

## On linking mechanism to invasive species impact

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## Abstract

Species invasion represents one of the major drivers of biodiversity change globally, yet there is widespread confusion and controversy about the nature of non-indigenous species (NIS) impact. This confusion stems from differing notions and understanding of what constitutes invasive species 'impact' and the scales at which it should be assessed. At local scales the mechanisms of NIS impact on potential competitors can be classified into four scenarios: 1) minimal impact from NIS inhabiting unique niche space; 2) neutral impact spread across the community and proportional to NIS abundance; 3) targeted impact on a small number of competitors with overlapping niches; and 4) pervasive impact that is disproportionate to NIS abundance and ostensibly caused by ecosystem modification that filters out other species. I develop a statistical test to distinguish these four mechanisms based on community rank-abundance curves. Using an example dataset, I show that in long-term plots that had high native plant diversity and where the dominant invasive vine, *Vincetoxicum rossicum*, increased, impact resulted in either targeted extirpations or widespread biodiversity loss. Regardless of whether NIS impact is neutral, targeted or pervasive, the net outcome will be the homogenization of ecosystems and reduced biodiversity at larger scales, perhaps reducing ecosystem resilience.

## Introduction

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

One facet of this confusion stems from differing notions and understanding of what constitutes invasive species 'impact' and the scales at which it is important to assess it (Parker *et al.* 1999; 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, to population level fitness, 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 fitness 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 measure of impact, there remains an important conceptual confusion about impact, namely, whether impact is proportional to the abundance of the NIS or if the NIS has a disproportionate impact relative to its abundance, harkening classic discussion about the role of dominant species versus ecosystem engineers (Jones, Lawton & Shachak 1994), or whether there are multiple pathways to being an invasive species with large impact.

I argue that the proximate mechanisms determining an invasive species impact happen at smaller scales where species actually 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 community, which we can then scale up to metacommunities or regional scales to quantify the fulsome impact.

### **Defining impact**

Here I will assume no difference between NIS and invasive species from the perspective of a recipient community. The point is that a NIS immigrates into a new community and its degree of impact, and mechanisms generating this impact, are what determines if it should be considered an invasive species. 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 (Hubbell 2001; Chave 2004). 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 are starting off closer to an abundance of zero. Yet, non-neutral impact can result in the exclusion of resident species that have the greatest niche overlap with the invading NIS (Shea & Chesson 2002; MacDougall, Gilbert & Levine 2009). This can happen because the NIS is simply a better competitor or that it has escaped its natural enemies from its native range and

so has higher local fitness in its adventive range (Keane & Crawley 2002; Heger & Jeschke 2018), 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. More specifically, some NIS, specifically those likely to be considered invasive, can have broad community wide impacts by altering niche and resource availability and modifying ecosystem-level processes (Crooks 2002; Charles & Dukes 2008), which results in wholesale changes to community diversity and composition. 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; 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 abundance or diversity (Case 1990; Shea & Chesson 2002; MacDougall, Gilbert & Levine 2009). The logic here is that the resident community inhabits a certain proportion of available resources, but that there are gaps where NIS might exploit unused resources because they possess unique traits and have evolved different ecological strategies than local natives.

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

### **The four types of impact**

The mechanisms of NIS impact on potential competitors outlined above results in four possible outcomes for community residents facing an increasing population size from an invader, namely, no 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). 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., 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., numbers 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:

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

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

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

Giving us the expected average rank of:

$$\bar{R} = \frac{\sum [R, \dots, S]}{\hat{k}}$$

eq(4)



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

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

The first impact scenario (Fig. 1B) is where the observed extirpations,  $\kappa_o$ , and the average observed rank of extirpated species,  $\bar{R}_o$ , conform to:

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

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

The second scenario (Fig. 1B) is simply our neutral scenario that generated our expectations.

We expect that if the invader 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). And for completeness:

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

In the third scenario, the NIS has high niche overlap with one or a few other species, and coupled with the increased fitness in the adventive range that made it invasive in the first place, it's competitive impact is concentrated on these overlapping species (Fig. 1B). Given this, we should expect likely fewer extirpations but of lower average rank, such that:

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

Finally, in extreme cases, the NIS that invades a community not only competes with other species, either neutrally or with those species with a high degree of niche overlap, but they also modify the local environment in ways that reduce fitness broadly and exclude a disproportionate number of species (Fig. 1B). In this case:

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

These four scenarios are testable with observational community data, with before and after invasion observations, assuming the community prior to invasion was at equilibrium. These scenarios can be statistically assessed by stochastically removing abundance units from resident species proportional to the invader abundance. This generates a neutral community where all individuals compete equally for the same resources (space) but are removed according to random processes. This stochastic simulation can then be run some number of iterations (e.g., 999) to generate a null expectation for the average number of extirpations ( $\overline{\hat{\kappa}_{null}}$ ) and the average rank ( $\overline{\bar{R}_{null}}$ ), as well as their standard deviations ( $\sigma_{\hat{\kappa}_{null}}$  and  $\sigma_{\bar{R}_{null}}$ , respectively). The standardized effect size (SES) of these two measures can be estimated as the z-values:

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

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

Significance can be assessed using either the rank of the observed value relative the full distribution of the randomized estimates and compared to the 95% confidence interval or, if

normality assumed, against the z-distribution, which is -1.96 for the lower tail (i.e., fewer extirpations or lower rank than expected) and 1.96 for the upper tail (more than expected) at the 95% confidence level.

Given this diagnostic test, the four scenarios can be distinguished based on whether the number of extirpations and their average ranks are lower, greater or indistinguishable from the null expectation ( $z = 0$ ; see Fig. 1C). Thus, when the invader occupies a unique niche with little impact (scenario 1), the SES values for both the number of extirpations and their ranks should be less than expected ( $z < 0$ ). Neutral community impacts (scenario 2) should exhibit  $z = 0$  for both measures. The case where the invader's impact is largely on the few species with a high degree of niche overlap (scenario 3) means that we should observe  $z \leq 0$  for number of extirpations and  $z > 0$  for their average rank. Finally, for invaders that have disproportionate impact (scenario 4), we should see  $z > 0$  for both measures (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, it becomes co-dominant with the most abundant resident). In scenario 1, only one extirpation occurs, for 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 invader 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 not likely 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 an invader increases over time. Even if the invader 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 conform to one of the four scenarios. In this case, the invader abundance,  $I_A$ , should not be its total abundance, but rather the increase in abundance,  $I_{A,t+1} - I_{A,t}$ .

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

then the way forward is to group them together and assess the impact of invasion, such that

$$I_A = \sum_i^I A_i.$$

### **Extending this spatially**

This framework can be used in the absence of data from repeatedly sampled plots so long as sufficient plots have been sampled spatially, and that include invaded and uninvaded plots in close proximity. Plots can be paired (e.g., Malloch *et al.* 2020) as invaded and uninvaded or perhaps better would be to create an average rank-abundance curve from multiple uninvaded plots to compare with the invaded ones. In this case, this regional rank-abundance curve can be resampled to produce average rank-abundance curves and we can assess the average difference in plots with the invader present. Such a spatial approach is laden with assumptions about the homogeneity of communities across scales and requires detailed system understanding to reinforce inferences.

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

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

To showcase how we can use observational data to assess which of the scenarios of impact community dynamics fit, I use an example long-term dataset where a dominant non-indigenous vine (*Vincetoxicum rossicum* or dog-strangling vine) has invaded large sections of the Rouge National Urban Park, located on the eastern edge of Toronto, Canada (Sodhi *et al.* 2019; Livingstone, Isaac & Cadotte 2020). We have been collecting species 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. 3A 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. 3B & C). Given the large number of plots where *V. rossicum* cover increased (Fig. 4A), it is reasonable to investigate the degree and type of impact.

I subsetting plots into those with four 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 104 plots that were analyzed for invader impact (shaded area in Fig. 4C). I then performed the SES analyses describe above and in Figs. 1 and 2.

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. 4D). 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. 4E). 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. 4E & 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. 4E), and highlighted that in many of these communities, rare species were not more likely to be extirpated than more abundant species.

### **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, they can also be extended to larger spatial scales, though mechanisms might differ. 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 an invasive species. In the data example above, *V. rossicum* did not appear to impact communities in a way that was consistent with neutrality, but rather exhibited targeted or broad extirpations (beyond what was expected based on its abundance) in species-rich communities, likely because it has been shown to release allelopathic chemicals (Douglass, Weston & Wolfe 2011). This invasive vine is currently spreading throughout eastern North America, and from these analyses, we would predict consistent species loss greater than would be predicted from its abundance.

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

## **Future directions**

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

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

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 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. 4: 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.

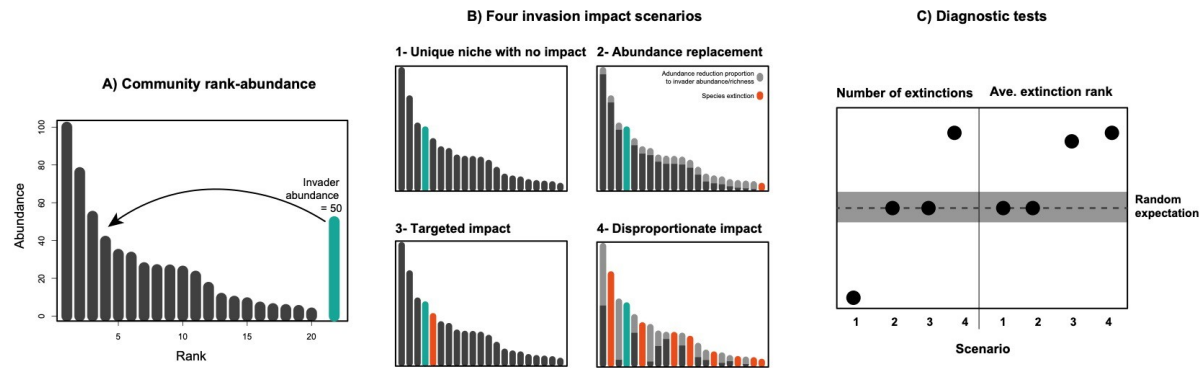


Fig. 1

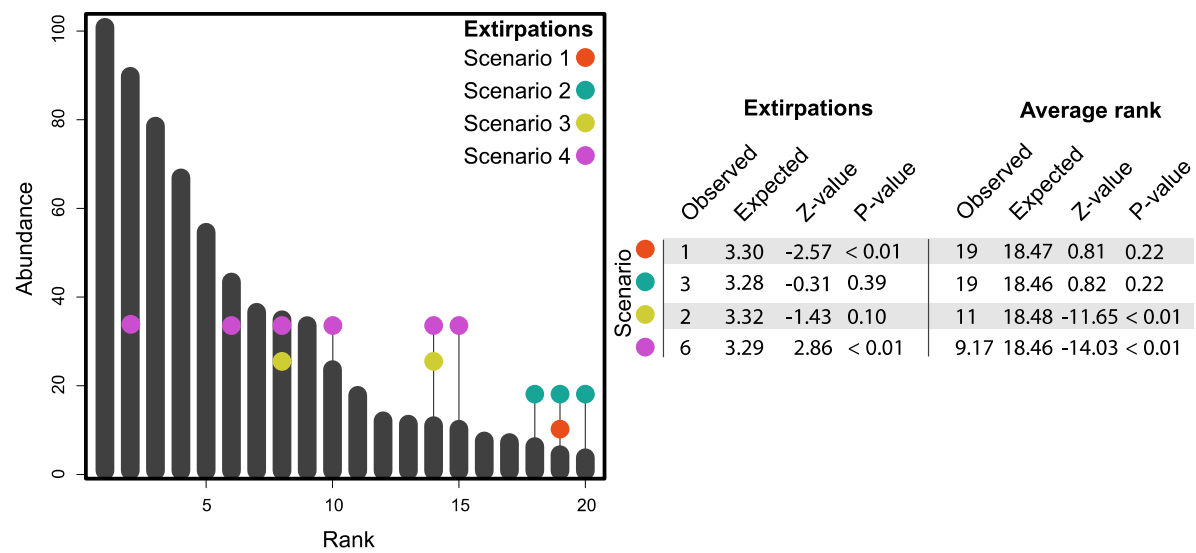


Fig. 2

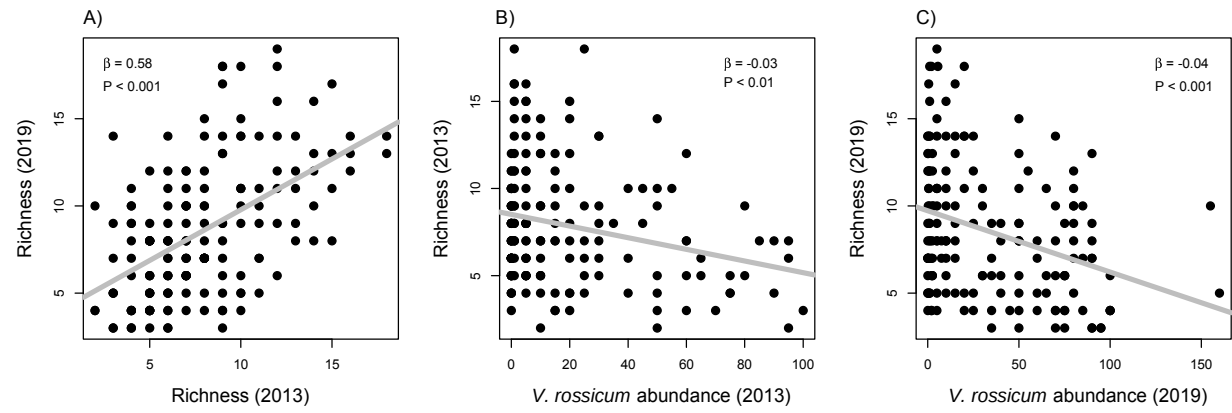


Fig. 3

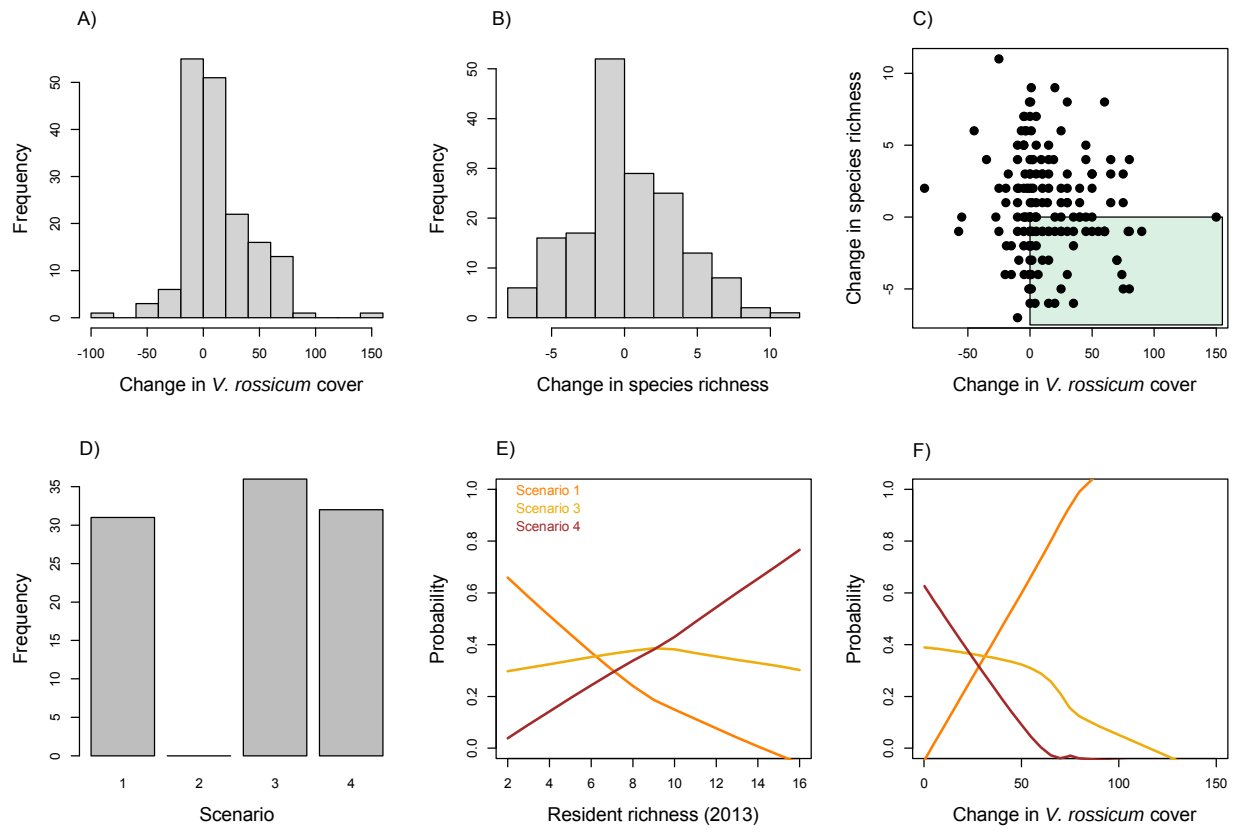


Fig. 4