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Perspective

Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species

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ABSTRACT

Though biological invasion studies have proliferated in recent decades, a consistent emphasis remains on the study of single-species invasions. Here, we juxtapose the number of invasive plants reported as co-occurring within conservation habitats in one of the most comprehensive global conservation management databases (The Nature Conservancy's Conservation Projects) with the number of published studies that address impacts of co-occurring invasive plants. We reviewed 86 conservation projects and 153 peer-reviewed publications and found that only one-third of studies mentioned co-occurring invaders, although over two-thirds of habitats were multiply invaded, indicating researchers are more likely to study single invaders, even though conservation managers are more often faced with multiple invaders in a given habitat. Of those studies focused on multiple invasives, the majority did not attempt to differentiate impacts caused by species when found alone or with other invaders and instead either treated co-occurring invaders together as a single, undifferentiated group or compared impacts between invasive plant monocultures. Less than 6% of all studies analyzed invader interactions. The high prevalence of co-occurring invasive plants should encourage more research on multiple invaders, which may better inform prioritization of which species to manage. Specifically, we suggest research on how effects of multiple invaders differ from those of single invaders, what types of interactions (facilitative, competitive, neutral) are most commonly found between invaders, and what effects interactions might have on the overall impact (additive or non-additive) of the individual invader. Though we acknowledge the challenge of studying multiple invaders, there is a critical need to address these questions to make invasion research more relevant to conservation programs.

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1. Introduction

Biological invasion research has burgeoned in the last few decades (Gurevitch et al., 2011; MacIsaac et al., 2011; Simberloff, 2011a), in part owing to growing recognition of negative ecological and economic impacts of invasive species (Mack et al., 2000; Pyšek and Richardson, 2010; Simberloff et al., 2013) and the shrinking of regions of the globe that remain substantially unaffected by invaders (Mooney and Hobbs, 2000). Historically, the focus of much invasion research has been on factors that characterize impacts of invasive species in their non-native ranges, with a strong emphasis on single-species invasions (Davis, 2006; Simberloff, 2011a).

Some of the best-studied invasive taxa are plants (Parker et al., 1999). This focus on plants has advanced our understanding of many facets of invasion biology. We now have better trait-based models to predict which exotic plant species might become invasive (Rejmánek and Richardson, 1996; Ordonez et al., 2010; Castro-Díez et al., 2011), an improved sense of potential factors that may influence community susceptibility to invasion (Levine and D'Antonio, 1999; Davis et al., 2000; Fridley et al., 2007; Drenovsky et al., 2008, 2012; Simberloff, 2009), better understanding of which mechanisms may produce larger invasion impacts (Levine et al., 2003), and a rich catalogue of individual invader impacts that include those driving major shifts in ecosystem functioning (Ehrenfeld, 2010; Vitousek et al., 1987; Zavaleta, 2000) and draining national economies (Olson, 2006; Vilà et al., 2010; van Wilgen et al., 2002).

Like much of the invasion literature in general, most invasive plant research considers only single invasive species and ignores the presence of co-occurring invaders. The effects of singleton plant invaders on native communities and ecosystems can be wide-ranging. Invasive plants can disrupt pollinator visitation rates and seed set of native species by exploiting pollinator visits (Brown et al., 2002) or by creating shaded, unfavorable habitats for pollinators (McKinney and Goodell, 2010). Other invasive plants are allelopathic, disrupting mutualistic relationships and decreasing native plant growth rates (Stinson et al., 2006). Many invasive plants can affect nutrient cycling through changes in litter quality or root exudates (Ehrenfeld, 2010; Liao et al., 2008) or affect timing and intensity of natural fire regimes (Brooks et al., 2004; D'Antonio and Vitousek, 1992). Sometimes invasive plants modify a habitat's structural components (Simberloff, 2011b), which can affect predation rates on native species (Schmidt and Whelan, 1999) or change food resource availability (Gosper, 2004).

Because the total number of species' introductions trends upward (Perrings et al., 2010; Ruiz and Carlton, 2003), the probability that multiple invasive species will co-occur in the same habitat should also be increasing, which would indicate a need to shift studies to include these co-occurring invaders. Furthermore, many invasion publications are couched in terms of providing helpful management information for mitigation of invader impacts. These studies may be less useful if the scenario they study—single invaders—is uncommon or the impacts of multiple invaders are non-additive.

While we have much evidence that single invaders can have notable impacts, we have limited knowledge of the effects of multiple co-existing invaders on communities and ecosystems. Broadly, impacts of co-occurring invasive species could be additive (i.e., the sum of the impacts of each invader individually) or non-additive, and this relationship might direct management of species when they co-occur. If the overall impact of multiple invaders is additive, then it might be easy to extrapolate from previous single-invader impact studies to predict what will happen when invaders co-occur. Non-additive impacts, however, will be less predictable because the presence of a second invasive plant might magnify (Simberloff, 2006; Simberloff and Von Holle, 1999) or mitigate the overall impact on the community.

Several previous publications have drawn attention to the need to focus research on understanding non-additive outcomes when multiple invasive species are present, primarily focused on mutualistic interactions among invaders (Crosby, 1986; Richardson et al., 2000). Simberloff and Von Holle (1999) coined the term "invasional meltdown," which described how positive interactions among invaders would result when co-occurring invaders benefit from each others' presence, which might lead to an increase in magnitude of the invaders' impacts or an increase in the probability of their survival. These ideas have propagated research on multiple invasions, much of this focused on co-occurring animal invasions and cases in which introduced animals interact with introduced plants (Green et al., 2011; Olesen et al., 2002).

Here we juxtapose data on how commonly co-occurring plant invaders are found within conservation habitats with data on how often invader impact studies address multiple invaders. We define invasive non-native species as those species transported by humans across fundamental biogeographical barriers that sustain self-replacing populations and have the potential to spread over long-distances in the novel non-native range (sensu Richardson et al., 2011). We focus on invasive non-native species because they tend to appear in higher abundances and densities than non-invasive non-natives and therefore are more likely to cause considerable impacts. We focus on conservation habitats because these properties are considered valuable sites in need of conservation, they are currently managed to reduce invasive plant species when these are present, and they represent a wide variety of habitat types. Finally, we review studies that address impacts of multiple invaders and identify research gaps that may hinder to understanding more about biological invasions, especially when multiple invasive plant species co-occur.

2. Material and methods

2.1. Invasions within conservation habitats

To address questions concerning the likelihood of encountering multiple plant invaders in conservation habitats we used the Conservation Project Database (ConPro), which contains conservation projects from over 30 countries in 5 continents (see TNC, 2011 for a complete listing of projects by country) and is compiled and curated by The Nature Conservancy (TNC), one of the largest international conservation organizations. ConPro is one of the most complete listings of conservation projects worldwide and contains over 1100 international conservation projects managed by TNC and their partner organizations (TNC, 2007, 2011). Although not all countries are included in this database and some regions have more representation than others (e.g., the Americas have more projects than Asia), it has been successfully used as a source of information in other projects concerning broad conservation questions such as ours because it provides a large sample of conservation efforts that use the same methods for ranking and describing projects (Goldman et al., 2008; McDonald et al., 2009).

For each project listed in ConPro, TNC project leaders specified conservation targets (e.g., Ecological System, Single Species, or Species Assemblages) and threats to those targets (e.g., "Pollution", "Climate Change & Severe Weather", "Natural System Modification", or "Invasive & Other Problematic Species & Genes"). Single projects in the database may contain multiple entries that vary in habitat type, conservation target, and/or threat. Conservation targets and threats were categorized by an IUCN-CMP threat classification scheme (Salafsky et al., 2008; TNC, 2007).

We extracted all entries from the database that listed invasive species as a conservation threat. Beginning with over 4500 entries, because invasive species are by far the most commonly listed threat (J. Fisher, *personal communication*), we refined this list to 1700 entries that met the following criteria: (1) conservation threats that specified invasive non-native terrestrial plant species (i.e., excluding invasive animals or aquatic plants), and (2) conservation targets that specified habitat-based target types (i.e., plant species assemblages or ecological systems). We further refined this list to contain only entries that specified the invasive plant species of concern ($N = 137$). These restrictions insured that we counted only "invasive plant threats" that co-occurred within the same habitat. To obtain more detailed information on database listings, we queried an additional 106 public project managers (in English and their mother tongues) for more specific data concerning which particular invasive plant(s) threatened listed conservation targets and if those species were found adjacent to one another (n.b., the ConPro database comprises public entries, which can be reviewed online (TNC, 2011), and more sensitive private projects whose details are not available online). A second question provided additional confirmation that managers were listing co-occurring invasive plant species. We received answers from 43 (41%) of project leaders. This survey increased the dataset to 311 entries, detailing 86 conservation projects, for which we could identify the habitat-type and specific plant invader(s) of concern. Once we refined the subset of entries, we identified the number of invasive species for each threat listing. Number of invasive species was scored from 1 to 5 species and entries with more than 5 invasives listed were combined into a 6+ category.

The ConPro database aims to collect information on conservation projects globally and reports these projects in a systematic fashion. Because this database collects information on projects from developing and developed nations, there may be inherent biases stemming from organizational and managerial differences between cultures (Nuñez and Pauchard, 2010). Understanding this limitation, we argue that the ConPro database provides us with the unique opportunity to systematically survey habitats globally. Finally, ConPro is not an exhaustive list of all non-native species within a conservation project, but instead a list of species considered "threats" to listed conservation targets. We can therefore be confident that our analysis of listed invasive plant threats represents only those exotic, invasive plant species that conservation practitioners consider of management concern.

2.2. Invasions in the literature

To assess how often plant invasion impact studies considered more than one invasive species, we queried the database Web of Science (v. 5.2 Thomson Reuters 2011) for all published articles in the past 5 years (2006–2011) using the search terms from Simberloff and Von Holle's (1999) previous literature search on invader–invader interactions: 'species AND inva* OR introduced OR alien OR exotic OR non-native OR non-indigenous'. We used these search terms because they have been used in previous invasion literature reviews as reliable terms for locating published material on non-native species research. However, because the number of invasive-related articles has increased nearly 5-fold in the past decade (Simberloff and Von Holle (1999) found over 5000 articles with these search terms; we found over 27,000), we added the additional search terms 'AND plant* AND impact*' to mimic the results from the previous search on invasion in natural habitats and to filter some articles that were likely to be irrelevant. This reduced the database size to 1692 articles. Again, following the protocol of Simberloff and Von Holle (1999), we then selected the database articles published in the 12 journals that had the highest total number of invader publications. One journal, *Biological Invasions*, had triple the amount of articles of each of the other top 11 journals. Each of the remaining journals (*Biological Conservation*, *Biological Control*, *Diversity and Distributions*, *Ecological Applications*, *Ecology*, *Forest Ecology and Management*, *Journal of Applied Ecology*, *Journal of Ecology*, *Oecologia*, *Plant Ecology*, and *Restoration Ecology*) had at least double the number of articles of any other single journal within the database. This literature search produced an incomplete sample of publications on the impact of invasive plants. Nevertheless, because our aim was to assess how commonly plant invasion impact studies address multiple invasive plants, we believe this survey is an appropriate sample of ecological studies for our question. We examined 562 articles from these 12 journals and found 153 articles that specifically considered plant invasion impacts that included observation and experimental studies in field or greenhouse settings. From these articles, we assessed the number of plant invaders the authors studied and recorded the species, habitat types where the study took place, and whether the authors considered invader–invader interactions. We acknowledge that this literature search has limitations. For example, relevant papers may be published in other journals or the grey literature, or our keywords may not be ideal to capture all the research on this topic (Fazey et al., 2005). However, we believe this search allows an adequate assessment of current scientific work on invasive species and speaks towards our goal of assessing the relative publication rates of research on single and multiple invaders.

To compare the results obtained from the managers in the ConPro database and what is published in the literature on the topic, we compared the distribution of observed values with the distribution of expected values with a *G*-test, an alternative to Pearson's chi-square test that is appropriate for observational studies that do not assign observations a priori to each category (i.e., a Model I design; Gotelli and Ellison, 2004). For our purposes, we compared the distribution of single versus multiple invasive plant impact studies in the published literature to the distribution of single versus multiple invasive plant reports in the ConPro database.

3. Results

3.1. Invasions within conservation habitats

An overwhelming 69% ($N = 214$) of entries from the ConPro database were concerned with more than one invasive plant species in a single habitat (Fig. 1). For multiple invasions, the reported number of invasive species per habitat ranged from 2 to 12 with a median of 3, and the mean number of invasive species was 4.27 ± 2.44 SD. Looking within those entries concerned only with single-species invaders (31% of the total; $N = 97$), we see that 47% ($N = 42$) of the listed invaders were grasses. The graminoid giant reed (*Phragmites australis*) ($N = 12$) and cheatgrass (*Bromus tectorum*) ($N = 12$) were especially likely to be cited as solo invaders. When we sorted entries by habitat type, forest and wetland habitats tended to have multiple species of concern (>75% of entries

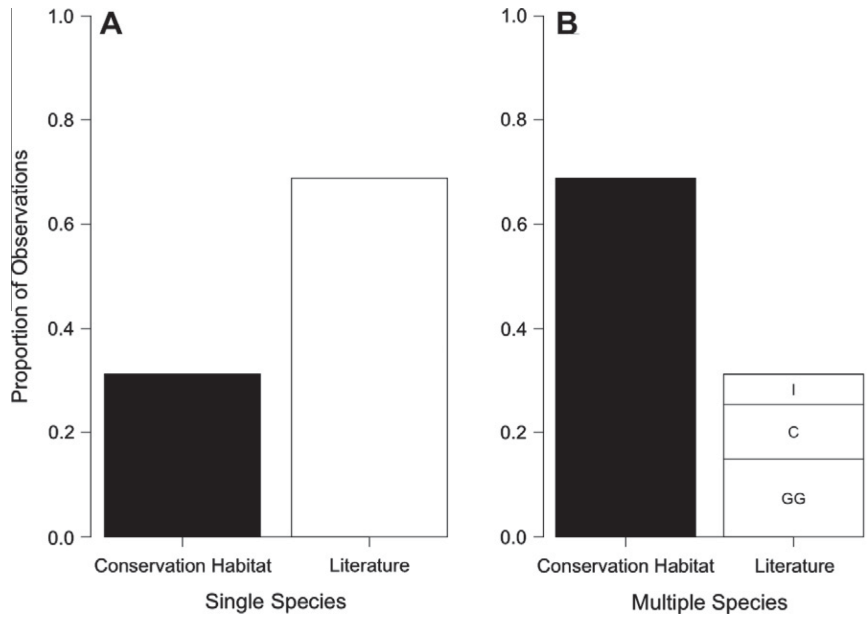

Fig. 1. The proportion of times single (A) or multiple (B) invasive plant species were of concern within conservation habitats and in the published literature. Habitat data are frequency counts when "invasive plant species" were listed as a conservation threat for 86 projects listed in The Nature Conservancy's Conservation Projects database. Literature data are frequency counts of 153 published studies from 2006 to 2011 that dealt with the impacts of invasive plant species in their invaded range. Of those studies that reported on the impacts of multiple invasive species (Fig. 1B), less than 6% explicitly tested for impacts of invader–invader interactions (I). The majority of multiple invader studies either compared the impacts among multiple invasive plants [e.g., Rodewald et al. (2010) compared nesting success of Northern Cardinals (*Cardinalis cardinalis*) between two invasive woody shrubs, *Rosa multiflora* and *Lonicera maackii*; (C)] or considered the invasive plant community as a grand group, studying plots with and without invasive species [e.g., Corbin and D'Antonio (2010) compared the competitive ability of a group of exotic perennial grasses to a group of native perennial grasses; (GG)].

were for multiple invasions), while littoral communities were more likely to report only a single problematic invader (>75% of entries were for single invasions). We should interpret these habitat susceptibility patterns cautiously because the conservation projects are not a random or stratified sample of natural habitat types and may reflect a bias towards some ecosystems, but they support previous findings that there is great variability in invasibility across habitat types (Chytrý et al., 2008a,b) and that there is a need to quantify invasion level objectively for comparisons across habitats (Catford et al., 2012).

3.2. Invasions in the literature

Of the 153 published articles we analyzed that studied plant invasion impacts, only 31.4% ($N = 48$) considered more than one plant species in their studies (Fig. 1). These results contrast with what we found in conservation areas. The number of species studied in surveyed publications with multiple invaders ranged from 2 to 14 with a median of 3; the mean number of invasive species was 3.98 ± 3.02 SD. The *G*-test detected significant differences between observations of single and multiple invaders in the literature and analogous reports in the ConPro database ($G = 115.343$, $p < 0.0001$), showing that the published literature is significantly more likely to consist of studies on single invaders while conservation managers are more likely to report multiple invaders of concern.

Over three-fourths ($N = 39$) of the published articles that focused on multiple species did not specifically address how impacts between single and multiple invasive plants might differ. One large subset (33.3%; $N = 16$) of multiple-invader studies compared how monospecific stands of different invasive plants affected particular response variables (such as native plant diversity or soil nutrient properties). Another subset (47.9%; $N = 23$) acknowledged the presence of multiple invasive species within a study system and manipulated the invasive community as an entire unit or homogeneous group (i.e., plots with all invasive plants or plots with no invasive plants). These two types of studies will inform our understanding of multiple invader impacts only if impacts are additive. The remainder of the multiple invasive species publications (19%, $N = 9$, constituting only 6% of the total studies) explicitly tested for interactions between co-occurring invasive plant species. One reported a facilitative interaction, three reported neutral interactions, and five reported competitive interactions (Table 1).

Across all invasion-impact studies, focus was heavily on invasive plants found in forest (25%, $N = 39$) and grassland (23%, $N = 36$) habitats. Forest invasion studies were primarily focused on single invasive species (82%, $N = 32$), whereas grassland studies were almost evenly split between those on single (52%, $N = 16$) and multiple (48%, $N = 20$) invaders.

4. Discussion

4.1. Evident mismatch between invasion research and conservation management

These results show that when invasive plants are present in conservation habitats, it is more common to find multiple, rather than single, species covered by conservation projects. This pattern contrasts with current research activity, which focuses primarily on effects of single species. Invasion biologists have begun to address issues surrounding multiple invaders in terms of 'levels of invasion'; for example, documenting the wide variability in invasion level (Chytrý et al., 2008a) and quantifying consistent metrics for measuring invasion level in terms of abundance, evenness, and richness of invasives (Catford et al., 2012). However, while studies indicate that some habitats have high levels of invasion, we still have limited knowledge of the effects of multiple co-existing invaders on communities and ecosystems. We suggest that the

Table 1
The three potential outcomes of interactions of co-occurring invasive plant, where they fit into current invasion biology paradigms, and published examples of each.

Scenario	Facilitative	Neutral	Competitive
	Invasive plants exacerbate the impact of the other invasive plants	Invasive plant species do not interact or have weak, inconsequential interactions with each other	Invasive plant species reduce the impact (via reducing fitness or population density) of other invasive species
Examples of theoretical framework(s)	*Invasional meltdown* (Simberloff, 2006; Simberloff and Von Holle, 1999)	Standard invasion hypotheses including *propagule pressure* (Simberloff, 2009), *enemy release* (Keane and Crawley, 2002), *evolution of increased competitive ability* (*EICA*) (Blossey and Nötzold, 1995), or *fluctuating resources* (Davis et al., 2000) which assume the characteristics of the invading plant or invaded ecosystem trump all other biotic interactions	Non-typical cases of *biotic resistance* (Elton, 1958) where existing invasive plant(s), as part of the local community, resist invasion. When *novel weapons* (Callaway and Aschehoug, 2000) of one plant invader may negatively affect another plant invader that is native to a different region from the first
Possible management strategies and goals	Keep invasive plant richness low. Identify the species that promote other plant invasions and target them for management	Do not need to make special management recommendations. Invasive plant populations can be treated individually, with no presumed effect on populations of other invasive species	Removing one invasive plant may trigger the invasion of another, relatively rare, invader. If certain invasive plants prevent establishment or decrease fitness of other invaders, managers may choose to allow those populations to persist and focus on other invasive issues. Need to identify which of the co-occurring invasive species have the most negative effects on the other invaders but the least effects on the target native community
Published examples from our literature search	(1) Invasive grass, *Ehrharta calycina,* grows more frequently in association with invasive shrub, *Carpobrotus edulis* and invasive grass *Ammophila arenaria* (and native *Baccharis pilularis*); proposed mechanism is invader released from herbivory when growing in close proximity to these other invaders (Cushman et al., 2011)	(1) Two common riparian invaders, *Arundo donax* and *Vinca major*, decrease native plant community richness, abundance and seedling performance when found in monoculture or in mixture patches (Cushman and Gaffney, 2010)	(1) The invasive grass *Avena barbata* reduced biomass of *Centaurea solstitialis* when grown together in a greenhouse competition experiment. Likewise, *A. barbata* biomass decreased when *C. solstitialis* leaves were clipped (herbivory) (Callaway et al., 2006)
		(2) The canopy of the invasive tree *Prosopis* spp. was no more likely to harbor exotic fleshy-fruited species than the native tree *Acacia tortilis* in a South African savanna. Instead, distance from host/source plant was most important in determining exotic plant presence (Milton et al., 2007)	(2) The spread of the shrub invader *Cinchona pubescens* on Santa Cruz Island, Galapagos was negatively correlated with the presences of the invasive herb *Stachys agraria*; when *C. pubescens* populations decreased, the two invaders *S. agraria* and invasive shrub *Psidium guajava* cover increased (Jäger et al., 2009)
		(3) In a greenhouse competition experiment, the invasive shrub *Cytisus scoparius* did not impact the growth of the invasive grass *Dactylis glomerata* (Shaben and Myers, 2010)	(3) In a greenhouse competition experiment the invasive grass *Lolium multiflorum* decreased biomass of the invasive grass *Schedonorus arundinaceus* across moisture and nutrient treatments (Pfeifer-Meister et al., 2008)
			(4) The invasive tree *Ailanthus altissima* and shrub *Elaeagnus umbellata* lost biomass when grown in pots conditioned by the invasive grass *Lolium arundinaceum* and its symbiotic endophyte *Neotyphodium coenophialum* (Rudgers and Orr, 2009)
			(5) Two invasive old world bluestem grasses, *Bothriocholoa bladhii* and *B. ischaemum,* inhibit the growth of the other when grown as "neighbors" in a controlled field experiment (Schmidt et al., 2008)

prevalence of co-occurring invasive plant species should encourage more multiple-species plant invasion studies that address three interrelated, but distinct, questions. Below we outline these three avenues of future research and how they might better inform management practices.

4.2. Are multiple plant invader impacts additive or non-additive?

Distinguishing between additive and non-additive impacts of invaders will be important for management of sites with multiple invaders. For example, two common forest invaders in the eastern United States are garlic mustard (*Alliaria petiolata*) and Japanese stiltgrass (*Microstegium vimineum*). Both species are reported to reduce native herbaceous species biomass when found alone (Flory and Clay, 2010; Rodgers et al., 2008). However, in forests where both species co-occur (Fig. 2c) we do not know the species' combined impacts on understory plants. If multiple invader impacts are additive, their overall impact should be predictable—the sum of their individual impacts—and a manager can more easily extrapolate from single-invader impact studies to predict how management will change the co-occurring invaders' overall impact. If *A. petiolata* and *M. vimineum* have additive impacts, treatment of only one species should allow a fraction of the understory plant community to recover, based upon the impact of either species singly. The majority of multiple invader studies we reviewed either compared impacts between monocultures of multiple invasive species

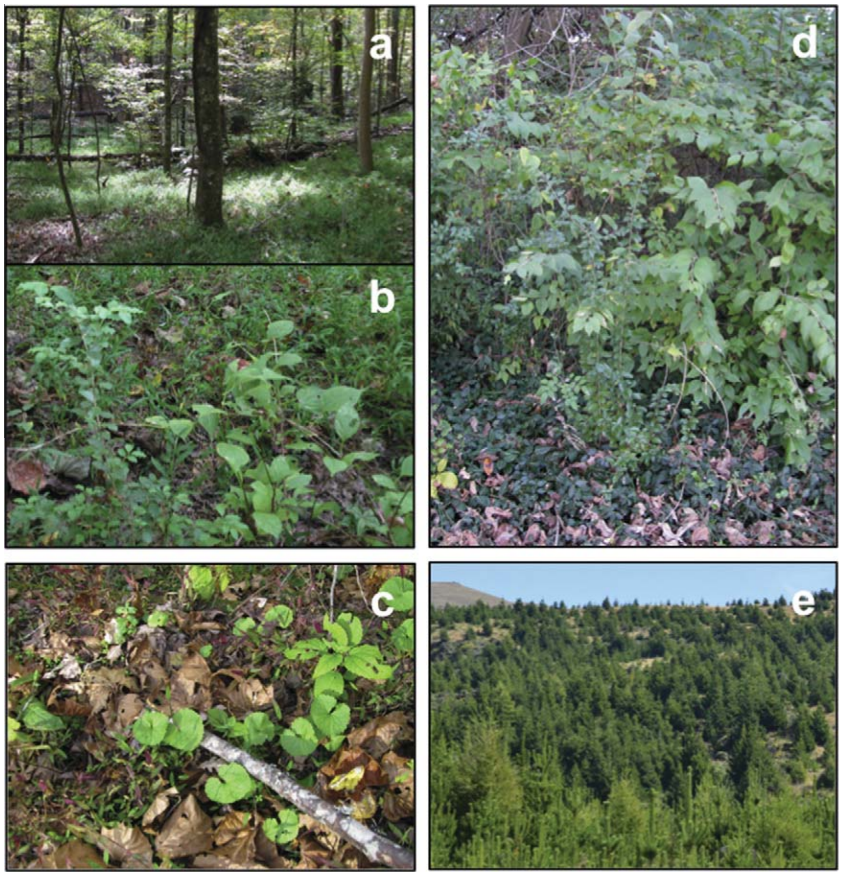

Fig. 2. The presence of co-occurring invasive plant species is increasing, creating a variety of multiple invasion scenarios. Examples include a southeastern United States forest understory containing "strong" invader Japanese stiltgrass (*Microstegium vimineum*) (a), and "weak" invaders Chinese privet (*Ligustrum sinense*) and Asiatic bittersweet (*Celastrus orbiculatus*) (b); southeastern forest with herbaceous invader garlic mustard (*Alliaria petiolata*) and annual grass Japanese stiltgrass (*Microstegium vimineum*) (c); southeastern forest with co-dominant woody shrub invaders Chinese privet (*Ligustrum sinense*) and bush honeysuckle (*Lonicera maackii*), and woody vine wintercreeper (*Euonymus fortunei*) (d); and invasive trees *Pinus contorta* and *Larix decidua* in New Zealand (e). Photos by Sara Kuebbing (a–d) and Martin Nuñez (e).

or lumped all non-native species together in one group (Fig. 1b). If invader impacts are additive, then these comparative and total removal experiments will help in predicting what to expect when species' co-occur.

Multiple invasive species may also have non-additive impacts, and thus the impact of multiple invaders may be greater or less than the impact of either invader in isolation and cannot be predicted based on the impact of each species in isolation. For example, it is possible that *A. petiolata*, an invader whose biomass is greatest in the early spring and summer, and *M. vimineum*, an invader whose biomass is greatest in the late fall, will cause a non-additive decrease in native ground cover because their greatest impacts do not overlap temporally and we might see a greater decrease of the understory plant community. Managers currently have no tools to assess how adding or removing an invader will impact the native community or ecosystem when impacts are non-additive (Zavaleta et al., 2001), and only studies that compare single and multiple invasion scenarios will allow sound prediction of the overall impact of co-occurring invaders (for example, Rauschert and Shea, 2012).

4.3. What types of interactions are most common among invasive plants?

Based upon the invader interaction studies we found, we outline the three broad types of interactions we might expect to see when invasive plants co-occur, how these interactions fit into contemporary invasion theory, and possible management recommendations these interactions would suggest (Table 1).

4.3.1. Facilitative interactions

Facilitative interactions arise when one invader promotes the invasion or increases the fitness of the other. One scenario could be a case of "invasional meltdown," in which the presence of multiple invasive species increases the probability of survival and spread over that of any single invader (Simberloff and Von Holle, 1999). In our search we found only a single study that indicated the growth of an invasive plant was increased when it was growing near other invasive plants (Cushman et al., 2011). Other studies have shown plant invaders can create more favorable environments for the establishment of new invaders through soil nutrient modification (Fisher et al., 2006; Vitousek et al., 1987) or nurse plant effects (Tecco et al., 2007).

If facilitative interactions lead to non-additive impacts, this could indicate an important prioritization consideration for invasive plant management. A central question in predicting invasions is whether non-native species act as "drivers" or "passengers" of community change (MacDougall and Turkington, 2005). As drivers, invaders are hypothesized to enter intact and undisturbed habitats and cause notable effects on native species. As passengers, invaders enter degraded habitats that have already lost native diversity and thus are not the direct cause of diversity declines. However, if habitats contain multiple invasive species then this question widens to what role do previous invaders play in facilitating further invasion? Scenarios of ecosystem "hijacking" could occur in which an invader enters a community as a "passenger" but subsequently modifies the community, "driving" future invasions. Ecosystem "hijacking" may have important conservation implications. Such a phenomenon would suggest that if managers can reduce disturbance and prevent the first invader from entering a community, then future invasions may not occur.

4.3.2. Competitive interactions

Competitive interactions comprised the majority of invader–invader interaction studies we reviewed (Callaway et al., 2006; Jäger et al., 2009; Pfeifer-Meister et al., 2008; Rudgers and Orr, 2009; Schmidt et al., 2008). Other studies show that some invasive plants can restrict the growth of other invasive plants through competition for light, space, or other limiting resources (Belote and Weltzin, 2006; Rice and Nagy, 2000; Tecco et al., 2007) and that interactions with co-occurring native species can moderate this competition (Metlen, 2010). Competition among non-natives may help explain the observed pattern of decline of some populations (Simberloff and Gibbons, 2004) when one invasive species is replaced by another (Jäger et al., 2009; Morrison et al., 2007). This apparent natural succession may not be due to the suggested transient nature of biological invasions (Davis et al., 2001) but rather to specific invader–invader interactions.

If interactions between invasive plants are commonly competitive, this information could be critical for decisions of how and when to manage for invasive populations. Competitive interactions might be particularly relevant in habitats that have a numerically dominant 'strong' invader and fewer individuals of 'weak' invaders (Ortega and Pearson, 2005). Management strategies in these instances may choose to focus on the more abundant invader, but if this is competitively suppressing other invasives, management of only the 'strong' invaders may result in a release of secondary invaders, or acceleration of "invasion succession" to a different invasive plant (Loo et al., 2009; Ortega and Pearson, 2010) Thus, if the removal of one species leads to the re-invasion of a site by another invader, management schemes would need to incorporate this possibility and adequately prepare for secondary invasions (Ruscoe et al., 2011). Likewise, if the impact of the primary invader is deemed less harmful than the future impacts of a suppressed invader, managers with limited resources might decide to forgo management of the former plant population until enough resources are available to treat both populations.

4.3.3. Neutral interactions

Though competitive and facilitative interactions among plant invaders have been documented, we cannot assume there will always be strong interactions between co-occurring invaders. A last possible scenario is that interactions among invaders are neutral or weak; we found this situation in three examples (Cushman and Gaffney, 2010; Milton et al., 2007; Shaben and Myers, 2010). However, interactions might differ between life stages of the plant (Tecco et al., 2006, 2007), based on presence of native species (Metlen, 2010), or under changing environmental contexts (Besaw et al., 2011).

4.3.4. How do invader interactions affect the overall impact of a species?

We currently have limited knowledge on how overall impacts of multiple invaders differ from those of single invaders, which seems a critical lacuna in light of the evidence that co-occurring invaders are common. Understanding differences in impact and management between multiple and single invasions will arise, in part, through better understanding of interactions between invaders. It is necessary to remember, however, that the direction of invader–invader interactions may not lead to an obvious overall impact on the native community. For example, even when species compete by having different but substantial negative effects on the native community, they may have still more detrimental effects together than in isolation, since low-density species can still exert significant effects (Peltzer et al., 2009). Building a larger body of case studies on co-occurring invasive plant species would be prudent, because our limited results restrict our ability to suggest whether any of these scenarios is a rule or an exception, whether invasive plants might tend to interact in certain directions, and how temporal or spatial variability of invasions might moderate interactions.

4.4. How researchers and managers can adapt to multiple invader scenarios

Though we acknowledge the challenges to studying multiple invaders, especially in field settings, we feel there is a critical need to begin addressing this issue. The many cited studies in this manuscript provide an excellent framework for applicable methods, including observational, field manipulation, or greenhouse experiments on how to address these questions. Observational studies can confirm if certain patterns of co-occurrence among invaders exist and experimental research can begin to decipher mechanisms of interactions. The large body of research on single-invader impacts has allowed researchers to use meta-analytic techniques to compare impacts of invaders on single species, communities, and ecosystem processes (Liao et al., 2008; Vilà et al., 2011), but we seem to lack a comprehensive set of studies on cases of multiple invasions for similar analyses.

Though there is less research on the impacts and interactions of multiple invasive species, managers should adapt management plans to encompass co-occurring invaders; probably many are already doing so. Because limiting resources typically constrain management budgets, managers must decide which habitats to target and, under multiple invasion scenarios, which species within these habitats they should manage. One recommendation that could arise from this study is that if the costs associated with managing additional invasive species are low (e.g., both invasives respond to the same treatment, such as co-occurring woody shrubs; Fig. 2b), managers should target all invasive species. Where this is feasible, management strategies should avoid treating only the 'strong' invaders, because as mentioned above, removal of dominant invaders may lead to the release of secondary invaders or propel "invasion succession". If limited resources prevent managers from targeting multiple species, then specific knowledge of the impacts and interaction of co-occurring species would be essential to prioritizing management, but unfortunately this is likely to be context-specific for the habitat type and co-occurring species at that location. However, if information on the particular invasive species is not available (either in the published literature or through management networks), then managers could conduct trial removal experiments in which they treat smaller areas to assess how management of single invasive species is likely to affect outcomes when multiple species are present. Alternatively, gathering information on the effect of single-species removal in comparable habitats could provide precious information on the management of multiple invaders.

5. Conclusions

Overall, our data show a disconnect between what is occurring in many conservation habitats and what is typically published in the invasion biology literature. This suggests that application of current invasion theory and research for conservation purposes might be pertinent only for practitioners dealing with single invader scenarios, or where the co-occurring invasive species have non-interactive additive effects. The divergence between research and on-the-ground needs has been recognized for many areas of invasion biology, where scientific research rarely translates into useable management practices (Hulme, 2003; Papeş et al., 2011). This issue mirrors, but is distinct from, the acknowledged ''knowing-doing'' gap in conservation (Knight et al., 2008) and invasion (Esler et al., 2010) research. Mismatches between research and conservation reality—a ''not-knowing-doing'' gap—might be just as significant a hindrance to effective conservation. This insight has important implications for how we currently study plant invasions and, potentially more importantly, how relevant scientific results may be for those managing invasive plant populations.

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