



# Moving forward in understanding the impacts of biological invasion rates on ecosystem sustainability: reply to Haubrock

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Rates of biological invasion are increasing globally. All regions, biomes, and virtually all known habitat types are experiencing rising numbers of established non-native species and their impacts (Seebens et al. 2017; Seebens et al. 2018; Mormul et al. 2022; IPBES 2023). Invasions can alter ecosystem function by (e.g.) disrupting key ecological interactions, restructuring biological communities, modifying resource availability and physical habitat conditions, and causing shifts in disturbance regimes; these changes benefit some resident species while disadvantaging others (Ehrenfeld 2010; Simberloff et al. 2013; Garcia et al. 2022; IPBES 2023). Moreover, invasions are eroding native biodiversity across multiple spatial scales (Blackburn et al. 2005, 2019; Bellard et al. 2016; Doherty et al. 2016; Thakur et al. 2025), while substantially altering the provision of ecosystem services

(Vilà and Hulme 2017) and threatening human well-being and livelihoods (IPBES 2023).

It is empirically demonstrated that the probability of a disruptive invader appearing in an ecosystem increases with the number of invasions (Rejmánek and Randall 2004; Ricciardi and Kipp 2008; Ricciardi and MacIsaac 2011). However, the identities of the invaders and the timing of their arrivals are largely unpredictable (Ricciardi et al. 2021), and the mechanisms relating the rate of invasion and cumulative impacts to changes in ecosystem function have hardly been studied. Adding to their unpredictable nature, invaders that first appear innocuous can be triggered to become disruptive long after their introduction (Spear et al. 2021). Furthermore, invaders can interact with each other and with other stressors to produce impacts that are virtually impossible to anticipate (Ricciardi and Simberloff 2025). Finally, invasions can destabilize communities by increasing temporal variability and disrupting stabilizing interactions (Erős et al. 2020; Vetter et al. 2020; Frost et al. 2024; Czeglédi et al. 2025). For these and other reasons, frequent invasions can jeopardize the reliability and management of ecosystem services.

The problem is not simply a matter of ecosystems worldwide being increasingly threatened by the same small minority of invaders. Given that new species source pools are continuously accessed due to expanding trade networks and environmental change, and new records of non-native species with no previous invasion history are rising (Seebens et al. 2018),

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it follows that the composition of invading species is also broadening globally. As shown for many previous invasions, the impacts of these emerging invaders will be highly context-dependent and affected by myriad environmental stressors (Ricciardi et al. 2013), resulting in diverse combinations of effects and ecological surprises that confound risk assessment and management (e.g., Messner et al. 2013). Therefore, I have argued that burgeoning rates of invasion are a crucial challenge for ecosystem sustainability (Ricciardi 2026) that justifies the Kunming-Montreal global biodiversity framework's target of a substantial reduction in rates of establishment of invasive species.

### Misapplied criticisms

Haubrock (2026) asserts that my paper (Ricciardi 2026) oversimplifies invasion dynamics by “conflating introduction with impact and underrepresenting probabilistic filters, interaction structures, context dependence and non-additive effects.” He extends this long inventory of factors in subsequent sentences. Among other things, he claims that I “conflate [species] arrival with impact” and ignore the sequential filters, Allee dynamics and stochasticity that result in most introduced species failing to establish, while I am “over-focusing on introduction rates”. This collection of claims is unfounded because my paper does not focus on introduction rates. The models and arguments that I presented are clearly focused on rates of *invasion*—that is, the rate of accumulation of non-native species that have established self-sustaining populations. Consequently, the dynamics of arrival, introduction and establishment, which are highlighted throughout Haubrock's (2026) critique and are indisputably important to invasion risks in general, are not directly relevant to the issue that I have addressed.

Invoking another false premise, Haubrock (2026) criticizes my paper for treating invasion rate as a “proxy” for sustainability. In fact, my paper does not *equate* the two concepts; it *relates* them as cause and consequence—in the same way, for example, that greenhouse gas concentration is related to climate change. Obviously, as in climate change, the relationship is complicated by diverse mechanistic factors and feedbacks, which remain to be fully elucidated, but compelling evidence supports a positive

correlation between the rate of invasion and risk of ecological disruption (see below).

Haubrock (2026) also condemns my supposed “implicit assumption that non-native species contribute to cumulative risk largely independently, or at least without systematically reducing each other's impacts”, and then he reminds us that antagonistic interactions can dampen impacts and violate the assumption of additive risk accumulation that he says dominates my narrative. Once again, his framing of the paper is misleading. I presented two scenarios for consideration. The simpler one (named *ecological roulette*) assumes a linear increase in the risk that at least one invader will prove to be disruptive—and thus a threat to ecosystem stability—as more invaders succeed. This process is about the frequency of disruption and it neither assumes nor requires that invaders avoid forming antagonistic relationships. Regardless of how oversimplified it may appear, the ecological roulette scenario has empirical support from terrestrial and aquatic systems (Rejmànek and Randall 2004; Blackburn et al. 2005; Ricciardi and Kipp 2008; Ricciardi and MacIsaac 2011). In my paper, I explicitly noted that the risk of disruption can be compounded by several factors such as emerging invaders from new source pools, sleeper populations, and interactions with other invaders and environmental stressors. The latter factor points to the second scenario (named *facilitation-synergy*), in which synergistic impacts can arise from multiple interacting invaders and stressors. There is some empirical evidence for this scenario as well (Ricciardi and Simberloff 2025). Neither scenario assumes “a stationary or homogeneous source pool”, contrary to Haubrock's (2026) depiction.

Haubrock's (2026) claim that I failed to properly consider antagonistic interactions among invaders is contradicted by multiple paragraphs of my paper that address the biotic resistance model—which posits that dampening effects become increasingly prevalent and stabilizing as the number of established non-native species increases (Case 1990). There is no doubt that invaders sometimes interfere with each other in such a way as to change or dampen their impacts; I clearly acknowledged this by stating “non-native species can also replace, inhibit, or interfere with each other, resulting in an attenuation of some of their respective impacts” (Ricciardi 2026). However, the competitive displacement of functionally similar

invaders can still maintain negative impacts (Russell et al. 2014). It must also be recognized that synergies and antagonisms are more complex in nature than their simple categorizations imply (Piggott et al. 2015). The same co-invaders can have simultaneous synergistic, additive, and antagonistic effects on various ecosystem components (Lone et al. 2024). Even when co-invading species have strong antagonistic interactions, their combined impacts can still be significant since they rarely cancel each other (Ahmad et al. 2025). It is doubtful whether the biotic resistance model is more generally applicable than either the ecological roulette or facilitation-synergy models, or variations thereof, under current levels of propagule pressure—which can overwhelm the intrinsic resistance of natural ecosystems (Von Holle and Simberloff 2005; Hollebone and Hay 2007; Clark and Johnston 2009).

Along a similar line, Haubrock (2026) expresses concern that my paper consistently frames positive contributions of invaders as “transient or reversible, whereas negative outcomes are treated as persistent and cumulative”. Obviously, some negative effects are indeed persistent (Doody et al. 2017) or even permanent (Doherty et al. 2016), whereas other disruptive effects (e.g., changes to soil chemistry) may diminish over time (Thakur et al. 2025). Overall, invaders have both positive and negative effects on various resident taxa and ecosystem properties (e.g., Higgins and Vander Zanden 2010), but the threat of high invasion rates to sustainability does not depend on the relative persistence of these effects. Successive invaders can change the abundance of resident species and alter ecosystem functions in myriad ways, resulting in increased temporal variance (Frost et al. 2024; Czeglédi et al. 2025)—i.e., greater instability. Even ecological stable states resulting from previous invasions can be disrupted by new invasions (Ricciardi and Simberloff 2025). I know of no empirical evidence that positive effects of invaders stabilize ecosystems under rising colonization pressure. Given the unpredictable and increasingly frequent perturbations caused by high invasion rates, the task of managing ecosystems to the benefit of society becomes increasingly challenging regardless of how transitory positive or negative effects on various ecosystem components prove to be.

Finally, Haubrock (2026) insinuates that I ignored an existing body of work when he remarks that my

paper “makes it sound as if biological invasions have been ‘rarely framed as a sustainability issue’ despite biological invasions having long been recognized as a major driver of biodiversity loss and ecosystem change in global assessments...” On the contrary, in a statement that Haubrock (2026) misquoted, I actually said “Even though non-native species are now widely recognized as a major threat to biodiversity and ecosystem services (IPBES 2023), uncontrolled *rates of invasion* have rarely been framed as a sustainability issue.” I supported this statement with the results of a Clarivate Web of Science search that found that only <6% of articles explicitly identified invasions as a threat to sustainable ecosystems, and no article elaborated on how sustainability is affected by invasion rates or colonization pressure (Ricciardi 2026).

In summary, Haubrock’s (2026) attempt to call attention to important nuances of invasion dynamics, context dependencies, and their potential roles in mediating impacts is undermined by a series of misapplied criticisms.

## Moving forward

The speculative propositions in Ricciardi (2026) are intended to encourage thoughtful consideration of the mechanisms by which invasion rates can potentially destabilize ecosystems and thus impede sustainability. Sustainable ecosystem management requires a framework for understanding cumulative and long-term impacts of increasing numbers of invaders. Such a framework must consider complex indirect effects of antagonisms and synergies (Lone et al. 2024) as well as the influence of invader residence time in the system (Thakur et al. 2025). Indirect effects remain among the most understudied consequences of invader interactions (Kuebbing et al. 2020), yet even mixed positive and negative interactions can have profound impacts on community stability (Ricciardi and Simberloff 2025). Essentially, a coordinated research effort is needed to relate invasion rates to stability using modelling approaches, analyses of long-term data from invaded natural systems, and whole-ecosystem experiments that incorporate ecological complexity—similar to those that manipulate rates of intensity of external drivers to examine effects on ecosystem resilience (e.g., Brock et al. 2026). Nevertheless,

there already exists ample evidence that uncontrolled invasion rates threaten sustainability and thus require urgent management action, as directed by the Kunming-Montreal Global Biodiversity Framework.

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#### Ethics declarations

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