prediction; resources*

INTRODUCTION

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Habitat invasibility and species invasiveness have together been a central focus in the field of invasion biology, not only because of their importance for invasion management, but also for our need to understand basic ecological patterns and processes. Nonetheless, “invasibility” is among the most elusive metrics, difficult to compare across habitats, and thus the terminology is perhaps frequently misused in ecology. Many hypotheses have been proposed to understand the relationships between invasibility and habitat features such as biodiversity (Elton 1958). However, empirical studies and meta-analyses into these relationships to date have produced inconsistent and even conflicting results (e.g., Jeschke et al. 2012, Catford 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: degree of invasion (*DI*) or level of invasion, which measures the extent to which a community has already been invaded (e.g., based on the number of exotic species, exotic fraction; see Catford 2009, Gurivitch et al. 2011). In most cases, *DI* increases over time. Historically, the terminology 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 usage 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 invisibility and habitat features.

The lack of commonly defined invasion metrics also makes it difficult to compare

61 invasion ecology studies and to generalize patterns and processes in invasion ecology. A review
62 of all articles indexed by Web of Science in 2013 (119 total; Table S1) that listed invasibility as a
63 keyword reveals that although most researchers seem to agree about what invasibility means in
64 general, no consistent measurements of this phenomenon exist. While the majority of studies to
65 date, especially those on large scales, have used the number of exotic species as an indicator of
66 invasibility (Elton 1958, Planty-Tabacchi et al. 1996, Lonsdale 1999, Moore et al. 2001, Fridley
67 et al. 2004, Herben et al. 2004), others have used density, biomass, cover, growth rate, or
68 survivorship of exotics (e.g., Smith et a. 2004, Catford et al. 2012). Yet, even within the same
69 community and time period, using different variables to quantify invasibility such as richness,
70 density, and biomass can generate different conclusions (e.g., Guo and Symstad 2008, Miller et
71 al. 2014).

72 Invasibility seems easier to define (below) but difficult to measure, whereas *DI* is easier
73 to measure but has not been consistently defined (but see Catford 2012). The combination of (1)
74 the lack of precise definitions and indiscriminant use of these two terms and (2) lack of common
75 metrics continues to lead to inconsistent or even conflicting results regarding the relationships
76 between invasibility and habitat features, hindering the comparison of otherwise comparable
77 studies and therefore the formation of more robust generalizations. In this article, we intend to
78 clarify the definitions of invasibility and degree of invasion (*DI*) and propose common metrics to
79 quantify these two concepts that can be broadly used for comparisons across different habitats.
80 To demonstrate the feasibility of our proposed metrics, we present an example using data
81 collected from 2,475 plots in three forest ecosystems in the United States by the Forest Inventory
82 and Analysis Program (FIA-<http://www.fia.fs.fed.us/>; [Bechtold and Patterson 2005](#), Woudenberg
83 et al. 2010). As invasive species continues to be one of the major challenges to nearly all

84 ecosystems (Simberloff 2012, Fei et al. 2014), our proposed common metrics will help to reduce
85 the hurdle for unifying theories in invasion ecology and better inform future land management
86 and policy making.

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88 DIFFERENCE BETWEEN INVASIBILITY AND DEGREE OF INVASION

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

99 In contrast to invasibility, which is a pre-invasion habitat property, “degree of invasion
100 (*DI*)” measures how much the community has already been invaded by exotic species, and thus
101 is an outcome of interactions between intrinsic (invasibility) and extrinsic factors. The extrinsic
102 factors may include invasion pressure (e.g., propagule/colonization pressure due to the
103 combination of proximity to exotic species sources such as ports, large cities and invader
104 identity/traits; Williamson 1996, Lockwood et al. 2009), disturbance, and time since invasion
105 (e.g., Clark and Johnston 2011, Miller et al. 2014; Fig. 1).

106 Given the above definitions, communities with similar *invasibility* could have very

107 different *DI*s, and *vice versa*, despite the fact that the two terms are often positively related to
108 each other. A community with low invasibility cannot have high *DI*, but one with high
109 invasibility could show either low or high *DI* depending on extrinsic factors. Furthermore, the
110 concept of “invasibility” is more valuable for theoretical and even tightly controlled
111 experimental studies (e.g., Case 1990, Robinson et al. 1995, Drake et al. 1996, Dukes 2001,
112 Wardle 2001), whereas *DI*, as a measure of exotic abundance and a potential correlate of impact,
113 is what we measure in observational (non-manipulative) field studies and compare among
114 empirical studies. In practice, invasibility is more difficult to measure due to its intrinsic nature
115 and the absence of pre-invasion historical data on communities that are already invaded.
116 Correspondingly, knowledge about invasibility is more informative for the prevention of future
117 invasions, whereas *DI* is more related to how to better prioritize the management of existing
118 exotics species.

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120 CRITICAL ELEMENTS OF QUANTIFYING INVASIBILITY

121 *Contribution of species richness vs. dominance*

122 There are several problems with using species richness or dominance alone in measuring
123 habitat invasibility (Levine and D’Antonio 1999). First, as argued above, at large scales and
124 especially under environmental fluctuations, there is little evidence that any habitat could have
125 stable long-term species saturation (Shurin and Srivastava, 2005); that is, all habitats are likely
126 invisable to some degree. In other words, short-term or transitional invasions could take place
127 even in “saturated” habitats due to temporal population fluctuations of dominant species.

128 Species richness is only one part of community structure, which also includes species
129 composition, evenness, abundance, and the age structure of each component species. Even if a

130 species has a unique niche, it still needs time to fill its niche space (consider a community in
131 early succession versus a clearly less invasible, pure, and dense forest stand; Clark and Johnston
132 2011). Also, in a highly fluctuating environment (e.g., one experiencing frequent disturbances),
133 high native species richness does not necessarily equate to high biomass and subsequent niche
134 occupancy because under such dynamic conditions species will rarely have the time necessary to
135 fully occupy niches. In other cases, richness of exotics and natives may be positively correlated;
136 both variables accumulate with area and heterogeneity, and can respond similarly to other factors
137 (Moore et al. 2001).

138 Biomass, on the other hand, can be another good indicator of controlling factors such as
139 resource uptake (e.g., as affected by disturbance; Crawly 1987) and resource supply (Davis et al.
140 2000). However, using biomass alone to quantify invasibility can also be misleading because it
141 misses the importance of invader identity and sampling effects - higher exotic richness may
142 contain more aggressive invaders that could penetrate even highly crowded communities
143 (Huston 1997). Therefore, predicting invasibility must take the two dominant factors (richness
144 and biomass) into account, and the approach must be simple and practical for broad comparisons
145 across communities and regions. However, for each particular community and for detailed
146 research, predicting invasibility with higher precision should also consider any special conditions
147 attached to it. For example, invasibility is after all often linked to the (phylogenetic) traits of
148 particular invaders *versus* that of competitors or facilitators in residence (Richardson and
149 Cowling 1992, Proches et al. 2008). If an invader has strong mutualistic relations with certain
150 resident species, it can successfully invade by outcompeting and/or replacing some resident
151 species.

152

153 *Absolute vs. relative values as estimates*

154 Using absolute or relative value (e.g., total number *versus* percentages) to measure
155 invasibility can lead to very different conclusions (Guo and Symstad 2008, Catford et al. 2012).
156 As argued earlier, invasions depend largely on the availability of unused resources. When a
157 habitat is still open with many niches available (e.g., in early succession), it is natural that other
158 species (native or exotic), if not dispersal limited, will invade (Williamson 1996). Because
159 communities are rarely saturated with species, high richness or biomass at a particular time does
160 not necessarily indicate low invasibility; natural or human-made habitats have varying carrying
161 capacities in total abundance or biomass and some can support higher richness and biomass of
162 both natives and exotics than others. Thus, assessing invasibility by using relative measures (i.e.,
163 fractions) would facilitate cross-community comparisons (Fig. 2).

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

173 On the other hand, estimating the maximum richness and biomass in a habitat can be
174 achievable through either direct field sampling or using historical records that are becoming
175 increasingly available and assessable. In practice, for small areas, the maximum species richness

176 and maximum biomass would be estimated with a relatively higher degree of accuracy than for
177 larger areas, but comparisons of invasibility or *DI* measures can still be compared over larger
178 scales using these estimates, especially for the same type of communities. One possible source of
179 data is historically accumulated vegetation sampling completed during the past century.
180 Additionally, large sampling efforts and datasets are becoming increasingly available around the
181 world (e.g., Global Biodiversity Information Facility: www.gbif.org; Chinese Forest Biodiversity
182 Monitoring Network: <http://www.cfbiodiv.org/>; and Forestplots.net:
183 <https://www.forestplots.net/en>). For many of these long-term monitoring datasets, estimates of
184 the maximum richness and biomass can be obtained for individual plots from the highest values
185 inventoried from many years of sampling. This is especially the case if the data cover entire
186 successional cycles and can therefore encompass the maximum richness and biomass values. An
187 alternative approach is to use data from nearby similar vegetation plots or to use the space-for-
188 time method if succession is taking place.

189 190 A UNIFIED MEASURE OF INVASIBILITY

191 Based on the above premises that invasibility is the intrinsic property of a community, in
192 contrast to previous studies that often use exotic richness as a measure of invasibility or *DI*, we
193 propose a generic metric for predicting invasibility (I_p) based on relative resident species
194 richness and abundance as,

$$195
196 I_p = 1 - (S_{\text{obs}}/S_{\text{max}} + B_{\text{obs}}/B_{\text{max}})/2 \quad (1)$$

197
198 S_{obs} and B_{obs} are the observed plot-level richness and biomass, and S_{max} and B_{max} are maximum

199 plot-level richness and biomass, respectively, within the habitat type (*i.e.*, resource-based
200 carrying capacity). Both S_{\max} and B_{\max} can be estimated from field measurements or inferred
201 from published literature (e.g., successional studies; see above). The values for I_p are scaled
202 between 0 and 1, with higher values equating to higher invasibility (e.g., Terborgh and Faaborg
203 1980, Wilson et al. 2012). Predicted invasibility (I_p) defined here is both standardized and
204 unitless, and can therefore be used to compare different ecological communities regardless of
205 successional stage. The relative importance of richness and biomass of resident species in
206 controlling I_p could switch over time (e.g., succession) or space (different habitat types or plots
207 of the same habitat; Fig. 2). Further work is needed to estimate the weighted contribution of
208 biomass and richness to I_p for certain habitat types. To predict future invasibility in a
209 community that has already been invaded, existing invaders should also be included as “resident”
210 (native and exotic species) species in the calculation.

211 To illustrate the utility of our proposed I_p metric, we used field-based measurements from
212 the U.S. Forest Service Forest Inventory and Analysis (FIA) program (Bechtold and Patterson
213 2005). We first developed a relative biomass-richness space by randomly selecting three forest
214 ecosystems, Midwest Broadleaf Forest, Prairie Parkland forest, and Adirondack-New England
215 mixed forest, from the FIA program (Fig. 3). Biomass and richness for resident tree species in
216 each plot were calculated. Relative biomass and richness for each plot were then calculated
217 using the observed biomass (B_{obs}) and richness (S_{obs}) divided by the observed plot-level
218 maximum biomass (B_{\max}) and richness (S_{\max}) within each forest ecosystem, respectively.

219 The zone with a slope of -1 in the upper-right corner of Fig. 3 encompasses the highest
220 values of S_{obs}/S_{\max} and B_{obs}/B_{\max} for the three forest ecosystems and represents possible habitat
221 saturation (see also Fig. 2) and/or trade-offs in the role of richness and biomass in resisting biotic

222 invasions. Within this zone, a community cannot have the highest richness and biomass at the
223 same time even though the two variables are often positively correlated when both values are
224 low. The biomass and richness ratios within this zone are inter-changeable in measuring and
225 controlling I_p , and this agrees with our equation (1) that one unit of relative biomass is
226 equivalent to one unit of relative richness. For the three forest ecosystems examined here,
227 richness appears to be closer to the saturation level while biomass is not, as suggested by the
228 majority of forest plots (> 60% in all three forests) distributed under the diagonal $x = y$ line (Fig.
229 3). Similarly, the large number of plots in the lower-left corner indicates great potential of future
230 invasions if exotic species pool becomes available.

231 Our proposed I_p index, a composite value based on richness and biomass for each plot,
232 allows comparisons across habitat types or successional stages. For example, in our case study,
233 there was no significant difference in the mean I_p value between Midwest Broadleaf Forest and
234 Prairie Parkland Forest (0.72 vs. 0.73, t - test, $df = 1,791$, $p = 0.248$). However, mean I_p of
235 Midwest Broadleaf Forest and Prairie Parkland Forest was significantly higher than that of
236 Adirondack-New England Mixed Forest (0.72 vs. 0.62, $df = 1,569$, $p < 0.0001$ and 0.73 vs. 0.62,
237 $df = 1,493$, $p < 0.0001$, respectively). Although our estimated mean I_p values only represent the
238 current status of these forests ecosystems and may change over time, the comparative results
239 from the above analyses offer important information for management prioritization and policy
240 making.

241

242 MEASUREMENT OF DEGREE OF INVASION

243 The reasoning behind our proposed I_p prediction leads us to re-evaluate and to improve
244 existing measures for DI . Similar to the predictive measure of invasibility (i.e., critical elements,

245 absolute vs. relative values), we also propose a common metric to measure degree of invasion
246 (*DI*). We argue that both number and dominance of exotic species are important to measure *DI*.
247 A single highly invasive species can disrupt ecosystem functioning in one community, with
248 typical examples such as kudzu (*Pueraria lobota*; Li et al. 2011) and reed canary grass (*Phalaris*
249 *arundinacea*; Green and Galatowitsch 2002). In such well-established pure stands of only one
250 invasive species, it can be difficult for other species (native or exotic) to invade. In contrast,
251 some other communities may harbor many non-invasive exotics but the functioning may remain
252 relatively unaffected (Guo and Symstad 2008). We propose to measure degree of invasion (*DI*)
253 as follows,

$$255 \quad DI = (S_{\text{exo}}/S_{\text{tot}} + B_{\text{exo}}/B_{\text{tot}})/2 \quad (2)$$

256
257 S_{exo} and B_{exo} are observed exotic richness and biomass, and S_{tot} and B_{tot} are total (native plus
258 exotic) richness and biomass in the community, respectively (see also Fig. 2 in which S_{max} and
259 B_{max} can be replaced by S_{tot} and B_{tot} for measuring *DI*). In order to make comparisons of *DI*
260 among communities, the value for *DI* is also scaled between 0 and 1, with higher values equating
261 to higher degree of invasion. We provided an example of applications of the *DI* metric in
262 Supporting Information (Fig. S1).

263

264

FUTURE DIRECTIONS

265 The factors affecting I_p and *DI* are inevitably interrelated (e.g., Sobrino et al. 2002; Fig.
266 4). Disturbance usually reduces the ratio of existing biomass to the maximum biomass ($B/B_{\text{max}} =$
267 R_B) in mature, stable communities but its effects on species richness are more complex (e.g., the

268 intermediate disturbance hypothesis or IDH; Grime 1973). Both I_p and DI would increase with
269 decreasing R_B . High richness and biomass could indicate a high level of species saturation (all or
270 most niches are occupied) and thus resistance to opportunistic invasions. Correspondingly, the
271 determinants of invasibility may not be the number of native species only; biomass must be
272 jointly considered as it is more directly related to competition (Bonser and Reader 1995). Based
273 on such arguments, we strongly suggest that habitat invasibility I_p should be evaluated as the
274 relative values of observed richness and biomass to community carrying capacity (or maximum
275 values), (2) DI measures should be based on the relative value such as proportion or fraction of
276 exotic richness and biomass in the community rather than absolute values of those measures, and
277 (3) additional and improved strategies to estimate maximum diversity and biomass should be
278 explored. For example, Potter and Woodall (2014) recently used site productivity classes and a
279 proxy for stand development when investigating the relationship between biomass and
280 biodiversity on FIA plots.

281 It is essential to note that time plays different roles in invasibility vs. DI and that the roles
282 vary at different temporal scales; that is, invasibility may change with the population fluctuation
283 of dominant species (e.g., Wiser et al. 1998, Clark et al. 2013). Over a relatively short period of
284 time such as a successional cycle, a community in early stages is more invulnerable than in later
285 stages (Fig. 4). Over longer-term (e.g., across multiple successional cycles), however, as exotic
286 species may continue to invade and some of them could stay and persist, DI almost always
287 increases (Fig. 4; Heard et al. 2012) unless management activities can act to slow or even reverse
288 this pattern. These differences will result in the long-term trend of invasibility varying in
289 relation to a more-constant mean and the DI trend steadily increasing or stabilizing.

290 In short, how invasibility and DI are defined and measured can strongly influence pattern

291 description and interpretations. In addition, clear distinction and appropriate use of habitat
292 invasibility vs. *DI* are critical for comparative purposes and for informing management (Catford
293 et al. 2012). The former is an intrinsic property of a habitat while the latter is an outcome of
294 species invasion controlled by both intrinsic and extrinsic factors. Because carrying capacity
295 varies over space and time, measures of invasibility should reflect niche availability for potential
296 invasions, and measures of *DI* should reflect the fractions of invaded species richness and
297 biomass in the community. The resource-based, unified indexes for both invasibility and degree
298 of invasion (*DI*) proposed here represent a step forward for both research in basic ecology and
299 informing land management and ecological restoration.

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301

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432

433 SUPPLEMENTAL MATERIAL

434 **Table S1**

435 A review of all articles indexed by Web of Science in 2013 (119 total) that listed
436 invasibility as the keywords reveals that although most researchers seem to agree about what
437 invasibility and *DI* mean in general, neither has a consistent measure.

438 **Fig. S1**

439 An example of applications of the proposed DI metric based on data from various
440 sources: Blue - northern California coastal grassland; Brown - North Coast Range, California;
441 Pink - northern Great Plains; Black - California chaparral; Green – mountain/desert shrub lands
442 and wetlands. For detailed descriptions about the data, see Guo, Q.F., and A. Symstad. 2008. A

443 two-part measure of degree of invasion for cross-community comparisons. *Conservation Biology*
444 22:666-672.

445

Supporting references

Figure legends

446

447

448 Fig. 1. The differences between invasibility and degree of invasion or DI in habitats across a
449 hypothetical landscape (note that propagule includes invader identity; Simberloff 1989).
450 The outcome of the interactions between invasibility (a) and invasion pressure (b) at a
451 specific time (t) leads to measured DI_t (c).

452

453 Fig. 2. The conceptual model showing the constraints of possible habitat saturation (i.e., S_{\max}
454 and B_{\max}) on invasibility, Ip (e.g., $IpA = IpB < IpC$) or degree of invasion, DI . The plots
455 on the dashed blue line have the same Ip . The relative importance of richness and
456 biomass could switch between early and late succession and across habitat types. Note
457 that replacing S_{\max} and B_{\max} with S_{tot} and B_{tot} would be for comparing DI values among
458 plots or habitats.

459

460 Fig. 3. An example of using the proposed definition and measure for invasibility using the US
461 FIA data (<http://www.fia.fs.fed.us/>): Midwest broadleaf forest (brown; $n = 969$), Prairie
462 Parkland forest (black; $n = 845$), and Adirondack-New England mixed forest (blue; $n =$
463 661). The forest plots close to the lower-left corner are more invisable than those in the
464 upper-right corner. The line in the upper-right corner connects the highest values of
465 S_{obs}/S_{\max} and B_{obs}/B_{\max} for each of the three forest ecosystems and represents possible
466 habitat saturation levels which vary among ecosystems. The diagonal red line ($x = y$)
467 separates the forest plots more saturated with richness (usually in early succession; i.e.,
468 plots below the line) and those more saturated with biomass (usually in late succession;

469 i.e., plots above the line).

470

471 Fig. 4. Differences between invasibility and *DI* based on the hypothetical and simplified temporal
472 trajectories in a community with varying a roughly 50-yr successional cycle. Invasibility
473 peaks in early succession and fluctuates around the mean during succession (short-term)
474 but may not show long-term trends. *DI* also increases in early succession due to high
475 invasibility but will show long-term increase as a consequence of continuing species
476 introductions but especially if “invasion meltdown” takes place (Simberloff and Von
477 Holle 1999), which may lead to extinction of native species. However, under extreme
478 conditions such as right after total habitat destruction due to volcanic eruption, *DI* could
479 briefly reach the maximum value of invasibility.

480

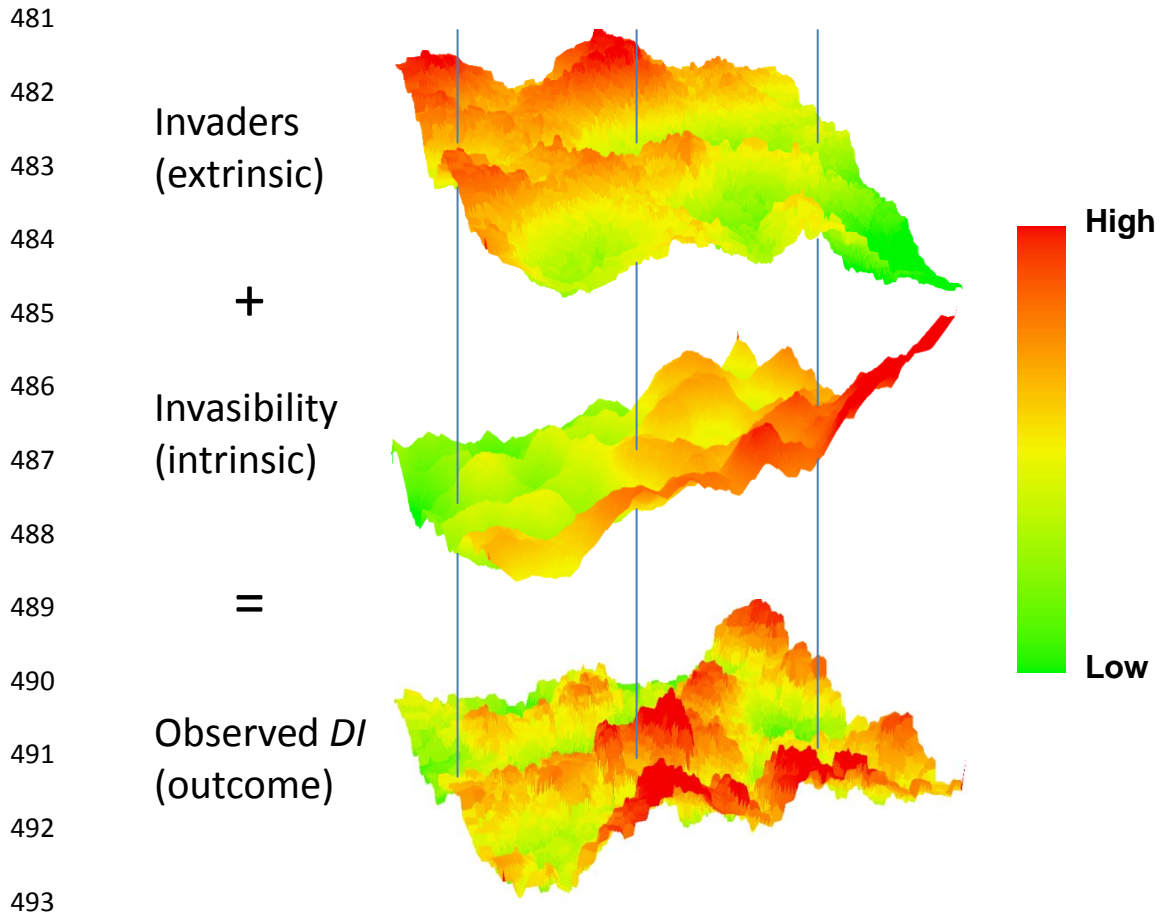
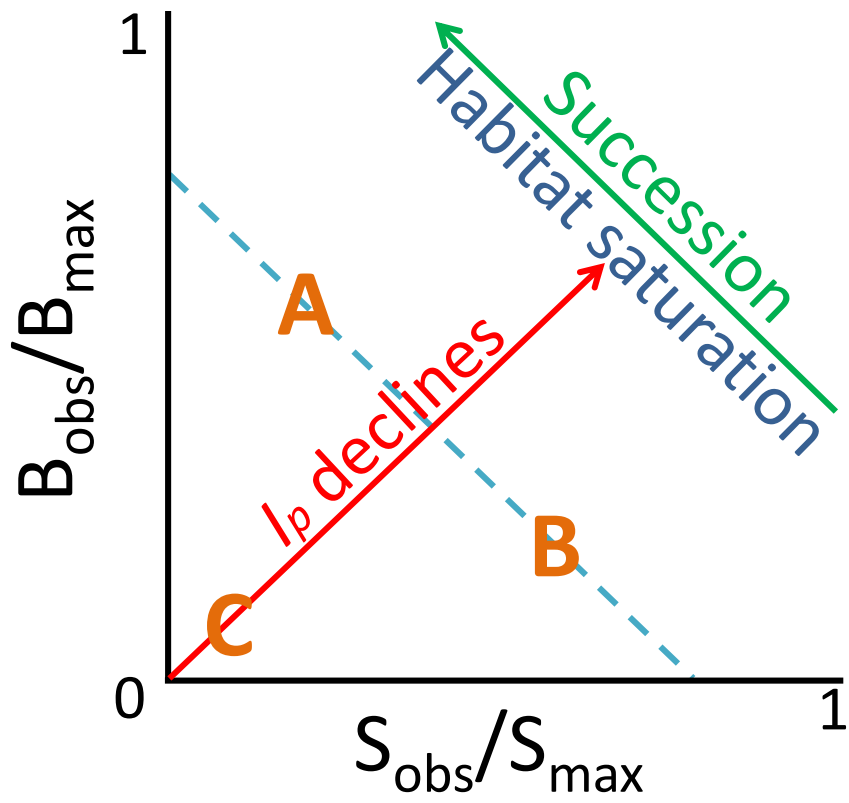


Fig. 1



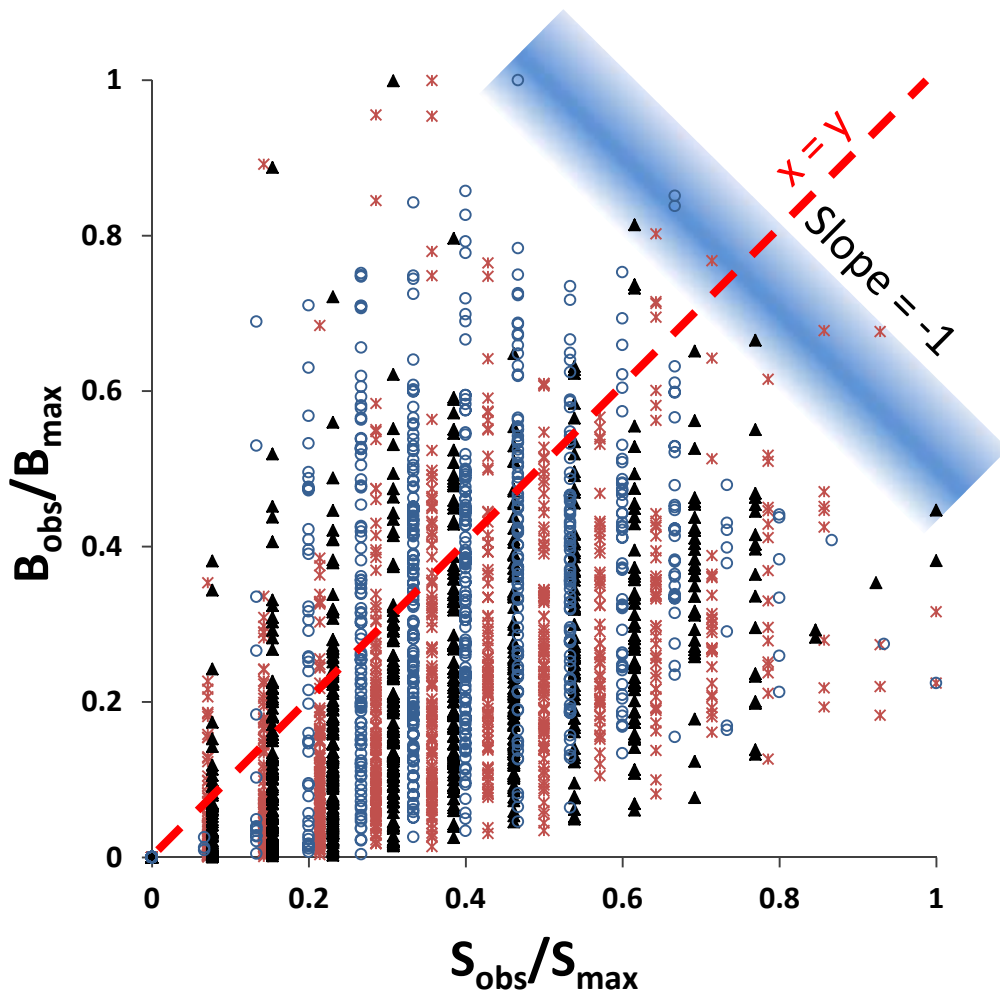
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500 Fig. 2

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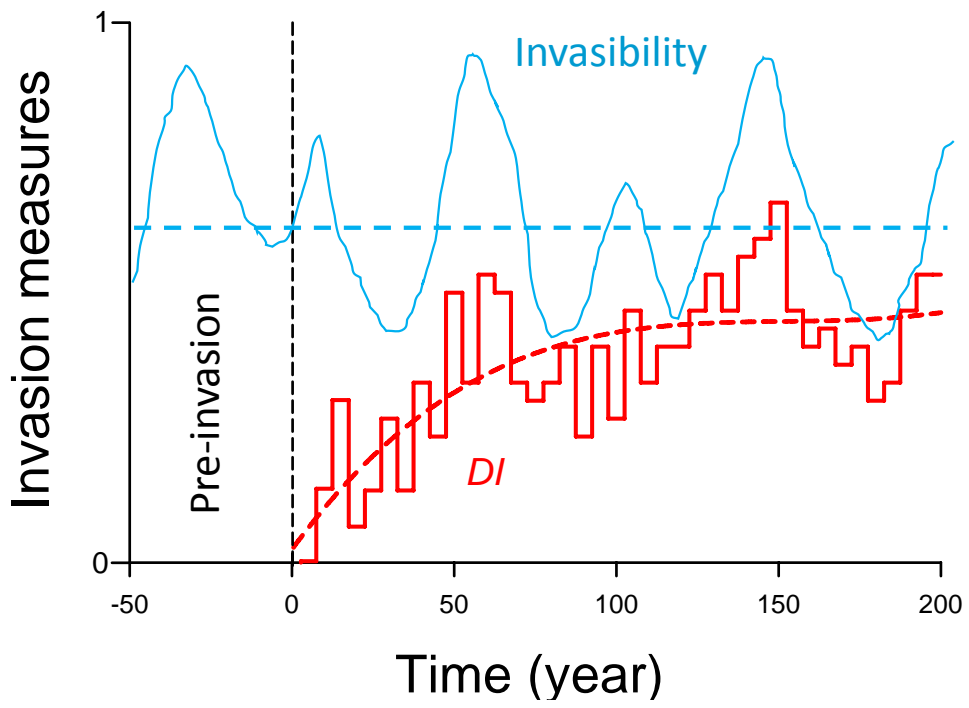


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504 Fig. 3

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510 Fig. 4

SUPPLEMENENTAL MATERIAL

Table S1

A review of all articles indexed by Web of Science in 2013 (119 total) that listed invisibility as the keywords reveals that although most researchers seem to agree about what invisibility and *DI* mean in general, neither has a consistent measure.



SUPPORTING TABLE S1.mht (Command Line)

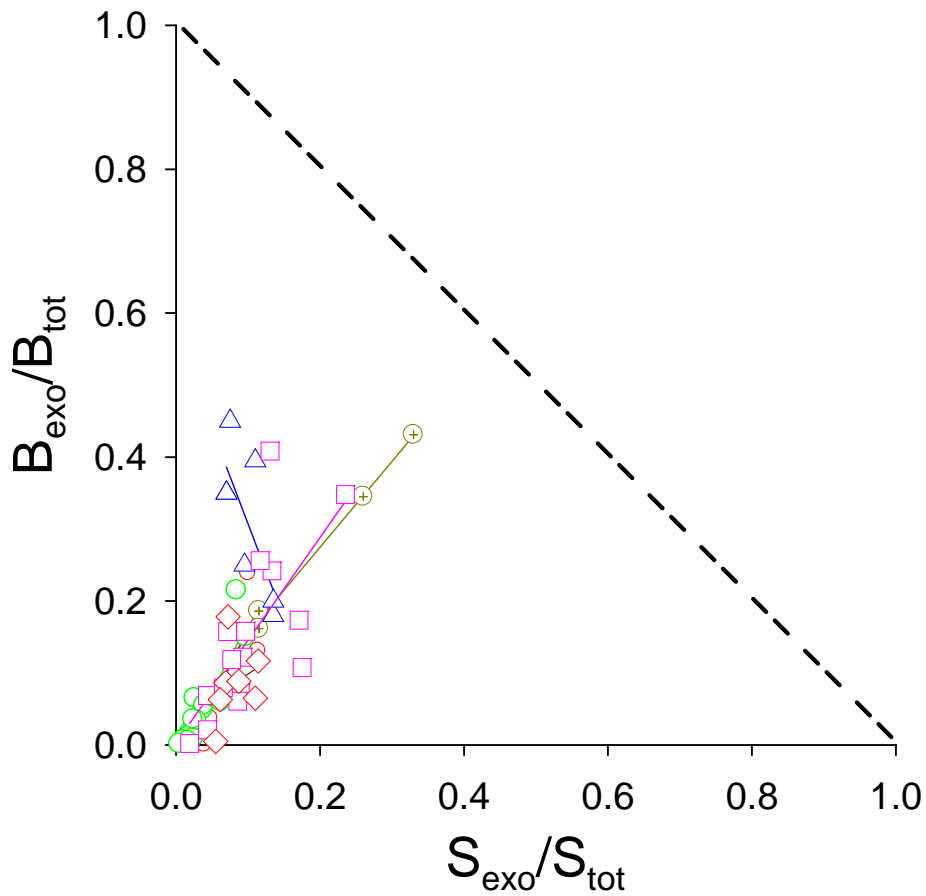


Fig. S1. An example of applications of the proposed DI metric based on data from various sources: Blue - northern California coastal grassland; Brown - North Coast Range, California; Pink - northern Great Plains; Black - California chaparral; Green – mountain/desert shrub lands and wetlands. There are large variations in *DI* both among and within habitat types (plots). For detailed descriptions about the data, see Guo, Q.F., and A. Symstad. 2008. A two-part measure of degree of invasion for cross-community comparisons. *Conservation Biology* 22:666-672.

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