

Temporal Dynamics of Alien Species' Impacts

Lara Volery¹, Lara.volery@unifr.ch

Daniel Wegmann^{1,2*}, Daniel.wegmann@unifr.ch

Sven Bacher^{1*}, Sven.bacher@unifr.ch

¹Department of Biology, University of Fribourg, Chemin du Musée 10, CH-1700 Fribourg, Switzerland

²Swiss Institute of Bioinformatics, Chemin du Musée 10, CH-1700 Fribourg, Switzerland

* These authors contributed equally to this work

Corresponding author: Lara Volery, Lara.volery@unifr.ch, +41 26 300 88 59

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Abstract

Alien populations keep establishing at alarming rates and often have highly detrimental impacts on recipient environments. Quantifying the magnitude of their impact is essential for prioritization and management and is commonly done by comparing ecological variables between invaded and uninvaded states. Such estimates are highly uncertain and often biased because they ignore the temporal dynamics of the system. This has hampered the understanding and prediction of impacts, and hence management. To address this, we propose a framework to quantify impacts by contrasting the trajectory of ecological variables in presence of an alien with that forecasted in the absence of the alien. We discuss how trajectories in absence of the alien can be forecasted statistically and how uncertainty in these forecasts can be accounted for when estimating impacts. This framework readily allows for comparisons of alien species' impacts across taxa and regions, as well as with impacts caused by other stressors.

Keywords: Biological invasions, Non-native species, Stressors interactions, Impact magnitude, Synergistic interaction, Antagonistic interaction

Introduction

Alien species are species introduced by humans (accidental or intentional) into novel environments where they do not occur naturally. Alien species are establishing at alarming rates (Seebens *et al.* 2017) and their number is predicted to keep increasing in the next decades (Seebens *et al.* 2021). Alien species cause varied environmental and societal changes in invaded environments (Bellard *et al.* 2016; Bacher *et al.* 2018; Nentwig *et al.* 2018; Shackleton *et al.* 2018; IPBES 2019; Pyšek *et al.* 2020; Diagne *et al.* 2021), which are referred to as impacts. To understand and predict these changes and to optimize the management of alien species, it is crucial to accurately quantify their impacts.

Evidence is accumulating that the current practice of punctual impact quantification is error-prone and that the temporal dynamics of the studied systems (e.g. natural variability, long-term temporal trajectories) must be accounted for (e.g. Wolkovich *et al.* 2014; McCain *et al.* 2016; Christie *et al.* 2019; Ryo *et al.* 2019; Büntgen *et al.* 2020; Jackson *et al.* 2021; Wauchope *et al.* 2021). Considering temporal dynamics when quantifying impacts, for instance, revealed that driver-response relationships are not necessarily constant but may vary over time (Ryo *et al.* 2019). In invasion science, however, alien species' impacts are still mainly measured by comparing snapshots (i.e. measurements taken at single time points) of the situation with ('invaded state') and without the alien ('uninvaded state'; e.g. before introduction, Simberloff *et al.* 2013; Kumschick *et al.* 2015; Gallardo *et al.* 2016; Crystal-Ornelas & Lockwood 2020; Ricciardi *et al.* 2020). Such comparisons implicitly assume that the impacted variable (e.g. a native population) follow stationary trajectories and show little variability, both in the uninvaded and invaded states. When these assumptions are not met, impacts can be misinterpreted (Christie *et al.* 2019; Wauchope *et al.* 2021). In addition, such comparisons do not capture temporal variation in alien species' impacts themselves, which provide crucial information for management. Temporal variation is also not considered in popular impact frameworks (e.g. Baker *et al.* 2008; Brunel *et al.* 2010; Essl *et al.* 2011; Dick *et al.* 2014; D'hondt *et al.* 2015; Bacher *et al.* 2018; Roy *et al.* 2018, 2019), including the Environmental Impact Classification for Alien Taxa (EICAT; Blackburn *et al.* 2014;

IUCN 2020), which has recently been adopted by the IUCN as its official classification system for alien species. As these issues may have led to a distorted understanding of alien species' impacts, we here propose a conceptual framework to accurately quantify the impacts of alien species under dynamic conditions and discuss how this can be done in practice.

Why should we stop quantifying alien species' impacts by comparing snapshots?

Impact mis-quantification

Ignoring temporal dynamics in impact assessments can lead to mis-quantification. Consider an alien population affecting the temporal trajectory of a native population (Fig. 1). A classic measure of impact is obtained by comparing snapshots of the abundance of the native population before and after the alien introduction. While this measure may be meaningful if the native population was stationary (Fig. 1A), it is problematic if the native population followed a temporal trend independently of the presence of the alien species (Fig. 1B-F). This is likely a common situation as alien species frequently co-occur and interact with other anthropogenic stressors like climate change, harvesting, habitat loss or pollution (Russell *et al.* 2017; Geary *et al.* 2019; Pyšek *et al.* 2020). In such cases, simply comparing snapshots of abundances before and after an alien introduction may lead to biased impact estimates in terms of their magnitude and potentially even in their sign. In case the native population was already decreasing in absence of the alien, for instance, the impact would be overestimated (Fig. 1B). In case it was increasing, the impact might even be wrongly inferred as positive (Fig. 1C,D). Similarly, a positive impact could be wrongly inferred as negative if the native was heading towards extinction (Fig. 1E). In addition, stochastic (natural variability) and deterministic processes (biotic interactions) can lead to fluctuating abundances; ignoring this variability by measuring snapshots can result in inaccurate assumptions about the native population's baseline state and on the effect of the alien (Fig. 1F), as was argued for other stressors (McCain *et al.* 2016; White 2019; Büntgen *et al.* 2020; Didham *et al.* 2020).

Lack of understanding of impacts' temporal variation

Some of the above issues can be mitigated by comparing snapshots from invaded to snapshots from uninvaded control sites (Christie *et al.* 2019). But such comparisons would still not shed light on the temporal dynamics of impacts themselves (Wauchope *et al.* 2021), which is indispensable to understand how and why impacts evolve over time and across taxa and contexts, for which data is currently scarce.

The few studies that investigated temporal variation in impacts of alien species have identified three distinct patterns of trends in negative impacts (Strayer 2012): The first pattern shows monotonously increasing impact magnitudes until they either reach the maximally possible impact (e.g. by leading to a local extinction, Fig. 1A,B), or level off at a lower value (e.g. Fig. 1C). The second pattern shows boom-bust dynamics, in which impacts decrease after an initial, acute phase. This pattern can occur because of accumulation of alien's enemies (Simberloff & Gibbons 2004; Strayer *et al.* 2017), or behavioral, phenotypic or genotypic adaptation of the native (Carthey & Banks 2016; Langkilde *et al.* 2017; Leger & Goergen 2017; Anton *et al.* 2020). The third pattern shows abrupt instead of continuous changes (Strayer 2012), e.g. when alien populations interact with rare events such as wildfires and suddenly become dominant (e.g. D'Antonio *et al.* 2017; Klinger & Brooks 2017), or experience mass mortality (e.g. Leuven *et al.* 2014). The relative frequency of these patterns is not known, however, and neither are the timescales at which these dynamics are at play, despite their relevance for predictions (Strayer 2012). While adaptation of native species to the alien can sometimes be rapid due to phenotypic plasticity, other evolutionary processes can last over many generations (Saul & Jeschke 2015).

Discriminating between stable, increasing, or decreasing temporal trends in impacts would also inform decisions on if and when management interventions are relevant, and how to avoid unnecessary costs and efforts. Impacts that decrease over time, for example, may not require urgent management, even if they are currently at a high level. By contrast, impacts that are currently at a low level, but increasing, may call for management to prevent high impacts in the future.

Quantifying alien species' impacts and their temporal variation

Quantifying impacts

Alien impacts are often quantified through caused changes in the abundance of a native population, a strategy recommended by the IUCN (see IUCN 2020), and a case we adopt here for illustration. To quantify such an impact properly, the trajectory of the native population in the invaded state must be compared with its trajectory in the uninvaded state. For the impact $R(t)$ at time t , we propose the relative measure

$$R(t) = \log(N^*(t)/N(t))$$

of the abundance of the native population in the absence ($N(t)$) and presence ($N^*(t)$) of the alien introduced at t_0 (Fig. 1). Before the introduction of the alien ($t \leq t_0$), we define $N^*(t) = N(t)$, in which case there is no impact ($R(t) = 0$).

A negative impact ($R(t) < 0$) denotes a decrease of the native population due to the alien (Fig. 1A-C), and reaches $R(t) = -\infty$ if the alien causes the extinction of the native population (Fig. 1A,B). Similarly, a positive impact ($R(t) > 0$) denotes an increase of the native population due to the alien, and reaches $R(t) = +\infty$ if the alien prevents the extinction of the native population (Fig. 1D). Note that the alien continues to cause an impact even after it led to a local extinction (Fig. 1A,B), but that the impact is not defined once the native species would have gone extinct in the absence of the alien, i.e. for reasons unrelated to the alien (Fig. 1B).

Importantly, the measure $R(t)$ can be calculated regardless of the mechanism of interaction between alien and native (e.g. predation, hybridization, etc. [Blackburn *et al.* 2014; IUCN 2020]). Further, the measure, while presented in terms of population abundances, is readily applied to other impacted

variables such as biodiversity indicators (e.g. local species richness, evenness, diversity, Red List Index) or impacts on abiotic characteristics of the environment (e.g. nitrogen content, frequency of fire events, nutrient availability, water quality), human well-being (Bacher *et al.* 2018) or the economy (Diagne *et al.* 2021). However, depending on the variable or indicator of interest, one would need to carefully reflect on the interpretation of the sign of the impact (e.g. is a positive impact on soil nitrogen beneficial or detrimental to e.g. local biodiversity? [Vimercati *et al.* 2020]).

Quantifying impact dynamics

To quantify the temporal dynamics of impacts, we propose a second metric, $\rho(t_1, t_2)$, which quantifies the average rate of change in $R(t)$ between two time points t_1 and t_2 and is given by

$$\rho(t_1, t_2) = 1/(t_2 - t_1) \cdot \log(N^*(t_2)N(t_1)/N^*(t_1)N(t_2))$$

Here, $\rho(t_1, t_2) = 0$ indicates a constant (negative or positive) impact over time, while $\rho(t_1, t_2) < 0$ indicates either that the magnitude of a negative impact is increasing, or that a positive impact is decreasing, and vice-versa for $\rho(t_1, t_2) > 0$. This metric is particularly useful for the prioritization of management actions: two alien populations causing impacts of the same magnitude ($R_1(t) = R_2(t)$) may warrant different management actions if their impacts differ in their dynamics ($\rho_1(t_1, t_2) \neq \rho_2(t_1, t_2)$, e.g. Fig. 1C,D). Rapidly increasing impacts (e.g. Fig. 1D), for instance, may be prioritized over stable impacts (e.g. Fig. 1C).

Interactions among multiple stressors

The $R(t)$ and $\rho(t_1, t_2)$ measures can also be used to compare impact magnitudes and dynamics caused by different stressors. Under our definition, two alien populations leading to the same relative reduction of a native population, for instance, cause impacts of the same magnitude ($R_1(t) = R_2(t)$), regardless of the initial native abundances. If multiple stressors act simultaneously, the measures allow

to quantify their joint impact by comparing the abundance in the presence of all stressors with that in their absence. To quantify the individual impact of one out of several stressors, two strategies can be used: To compare the relative importance of stressors, the abundance of the native in the presence of a single stressor should be compared against the abundance in the absence of all stressors. To prioritize stressors for management, however, the abundance of the native in the presence of all stressors should be compared against that in the presence of all but the stressor in question.

To illustrate these two strategies, we use the well-known example of the debated role of the introduced Zebra mussel (*Dreissena polymorpha*) in native freshwater mussel extinctions in North America (Gurevitch & Padilla 2004a, b; Ricciardi 2004). Ricciardi (2004) argues that Zebra mussel introductions should be considered as major driver of native mussel extinctions in lakes, as they greatly accelerated these extinctions. Gurevitch & Padilla (2004b) oppose this view and argue that Zebra mussels are not a major driver of extinctions, as these would have happened anyway in a near future (because of pollution, habitat destruction, harvesting, etc.) and could not have been avoided by managing the alien alone. Accounting for temporal trends in the impacted native freshwater mussels could aid in interpreting the roles of multiple, interacting stressors, which is critical for the management of such scenarios (Ricciardi *et al.* 2020), and brings quantitative terminology to the debate. To rank stressors by their importance, their individual impacts can be compared, e.g. based on their respective impact in the absence of the other stressor(s), or on whether or not each stressor would have caused a local extinction on their own and on the time needed to cause an extinction (Fig. 2). To identify the most effective management strategy, however, what matters is how much the overall impact can be reduced by removing one of multiple stressors. Consider the two hypothetical scenarios represented in Fig. 2: while native mussels can be more effectively preserved in Scenario (A) by reducing the impact of pollution rather than of the Zebra mussel, this is not the case under Scenario (B), in which the impacts of both stressors would need to be reduced.

In stressors' interactions, the impact of a stressor in the presence of all other stressors is identical to the impact that stressor would have had alone if the interaction is additive (the total impact equates the sum of individual impacts; Fig. 3A), but differs if the interaction is synergistic or antagonistic, in which case the total impact is larger or smaller than the sum of individual impacts, respectively (Fig. 3B,C) (Piggott *et al.* 2015; Côté *et al.* 2016; Birk *et al.* 2020; Braga *et al.* 2020; Jackson *et al.* 2021). Importantly, interactions may also be subject to temporal dynamics and change in both strength (e.g. increasing synergistic effect in Fig. 3B, or decreasing antagonistic effect in Fig. 3C) and type (e.g. antagonistic becomes synergistic; Fig. 3D) (Garnier *et al.* 2017; Romero *et al.* 2019). This can happen because the dynamics of multiple stressors are rarely synchronized (Ryo *et al.* 2019; Jackson *et al.* 2021), or because populations adapt to the co-occurrence of stressors, which decreased their combined effect and leads to antagonistic interactions over time (e.g. Romero *et al.* 2019). However, studies rarely capture this variation, and thus overlook important features of interactions between multiple stressors that can shed light on their evolution (Jackson *et al.* 2021). Understanding the mechanisms of interactions is also informative for management actions (Didham *et al.* 2007; Geary *et al.* 2019): If a synergistic interaction evolves towards an additive rather than an antagonistic one, for instance, suggests that the interaction should be targeted directly by management actions (e.g. Fig. 3B).

How to estimate alien species' impacts and their evolution over time in practice?

To estimate impacts under the framework proposed above, the trajectory of the variable of interest (e.g. the abundance of a native species) must be compared in the presence and absence of the alien. While the former can be directly measured, the latter must be estimated, either by extrapolating from measurements prior to the introduction of the alien, from populations in a similar context but at uninvaded sites, or from a combination of both. These setups are similar to the designs classically used to quantify the impact of alien species (Kumschick *et al.* 2015; Crystal-Ornelas & Lockwood 2020), namely the Before-After (BA), Control-Impact (CI) or combined Before-After-Control-Impact (BACI)

designs (Christie *et al.* 2019; Wauchope *et al.* 2021), but used here to model the temporal trajectory of the native species in the absence of the alien. Such forecasted trajectories are likely associated with uncertainties from multiple sources: First, any forecast requires a statistical model and hence relies on specific assumptions (e.g. exponential change). Second, once the alien was introduced, there exist no measurements of the native in absence of the alien, which results in increased uncertainty through time (Fig. 4A; Oliver & Roy 2015). And third, trajectories often exhibit substantial, inherent stochasticity not well characterized by covariates (Fig. 4B; Connors *et al.* 2014; d'Eon-Eggertson *et al.* 2015; McCain *et al.* 2016; Fox *et al.* 2019; White 2019; Didham *et al.* 2020).

Uncertainty stemming from the former two sources may be reduced, either by increasing survey efforts such that more realistic models can be learned (Oliver & Roy 2015; Fox *et al.* 2019; White 2019), or through BACI designs in which regional effects such as specific weather conditions affecting all populations can be captured (Christie *et al.* 2019; Wauchope *et al.* 2021). However, substantial uncertainty will likely remain, particularly in cases with high natural variability in abundances.

To deal with this uncertainty, we recommend three steps in impact quantification: First, the uncertainty associated with the forecasted trajectories should be accounted for when quantifying impacts and be reflected in the uncertainty associated with impacts (e.g. Fig. 4). This applies equally to any additional uncertainty that stems from measuring the impact variable in the presence of the alien (e.g. measurement error, e.g. Didham *et al.* 2020). Second, we recommend quantifying impacts jointly from multiple sites or populations, if the research question permits, and thus to spread the survey effort across multiple sites. By aggregating information across sites, shared impacts can be quantified at much higher accuracy than for any site individually, particularly in case of high variability in the native abundance (Christie *et al.* 2019). This equally applies when investigating context-dependency of impacts: although between-sites differences are important for such research questions, replicating measures for each context variable of interest improves the quality and relevance of the

findings. Third, we recommend focusing on probabilistic statements rather than impact estimates themselves whenever possible (see also Probert *et al.* Under review). Even if impact estimates are associated with high uncertainty, it may for instance still be possible to confidently conclude that there is a negative impact ($R(t) < 0$), in many cases already shortly after the alien introduction (Fig. 4). Similarly, two species may be ranked based on the probability that $R_1(t) < R_2(t)$ rather than their impact point estimates.

Conclusion

The necessity to account for temporal dynamics when quantifying impacts has been recognized in other areas of ecology (De Palma *et al.* 2018; Chevalier *et al.* 2019; Christie *et al.* 2019; Ryo *et al.* 2019; Büntgen *et al.* 2020; Jackson *et al.* 2021; Wauchope *et al.* 2021), and the impacts of alien species are no exception. The quantification of impacts of alien species therefore needs to shift from simple before-after or other two-point comparisons to the comparison of long-term temporal trends and modelling studies, for which we introduce a coherent conceptual framework that can also be generally applied to compare ecological impacts. Most of our current knowledge about alien species' impacts relies on comparisons of point estimates, but such estimates contain unknown biases that may distort our understanding of impacts. It is critical to address the challenges of accurately measuring impacts to improve our understanding and to better predict future impacts of invasions and other drivers of global change.

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272 ***Conflicts of interest***

273 The authors declare they have no conflict of interest.

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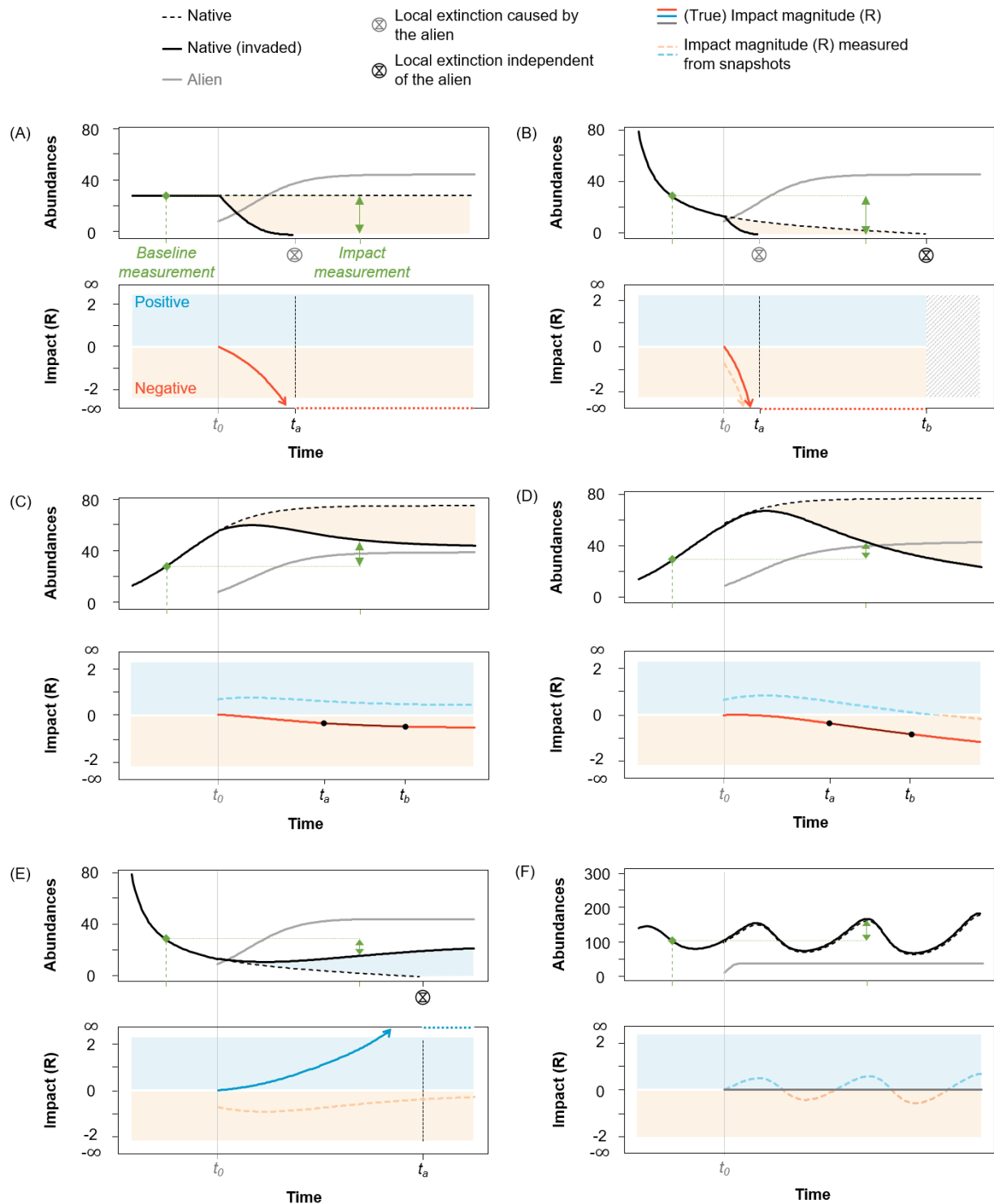
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433 decreasing independently of the alien (B); a positive impact is wrongly inferred when the native was
434 increasing independently of the alien (C & D) and a negative impact is wrongly inferred when the alien
435 prevents the extinction of the native (E). When the native's trajectory is cyclical (e.g. prey-predator
436 oscillations) but the alien has no impact (F), a positive or negative impact may be wrongly inferred,
437 depending on when the snapshots were taken. In (A) and (B), the alien causes a local extinction of the
438 native at time t_a : the aliens' impact magnitude reaches $-\infty$. At time t_a in (E), the alien prevents the local
439 extinction of the native: its impact magnitude reaches $+\infty$. At time t_b in (B), the native would have gone
440 extinct independently of the alien: quantifying the alien's impact is not meaningful afterwards (shaded
441 grey area). In (C) and (D), the alien causes the same impact at time t_a , but the rate of change between
442 t_b and t_a , $\rho(t_a, t_b)$, is larger in (D).

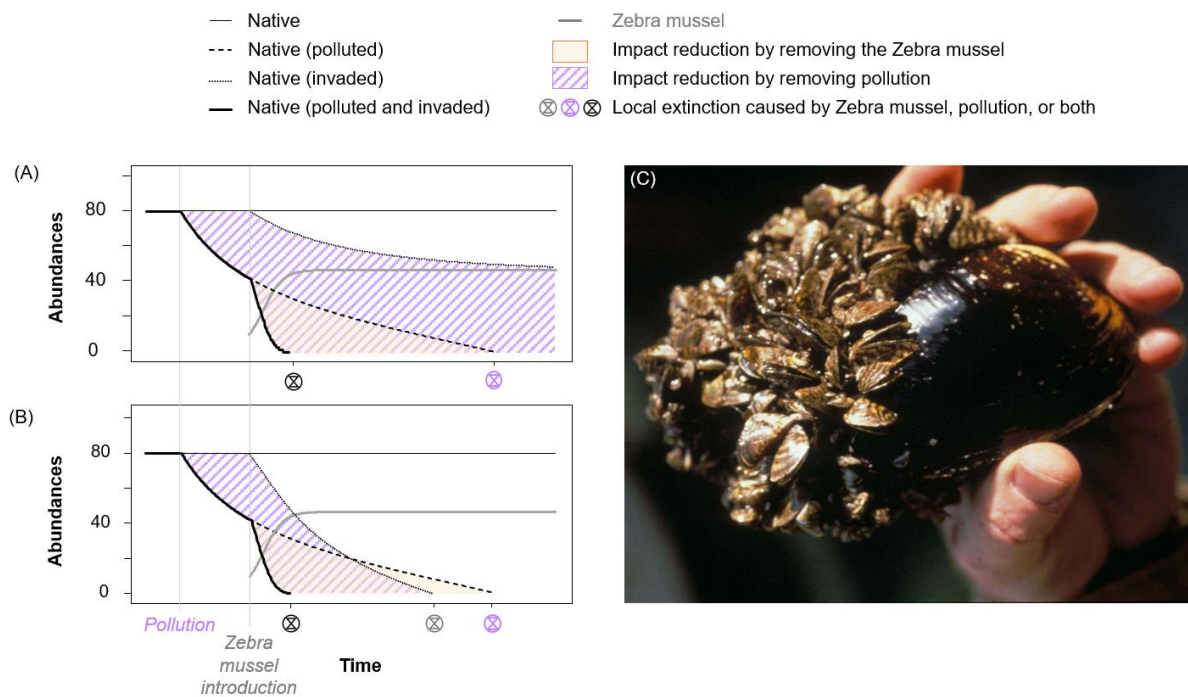


Figure 2. Hypothetical scenarios of interaction between the alien Zebra mussel and pollution. While both scenarios show the same total impact of both stressors, they differ in the relative impacts of the two stressors. In (A), pollution plays a dominant role leading to a local extinction because, contrary to the Zebra mussel, it would also have led to an extinction alone (in absence of the Zebra mussel). In (B), both stressors play dominant roles: Zebra mussel and pollution would both have caused an extinction alone, but it would have taken less time to the Zebra mussel to cause it than to pollution. (C) Zebra mussels biofouling on a native mussel (<http://www.public-domain-image.com>).

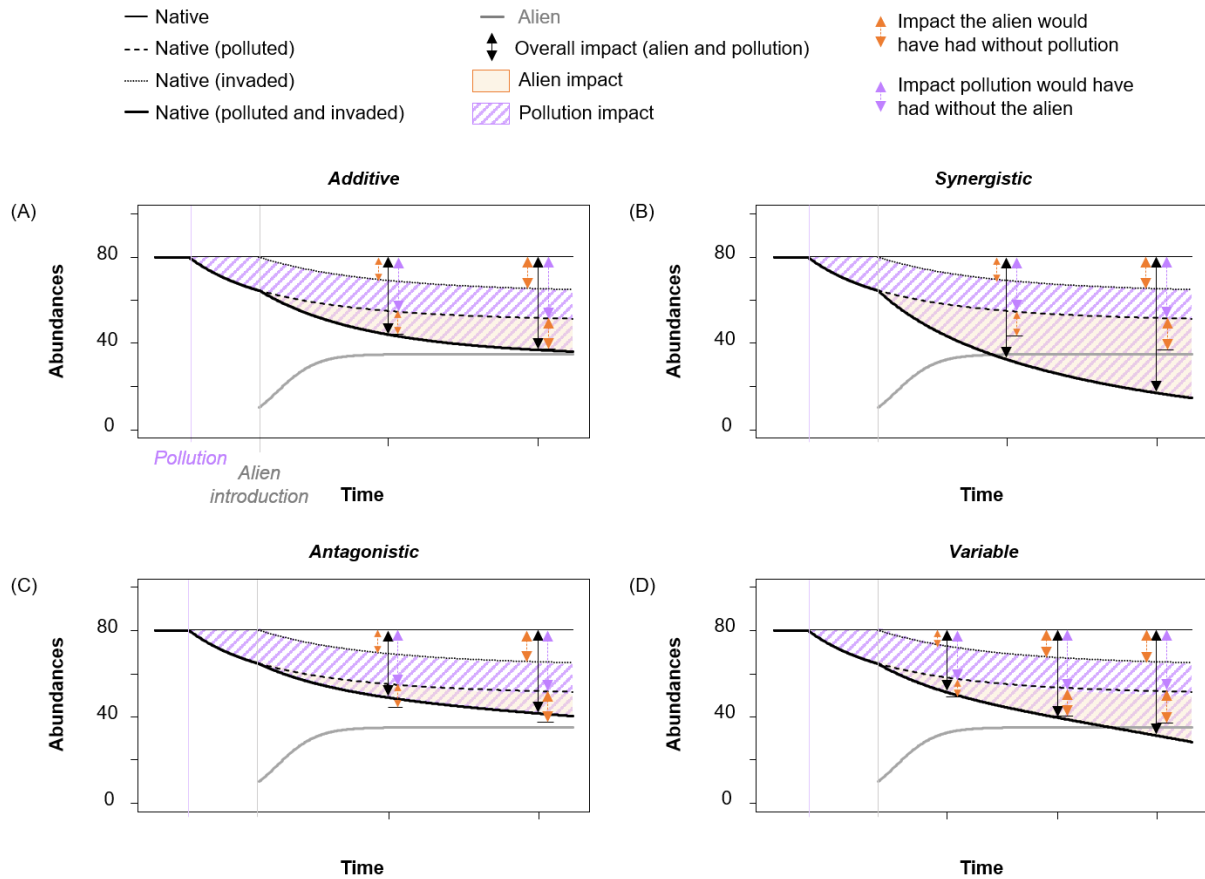


Figure 3. Types of interactions between multiple stressors (e.g. an alien species and pollution). When the joint pressure of the alien and pollution (black arrow) equates the sum of their individual pressures in absence of the other stressor (orange and violet arrows), the interaction is additive (A); when it is larger, the interaction is synergistic (B); and when it is smaller, the interaction is antagonistic (C). The strength of the interaction can change over time: for instance, the synergistic and antagonistic effect between the two stressors increases over time in (B) and decreases in (C). Interaction type can also change over time: e.g. in (D), the interaction is first antagonistic, then additive, and finally synergistic. For simplicity, we assumed that the impact dynamics of both stressors are similar: however, disturbances can have different shapes (e.g. continuous vs discrete events), evolve over very different time scales, occur at different frequencies, etc. (Ryo *et al.* 2019; Jackson *et al.* 2021).

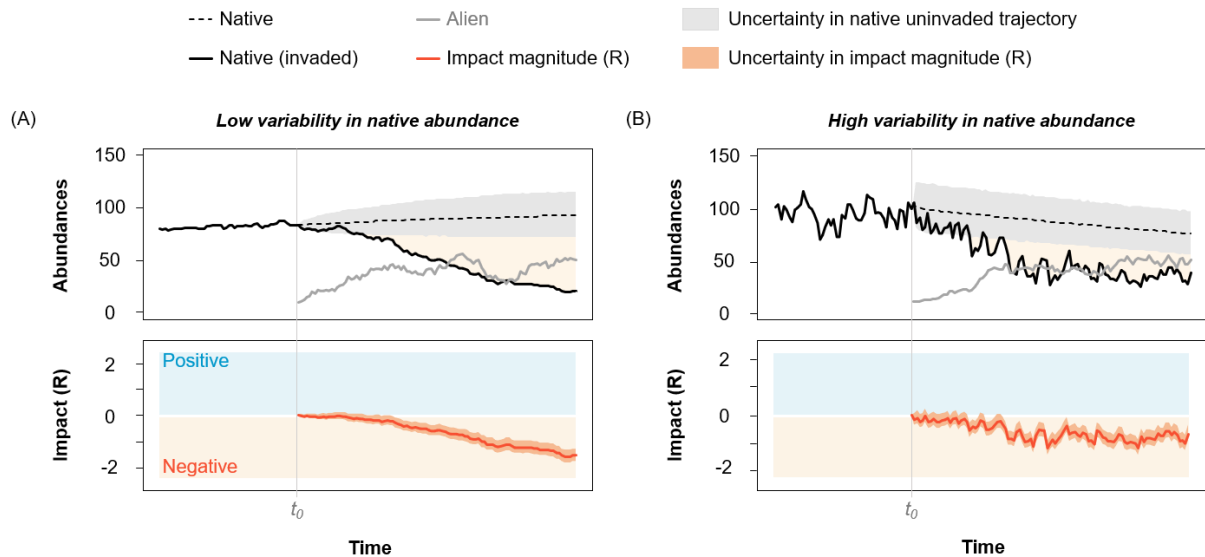


Figure 4. Uncertainty in estimations of alien species' impacts. This figure illustrates two of the main sources of uncertainty in impact estimations: that the native trajectory in the uninverted state cannot be measured after the alien introduction at t_0 , and that substantial variability renders trajectory forecasts difficult (here done solely from data prior to t_0). When variability in native abundance is low (A), uncertainty in the native trajectory in the uninverted state is small just after t_0 , but increases over time. When variability in native abundance is high (B), uncertainty is already large just after t_0 , but does not increase much. In real impact studies, the statistical model chosen to forecast the native trajectory in the uninverted state might not be suitable, which would result in increased uncertainty. Furthermore, uncertainty would likely also exist in the native trajectory in the invaded state, for instance because of measurement error.