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3 **On linking mechanism to invasive species impact**

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23 **Abstract**

24 Species invasion represents one of the major drivers of biodiversity change globally, yet there is
25 widespread confusion about the nature of non-indigenous species (NIS) impact. This stems
26 from differing notions of what constitutes invasive species 'impact' and the scales at which it
27 should be assessed. At local scales, the mechanisms of impact on competitors can be classified
28 into four scenarios: 1) minimal impact from NIS inhabiting unique niche space; 2) neutral
29 impact spread across the community and proportional to NIS abundance; 3) targeted impact on
30 a small number of competitors with overlapping niches; and 4) pervasive impact that is
31 disproportionate to NIS abundance and caused by modifications that filter out other species. I
32 developed a statistical test to distinguish these four mechanisms based on community rank-
33 abundance curves and then created a scale-independent standardized impact score. Using an
34 example long-term dataset, that has high native plant diversity and an abundance gradient of
35 the invasive vine, *Vincetoxicum rossicum*, I show that impact resulted in either targeted
36 extirpations or widespread biodiversity loss. Regardless of whether NIS impact is neutral,
37 targeted or pervasive, the net outcome will be the homogenization of ecosystems and reduced
38 biodiversity at larger scales, perhaps reducing ecosystem resilience.

39

40 **Introduction**

41 For the past 20 years, species invasions have consistently been ranked as one of the top five
42 causes of biodiversity decline globally (Sala *et al.* 2000; Butchart *et al.* 2010). Yet, no subject
43 area in applied ecology and conservation has elicited more scientific and popular confusion and
44 controversy than the nature of invasive species impact. There have been well-intentioned
45 scientific disagreements about whether non-indigenous species (NIS) generally, and specifically
46 those that become invasive, have negative impacts in ecosystems and whether these result in
47 species extinctions (Gurevitch & Padilla 2004; Ricciardi 2004; Simberloff 2005). Further, some
48 analyses of smaller scale diversity change potentially conflate native species losses with
49 increases from the arrival of NIS (Vellend *et al.* 2013; Vellend *et al.* 2017; Schlaepfer 2018), thus
50 not adequately capturing the myriad of spatial and temporal changes in biodiversity at local and
51 regional scales (Hillebrand *et al.* 2018; Tatsumi *et al.* 2020). These disagreements have spread
52 into larger, and perhaps, less scientific debates about whether NIS should in fact be managed as
53 a threat to biodiversity or if they should be accepted and even celebrated as symbolic of the
54 potential for resilience in a changing world (Shrader-Frechette 2001; Davis *et al.* 2011;
55 Simberloff 2011; Cadotte 2015; Pearce 2015; Pauchard *et al.* 2018; Ricciardi & Ryan 2018;
56 Schlaepfer 2018).

57

58 One facet of this confusion stems from differing notions and understanding of what constitutes
59 invasive species 'impact' and the scales at which it is important to assess it (Parker *et al.* 1999;
60 Crystal-Ornelas & Lockwood 2020; Flory & Lockwood 2020) and further how we manage these

impacts (García-Díaz *et al.* 2020). Impact, whether it be ecological, on native diversity and ecosystem functioning, or social, on economic and agricultural systems, is a central component of the definitions and guidelines for invasive species prioritisation (Robertson *et al.* 2003; Catford, Jansson & Nilsson 2009; Blackburn *et al.* 2011; Kumschick *et al.* 2012; Lockwood, Hoopes & Marchetti 2013; Hawkins *et al.* 2015; Obama 2016). Even though impact is the cornerstone of the definition of invasive species, the differing conceptualizations and interpretation of what constitutes impact can impair the implementation of best practices for identifying and controlling invasive species. Crystal-Ornelas & Lockwood (2020) show that evaluations of impact range from impacts on individual growth and reproduction on native species, to population changes, to community level diversity and to ecosystem level nutrient cycling and productivity. Widely used impact assessment tools, like the EICAT framework (Hawkins *et al.* 2015), delineates NIS based on their degree of impact, including ‘minor impact’ that might result in reduced population sizes of native species all the way up to ‘massive impact’ that results in irreversible changes like extinction. However, even if we specify a target biological scale and the appropriate measure of impact, an important conceptual confusion remains pertaining to the ratio of NIS abundance to impact. There is currently no clarity about whether impact is proportional to the abundance of the NIS or if the NIS has a disproportionate impact relative to its abundance (Parker *et al.* 1999), harkening classic discussion about the role of dominant species versus ecosystem engineers (Jones, Lawton & Shachak 1994), or whether large impact of an invasive species arises from multiple pathways.

I argue that the proximate mechanisms determining an invasive species impact happen at smaller scales where species interact, including competition for shared resources or interactions based on consumptive and exploitative relationships. Further, the larger-scale manifestations, like ecosystem impacts or extinction, are the sum of these local impacts. Thus, we need to evaluate how a specific NIS impacts local communities, which we can then extend to metacommunities or regional scales to quantify the fulsome impact.

Defining impact

In the analytical framework I present below, 'invader' is not a discretely defined entity, but rather it refers to a NIS whose increasing abundance has a measurable impact on local community diversity. Further, I am only considering competitive interactions, but as I indicate later, this framework can be extended to other trophic levels and even other stressors. NIS impacts within single trophic levels happen through the various types of interspecific competition (Holt 1977; Kawata 1997; Hubbell 2005; MacDougall, Gilbert & Levine 2009), including neutral, interference, exploitative and apparent competition. These mechanisms can result in different patterns and magnitudes of impact on community diversity. Within local communities, NIS, even if under neutral dynamics, can displace residents through random birth-death processes and eventually occupy space and pre-empt resource access simply through numerical dominance in a zero sum outcome -one's gain only comes at another's loss (Hubbell 2001; Chave 2004; Daleo, Alberti & Iribarne 2009). In this case, numerically rare resident species are the most likely to be excluded from a community first because all species have an equiprobable chance of having their abundances reduced, and the rarest species begin with an

abundance closer to zero. On the contrary, non-neutral impact can result in the exclusion of resident species that have the greatest niche overlap with the NIS as it's abundance increases (Shea & Chesson 2002; MacDougall, Gilbert & Levine 2009). This can happen because the NIS is simply a better competitor, or through release from the natural enemies in its native range, the NIS obtains higher growth and reproduction in its adventive range (Keane & Crawley 2002; Heger & Jeschke 2018), thereby outcompeting resident species with a high degree of niche overlap.

NIS could also impact the resident community in more pervasive ways than through simple resource competition. Some NIS can have broad community wide impacts by altering niche and resource availability and modifying ecosystem-level processes (Crooks 2002; Charles & Dukes 2008), and such invasions can cause wholesale changes to community diversity and composition, resulting in diversity loss and reduction in trait diversity, or alter the occupancy of trait space (Sodhi *et al.* 2019). These NIS can shift ecosystems by exuding novel chemicals which hinder native biota (Hierro & Callaway 2003; Zhang *et al.* 2020), by changing fires cycles (Brooks *et al.* 2004; Sugihara *et al.* 2006), or by influencing fundamental resource or environmental conditions (Herr *et al.* 2007; Broadbent *et al.* 2018). Such invasions can cause widespread diversity loss and reduce trait diversity or alter the occupancy of trait space (Hejda & de Bello 2013; Borer *et al.* 2014; Sodhi *et al.* 2019; Livingstone, Isaac & Cadotte 2020).

Conversely to these impact scenarios, a NIS can have no impact, if for example, the NIS occupies a unique niche and its presence does not appreciably reduce resident species

126 abundance or diversity (Case 1990; Shea & Chesson 2002; MacDougall, Gilbert & Levine 2009).
127 The logic here is that the resident community only inhabits a certain proportion of available
128 resources, thus allowing NIS to exploit unused resources, either because they possess unique
129 traits and have evolved different ecological strategies than natives, or perhaps that
130 disturbances or other external influences provide opportunity for the NIS (Catford, Jansson &
131 Nilsson 2009).

132

133 Superficially then, we can define impact as the magnitude of the change in the abundances and
134 richness of resident species, with the expectation that impact entails that both decline in
135 response to an increasing NIS abundance, with declines in richness being a more conservative
136 threshold for identifying impact. However, an observation of abundance and richness declines
137 in itself is not sufficient to determine how differing competitive mechanisms impact local
138 diversity. Beyond the scientific relevance for uncovering potential mechanisms, it might be
139 important to a manager or policy maker to quantitatively distinguish between diversity declines
140 that result from stochastic removal of resident individuals versus widespread impacts that are
141 disproportionate to the abundance of the NIS in question. These mechanisms certainly matter
142 for prioritizing which NIS should be managed, given limited resources (García-Díaz *et al.* 2020).

143

144 **The four scenarios of impact**

145 The scenarios of NIS impact on potential competitors outlined above results in four possible
146 outcomes for community residents facing an increasing NIS population size, namely, no
147 appreciable impact (scenario 1), exclusion of individuals proportion to NIS abundance (scenario

2), impact focussed on a few focal competitors (scenario 3), or broad and disproportionate impact (scenario 4). To evaluate these different types of impact, we need to view a community through the classic rank-abundance perspective of communities (Whittaker 1965) as intimated by Parker and colleagues (1999). Here species abundance is on the y axis and their rank on the x axis (Fig. 1A), such that the most abundant species is given a rank of 1. For our purposes here, let's assume that the resident community's rank-abundance curve is estimated at time t and a new NIS (i.e., a species that colonizes with an existing community and increases in population size, or ecological 'invader' -which will be used for simplicity below) colonizes the community and reaches equilibrium abundance, I_A , by $t + 1$. Under neutral dynamics, our expected impact should be simply stochastic competition for space, and assuming that each unit of abundance (i.e., number of individuals, biomass or percent cover) represents an equivalent per capita effect on the resource (space), then the community wide effect of the invader is an average decrease in abundance of residents proportional to the invader's abundance. Each resident species' abundance at $t + 1$ is then:

$$A_{i,t+1} = A_{i,t} - \frac{I_A}{S} \quad \text{eq(1)}$$

Where A_i is the abundance of species i and S is the total number of resident species. For any resident species where $A_{i,t+1} \leq 0$, they will be locally extirpated. Thus, the expected number of such extirpations, \hat{k} , in the set of abundances in a community rank abundance curve, A , is:

$$\hat{k} = \left| a \in A : a < \frac{I_A}{S} \right| \quad \text{eq(2)}$$

168 Given the deterministic nature of this expectation, the ranks of these species will simply be all
 169 those species at the end of the rank-abundance curve with abundances below the threshold
 170 and so the expected lowest rank, R , to be extirpated will be:

$$171 \quad R = S - \hat{\kappa} \quad \text{eq(3)}$$

172 Giving us the expected average rank of:

$$173 \quad \bar{R} = \frac{\sum [R, \dots, S]}{\hat{\kappa}}$$

$$174 \quad \text{eq(4)}$$

175 The expected number of extirpations, $\hat{\kappa}$, and the average expected rank of extirpated species, \bar{R}
 176 , provides us with baselines to compare to observed number and rank of extirpated residents.

177 From these comparisons, there are four different possible impact scenarios.

178

179 The first impact scenario (Fig. 1B) is where the observed extirpations, κ_o , is lower than the
 180 expected and the average observed rank of extirpated species, \bar{R}_o , is greater or equal to the
 181 expectation:

$$182 \quad \kappa_o < \hat{\kappa}; \bar{R}_o \geq \bar{R} \quad \text{eq(5)}$$

183 And this would be the logical outcome if the NIS occupied a unique niche with limited
 184 competitive impact on the resident species, causing lower abundance reduction and thus fewer
 185 extirpations than expected under neutral dynamics (Fig. 1B).

186

187 The second scenario (Fig. 1B) is simply our neutral dynamics scenario that generated our
 188 expectations. We expect that if the NIS is filling space and impacting residents proportional to

its abundance, we should see, on average, a constant decline in each resident's abundance (Fig. 1B). The observed number of extirpations and their average ranks should be the same as the expected:

$$\kappa_o = \hat{\kappa}; \bar{R}_o = \bar{R} \quad \text{eq(6)}$$

In the third scenario, the NIS has high niche overlap with one or more specific residents, and coupled with a potentially increased competitive ability in the adventive range, it's impact is predominately concentrated on the overlapping species (Fig. 1B). Here then, we might expect the impact of a NIS to be focused on a similarly ranked species in the rank abundance curve, resulting in fewer extirpations, which occur at a lower average rank, than if the abundance of the NIS was spread across the community, such that:

$$\kappa_o \leq \hat{\kappa}; \bar{R}_o \leq \bar{R} \quad \text{eq(7)}$$

Finally, in extreme cases, a NIS can not only compete with other species, but also modify the local environment, such that there is a greater reduction in abundance and disproportionate exclusion of natives, than predicted by the NIS abundance:

$$\kappa_o \geq \hat{\kappa}; \bar{R}_o \leq \bar{R} \quad \text{eq(8)}$$

To test these four scenarios are testable with observational community data, with observations before and after a NIS arrives and increases in abundance, are needed, with the assumption that the community prior to invasion was at equilibrium. These scenarios can then be statistically assessed by stochastically removing abundance units from resident species

211 proportional to the NIS abundance. This generates a neutral community where all individuals
 212 compete equally for the same resources (i.e., space) and are removed according to random
 213 processes with the rarest species most likely to be extirpated. This stochastic simulation can
 214 then be run for some number of iterations (e.g., 999) to generate a null expectation for the
 215 average number of extirpations ($\overline{\hat{\kappa}_{null}}$) and the average rank ($\overline{\hat{R}_{null}}$) of those extirpations, as well
 216 as their standard deviations ($\sigma_{\hat{\kappa}_{null}}$ and $\sigma_{\hat{R}_{null}}$, respectively). The standardized effect size (SES) of
 217 these two measures can be estimated as the z-values:

$$218 \quad SES.\kappa = \frac{\kappa_o - \overline{\hat{\kappa}_{null}}}{\sigma_{\hat{\kappa}_{null}}} \quad eq(9)$$

219

$$220 \quad SES.\bar{R} = \frac{\bar{R}_o - \overline{\hat{R}_{null}}}{\sigma_{\hat{R}_{null}}} \quad eq(10)$$

221 Significance can be assessed using either the rank of the observed value relative the full
 222 distribution of the randomized estimates and compared to the 95% confidence interval or, if
 223 normality assumed, against the z-distribution, which is -1.96 for the lower tail (i.e., fewer
 224 extirpations or lower rank than expected) and 1.96 for the upper tail (more than expected) at
 225 the 95% confidence level.

226

227 Given this diagnostic test, the four scenarios can be distinguished based on whether the
 228 number of extirpations and their average ranks are lower, greater or indistinguishable from the
 229 null expectation ($z = 0$; see Fig. 1C). Thus, when the NIS occupies a unique niche with little
 230 impact (scenario 1), the SES values for both the number of extirpations and their ranks should
 231 be less than expected ($z < 0$). Neutral community impacts (scenario 2) should exhibit $z = 0$ for

both measures. In a case where the impact of the NIS is largely on a few species with a high degree of niche overlap (scenario 3), we should observe $z \leq 0$ for number of extirpations and $z < 0$ for their average rank. Finally, for NIS that have disproportionate impact (scenario 4), we should see $z \gg 0$ for extirpations and $z < 0$ for average rank (Fig. 1C).

A hypothetical example

To highlight the utility of the method presented above, I use a simple hypothetical community. Code, in the R programming language, to calculate SES values and the following example, is available at <https://github.com/mcadotte/impact>.

The example community includes 20 species exhibiting a lognormal distribution (Fig. 2), with maximal resident abundance of 100. From randomizations, we can determine the average number of extirpations expected with any I_A value, and in this example, $\overline{\hat{K}_{null}} \approx 3.3$ species when $I_A = 100$ (that is, the NIS becomes co-dominant with the most abundant resident). In scenario 1, only one extirpation occurs, of a rare species, in line with the NIS occupying a niche with limited overlap with residents. In this case, we see significantly fewer extinctions ($z = -2.49$; $P = 0.008$) but the rank is not significantly different than the random expectation ($z = 0.80$; $P = 0.218$) (Fig. 2).

In scenario 2, the number of extirpations was similar to the expected number ($n = 3$) and the rarest residents were the ones that went extinct. Neither the number of extirpations ($z = -0.31$;

P = 0.394) nor the average rank of extirpated species ($z = 0.82$; $P = 0.220$) were significantly different than the null expectation (Fig. 2), supporting neutral replacement.

In scenario 3, the number of extirpations was slightly fewer than expected ($n = 2$) but these were not the rarest species. In this case the number of extirpations was not significantly different than expected ($z = -1.43$; $P = 0.104$) but the average rank of extirpated species was significantly lower (i.e., more abundant species) than expected ($z = -11.65$; $P = 0.001$) (Fig. 2).

Finally, scenario 4 represents the case where the NIS had a disproportionate negative impact on resident diversity. In this case, there were significantly more extirpations than expected ($z = 2.86$; $P = 0.003$) and a significantly lower average rank ($z = -14.03$; $P = 0.001$) (Fig. 2).

Using this in real world settings

The framework described in this paper is for an idealized case where we have richness and abundance data for a community pre-invasion, at what we assume is its equilibrium, as well as post-invasion, once species interactions have had sufficient time to alter resident diversity. This type of data is not commonly available, and more importantly, real world data would likely not conform to the assumption of equilibrium before invasion and post-invasion equilibrium.

However, this framework can be applied to any repeatedly sampled plot where the abundance of a NIS increases over time. Even if the NIS is already established at time t , and it has likely had some impact, if it continues to increase in abundance substantially, its impact might still

274 conform to one of the four scenarios. In this case, the NIS abundance, I_A , should not be its total
275 abundance, but rather the increase in abundance, $I_A = I_{A,t+1} - I_{A,t}$.

276

277 Moreover, most real communities will be invaded by multiple species or have a number of non-
278 invasive naturalized NIS. The researcher will need to decide what constitutes the resident
279 community. If some non-dominant NIS are long-term residents of a community, then it makes
280 logical sense to include them as members of the recipient community since they are apparently
281 kept in check by the mechanisms that structure the community. This method is useful in the
282 case where a NIS arrives and increases to high abundance in a relatively short amount of time.
283 What about when multiple NIS arrive and obtain high abundances (Von Holle & Simberloff
284 2005)? In this case, unless there are multiple plots with variable NIS abundances, where
285 differences in their abundances can help us infer specific NIS impacts, then the way forward is

286 to group them together and assess the impact of invasion, such that $I_A = \sum_i^I A_i$.

287

288 **Extending the framework spatially**

289 This framework can be used in the absence of data from repeatedly sampled plots so long as
290 sufficient plots have been sampled spatially, and that include invaded and uninvaded plots in
291 close proximity. Plots can be paired (e.g., Malloch *et al.* 2020) as invaded and uninvaded ,
292 assuming that both plots would have identical composition and rank abundance curves, which
293 might be plausible if assessed across large numbers of plot pairs. Another option could be to
294 create an average rank-abundance curve from multiple uninvaded plots to compare with the

295 invaded ones and then assess the average number of extirpations with increasing NIS
296 abundance. In this case, this regional rank-abundance curve can be resampled to produce
297 average rank-abundance curves and we can assess the average difference in plots with the
298 invader present. Such a spatial approach is laden with assumptions about the homogeneity of
299 communities across scales and requires detailed system understanding to reinforce inferences.

300

301 An alternative approach could be to use occupancy at a larger scale in invaded and uninvaded
302 plots. Here then we analyze a rank-occupancy curve across multiple plots. While the scenarios
303 and mechanisms outlined in Fig. 1 might play out at larger scales, analyzing occupancy might
304 intermingle with other mechanisms beyond local competition (e.g., colonization differences).
305 However, see the next section to scale up impact.

306

307 **Scaling up impact**

308 In a classic paper on NIS impact, Parker and colleagues (1999) conceived a way to quantify
309 impact as the product of three quantities: range size (in m^2), average abundance (per m^2) and
310 the per capita effect of the NIS on native diversity. This equation, for the first time, provided
311 researchers with a way to compare the relative impact of different NIS within a region.

312 However, comparing this impact measure between regions is difficult if physical area is
313 different (e.g., island versus mainland) and if the underlying environment supports different
314 average abundances (e.g., an arid versus moist habitat). Further, the multiplicative nature of
315 their formula can result in large numerical differences with minimal ecological differences. As
316 Parker and colleagues (1999) note, their measure is scale dependent.

317

318 Using the scenarios outlined in Fig.1, we can adapt the Parker impact measure to be scale
319 insensitive thereby allowing us to compare between regions, since the per capita effect is
320 capture by $SES.K$, described above. We can create within-region, scale-independent range and
321 abundance measures that are also standardized effect sizes (SES). The abundance and range
322 estimates rely on a species by site matrix, where cells are estimates of local abundance for each
323 species observed. The standardized effect size of abundance ($SES.ab$) compares the observed
324 average abundance of the focal NIS (ab_o), standardized by the mean and standard deviation
325 from randomizing the abundances for each site and calculating mean abundance for a single
326 species some number of iterations (e.g., 999), calculated as:

327

328
$$SES.ab = \frac{ab_o - \overline{ab_{null}}}{\sigma_{ab_{null}}} \quad eq(11)$$

329

330 If we use sampled occupancy for our measure of range (i.e., number of community samples,
331 from plots or sites across a protected area, city, county, etc., where the NIS is observed), the
332 observed range (occupancy, occ_o) of the NIS is simply the summation of observations across W
333 sites. Again, we can randomize the matrix and sum presences to get the null distribution to
334 calculate $SES.occ$:

335

336
$$SES.occ = \frac{occ_o - \overline{occ_{null}}}{\sigma_{occ_{null}}} \quad eq(12)$$

337

338 All three of these *SES* values are z-values and so significantly greater than expected when *SES* >
 339 1.96 and significantly lower than *SES* < -1.96 (from a two-tailed test). These additional
 340 geographic components of an NIS distribution, combined with *SES*. κ , highlight four possible
 341 invasion scenarios (Fig. 3). In line with Parker et al. (1999), except using an additive formulation
 342 rather than a multiplicative one so that we retain the z-value distribution, we can calculate a
 343 standardized impact score (*SIS*):

$$344 \quad \quad \quad SIS = \frac{SES.\kappa + SES.ab + SES.occ}{3}$$

345 eq(13)

346

347 Since the *SIS* is a z-value, the deviation from a value of 0 (outside of -1.96 and 1.96) indicates
 348 deviation from a neutral or average expectation. These z-values can then be directly compared
 349 across different taxa and regions to identify the most invasive species regardless of biome size
 350 or productivity.

351

352 **Assessing the impacts of a dominant invader in a natural system**

353 To showcase how we can use observational data to assess which of the scenarios of impact
 354 community dynamics fit, I use an example long-term dataset where a dominant non-indigenous
 355 vine (*Vincetoxicum rossicum* or dog-strangling vine) has invaded large sections of the Rouge
 356 National Urban Park, located on the eastern edge of Toronto, Canada (Sodhi et al. 2019;
 357 Livingstone, Isaac & Cadotte 2020). Collaborators and I have been collecting species
 358 composition and abundance data in hundreds of plots distributed across 14 sites in the Park

annually since 2013 (for methodological details, see: Livingstone, Isaac & Cadotte 2020). The data used in this analysis is available at: [Dryad link to be added]. Here I consider plots sampled in 2013 as $t = 1$ and compare these to a 2019 sampling ($t = 2$). While plot richness is correlated between these two sampling periods, there has been a net loss of species (Fig. 4A slope $\beta < 1$, and Fig. 4B mode of richness change < 0). Further, plot richness is negatively correlated with *V. rossicum* cover for both years (Fig. 4B & C). Given the large number of plots where *V. rossicum* cover increased (Fig. 5A), it is reasonable to investigate the degree and type of impact.

I subsetting plots into those with five or more resident species recorded and that have *V. rossicum* present in the 2019 plots, and then those that experienced increases in *V. rossicum* cover, resulting in 90 plots that were analyzed for invader impact. I then performed the SES analyses describe above and in Figs. 1-3.

In virtually every instance where *V. rossicum* cover increased and resident species declined, the SES analyses for number of extirpations and average rank was significantly different from random expectations (Supplemental Table S1). Surprisingly, no instances of neutral impact (scenario 2-Fig. 1) were detected, and the plots were evenly distributed amongst the other three scenarios (Fig. 5D). I then examined how resident richness in 2013 and change in *V. rossicum* cover influenced the probability of which scenario a plot fit using multinomial Log-linear models (using the `multinom` function in the `nnet` package in R). Scenario membership was significantly influenced by both 2013 richness and change in *V. rossicum* cover ($P < 0.001$, AIC = 122.14 for full model vs. 149.98 for change in *V. rossicum* cover only and 211.24 for 2013

richness only, and 2013 richness and change in *V. rossicum* cover were not significantly correlated; $r = -0.11$, $P = 0.17$). Interestingly, the probability of a plot showing that *V. rossicum* had no appreciable impact (i.e., unique niche space, scenario 1) was negatively correlated with resident richness, meaning that *V. rossicum* invading species poor assemblages had relatively little impact (Fig. 5E). The probability of a plot exhibiting changes consistent with large and disproportionate impact of *V. rossicum* increases (scenario 4) increased with resident richness, but decreased with *V. rossicum* cover change (Fig. 5E & F). This means that small abundance changes had disproportionate impact in species rich assemblages. Finally, targeted impacts (scenario 3) were largely independent of resident richness (Fig. 5E), and highlighted that in many of these communities, rare species were not more likely to be extirpated than more abundant species.

Final, I estimated the three *SES* components of the standardized impact score (*SIS*), and all three were greater than zero: $SES_{.K} = 1.11$, $SES_{.ab} = 51.87$, and $SES_{.K} = 29.63$. Overall, $SIS = 27.54$, indicating that *V. rossicum* deviates greatly from random expectation with major impact and should be of high concern (the red area in Fig. 3).

On what impact means and why we should be concerned

While the methods and concepts presented here make inferences about small-scale interactions and local extirpations, I also show that impact can be extended to larger spatial scales. Recurrent evidence of substantial impact within small-scale plots can be used to scale-up estimates of large-scale impacts or to predict the consequences of future spread of a NIS

403 species that is newly spreading (i.e., yellow region of Fig. 3). In the data example above, *V.*
404 *rossicum* did not appear to impact communities in a way that was consistent with neutrality,
405 but rather exhibited targeted or broad extirpations (beyond what was expected based on its
406 abundance) in species-rich communities, likely because it has been shown to release
407 allelopathic chemicals (Douglass, Weston & Wolfe 2011). This invasive vine is currently
408 spreading throughout eastern North America, and from these analyses, we would predict
409 consistent species loss greater than would be predicted from its abundance.

410

411 Not only is it scale independent, the framework presented here also aligns with other concepts
412 of impact, while providing mechanistic inferences underpinning different modes and
413 magnitudes of impact. The commonly employed impact scheme, the IUCN's Environmental
414 Impact Classification for Alien Taxa-EICAT (Blackburn *et al.* 2014; Hawkins *et al.* 2015) classifies
415 non-indigenous species into impact categories that include: *Minimal*, with little impact on
416 resident species reproduction or growth; *Minor*, with reproduction and growth impacts but no
417 population-level consequences; *Moderate*, resulting in the decline of at least one population;
418 *Major*, causing local extirpation of at least one species; and *Massive*, causing extirpations that
419 are irreversible. The framework presented here can distinguish among the classes from
420 *Moderate* to *Massive* impact. But more importantly, this framework can determine if the non-
421 indigenous invader impacts are predicted by per-capita effects that are correlated with its
422 abundance or if it has large and pervasive impacts even at low abundance. These two scenarios
423 would elicit different levels of concern and management and would be able to predict if a new
424 NIS will fall into, for example, EICAT's *Moderate* or *Massive* impact levels. This framework

quantifies impact statistically, and does not rely on the determination of concepts like 'several' and 'irreversible', which might vary subjectively with differing assessors. Furthermore, this framework could be extended to other types of interactions, such as invasive predator impacts on prey communities, with changes to the underlying mechanisms.

While this impact framework clearly shows that different mechanisms result in different forms of community impact, all forms of impact, except for when an invader occupies a unique niche (scenario 1) and has low occupancy and average abundance, are forms of impact that we should be concerned about. It might seem intuitive to think of within-community neutral dynamics as not giving rise to negative impact, it in fact does. If stochastic or external factors (e.g., propagule pressure from gardening activities; Dehnen-Schmutz & Touza 2008) result in high relative abundance of NIS, then these species will result in reduced abundance of resident species and potentially the loss of rare species, followed by the loss of more abundant species as the NIS abundance increases. No general decline in plant species richness was observed in a global meta-analysis by Vellend and colleagues (Vellend *et al.* 2013), but they did observe native species loss with replacement by non-indigenous species. This is a sinister form of impact, and can result from neutral-type impact, where the net result is that communities are homogenized and species diversity declines at larger spatial scales (Hillebrand *et al.* 2018). This is a good example of how local impact can potentially scale up to biodiversity loss and with the standardized impact score (SIS), even if a species has neutral-type replacement of community residents and so $SES_K = 0$, if it has a larger occupancy or abundance values, then it would still be listed as being of concern.

447

448 **Future directions**

449 The method introduced here can be used to assess non-indigenous species impact in
450 observational and experimental systems and to reduce definitional uncertainty with defining
451 and evaluating invasion impacts (e.g., Latombe *et al.* 2019). Work needs to be done to
452 determine how sensitive or limited this method is to non-ideal conditions where the invader
453 might have already been present for a long period of time and exerted impact prior to data
454 collection. Further, NIS can impact resident species by mechanisms other than competition,
455 including by potentially altering pollinator communities (Schweiger *et al.* 2010), through
456 predator-prey relationships (Roemer, Donlan & Courchamp 2002) or serving as pathogen
457 reservoirs (Sébastien *et al.* 2015), and it is not clear how this method would identify these, but
458 it would pick up community level changes. Clearly, this method need not be limited to within-
459 trophic interactions or even biotic impacts. Given a clear set of predictions about the potential
460 impacts of pathogens or predators, this method could be adapted to assess impacts of the
461 invasion of species from higher trophic levels or increases in the abundance of natural enemies,
462 where per-capita effects are consumptive (e.g., Griffen *et al.* 2020).

463

464 Conceivably, this method can be further adapted to assess the impact of any external driver
465 that might have species-specific or community level effects, like pollution or drought. In these
466 cases, translating the amount of stressor into a per-capita effect is more complicated and
467 requires additional information. This last application is currently being developed.

468

Finally, the framework developed here focussed explicitly on the negative impacts of invasive species. However, it is reasonable to assume that this method could also be used to detect the impacts of changes in abundance of native species on local competitors to test general hypotheses about the temporal dimensions of diversity change. Further, this method can detect positive (e.g., facilitative) effects of species that either increase in abundance or colonize a new area, for example in cases of invasional meltdown (Von Holle & Simberloff 2005).

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Figure legend

Fig. 1: The conceptual framework for detecting the degree and likely mechanism of non-indigenous species (NIS) impact on a community. A) The change in the species number and abundance from a rank-abundance curve can allow for the determination of likely mechanism of impact. B) These impacts can be the outcome of one of four mechanisms: 1) minimal impact from NIS inhabiting unique niche space; 2) neutral impact spread across entire community and proportional to NIS abundance; 3) targeted impact on species with overlapping niche requirements and which compete with NIS; and 4) pervasive impact that is disproportional to NIS abundance and ostensibly caused by ecosystem modification that filters out other species. C) To differentiate likely mechanisms underpinning patterns of community change, we can employ randomization tests and calculate the standardized effect sizes of the expected number of extirpations and the rank of extirpations based on the abundance of the NIS.

Fig. 2: The output of the standardized effect size tests for four different impact scenarios, including low impact (scenario 1), neutral-type impact proportion to the invader's abundance (scenario 2), targeted impact where species are extirpated independent of their abundance (scenario 3), and finally broad community scale impacts (Scenario 4).

Fig. 3: The combination of standardized effect sizes from expected extirpations (SES_K) and from either occupancy (SES_{occ}) or abundance (SES_{ab}) can identify the magnitude of non-indigenous species impact and the degree of management concern.

Fig. 4: The observed patterns of diversity change and degree of invasion by *Vincetoxicum rossicum* in the Rouge National Urban Park, Canada. A) Observed plot richness is correlated between the two sampling years used in this analysis. Species richness in plots is negatively correlated with *V. rossicum* abundance for both B) 2013 and C) 2019.

Fig. 5: Patterns of change in the sample plots between the 2013 and 2019 samplings, including: A) change in percent cover of *V. rossicum*, B) change in plot richness and C) the relationship between the two. The shaded box in C corresponds to the plots where impact of *V. rossicum* was assessed. D) *V. rossicum* impact was evenly divided into three of the four scenarios outlined in Fig. 1. The probability of plots belonging to these three scenarios depended on E) species richness in 2013 and F) the amount of *V. rossicum* change.

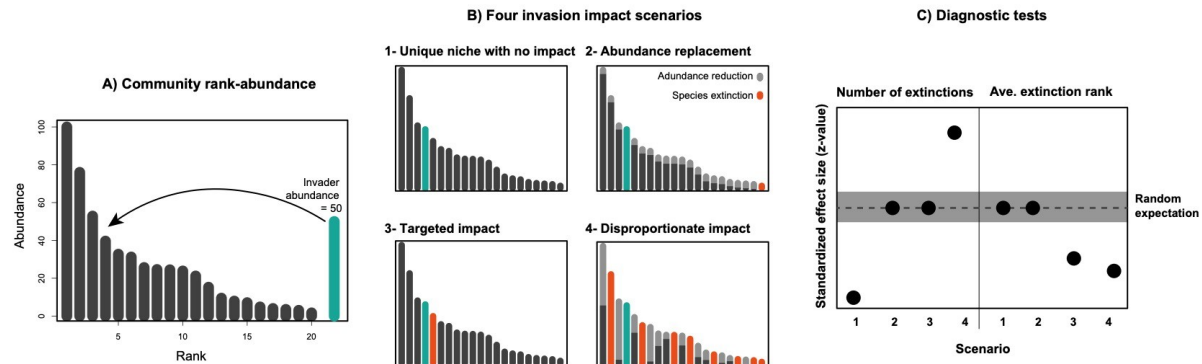
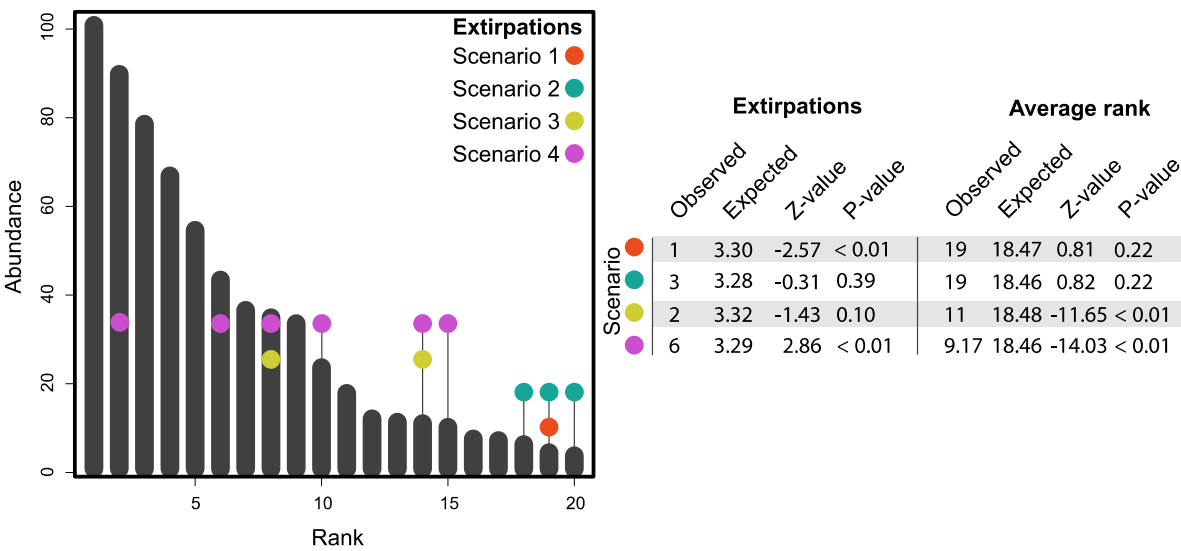


Fig. 1

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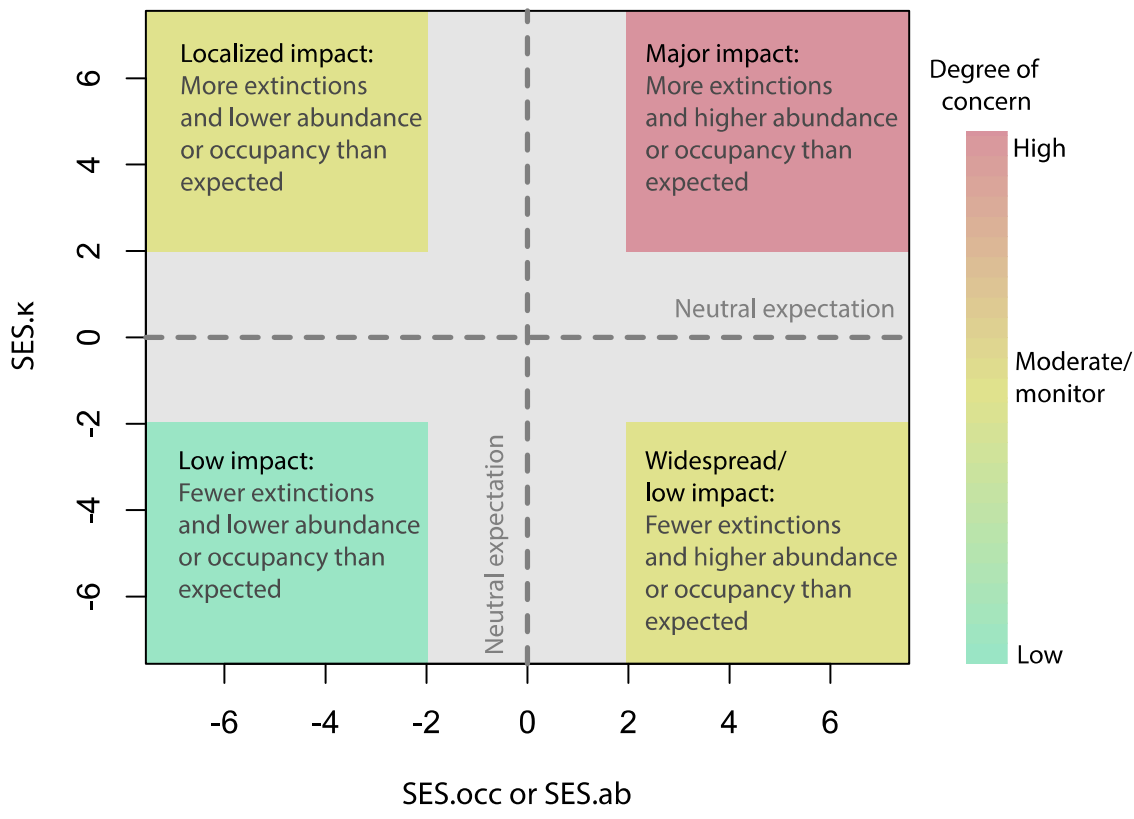


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702 Fig. 2

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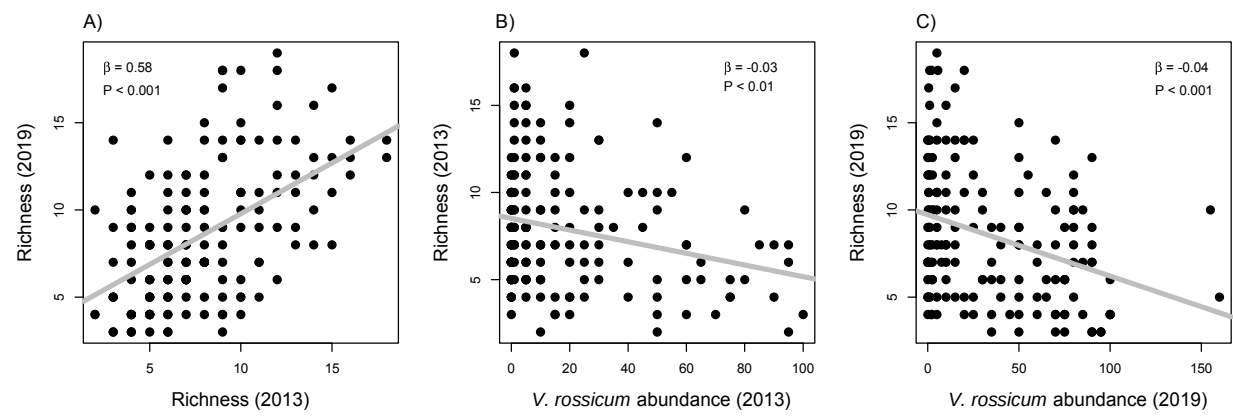
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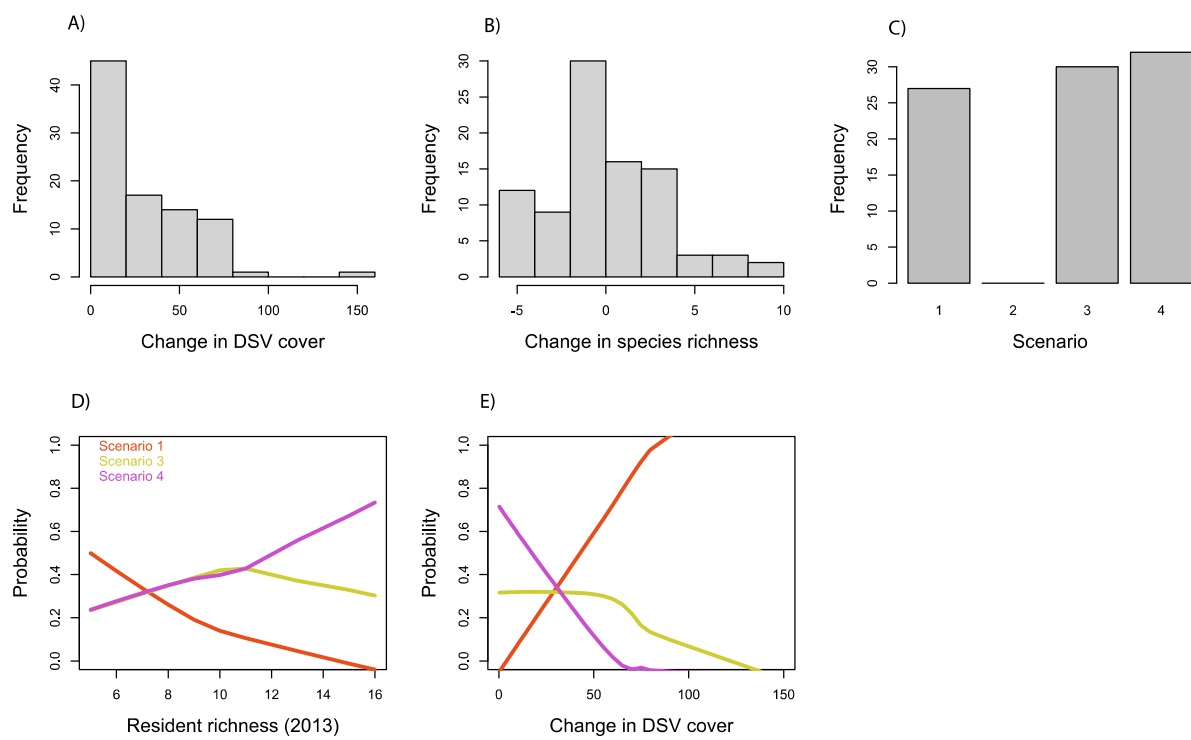
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712 Fig. 4

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717 Fig. 5

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