Managing multi-species plant invasions when interactions influence their impact

Angela J Brandt[1*], G Kenny Png[2], Insu Jo[3], Chris McGrannachan[4], Kara Allen[3], Duane A Peltzer[3], Carla D'Antonio[5], Ian A Dickie[6], Kristine French[7], Michelle R Leishman[8], Rebecca Ostertag[9], Ingrid M Parker[10], Margaret C Stanley[11], Katharine N Suding[12], and Peter J Bellingham[3,11]

Invasions by multiple non-native plant species are common, but management programs often prioritize control of individual species that are expected to have the highest impacts. Multi-species invasions could have larger or smaller impacts than single-species invasions depending on how multiple co-occurring invaders interact to alter their abundance or per capita impacts. Synergistic interactions, such as facilitation, may lead to greater combined impacts. However, if management focuses on a single invader, suppressive interactions could produce unintended consequences, such as the release of a co-occurring invader with a stronger impact. The mechanisms described here highlight where better evidence is needed to predict the combined impacts of co-occurring invaders and which mitigation strategies are most effective. Focused research is required to provide such evidence, which can aid managers in prioritizing which plant invaders to target and in determining the best sequence of invader removal – one that minimizes detrimental impacts on communities and ecosystems.

Front Ecol Environ 2023; doi:10.1002/fee.2658

The accumulating number of widespread and abundant non-native plant species has driven major efforts in research and management to understand and mitigate their harmful effects (eg Gurevitch *et al.* 2011; Pyšek *et al.* 2012). Many studies have focused on the causes of invasions by single plant species and their impacts on ecological processes and community structure (eg Vilà *et al.* 2011; Pyšek *et al.* 2012; Bradley *et al.* 2019). However, surprisingly few studies have considered how interactions among multiple invaders influence their combined impacts (Kuebbing *et al.* 2013; Pearson *et al.* 2016a), despite invaders co-occurring frequently and interactions among them differing in both magnitude and direction (ie from facilitative to competitive; Kuebbing *et al.* 2013). This suggests that the consequences of multi-species invasions are likely to be complex, and that different strategies are needed to successfully mitigate the combined impacts of co-occurring invaders.

In a nutshell:

- Management of non-native plant species mostly focuses on single invaders, but many sites contain multiple invaders
- Interactions between invaders may be positive or negative, potentially amplifying or dampening an invader's impacts on communities or ecosystems
- Selecting individual species for management could result in no overall improvement following invader control, or even increase adverse ecological impacts due to release of co-occurring invaders
- Understanding interactions among co-occurring invaders is essential for selecting the best management approach, such as targeting multiple species simultaneously or in a deliberate order

Multiple non-native plant species have invaded many ecosystems globally (Figure 1). For example, over two-thirds of areas managed for conservation (Kuebbing *et al.* 2013) and over half of grassland plots across 13 countries and six continents (Seabloom *et al.* 2013) contain more than one invader. Moreover, in areas where multiple invaders co-occur, the most dominant (that is, the single most abundant) invader may be numerically less abundant than all subordinate invaders combined (Panel 1 and Figure 2). Yet empirical data on how co-occurring invaders influence community structure, ecosystem processes, or responses to management remain scarce.

How co-occurring invaders interact to produce combined impacts differs among species and invaded ecosystems. Plant invaders can facilitate one another, altering community structure and ecosystem processes in a manner that promotes subsequent invasion (ie "invasional meltdown"; Simberloff and Von Holle 1999). In contrast, "invasional interference" through competition could reduce abundance or spread of co-occurring invaders (D'Antonio and Mack 2001; Rauschert and Shea 2017). However, invasion outcomes of plant interactions are likely more complicated than this dichotomy suggests. For instance, according to meta-analyses, competition between co-occurring invaders is often weaker than competition between invaders and native species (Kuebbing and Nuñez 2016), and invaders exhibit greater tolerance to competition than natives (Golivets

[1]*Manaaki Whenua – Landcare Research, Dunedin, New Zealand* [*]*(brandta@landcareresearch.co.nz);* [2]*Asian School of the Environment, Nanyang Technological University, Singapore City, Singapore;* [3]*Manaaki Whenua – Landcare Research, Lincoln, New Zealand;*
(continued on last page)

Figure 1. (a) The perennial grass *Melinis minutiflora* growing under and around the nitrogen-fixing tree *Morella faya* in Hawai'i. Photo credit: C D'Antonio. (b) Initial invasion and management of *Pinus contorta* stimulates both pine reinvasion and invasion by non-native grasses in New Zealand. Photo credit: IA Dickie. (c) The vines *Mikania micrantha* (upper left), *Passiflora rubra* (upper right), and *Cardiospermum grandiflorum* (bottom right) grow together in Rarotonga, Cook Islands. Photo credit: Q Paynter. (d) The fern *Nephrolepis cordifolia* (foreground), with the shrub *Lantana camara* and vines *C grandiflorum* and *Lonicera japonica* surrounding it along an urban bushland edge in Australia. Photo credit: MR Leishman. (e) The perennial forb *Zantedeschia aethiopica* alongside the tree *Paraserianthes lophantha* on a forest edge in New Zealand. Photo credit: MC Stanley. (f) Native species of California grasslands, such as *Lupinus nanus* and *Eschscholzia californica*, share a field with over a dozen non-native annual grasses and forbs, including *Avena barbata* and *Silene gallica*. Photo credit: AJ Brandt.

and Wallin 2018). Whether competition between co-occurring invaders results in suppression of one or more invaders may therefore depend on other interactions within the community. Due to these varying interaction outcomes, co-occurring invaders can have profound (but sometimes unanticipated) effects on communities and ecosystems. The potential for interactions to enhance or reduce the combined impacts of co-occurring invaders underscores the need for novel management strategies that effectively mitigate invasion impacts in ecosystems invaded by multiple non-native plant species.

Management often focuses on single "priority" species because they have known detrimental impacts (eg Pheloung *et al.* [1999]; see also Hulme [2012]). However, management targeting primary invaders can result in a surge of non-target invaders – either those co-occurring with the targeted invader or those establishing from outside of the managed area (Pearson *et al.* 2016b). This is a common management challenge: for example, approximately 25% of selected global studies reported that control efforts promoted invasion (Kettenring and Adams 2011), 44% of selected studies assessing the efficacy of non-native plant management in US National Park Service lands found increases in non-target invaders (Abella 2014), and 52% of respondents to land manager surveys in Australia reported increases in invasions post-management (Reid *et al.* 2009). Moreover, non-target invaders are often species that are identified in the region as noxious or invasive (Pearson *et al.* 2016b).

Previous studies have reviewed the types of interactions observed between co-occurring plant invaders (Kuebbing and Nuñez 2015) and, more narrowly, the release of non-target co-occurring invaders following single-species removal (Pearson *et al.* 2016b). We build on these earlier reviews by further assessing the potential interactive impacts of co-occurring plant invaders through a mechanistic lens, and the consequences of these interactions for management outcomes. First, we identify current knowledge gaps about the impacts of co-occurring invaders, and how filling these gaps is crucial for improving management strategies. We then demonstrate how different interaction mechanisms can affect the abundance or per capita impact (defined below) of an invader, and determine how the impacts of co-occurring invaders might differ from single-species invasions. Finally, we evaluate how understanding the mechanisms underpinning these impacts can generate new insight into how management of multiple invaders differs from a single-species approach.

The impacts of multiple plant invaders: more than the sum of their parts?

The effect of an invader depends on both its abundance and its per capita impact (the local-scale components of the impact equation described by Parker *et al.* [1999]).

Panel 1. How common are multi-species plant invasions?

We used regional databases of vegetation inventory plots from New Zealand and the US to illustrate how frequently invasions by multiple non-native species are recorded. More than 45% of all plots in each inventory contained at least one invader, with most invaded plots containing multiple invaders (Figure 2). Although many of the plots invaded by multiple non-natives contain a single dominant (most abundant) invader, the cumulative abundance of the co-occurring subordinate invaders often can match or surpass that of the dominant invader.

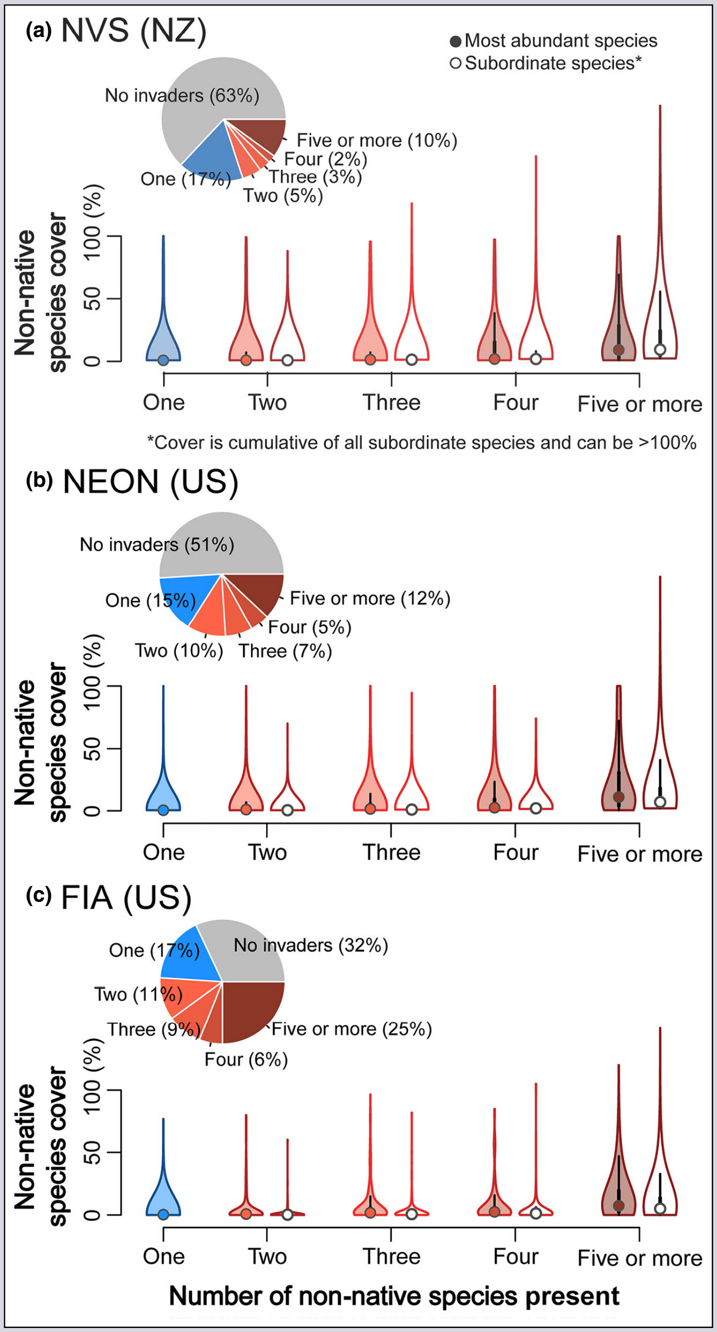

Figure 2. Frequency and abundance of co-occurring invaders in the (a) New Zealand National Vegetation Survey (NVS) databank (Wiser *et al.* 2001); (b) US National Ecological Observatory Network (NEON; NEON 2021); and (c) US Forest Inventory and Analysis (FIA) program (Gray *et al.* 2012). Pie charts show percentage of plots in each regional vegetation inventory database that contain zero, one, or multiple non-native plant species. Violin plots show the median and quartiles, as well as the kernel probability density, of cover of the single most abundant invader in these inventory plots (color-filled symbols) and combined cover (often exceeding 100%) of all subordinate invaders (open symbols) in each plot where multiple invaders are present. (Further details regarding the vegetation inventory databases are provided in WebTable 1.)

Quantitative measurements of invader impact usually scale with abundance (eg Bradley *et al.* 2019). Therefore, if co-occurring invaders can each alter the other's abundance (Figure 3), per capita impact, or both, their combined impact will differ from the simple sum of their individual impacts. (Although we recognize that more than two invaders can co-occur within a site and that multiple mechanisms may operate among species, for simplicity we evaluate pairwise interactions between two invaders.)

In scenarios where co-occurring invaders do not interact (that is, neither species alters the other's abundance or per capita impact), it would be expected that their combined ("additive") impact would be the sum of their individual impacts (Figure 3; see WebTable 2 for definitions, illustrative examples, and documented cases of each impact mechanism). This represents a "null model" for quantifying impacts of co-occurring invaders, resulting from an increase in total invader biomass at the site ("biomass effects"; Figure 3) or different types of impact from invaders having distinct traits ("complementarity").

It is also possible that interactions between co-occurring invaders could lead to a combined impact that is larger or smaller than expected from this null model. Most studies of interactions between co-occurring invaders have measured changes in abundance or performance of invaders rather than their net impacts (eg Kuebbing *et al.* 2013; Kuebbing and Nuñez 2015; but see Pearson *et al.* 2016a). Below, we discuss the few studies in which the combined impacts of co-occurring invaders have been appraised; although the authors of these studies demonstrated that both larger and smaller non-additive impacts can occur, they did not disentangle how abundance and per capita effects of co-occurring invaders determine their combined impacts.

Co-occurring invaders could produce a combined impact greater than the sum of their individual impacts ("non-additive – synergistic") if their interactions lead to an increase in each other's abundance ("facilitation"; Figure 3) or per capita impact ("impact synergy"). For example, in eastern US forests, carbon-degrading enzyme activity was higher in areas where two non-native shrubs, *Ligustrum sinense* and *Lonicera maackii*, co-occur (Kuebbing *et al.* 2014), and native plant root mass was reduced more than expected by each shrub's effect alone in a greenhouse experiment (Kuebbing *et al.* 2016). In the Brazilian Cerrado, the simultaneous removal of two co-occurring perennial grasses, *Melinis minutiflora* and *Urochloa decumbens*, increased native plant diversity and biomass to a greater degree than did the removal of each species separately – another synergistic impact (Zenni *et al.* 2020). However, these grass species appeared to be competing rather than promoting each other's growth, suggesting that this could represent a case of impact synergy rather than facilitation.

Co-occurring invaders could unexpectedly have a combined impact less than the sum of their individual impacts ("non-additive – suppressed") if their combined abundance or impact is equivalent to invasion by a single species ("redundancy"; Figure 3), or if their interactions lead to a decrease in abundance ("competition"; Figure 3) or per capita impact ("impact suppression"). Two grasses that invade understories of eastern US forests, *Microstegium vimineum* (an annual) and *Oplismenus undulatifolius* (a perennial), may be redundant because their combined impacts (reduction of native plant richness and effects on soil properties) when the grasses co-occur are similar to their individual impacts when they each invade separately (Tekiela and Barney 2017). In contrast, fields

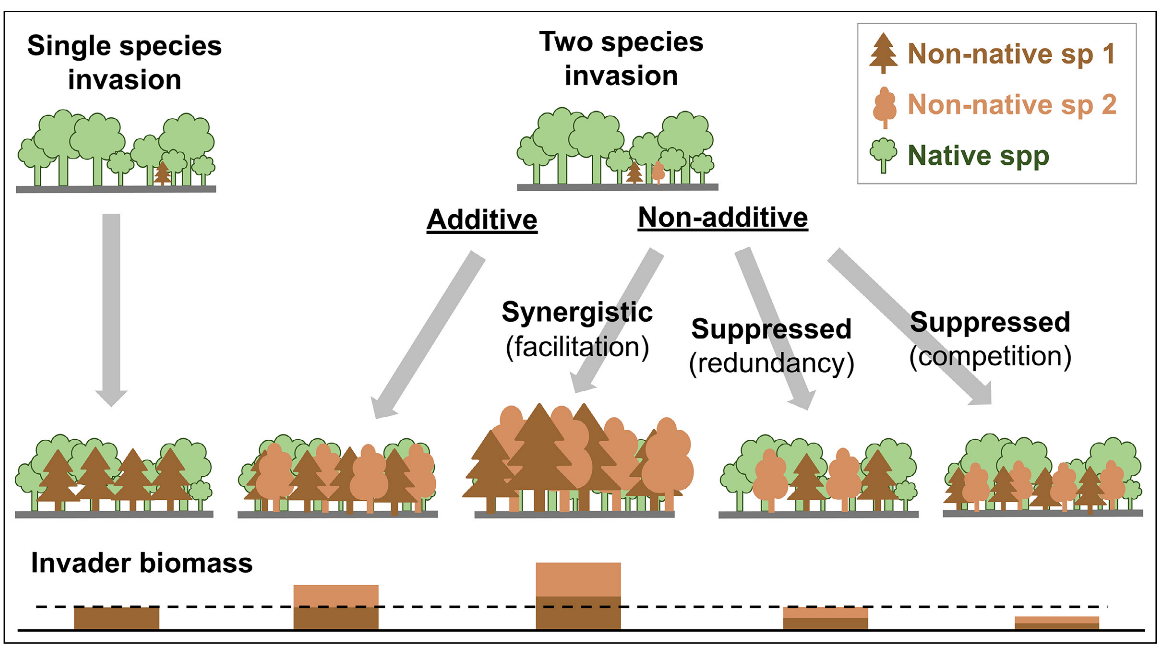

Figure 3. An additional non-native plant species at a site can influence total invader abundance or abundance of the first invader. As impacts tend to increase with abundance, the effect of co-occurring invaders on each other's abundance, as well as on total invader abundance at the site, will affect their combined impact.

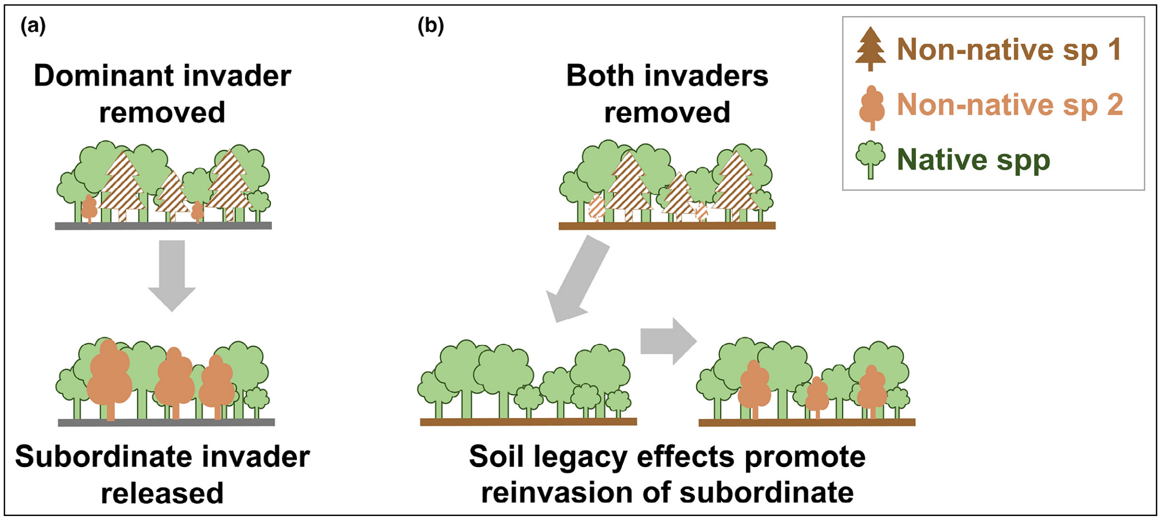

Figure 4. Unintended consequences can arise when management interventions fail to account for interactions between co-occurring non-native plant species. (a) Removal of one invader in competition with a co-occurring invader could lead to an increase in subordinate invader abundance, and subsequently its impact. (b) Facilitation between co-occurring invaders that operates via, for example, soil conditioning could leave legacies that persist even following control of the invader, which can promote reinvasion or spread of remaining invaders.

in Poland invaded by both *Juglans regia* trees and the perennial forb *Solidago canadensis* had higher native diversity than fields invaded by either species individually, likely due to competition that reduced *S canadensis* density where it co-occurred with *J regia* (Lenda *et al*. 2019).

Although interactions between co-occurring invaders can influence their combined impacts, outcomes can vary with the type of impact measured and interactions between natives and invaders. For example, additive effects of co-occurring grasses on soil properties in the Brazilian Cerrado (Zenni *et al*. 2020) and of co-occurring shrubs on non-native plant richness in eastern US forests (Kuebbing *et al*. 2014) were detected, although these co-occurring invaders synergistically affected other ecosystem properties, as described above. Furthermore, in microcosms of North American prairies, facilitation of the perennial forb *Cirsium arvense* by the perennial legume *Lotus corniculatus* was dampened in mixtures with native prairie species relative to two-species mixtures of the invaders, such that the invaders failed to synergistically reduce native biomass when they co-occurred (Oschrin and Reynolds 2019). In summary, co-occurring invaders in competition can generate synergistic, neutral, or suppressed impacts, and facilitation of a co-occurring invader does not always generate a synergistic impact. This highlights that measuring both interactions between and the combined impacts of co-occurring invaders is needed to improve predictions of multi-species invasion impacts.

Management strategies for multiple plant species invasion: avoiding perverse outcomes

Management to protect native species and ecosystem functioning usually focuses on removing invaders as the means of reducing or eliminating their impacts. Where invaders co-occur, they are often prioritized for removal based on their individual impacts (Kuebbing *et al*. 2013). Such an individual-species-led approach could be effective in reducing impacts of co-occurring invaders if their effects are additive, provided attention is given to minimizing reinvasion or invasion by other non-target invaders (Buckley *et al*. 2007; Pearson *et al*. 2016b). However, if impacts of co-occurring invaders are non-additive, management strategies are more likely to be successful if they recognize that interactions between invaders could influence the outcomes of control efforts.

Controlling a single invader can yield unintended consequences

Removal of an abundant invader could result in little or no change in overall invasion impacts at a site with co-occurring invaders that generate non-additive impacts (Figure 4). Such unintended consequences after invader removal can occur when suppressive interactions between co-occurring invaders reduce their combined impact (Figure 4a). In an example of the "worst-case" scenario, removing one invader could lead to a stronger detrimental impact, as the remaining invaders increase in abundance (Panel 2). In contrast, if co-occurring invaders are redundant, then removal of one invader may ultimately lead to no change in impact as the other invader fills the vacant space, as is predicted for forest understories where redundant grass invaders co-occur (Tekiela and Barney 2017).

Removal of only one invader involved in a synergistic interaction, such as facilitation, can also have unintended consequences, in some cases leading to more rapid invader recovery after management or other perturbations. For example, declines in *M minutiflora* populations after drought and wildfire in the submontane zone of Hawai'i were reversed following

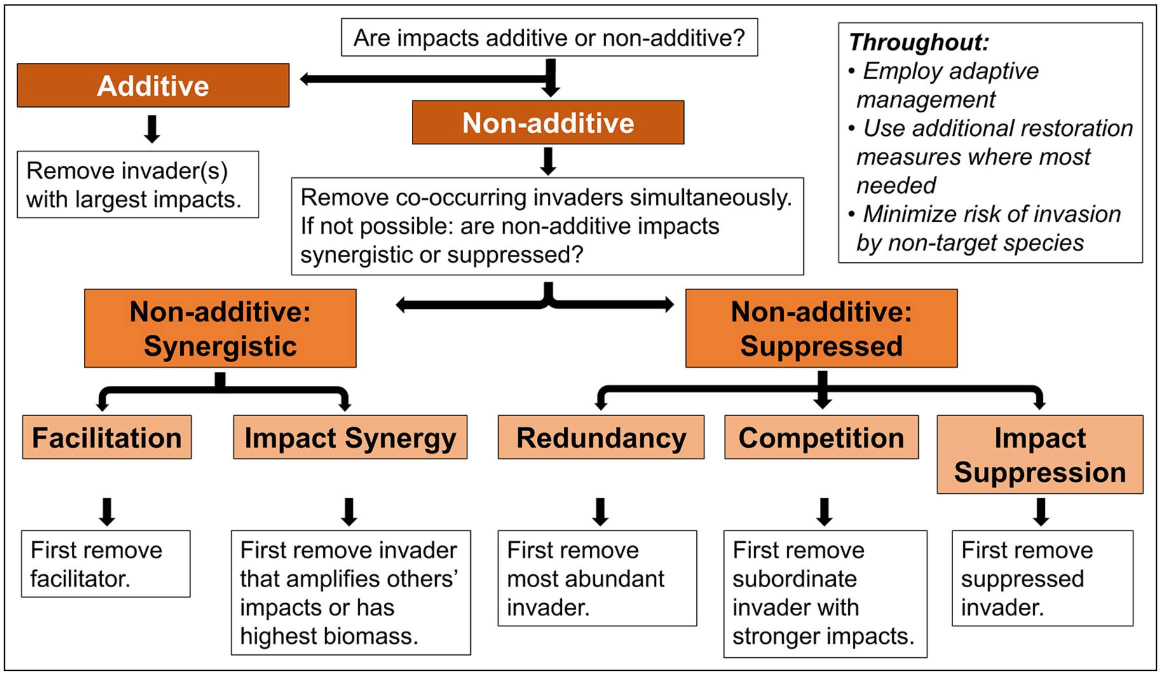

Figure 5. A decision-support pathway for applying management interventions based on the mechanisms underpinning the combined impact of co-occurring plant invaders. An adaptive management approach is recommended throughout, with potential non-target invaders monitored and additional restoration measures considered. In particular, revegetation alongside removal of invaders may be needed even when impacts are additive to minimize invasion by non-target species. Note that some management tools, including forms of herbicide application, may not support species-specific removal. We also recognize logistical and community-based values (eg harmful public health effects) will also be factored into management priorities.

Panel 2. Co-occurring invader case study – *Centaurea stoebe* and *Bromus tectorum* in North America

The complex nature of managing co-occurring invaders over time to mitigate their impacts is illustrated by studies of the co-occurring perennial forb *Centaurea stoebe* and the annual grass *Bromus tectorum* in Montana. Impacts of *C stoebe* include displacement of native plant species and alteration of forage for livestock and wildlife (DiTomaso 2005). In addition to reducing species diversity, *B tectorum* invasion increases wildfire frequency (Knapp 1996).

The plant community effects of treating *C stoebe* with a broadleaf herbicide were compared to untreated plots over 6 years (Ortega and Pearson 2010, 2011). Herbicide treatment initially reduced *C stoebe* cover by 70–80% as compared to untreated plots, whereas *B tectorum* increased about tenfold in the treated plots (Ortega and Pearson 2010). Six years after herbicide treatment, *C stoebe* cover remained lower (by more than 60%) in treated than in untreated plots (Ortega and Pearson 2011). Relative to pre-treatment levels, *C stoebe* cover was low and *B tectorum* cover high in both plot types. Ortega and Pearson (2011) posited that environmental factors independent of herbicide, such as drought, led to the decline of *C stoebe* in untreated plots and suppressed its recovery in treated plots, allowing *B tectorum* to increase in all plots.

To estimate the implications of a co-occurring invader being released from competition by management of a primary invader, Pearson *et al.* (2016a) used Parker *et al.*'s (1999) impact equation and abundance data for 25 plant invaders in Montana to rank the invasiveness and impact of each species. *B tectorum* ranked first for both metrics, suggesting that it is a "worse" invader than *C stoebe*. This case study highlights how managing a single invader may lead to perverse outcomes where it has been suppressing a co-occurring invader with stronger impacts. It also highlights that accounting for environmental effects on species abundance and interactions is critical for understanding and effectively managing combined impacts of co-occurring invaders.

invasion and soil enrichment by the non-native nitrogen-fixing tree *Morella faya* (Figure 1a; D'Antonio *et al.* 2017). Moreover, removal of an invader may not immediately remove its facilitative effects, such as those mediated by soils. For instance, altered soil nutrient cycling associated with the establishment of *Pinus contorta* in New Zealand persisted after pine removal, promoting invasion by non-native grasses and forbs (Figures 1b and 4b; Dickie *et al.* 2014).

Understanding co-occurring invader interactions can inform management decisions

Given that some co-occurring invaders produce non-additive impacts, effective management requires an understanding of the mechanisms underlying those impacts (Kuebbing *et al.* 2013). Such knowledge helps prioritize and manage invaders to reduce overall invasion impacts (Figure 5). Each case for management will be context specific (Kuebbing *et al.* 2013), with different focal invaders, other resident species, habitat types, levels of disturbance, and available resources for management. Managers' own expertise with local context will often strongly inform this understanding and can be leveraged with an adaptive management approach. In addition, meta-analyses and controlled experiments could shape guidelines to aid decision making by testing for mechanisms and generalizations based on functional group- or trait-based patterns (Kuebbing and Nuñez 2015; Ferenc and Sheppard 2020).

Manage co-occurring invaders simultaneously

Where possible, and especially where interactions between co-occurring invaders are anticipated, coordinated or simultaneous removal of these invaders may be the most effective means of avoiding or reducing perverse outcomes. For example, coordinated release of different, species-specific biocontrol agents for three perennial vines (*Cardiospermum grandiflorum*, *Mikania micrantha*, and *Passiflora rubra*) on Rarotonga, Cook Islands (Figure 1c), prevented the latter two vines from colonizing and dominating sites where *C grandiflorum* had once been abundant (Paynter *et al.* 2018).

Target the right species, in the right order

When management must focus on a single species at a time, considering how co-occurring invaders interact could change priorities of which species to target first (Figure 5). For example, one high-impact invader may be facilitated by a co-occurring invader. Prioritizing removal of the high-impact species might be less effective at reducing the overall invasion impact than by first removing the facilitator species, which could be promoting its fast recovery or further invasion by other high-impact species. Similarly, where suppressive interactions are occurring, prioritizing the most dominant invader for removal could lead to unintended consequences when a subordinate invader has stronger impacts (Panel 2). Managing synergistic or suppressive invaders could therefore involve a stepwise approach to first target a less abundant invader that amplifies other species' impacts or could be released from competition, respectively. Subsequent management would then work toward removal of any remaining invaders.

Tailor decision making to invasion context

Decisions on which invaders to manage, as well as when and how, should be based on which invaders co-occur at the site, how they interact, and how they are likely to respond to management interventions and environmental changes. For example, in cases where the combined impact of two co-occurring invaders was smaller than the individual impact of either species when they invaded alone (eg Lenda *et al.* 2019), focusing management on sites invaded by each species individually should be the priority. Notably, the nature of co-occurring invader interactions within a site can depend on the site's invasion history (ie which invader arrived first) as well as the identity of the invaders, where early arrival can confer a competitive advantage (Torres *et al.* 2022). Observing and collecting data for both target and non-target invaders, and their responses to changes in the environment (Panel 2; Sapsford *et al.* 2020), could determine whether management interventions achieve the desired outcome, and whether additional management interventions are required.

Identify when additional restoration measures are most needed

Removal of an invasive species entails the risk of reinvasion (Buckley *et al.* 2007). Additional restoration measures may be necessary in cases where a dominant invader with strong impacts is removed but its presence was suppressing the impacts of other problematic invaders. For example, the annual grass *M vimineum* suppresses growth of the perennial vine *Lonicera japonica* in eastern US forests (Belote and Weltzin 2006), and as such removal of the grass could inadvertently increase vine abundance. Targeting the dominant invader for removal in combination with planting native species could limit the expansion of subordinate invaders (Schuster *et al.* 2018), although additional control may be required to slow invader population growth and prevent the negation of gains from the initial removal efforts.

In addition to active revegetation, actions such as removal of invader litter and application of soil amendments might be necessary where, for example, legacy effects of target invaders promote other non-native species (Nsikani *et al.* 2017; Wardle and Peltzer 2017). Legacy effects such as altered soil microbial communities and nutrient cycling could enable synergistic impacts to continue following removal of the facilitator (Corbin and D'Antonio 2012; Nsikani *et al.* 2017). Together, these findings emphasize that a sequence of management interventions may be required to meet site-specific objectives of removing invaders or restoring ecological communities.

Prevention versus control

The interaction mechanisms we describe highlight a potentially counterintuitive conclusion: although synergistic interactions between co-occurring invaders are likely to produce the worst outcomes for ecosystems, suppressive interactions between co-occurring invaders may pose greater difficulties for achieving management goals. Thus, preventing additional species from invading a site should be a high priority regardless of whether the new invader might form synergistic or suppressive interactions with previously established non-natives, albeit for different reasons.

Research directions to support effective management of multi-species invasions

Interaction mechanisms between co-occurring invaders influence their combined impacts and the effectiveness of approaches to their management, which suggests that several lines of research are required to support management of multi-species invasions.

First, additional empirical data are needed to test the ideas we presented here. Few studies to date have linked interactions between co-occurring invaders with their impacts, particularly beyond effects on co-occurring invader abundance, or revealed the consequences of different management approaches. Aligning research on invasion impact with management interventions, particularly invader removals, could determine how co-occurring invaders interact across a wide variety of systems, and how often single-species management leads to perverse outcomes.

Second, improving predictions of which co-occurring invaders will produce non-additive impacts, and discerning which management approach will be most effective where these invaders co-occur, is crucial. Risk assessment frameworks using species characteristics can aid in prioritization of invaders for management when quantitative estimates of impacts are unavailable (Rayment and French 2021), but this approach must be coupled with estimated outcomes of co-occurring invader interactions. Similarly, characteristics related to the magnitude and direction of species interactions, such as life-history traits (lifespan, phenology) and functional traits (ability to fix nitrogen, flammability), could facilitate predictions of combined impact. For example, Kuebbing and Nuñez (2015) found that positive interactions (eg facilitation) were far more likely to occur when an invader's neighbor was a nitrogen-fixer or a woody plant and far less likely to occur when a neighbor was an annual plant rather than a perennial plant. In some cases, trait differences between co-occurring invaders may be better predictors of their interaction outcomes than an individual invader's trait value. In pairs of annual non-native species grown together, those that were taller, with lower specific leaf area, greater initial seed mass, and higher root investment than their neighbor attained greater biomass when grown in competition (Ferenc and Sheppard 2020). Such information on invader characteristics and distinctiveness from co-occurring invaders could generate spatially explicit predictions of co-occurring invader interactions, which could feed into a decision-support pathway (eg Figure 5). This area of research could also draw on the extensive knowledge and tools already developed for planning removals of animal invaders (eg Ramsey and Veltman 2005; Raymond *et al*. 2011). Enabling managers to apply such tools to inform site-specific interventions is the next essential step toward implementing a decision-support pathway as presented here. One example of incorporating local expert knowledge into interdisciplinary approaches is the recent development of a web-based interface for applying fuzzy cognitive maps to determine potential unintended consequences of species introductions or removals (Clark-Wolf *et al*. 2022).

Third, we identified a gap in understanding synergy and suppression of per capita impact independently of how invader interactions affect each other's abundance. These mechanisms suggest that facilitative interactions between co-occurring invaders will not always generate synergistic impacts, nor will competitive interactions always generate suppressive impacts, with the latter scenario observed in the Brazilian Cerrado (Zenni *et al*. 2020). Exploring different mechanisms of co-occurring invader interactions as well as their direction (ie competition versus facilitation), such as competitive tolerance versus suppression (Golivets and Wallin 2018) and indirect versus direct interactions (Kuebbing and Nuñez 2015), may enhance predictions of when, for example, competition will generate impact suppression.

Fourth, while research into synergistic interactions is needed to predict when multi-species invasions will have greater than expected impacts, we highlighted that research focused on suppressive interactions would greatly benefit management decision making, including the prioritization of invaders to target for management and the sequence in which invaders should be removed. Previous reviews support this need, given that competition between co-occurring invaders has been reported in the literature twice as frequently as facilitation (Kuebbing and Nuñez 2015), and because non-target invaders often increase in abundance after the removal of a target invader (Pearson *et al*. 2016b). However, accurate predictions will rely on understanding the outcomes of invader interactions rather than only their direction (ie competition versus facilitation), given that both direct and indirect interactions occur in natural communities (Kuebbing and Nuñez 2016) and competitive advantages can arise from tolerance to competition as well as suppression of co-occurring plants (Golivets and Wallin 2018).

Finally, we presented illustrative examples of each interaction mechanism for pairs of co-occurring invaders, but these interactions will be more complex given that three or more invaders often co-occur (Panel 1; eg Oschrin and Reynolds 2019). These mechanisms might occur in combination and all plants within the community may interact, including indirectly. Indeed, synergistic and suppressive mechanisms may operate simultaneously between co-occurring invaders. For example, abundance of the annual grass *Bromus diandrus* increases with invasion of the clonal succulent *Carpobrotus edulis*, possibly because the latter species captures and retains seeds of the former species in this environment with frequent high winds (Magnoli *et al*. 2013). However, belowground effects of *C edulis*, even after its removal, reduce germination of *B diandrus*. Native plants can also facilitate invaders (Cavieres 2021; Lucero *et al*. 2021), posing a challenge for management in cases where removal of all interacting species is not feasible. Appreciating the potential consequences of species interactions in combination with adaptive management is therefore the most pragmatic approach to managing multi-species invasions in complex ecosystems where data are lacking.

Management of non-native plant species has largely been based on studies of single dominant invaders with substantial impacts, and experimental data to guide management of multi-species invasions remain lacking. Using a community ecology approach can facilitate identification of invaders with high potential for non-additive impacts due to their interactions with other invaders or native species (Latombe *et al*. 2021), which would enable managers to target species whose removal would provide the greatest benefit. Supporting effective management to mitigate impacts of multi-species invasions is essential now that the UN Decade on Ecosystem Restoration is well underway (UNEP 2021).

Acknowledgements

We thank JL Firn and SJ Richardson for contributing to the ideas in this paper. Funding for the working group to draft this paper was provided by the Strategic Science Investment Fund of the Ministry of Business, Innovation and Employment of New Zealand to Manaaki Whenua – Landcare Research. Open access publishing facilitated by Landcare Research New Zealand, as part of the Wiley - Landcare Research New Zealand agreement via the Council of Australian University Librarians.

Data Availability Statement

Data used in this paper are already published and publicly accessible (Gray *et al*. 2012; NEON 2021; Wiser *et al*. 2001).

References

Abella SR. 2014. Effectiveness of exotic plant treatments on National Park Service lands in the United States. *Invas Plant Sci Mana* **7**: 147–63.

Belote RT and Weltzin JF. 2006. Interactions between two co-dominant, invasive plants in the understory of a temperate deciduous forest. *Biol Invasions* **8**: 1629–41.

Bradley BA, Laginhas BB, Whitlock R, *et al*. 2019. Disentangling the abundance–impact relationship for invasive species. *P Natl Acad Sci USA* **116**: 9919–24.

Buckley YM, Bolker BM, and Rees M. 2007. Disturbance, invasion and re-invasion: managing the weed-shaped hole in disturbed ecosystems. *Ecol Lett* **10**: 809–17.

Cavieres LA. 2021. Facilitation and the invasibility of plant communities. *J Ecol* **109**: 2019–28.

Clark-Wolf TJ, Hahn PG, Brelsford E, *et al*. 2022. Preventing a series of unfortunate events: using qualitative models to improve conservation. *J Appl Ecol* **59**: 2322–32.

Corbin JD and D'Antonio CM. 2012. Gone but not forgotten? Invasive plants' legacies on community and ecosystem properties. *Invas Plant Sci Mana* **5**: 117–24.

D'Antonio CM and Mack M. 2001. Exotic grasses potentially slow invasion of an N-fixing tree into a Hawaiian woodland. *Biol Invasions* **3**: 69–73.

D'Antonio CM, Ostertag R, Cordell S, and Yelenik S. 2017. Interactions among invasive plants: lessons from Hawai'i. *Annu Rev Ecol Evol S* **48**: 521–41.

Dickie IA, St John MG, Yeates GW, *et al*. 2014. Belowground legacies of *Pinus contorta* invasion and removal result in multiple mechanisms of invasional meltdown. *AoB PLANTS* **6**: plu056.

DiTomaso JM. 2005. Invasive weeds in rangelands: species, impacts, and management. *Weed Sci* **48**: 255–65.

Ferenc V and Sheppard CS. 2020. The stronger, the better – trait hierarchy is driving alien species interaction. *Oikos* **129**: 1455–67.

Golivets M and Wallin KF. 2018. Neighbour tolerance, not suppression, provides competitive advantage to non-native plants. *Ecol Lett* **21**: 745–59.

Gray AN, Brandeis TJ, Shaw JD, *et al*. 2012. Forest Inventory and Analysis database of the United States of America (FIA). *Biodivers Ecol* **4**: 225–31.

Gurevitch J, Fox GA, Wardle GM, and Taub D. 2011. Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecol Lett* **14**: 407–18.

Hulme PE. 2012. Weed risk assessment: a way forward or a waste of time? *J Appl Ecol* **49**: 10–19.

Kettenring KM and Adams CR. 2011. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *J Appl Ecol* **48**: 970–79.

Knapp PA. 1996. Cheatgrass (*Bromus tectorum* L) dominance in the Great Basin Desert. *Global Environ Chang* **6**: 37–52.

Kuebbing SE and Nuñez MA. 2015. Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications. *Glob Change Biol* **21**: 926–34.

Kuebbing SE and Nuñez MA. 2016. Invasive non-native plants have a greater effect on neighbouring natives than other non-natives. *Nat Plants* **2**: 16134.

Kuebbing SE, Classen AT, and Simberloff D. 2014. Two co-occurring invasive woody shrubs alter soil properties and promote subdominant invasive species. *J Appl Ecol* **51**: 124–33.

Kuebbing SE, Nuñez MA, and Simberloff D. 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biol Conserv* **160**: 121–29.

Kuebbing SE, Patterson CM, Classen AT, and Simberloff D. 2016. Co-occurring nonnative woody shrubs have additive and non-additive soil legacies. *Ecol Appl* **26**: 1896–906.

Latombe G, Richardson DM, McGeoch MA, *et al*. 2021. Mechanistic reconciliation of community and invasion ecology. *Ecosphere* **12**: e03359.

Lenda M, Skórka P, Knops J, *et al*. 2019. Multispecies invasion reduces the negative impact of single alien plant species on native flora. *Divers Distrib* **25**: 951–62.

Lucero JE, Callaway RM, Faist AM, and Lortie CJ. 2021. An unfortunate alliance: native shrubs increase the abundance, performance, and apparent impacts of *Bromus tectorum* across a regional aridity gradient. *Basic Appl Ecol* **57**: 41–53.

Magnoli SM, Kleinhesselink AR, and Cushman JH. 2013. Responses to invasion and invader removal differ between native and exotic plant groups in a coastal dune. *Oecologia* **173**: 1521–30.

NEON (National Ecological Observatory Network). 2021. Plant presence and percent cover (DP1.10058.001). Boulder, CO: NEON.

Nsikani MM, Novoa A, van Wilgen BW, *et al*. 2017. *Acacia saligna*'s soil legacy effects persist up to 10 years after clearing: implications for ecological restoration. *Austral Ecol* **42**: 880–89.

Ortega YK and Pearson DE. 2010. Effects of picloram application on community dominants vary with initial levels of spotted knapweed (*Centaurea stoebe*) invasion. *Invas Plant Sci Mana* **3**: 70–80.

Ortega YK and Pearson DE. 2011. Long-term effects of weed control with picloram along a gradient of spotted knapweed invasion. *Rangeland Ecol Manag* **64**: 67–77.

Oschrin E and Reynolds HL. 2019. Co-occurring invasive plant interactions do not predict the impacts of invasion in experimental tallgrass prairie communities. *Biol Invasions* **21**: 2417–30.

Parker IM, Simberloff D, Lonsdale WM, *et al.* 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* **1**: 3–19.

Paynter Q, Poeschko M, Mitchell C, *et al.* 2018. A weed biocontrol program for the Cook Islands: progress report. In: Hintz HL, Bon M-C, Bourdôt G, *et al.* (Eds). Proceedings of the XV International Symposium on Biological Control of Weeds; 26–31 Aug 2018; Engelberg, Switzerland. Wallingford, UK: Centre for Agriculture and Bioscience International.

Pearson DE, Ortega YK, Eren Ö, and Hierro JL. 2016a. Quantifying "apparent" impact and distinguishing impact from invasiveness in multispecies plant invasions. *Ecol Appl* **26**: 162–73.

Pearson DE, Ortega YK, Runyon JB, and Butler JL. 2016b. Secondary invasion: the bane of weed management. *Biol Conserv* **197**: 8–17.

Pheloung PC, Williams PA, and Halloy SR. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *J Environ Manage* **57**: 239–51.

Pyšek P, Jarošík V, Hulme PE, *et al.* 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Glob Change Biol* **18**: 1725–37.

Ramsey D and Veltman C. 2005. Predicting the effects of perturbations on ecological communities: what can qualitative models offer? *J Anim Ecol* **74**: 905–16.

Rauschert ESJ and Shea K. 2017. Competition between similar invasive species: modeling invasional interference across a landscape. *Popul Ecol* **59**: 79–88.

Rayment J and French K. 2021. Uncertainty in research about key invasion characteristics limits the evaluation of exotic perennial grasses in natural systems in New South Wales, Australia. *Ecol Manag Restor* **22**: 53–63.

Raymond B, McInnes J, Dambacher JM, *et al.* 2011. Qualitative modelling of invasive species eradication on subantarctic Macquarie Island. *J Appl Ecol* **48**: 181–91.

Reid AM, Morin L, Downey PO, *et al.* 2009. Does invasive plant management aid the restoration of natural ecosystems? *Biol Conserv* **142**: 2342–49.

Sapsford SJ, Brandt AJ, Davis KT, *et al.* 2020. Towards a framework for understanding the context dependence of impacts of non-native tree species. *Funct Ecol* **34**: 944–55.

Schuster MJ, Wragg PD, and Reich PB. 2018. Using revegetation to suppress invasive plants in grasslands and forests. *J Appl Ecol* **55**: 2362–73.

Seabloom EW, Borer ET, Buckley YM, *et al.* 2013. Predicting invasion in grassland ecosystems: is exotic dominance the real embarrassment of richness? *Glob Change Biol* **19**: 3677–87.

Simberloff D and Von Holle B. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biol Invasions* **1**: 21–32.

Tekiela DR and Barney JN. 2017. Co-invasion of similar invaders results in analogous ecological impact niches and no synergies. *Biol Invasions* **19**: 147–59.

Torres AT, Rodríguez-Cabal MA, and Núñez MA. 2022. Do not come late to the party: initial success of nonnative species is contingent on timing of arrival of co-occurring nonnatives. *Biol Invasions* **24**: 557–73.

UNEP (UN Environment Programme). 2021. United Nations Decade on Ecosystem Restoration, 2021–2030. Nairobi, Kenya: UNEP.

Vilà M, Espinar JL, Hejda M, *et al.* 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecol Lett* **14**: 702–08.

Wardle DA and Peltzer DA. 2017. Impacts of invasive biota in forest ecosystems in an aboveground–belowground context. *Biol Invasions* **19**: 3301–16.

Wiser SK, Bellingham PJ, and Burrows LE. 2001. Managing biodiversity information: development of New Zealand's National Vegetation Survey databank. *New Zeal J Ecol* **25**: 1–17.

Zenni RD, da Cunha WL, Musso C, *et al.* 2020. Synergistic impacts of co-occurring invasive grasses cause persistent effects in the soil-plant system after selective removal. *Funct Ecol* **34**: 1102–12.

Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2658/suppinfo

[4]*Manaaki Whenua – Landcare Research, Auckland, New Zealand;* [5]*Department of Ecology, Evolution, and Marine Biology, University of California–Santa Barbara, Santa Barbara, CA;* [6]*School of Biological Sciences, University of Canterbury, Christchurch, New Zealand;* [7]*School of Earth, Atmospheric and Life Sciences, University of Wollongong, Wollongong, Australia;* [8]*School of Natural Sciences, Macquarie University, Sydney, Australia;* [9]*Department of Biology, University of Hawai'i at Hilo, Hilo, HI;* [10]*Department of Ecology and Evolutionary Biology, University of California–Santa Cruz, Santa Cruz, CA;* [11]*School of Biological Sciences, University of Auckland/Waipapa Taumata Rau, Auckland, New Zealand;* [12]*Department of Ecology and Evolutionary Biology, University of Colorado–Boulder, Boulder, CO*