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PERSPECTIVES AND PARADIGMS

Keys to enhancing the value of invasion ecology research for management

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Abstract Invasion ecology has grown to include scientists with diverse skill sets who focus on a range of taxa and biomes. These researchers have the capacity to contribute to practical management solutions while also answering fundamental biological questions; however, scientific endeavors often fail to meet the perceived needs of practitioners involved in on-the-ground invasive plant management. One way that researchers have sought to bridge the gap between research and practice is by surveying managers to identify areas of study that are underexplored in invasion ecology. In this paper, we build on these efforts by reviewing the current state of knowledge and suggesting new directions for research in seven areas of plant invasion ecology that are highly relevant to management: seedbanks, dispersal and spread, life history, impacts, climate change, distribution, and succession. These topics were previously identified as urgent research priorities by land managers and are underrepresented in the invasion ecology literature. In addition to highlighting key knowledge gaps for these seven areas of research, we propose steps that academics can take to cultivate academic–practitioner relationships and remove barriers to conducting

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management-focused research, such as co-producing research questions with managers, addressing issues of working at management-appropriate spatial and temporal scales, and considering non-traditional funding and labor sources for long-term monitoring. Greater communication and collaborative selection of basic research questions will ensure that the goals of management and invasive species research remain aligned.

Keywords Climate change · Functional traits · Impacts · Knowing-doing gap · Life history · Restoration · Seedbank · Succession

Introduction

Invasive plants contribute to biodiversity loss and changes in ecosystem processes (Pyšek et al. 2012), and management of these species is crucial for conservation. In recent decades, academics have increasingly placed invasion research into fundamental ecological or evolutionary frameworks to better connect patterns to theory, draw generalizations across species and systems, and bring together researchers from different disciplines (Cadotte et al. 2006; Sax et al. 2005). However, this effort often comes at the expense of tackling applied problems to bring about practical management solutions. While some academics have sought to work with land managers to identify research priorities for improving invasive plant control (D'Antonio et al. 2004; Matzek et al. 2014), or to address the technical and cultural challenges of effective policy-making (Keller et al. 2015), the ecology of plant invasions still suffers from a "knowing-doing gap" (Knight et al. 2008).

The knowing-doing gap (also known as the research-implementation gap, or knowledge-practice gap), is the phenomenon of scientific research failing to inform or improve on-the-ground conservation practice. Many explanations for this gap have been forwarded, including a perceived resistance of researchers to solve applied problems (Renz et al. 2009), in part because the incentives and timeline for cooperative work do not align with outcome-centered academic research culture (Hallett et al. 2017). Although extension agents are charged with tackling applied research problems and communicating findings to managers, many researchers primarily seek to understand the basic mechanisms underlying invasions (Bayliss et al. 2013; Esler et al. 2010). Furthermore, publications on such topics, grounded in ecological and evolutionary theory, are more highly cited than papers concerning applied research topics (Pyšek et al. 2006). However, surveys consistently show that managers urgently need fundamental ecology and life history information about many invaders and conclude that scientists pursuing basic research into plant invasions could align their questions to better meet this need (e.g., Beaury et al. 2020; Esler et al. 2010; Matzek et al. 2015).

We build on this work by reviewing seven underexplored areas of basic invasion research. These knowledge gaps were previously identified by surveying over 200 land managers working in a diverse array of ecosystem types and for a variety of governmental and non-governmental organizations throughout the state of California (Matzek et al. 2014) and broadly correspond to knowledge gaps identified by surveys in California and other regions of the world (Bayliss et al. 2013; Beaury et al. 2020; Renz et al. 2009; Robison et al. 2010). The management priorities of survey respondents from Matzek et al. (2014) were then compared to published research on invasive plants through a systematic literature review, which showed a severe mismatch between the scientific needs of practitioners and the work conducted by researchers (Matzek et al. 2015). In an effort to improve the relevance of ecological research to on-the-ground invasive plant management, we review these topics in order of decreasing mismatch (Fig. 1), with the most under represented areas discussed first. For each area, we briefly summarize what is known, identify knowledge gaps that urgently need to be filled, and describe how advances in these areas of basic research can inform management. We then discuss ways that academics can cultivate academic–practitioner relationships and remove barriers to conducting management-focused research. Our goal is to suggest a path

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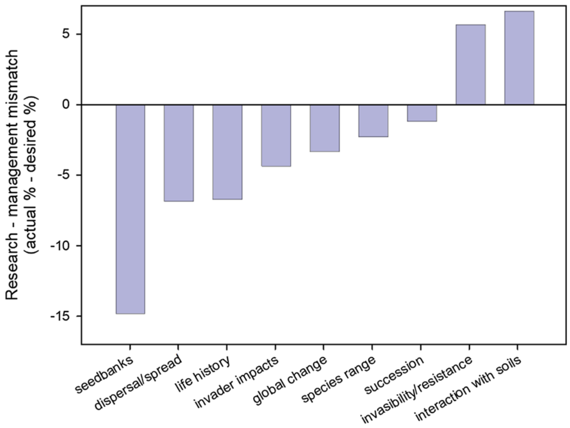

Fig. 1 A comparison of management priorities and published research shows a mismatch for specific topics in basic research. Negative values reflect underrepresentation of topics in the literature compared to what managers want. Sample sizes are N = 122 for manager-identified priorities and N = 243 for basic research papers. The survey was administered to managers in California, which is ecologically diverse and presents a variety of management challenges. Figure adapted from Matzek et al. (2015)

forward for invasion ecology that yields the greatest benefits for theoretical advancement and management (Fig. 2).

Seedbanks

Soil seedbanks, as reservoirs of germination potential for native and non-native species, can be major drivers of plant population and community dynamics, as well as potential indicators of habitat degradation or resilience (Frieswyk and Zedler 2006; Gaertner et al. 2014). Understanding seed behavior and the longevity of seedbanks is critical to management of invasive species that reproduce by seed (Gioria and Pyšek 2015). Invasive plants with persistent seedbanks exert strong legacy effects that exacerbate the difficulty of aboveground control (Richardson and Kluge 2008). Seedbanks can also cache secondary invaders that emerge after a more competitive primary invader is eradicated (Valliere et al. 2019).

The composition of the aboveground vegetation is not a reliable guide to the composition of the seedbank (Vilà and Gimeno 2007), nor is stand age or invasion intensity a reliable predictor of seedbank density (Alexander and D'Antonio 2003). These mismatches between what managers can see aboveground, and what they cannot see belowground, have major implications for control and restoration. They may cause managers to underestimate the time and resources needed to control invasions fully, or to abandon management efforts due to an unwarranted belief that control is infeasible. Uncertainty about seedbanks can also result in inadequate planning for invasive plant control after natural disturbances such as drought or fires (Keeley et al. 2005; LaForgia et al. 2018). Before removing a dominant invader, it may also be useful to know what native species are present in the seedbank, if restoration will require reseeding, and if secondary invaders are poised to emerge. Studies aimed at understanding the high spatiotemporal variability of seedbank composition, and how it is affected by variation in seed rain, seed dormancy/longevity, and biotic/abiotic constraints on germination potential (see Online Resource 1), would have immediate relevance to predicting the long-term impact of a plant invasion and planning an appropriate management response, such as topsoil removal or summer irrigation to flush the invasive seedbank (Funk et al. 2015). Researchers could also usefully contribute to the growing body of work on the responses of seedbanks to management intervention (Ma et al. 2015; Maclean et al. 2018).

Understanding differences in seed traits among invasive and native plants might also suggest successful management interventions. The seeds of co-occurring invasive and native species may vary with respect to phenology (Wainwright et al. 2012), response to disturbance (Emery et al. 2011), susceptibility to pathogens (Orrock et al. 2012), germination plasticity (Zimmermann et al. 2016), longevity in the seedbank (Saatkamp et al. 2019), or other traits (Fig. S1 in Online Resource 1). A better understanding of seed trait variability would allow managers to identify and exploit specific vulnerabilities. For example, Wainwright et al. (2012) used an artificial rainfall event to simulate an early start to the growing season in a scrubland invaded by non-native annual grasses ("grow-kill" cycle). Non-native grasses with more flexible germination cues germinated early and then died, depleting the seedbank in favor of native species, which did not respond to the early-season watering. Alternatively, detailed studies of seed traits may lead to a conclusion that the non-native seedbank is resistant to feasible intervention and that management should focus on diminishing seed rain

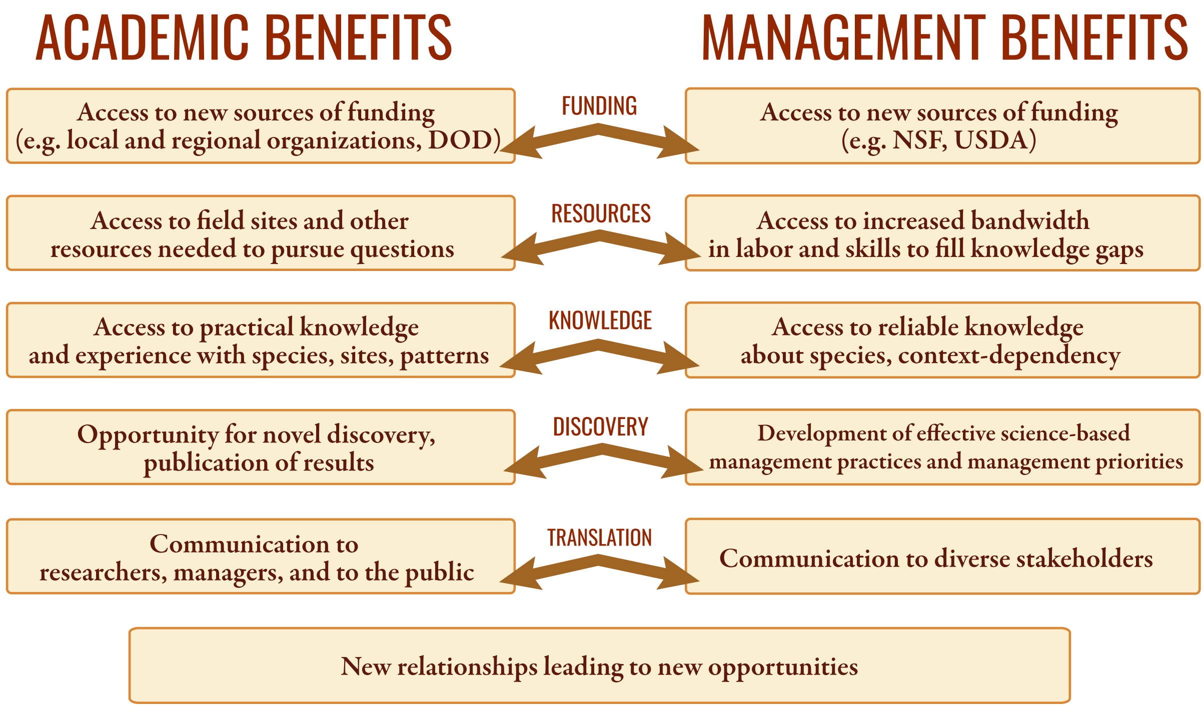

Fig. 2 The academic and management realms experience different potential benefits from interacting with each other. Recognizing and valuing the contrasting perspectives and goals helps to identify what academics and managers respectively could gain from collaboration. Abbreviations are Department of Defense (DOD), National Science Foundation (NSF), and USDA (United States Department of Agriculture)

(Richardson and Kluge 2008) or topsoil removal (Buisson et al. 2008).

Dispersal mechanisms and potential for spread

Managers need basic information about where invaders come from, their mechanisms of spread, how fast they are likely to spread, and what management actions are most likely to slow spread. Yet, for many high-priority invasive plants, specific data on dispersal mechanisms and distances remain limited. Global reviews and meta-analyses on plant invasiveness report little information on dispersal for many species beyond general characterizations of modality such as wind versus animal (Flores-Moreno et al. 2013; Pysek and Richardson 2007). Furthermore, management-focused online resources provide detailed references on dispersal for some widespread invasive plants (e.g. *Bromus tectorum*), but considerably less for others (e.g. *Bromus madritensis*, CABI Invasive Species Compendium, University of California Weed Research and Information Center).

There is a rich theoretical literature on dispersal and spatial spread of invaders going back nearly 70 years (Skellam 1951; for review, see Hastings et al. 2005; Lewis et al. 2016). This field continues to be highly productive in the academic sphere, exploring questions such as how adaptation (Andrade-Restrepo et al. 2019), density-dependence (Sullivan et al. 2017), or environmental variation (Kawasaki et al. 2017) may influence rates of spread. However, many such studies are designed with a primary goal of advancing theory, and not necessarily to provide information directly useful to managers.

Still, academic research on spread can provide valuable management guidance for some invasive species (Shea et al. 2010; Taylor and Hastings 2004). For example, models have been used to predict the effect of a biological control agent on decelerating rates of plant spread (Jongejans et al. 2008), which can be an important benefit of biological control even in cases where eradication is not possible. Nevertheless, to date much of this species-specific modeling concentrates on well-studied taxa such as *Carduus*, *Cirsium, Cytisus*, or *Spartina*. Use of model species can facilitate progress in theoretical understanding of dispersal and invasion, but may also limit the diversity of data available to test for generalizable patterns (Bullock et al. 2017; Tamme et al. 2014). A broader taxonomic focus would fill data gaps critical to managers while facilitating studies that relate species traits, such as seed and rhizome/stolon morphology, to dispersal and spread.

Beyond species-specific insights, research on spread can identify intervention strategies and provide broad rules of thumb for management. An example is Moody and Mack's classic 1988 paper, which used a simple mathematical model to show that eradicating small outlying patches (nascent foci) of invasive plants is more effective at slowing invasion than chipping away at one large patch (Moody and Mack 1988). Studies using more complex models have explored similar themes, demonstrating that controlling the "tail of the distribution" (far-dispersing outlier individuals or populations) is key to slowing invasion across a landscape (Lewis et al. 2016). Greater study of the role of extreme climate events, such as hurricanes, in promoting rapid spread is also needed and could be combined with modeling to help managers anticipate post-disturbance challenges in their region (Diez et al. 2012).

Research on spread has two other practical applications. First, researchers can identify processes or characteristics of invaders or sites that influence spread, informing prioritization of resources (such as to early detection and rapid response) and management efforts among species and locations (Jongejans et al. 2008). Similarly, researchers can evaluate how particular vectors of introduction (e.g. trade, construction, recreation) influence spread at the landscape scale (Chapman et al. 2016). For example, Meunier and Lavoie (2012) identified conversion of gravel roads to pavement as the key driver of *Galium mollugo* spread inside a national park. Successful site restoration may depend more on local seed rain than patterns of landscape spread; for example, Berleman et al. (2016) found that effective post-fire control of medusahead (*Elymus caput-medusae*) depended on controlling seed rain from adjacent areas. Understanding the role of seed rain falls under the conceptual framework of propagule pressure (D'Antonio et al. 2001), an active area of ecological research (Arruda et al. 2018). Determining landscape characteristics that correlate with propagule pressure can improve our ability to model risk (Table S1 in Online Resource 1). With their valuable on-the-ground perspective and access to landscape data, managers will be key partners for academics working to enhance models of spread and dispersal.

General life history of invaders

Basic life history information allows researchers to identify generalizations about invaders and suggest potential management strategies. While there are large amounts of accessible data for many well-known invasive species, bias towards researching well-known species (Matzek et al. 2015) also means that some newly-emerging invasive plants may be overlooked. This bias is unfortunate, because removal of species with limited distribution is far more cost-effective than waiting until such species become widespread and abundant (Leung et al. 2002). That said, the large scientific literature on key well-studied invaders has been used to develop life-history generalities that can be applied to nascent invaders (e.g., Pysek and Richardson 2007).

Since Baker (1974) devised the list of characteristics that define an 'ideal weed', ecologists have considered various aspects of species' life histories to determine their success as invaders. The most promising generality is that, compared to non-invasive plant species, invaders often grow faster (Dawson et al. 2011), reproduce earlier, produce smaller and more numerous seeds (Rejmanek and Richardson 1996), are able to capitalize on higher resource availability in disturbed habitats (Dawson et al. 2012), and spread through vegetative (clonal) propagation. While these general guidelines can be used as a starting point, life history traits of native and invasive species are context dependent, and land managers often lack knowledge of basic ecology and life-history of problematic and nascent invasive plants (Matzek et al. 2014). Ecologists are assembling trait databases (e.g., TraitNet, TRY), and an increasing focus on capturing intraspecific trait variation (e.g., Des Roches et al. 2018) may help managers understand differential responses and impacts of specific invaders across sites.

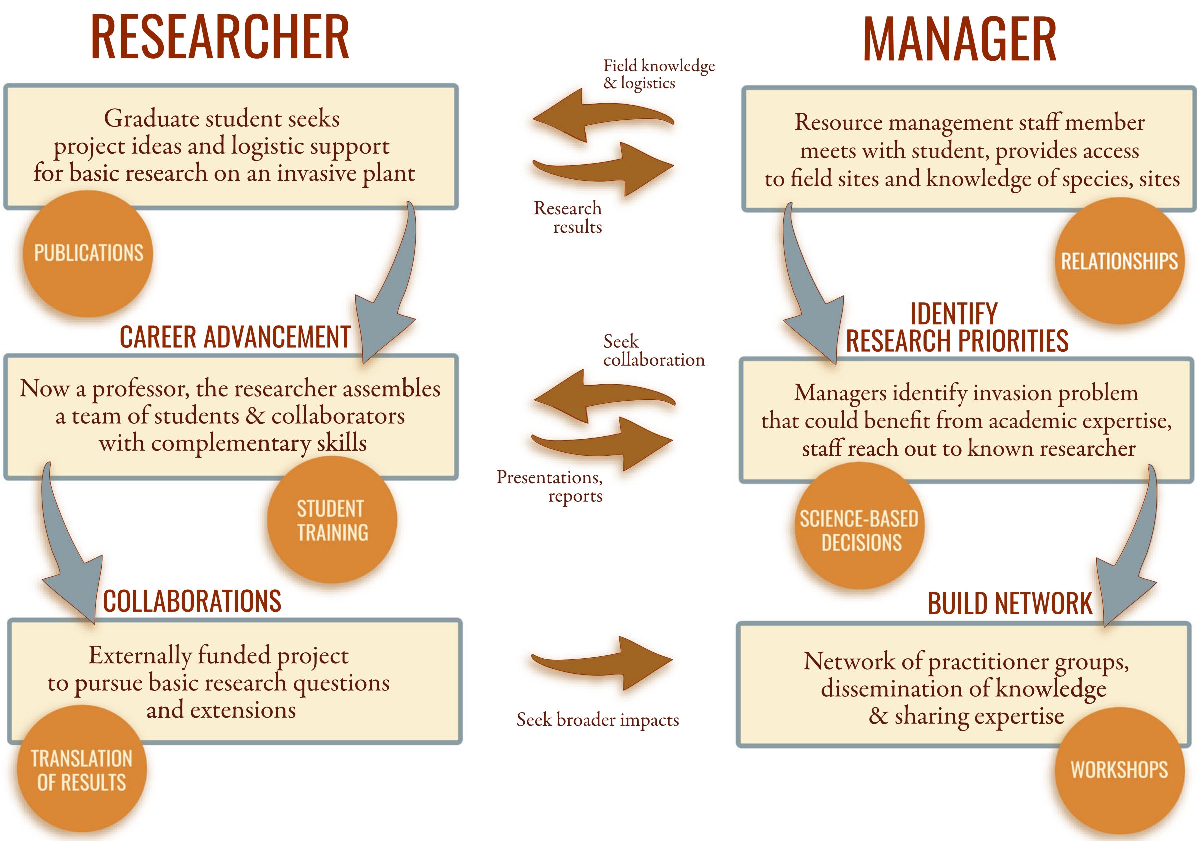

Fig. 3 Academic–manager partnerships can begin at any time in an academic's career and can catalyze the exchange of information and funding. In this case study, resource managers at Fort Lewis (Tacoma, WA, now Joint Base Lewis-McChord) provided generous logistical support for a graduate student conducting basic research on the invasive plant, Scotch broom (*Cytisus scoparius*) (Parker 1997). When managers at Fort Lewis needed help with a broom control problem ten years later, they called on the student, who was now a professor at a research university. The researcher, with collaborators and students, designed experiments together with managers, sharing results through regular in-person meetings and reports. Eventually they received National Science Foundation (NSF) funding to conduct additional basic research, using their collaborative work as preliminary data (e.g., Grove et al. 2019). As part of the Broader Impacts of their NSF grant, they helped plan and sponsor a networking workshop on broom control for nearly 300 resource managers from across Washington State. There are many potential variations of this partnership: graduate students may not continue in academia—many will cross over in career path to do applied invasion science—and several types of partnerships exist (e.g., industry, non-profit organizations)

Making these databases freely accessible, expanding coverage of invasive species and traits, and updating them frequently to include nascent invaders will enhance their utility for management.

Information about the life cycle, reproductive ecology, phenology, and breeding strategy of an invasive plant can be used to plan the timing and method of management (Funk et al. 2008). For instance, many managers mow (or graze by livestock) fields of annual invaders before flowering to reduce seed output. Similarly, understanding functional differences between native and invasive plant species can suggest management actions at the community level (Fig. S2 in Online Resource 1). For example, modifying disturbance regimes could be beneficial when existing disturbance facilitates the success of resource-acquisitive invasive species, such as where canopy gaps increase light availability (Funk and McDaniel 2010). By extending the large body of research about functional differences between natives and invaders and among invaders within individual habitat types, ecologists could identify management interventions that are suitable for specific communities (D'Antonio et al. 2017).

Many barriers exist to collecting basic life history information, particularly for nascent invaders.

Notably, it can be difficult to secure funding for species-specific, applied, or long-term monitoring projects. We see many ways for academics to overcome these barriers, including seeking smaller pools of funding (such as grants for undergraduate and masters theses), incorporating basic life history data collection into undergraduate lab curricula, contributing data to online databases or open-source publication archives, and strengthening communication with managers by attending or hosting workshops focused on local/regional invasive species management (see "Closing the knowing-doing gap" section below). Academics can source valuable life history information from managers who regularly record abundance and treatment data on the properties they manage.

Impacts of invaders

Invasive plants can have significant impacts on native species, including influencing their abundance, distribution, trophic interactions, and community composition. They may also alter ecosystem properties, such as nutrient cycling, primary production, and fire regimes (reviewed by Pyšek et al. 2012). One of the major problems with current studies of invader impact is that researchers often choose the impact they know something about (e.g., an entomologist would look at the effects of an invader on the insect community); yet many invaders have multiple impacts, some of which may be more persistent or difficult to reverse than others (Drenovsky et al. 2012). Given the variety of possible impacts, researchers should initiate interdisciplinary studies with a broad range of collaborators to devise a systematic approach to study the magnitude and persistence of impacts. Researchers must then work closely with managers to enhance the value of the research for management by encouraging management mitigation for significant impacts, or prioritizing removal of the most impactful invaders in a management area.

Studies on impacts are also biased towards particular species, functional groups, and biogeographic areas, greatly limiting their relevance for management (Hulme et al. 2013). Many species that are considered highly problematic by managers have been the subject of surprisingly few studies on impacts (Hulme et al. 2013). For example, kudzu (*Pueraria montana*) and Brazilian pepper (*Schinus terebinthefolius*) together have over 40,000 positive occurrence records online (eddmaps.org), and are the subject of large-scale management efforts, but very little quantitative information is available on their impacts (Hulme et al. 2013). Plant invaders can occupy wide geographic ranges but, in most cases, the context dependency of invader impacts is unknown (Hulme et al. 2013).

Finally, most studies on invaders monitor short-term impacts, and less is known about how invasive species alter communities and ecosystems on longer time scales, including whether impacts persist after removal. A review of over 400 plant invasion impact studies found that more than half of all studies lasted less than one year, and less than 8% of studies were conducted over four or more years (Stricker et al. 2015). Invader impacts may decline over time for several reasons. For example, invaders may accumulate enemies (e.g., herbivores, pathogens) from their home ranges or new enemies may emerge via evolution or 'ecological jumps' in the introduced range, leading to reductions in invader abundance and their impacts on ecosystems (Flory and Clay 2013). A better understanding of when, where, and what species or combination of species have the greatest impacts, and if impacts are expected to persist or decline over time, can improve decision-making when prioritizing species for management (see Online Resource 1).

Response of invaders to climate change

Climate change may alter the introduction, establishment, spread, and impacts of invasive plants (Dukes and Mooney 1999; Hellmann et al. 2008), with significant implications for management. The majority of studies to date have focused on how rising temperatures and alteration of precipitation patterns affect the survival, performance, and populations dynamics of invaders (Sorte et al. 2013). Because invasive species can disproportionately capitalize on greater resource availability following disturbance, nutrient addition, or reduced competition, climate change may increase their establishment (Sorte et al. 2013). Furthermore, higher inter- and intra-annual variation in temperature and precipitation (Pendergrass et al. 2017) may favor the establishment of invasive species, because many invaders have broader climatic tolerances and higher phenotypic plasticity than co-occurring natives (Davidson et al. 2011).

Species distribution modeling at the continental scale has predicted that many invaders will have greatly expanded ranges under future climate conditions, but ranges also may contract (see "Range and distribution of invasive species" section). While these model results are informative for management planning at the broadest scales (i.e., statewide or nationally), there is an urgent need for downscaled models that address the individual management unit (e.g., watershed, region).

While the field of invasion ecology has seen great advances in our understanding of how altered environmental factors influence establishment and spread, many knowledge gaps remain. Invasive species may evolve in response to environmental change on fast ($\sim$ 5 years) time scales (e.g., Nguyen et al. 2016), but our understanding of this phenomenon and its effect on community-level processes over the long-term is limited. Research has focused on how species will respond to changes in average climate (e.g., two degree increase in temperature, 50% reduction in precipitation) rather than climate extremes. However, extreme climatic events (e.g., hurricanes, floods, droughts) can enhance the transport, establishment, and impacts of invasive species through various understudied mechanisms (Diez et al. 2012). There is also a need to understand how the resident community responds to climate change, and whether it becomes more or less resistant to invasion (Beaury et al. 2020; Haeuser et al. 2017).

While filling these knowledge gaps, researchers need to strengthen the relevance of their research for management. Managers need information that bears on prioritization (Beaury et al. 2020), particularly in areas where climate change will have large impacts (e.g., island, estuary, and polar ecosystems). Understanding how invasive species will shift range or change in abundance with climate change will inform early detection and rapid response efforts in new ranges, and allow managers to reduce focus on invaders that may go locally extinct under new climate scenarios. Research may also inform the choice and effectiveness of management techniques (e.g., herbicides, biological control, altered disturbance regimes) under future climate scenarios. For example, changes in several abiotic factors can alter the fitness of biocontrol organisms and the phenological synchrony between them and their target invaders (Seastedt 2015). Fire is used to control invaders in some ecosystems (Pyke et al. 2010), but drier and hotter conditions may create larger logistical challenges to prescribed fire. Finally, restoration of native plant communities following invader removal has long focused on re-establishing historical native communities, but other species or genotypes may be needed for successful restoration under future climate scenarios (Bucharova et al. 2019; Butterfield et al. 2017).

Range and distribution of invasive species

Prevention and early detection of invasive species are the most effective forms of management (Westbrooks 2004). However, predicting which species are likely to arrive, establish, and spread is a complex task (Peterson and Vieglais 2001). Habitat suitability models leverage the known distributions of species in their native and non-native ranges to characterize essential niche dimensions and predict new areas of potential invasion (Peterson and Vieglais 2001). These models largely rely on environmental variables, such as climate, topography, land cover, and geology (Hirzel et al. 2006) and assume that local factors, biotic interactions, and demographic processes are captured inherently by working at large scales (Gallien et al. 2010). The underlying assumption of this approach is that all species require some level of environmental matching to shift ranges. Including the role of human activities in introductions (i.e., socio-economic, Bellard et al. 2016) and species-specific demographic processes (Gallien et al. 2010) can increase the accuracy of habitat suitability model predictions (Hirzel et al. 2006).

Models that predict establishment risk are not good predictors of the abundance of an introduced species or its ecological impact (Bradley 2013, 2016), which is essential information for land managers. Relying on climate variables to define habitat suitability also increases uncertainty about predicted future distributions because invasive species will likely respond to climate change in complex ways that could either expand or contract ranges (e.g., Bradley et al. 2009). Finally, realized niches in the native range may differ from those in the introduced range, due to biotic constraints in the former (Colautti et al. 2017) and evolutionary change of the invader in the latter (e.g., Nguyen et al. 2016).

Despite recent developments in modeling and a focus on predicting invasions, a knowing-doing gap exists between research and management in this area (Sofaer et al. 2019). First, spatially explicit predictive models are complex and increasingly focused on model validation and improvements rather than species-specific recommendations for managers (although see Bradley et al. 2009). Second, there is a mismatch in scale where models are often focused on establishment risk at regional or continental scales (e.g., Bellard et al. 2016), which is important for making regulatory decisions, but ineffective for prioritizing action for individual management units. Closing the knowing-doing gap will require a major shift in the way researchers build and communicate predictive models of invasion risk. Researchers must build models that include invasive species abundance, not just occurrence, in order to provide accurate and relevant predictions on the potential impacts of invaders (Bradley 2013; Uden et al. 2015). To this end, managers will need to be willing participants in data collection to ensure that model outputs are useful at the scale at which they wish to prioritize management actions. Adaptive models that include incremental improvements based on a feedback loop between model predictions and management data are labor intensive, but provide a framework for how academics and land managers can interact to develop management plans for invasive species across a broad range of spatial scales (Sofaer et al. 2019; Uden et al. 2015).

Succession

Plant invasions can strongly influence the successional trajectories of native plant communities through multiple mechanisms, including direct suppression of native species (Flory and Clay 2010), indirect facilitation of herbivores or seed predators (Orrock and Witter 2010), alteration of soil nutrient cycling (Vitousek et al. 1987), shifts in soil biota (Mangla and Callaway 2008), or changes to disturbance regimes (Mack and D'Antonio 1998). These mechanisms are not mutually exclusive; invaders may suppress natives though multiple pathways simultaneously. However, in some cases native species may reestablish in invaded communities (DeSimone 2011) or even be facilitated by invaders (Rodriguez 2006). Improved understanding of succession will help determine appropriate management and restoration strategies for invaded communities (Sheley et al. 2006). For example, if natives are able to reestablish in the presence of invaders, or if the abundance of or negative impacts of invaders decline over time (Dostál et al. 2013), it may be possible to succeed with lower levels of intervention (and less cost). On the other hand, if invaders exert a strong negative effect on ecosystem processes or lead to a new stable state of the community, or if native species are not available to colonize (Yelenik and D'Antonio 2013), more active intervention would be required (Suding et al. 2004). Therefore, researchers and managers should aim to understand whether and how invaders limit recruitment of native species, whether they create strong self-reinforcing feedbacks, and how effects might change over time.

Invasive plant removal may yield positive results for native species but invaders may have long-term legacy effects that hamper native community succession (Corbin and D'Antonio 2012). For example, some invasive species increase soil N availability, and this effect can persist following removal (Von Holle et al. 2013). This elevated N availability may reduce the ability of mid- and late-seral species to establish, necessitating management of soil N for successful restoration (Vasquez et al. 2008). To date, a limited number of studies have examined legacy effects of plant invasions (Corbin and D'Antonio 2012; Grove et al. 2015). Future research should explore potential legacies on biological, soil chemical, and physical properties of ecosystems and how long these impacts persist.

The recovery of native plant communities following invader removal may be limited by a depauperate native seedbank (see "Seedbanks" section) necessitating seed addition or transplanting nursery grown plants. Conversely, native species recruitment may occur without intervention, and in such cases passive restoration methods to further facilitate a desired successional trajectory may be more cost-effective (DeSimone 2011). Other important considerations are the mix of native species and the timing of their addition. By planting diverse mixes of native species or native species with similar functional traits to invasive species, practitioners may be able to increase the biotic resistance of restored communities and limit reinvasion (Byun et al. 2018; Funk et al. 2008). For example, in cheatgrass dominated rangelands of Utah, planting native grasses along with native shrub species increased restoration success compared to areas where only shrubs were planted (Cox and Anderson 2004). However, such an approach should not be assumed to always yield positive outcomes, and practitioners should test the efficacy of different species mixes on the establishment of natives that are the ultimate targets for restoration. For example, in coastal sage scrub of southern California, Bell et al. (2019) found that seeding native annuals along with native perennials did not limit the growth of invasive *Brassica nigra* and negatively impacted the survival of perennial species. Identifying general guidelines for the use of various restoration methods will require a better understanding of seedbanks, dispersal potential, and which mixes of native species will enhance resistance to reinvasion.

Managers should be mindful of unexpected consequences of invasive species management (Zavaleta et al. 2001). For example, removal of one invader may result in secondary invasion of potentially more problematic species (D'Antonio et al. 2017; Pearson et al. 2016). Thus, managers need to anticipate and control secondary invaders and include plans for the reestablishment of native vegetation that will increase resistance to future invasion (Funk et al. 2008). Studies that include long-term monitoring following control efforts, consistency in study design and data collection, and greater reporting of management outcomes by practitioners and invasion ecologists (e.g., through peer-reviewed publications, technical reports, and presentations to both scientific and management communities) will be useful for developing guidelines to mitigate secondary invasion.

Closing the knowing-doing gap

So far in this paper, we have principally discussed research approaches in invasion ecology that could provide information of relevance to management. However, we have not addressed how ecologists practice science. Indeed, throughout this paper we have tacitly supported the notion that scientists decide what is important to study, produce information, and then disseminate it for use by others, and that managers will adopt it if it is sufficiently useful and relevant.

There are two problems with this notion. First, failure to select a management-relevant topic of study, or a thematic gap, is but one way in which the knowing-doing gap comes about (Habel et al. 2013). Focusing here on what research topics are relevant to managers is unlikely to solve the whole problem, as surveys of managers frequently show that their biggest conservation challenges are fundamentally about social values, funding, stakeholder conflicts, and commitment to the process (Braunisch et al. 2012; Matzek et al. 2014; Moore et al. 2011). Researchers must also address issues of working at management-appropriate spatial and temporal scales (Bennett et al. 2012; Kettenring and Adams 2011), which may entail sacrificing some control over experimental conditions. They must also confront the challenge of translating research findings for managers and finding settings in which to disseminate them (Enquist et al. 2017; Lavoie and Brisson 2015). A large percentage of managers rely on their own experiences and information rather than results from scientific research. For example, one-third of 500 managers surveyed in California did not consult the peer-reviewed literature (Matzek et al. 2014). However, when presented with summarized scientific evidence, managers are more likely to adopt effective management strategies (Walsh et al. 2015). Open-access papers in journals focused on management or translational science (e.g., *Conservation Science and Practice, Ecology and Society*) may be more accessible and useful to practitioners. Research results presented at symposia and workshops attended by managers, shared through conversations with extension agents, or contributed to non-peer reviewed sources such as websites (e.g., plants.usda.gov, calflora.net) and newsletters (e.g., statewide invasive plant councils in the United States), are also more likely to reach a management audience.

The second problem is more fundamental. Promoting a one-way flow of knowledge from academics to managers endorses a world view that is likely to hold back progress in invasive species control. In reality, academics and managers are equal partners in this endeavor. Respectfully acknowledging how the goals of academics and managers differ, and how they can help each other meet their respective goals, is a step in the right direction (Fig. 2). The paradigm in which knowledge only flows in one direction, from academics to managers, is predominant in studies of the knowing-doing gap (Bertuol-Garcia et al. 2018). To truly close the gap, academics and managers should embrace a two-way flow of knowledge, with both groups cooperating to jointly source research questions, devise management-scale experiments, and coproduce knowledge (Fig. 3; Enquist et al. 2017; Gonzalo-Turpin et al. 2008). Co-production of research questions can increase the likelihood that results are implemented into practice and solidify stakeholder engagement (Shackleton et al. 2019).

There are several concrete steps that academics can take to cultivate academic–practitioner relationships and remove barriers to conducting management-focused research. Reaching out to managers or "information brokers" familiar with both researchers and managers (e.g., government scientist with an academic background) is the first step (Hallett et al. 2017). In addition to participating in management-focused workshops, conducting surveys of local managers is an effective method to identify urgent research needs and may lead to fruitful collaborations (Beaury et al. 2020; Dickens and Suding 2013; Rohal et al. 2018). Research questions will benefit from the real-world knowledge that managers gain from many hours of observing their landscapes (Fig. 2). For example, managers might notice that particular soil types are more invasion resistant, or that a particular native species serves as a nurse plant to other species. Both parties may need to invest in relationships without always seeing an immediate payoff (Fig. 3, Littell et al. 2017). Once partnerships are formed, academics must be mindful that managers need clear, timely answers rather than nuanced, complicated stories with limited practical applications. Researchers may also have to compromise on issues that are at odds with management goals, such as establishing control plots where invaders are not managed.

Additionally, researchers should consider how they incorporate applied questions into their research programs. While this review has focused on basic ecological research, there are many applied research areas that urgently need to be addressed, such as the timing of treatment, negative unintended consequences of management, herbicide effectiveness, and the development of early detection tools (Matzek et al. 2015). It is beyond the scope of this paper to review the need for research in these areas, but we can close with the observation that improving this situation will require some culture change within academia, particularly with respect to how management-driven research is valued within the community. In addition to encouraging academic institutions to provide recognition and career advancement for early-career faculty who conduct translational science (Hallett et al. 2017), researchers should emphasize the value of applied work to editorial boards of journals and grant program officers.

In the absence of widespread funding for applied work, researchers can pursue non-traditional approaches for conducting this type of research and outreach. Partnerships between academics and managers could pave the way for linking invasive species management to non-traditional funding mechanisms, such as federal funding for outreach and extension activities (Hallett et al. 2017), payment for ecosystem services (Funk et al. 2014), and cooperative grants to conduct research at management sites (Fig. 2, Renz et al. 2009). Undergraduate and graduate students often have access to small pools of money that could support studies of single invasive species. Long-term monitoring, which is difficult to achieve because of time and resources (Dickens and Suding 2013), could be incorporated into undergraduate lab courses which, over time, could yield decades worth of valuable data on the impacts and legacy effects of invasive species (e.g., http://erenweb.org) and management efficacy.

Conclusions

Our review highlights several areas where the goals of management and basic research align more now than in the past. An increased focus on trait-based approaches in the fields of ecology and evolutionary biology has enhanced databases of basic life-history data, which will provide urgently needed information about specific invaders to managers. In addition, the move towards enhancing taxonomic and spatial diversity in ecological research will benefit managers. Interactions between researchers and managers that are more intentional and collaborative will ensure that goals remain aligned, with positive benefits to research agendas and on-the-ground decision making.

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