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**Keys to enhancing the value of invasion ecology research for
management**

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32 **Abstract**

33 Invasion ecology has grown to include scientists with diverse skill sets
34 who focus on a range of taxa and biomes. These researchers have the
35 capacity to contribute to practical management solutions while also
36 answering fundamental biological questions; however, scientific endeavors
37 often fail to meet the perceived needs of practitioners involved in on-the-
38 ground invasive plant management. One way that researchers have sought
39 to bridge the gap between research and practice is by surveying managers
40 to identify areas of study that are under-represented in invasion ecology. In
41 this paper, we build on these efforts by reviewing the current state of
42 knowledge and suggesting new directions for research in seven areas of
43 plant invasion ecology that are highly relevant to management: seedbanks,
44 dispersal and spread, life history, impacts, climate change, distribution, and
45 succession. These topics were previously identified as urgent research
46 priorities by land managers and are underrepresented in the invasion
47 ecology literature. In addition to highlighting key knowledge gaps for these
48 seven areas of basic research, we propose steps that academics can take to
49 cultivate academic-practitioner relationships and remove barriers to
50 conducting management-focused research, such as co-producing research
51 questions with managers, addressing issues of working at management-
52 appropriate spatial and temporal scales, and considering non-traditional
53 funding and labor sources for long-term monitoring. Greater communication

54 and collaborative selection of basic research questions will ensure that the
55 goals of management and invasive species research remain aligned.

56

57 **Keywords:** climate change, functional traits, impacts, knowing-doing gap,
58 life history, restoration, seedbank, succession

59 **Introduction**

60 Invasive plants contribute to biodiversity loss and changes in
61 ecosystem processes (Pyšek et al. 2012), and management of these species
62 is crucial for conservation. In recent decades, academics have increasingly
63 placed invasion research into fundamental ecological or evolutionary
64 frameworks to better connect patterns to theory, draw generalizations across
65 species and systems, and bring together researchers from different
66 disciplines (Cadotte et al. 2006; Sax et al. 2005). However, this effort often
67 comes at the expense of tackling applied problems to bring about practical
68 management solutions. While some academics have sought to work with
69 land managers to identify research priorities for improving invasive plant
70 control (D'Antonio et al. 2004; Matzek et al. 2014), or to address the
71 technical and cultural challenges of effective policy-making (Keller et al.
72 2015), the ecology of plant invasions still suffers from a “knowing-doing gap”
73 (Knight et al. 2008).

74 The knowing-doing gap (also known as the research-implementation
75 gap, or knowledge-practice gap), is the phenomenon of scientific research
76 failing to inform or improve on-the-ground conservation practice. Many
77 explanations for this gap have been forwarded, including a perceived
78 resistance of researchers to solve applied problems (Renz et al. 2009), in
79 part because the incentives and timeline for cooperative work do not align
80 with outcome-centered academic research culture (Hallett et al. 2017).
81 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 forward for invasion ecology that yields the greatest benefits for theoretical advancement and management (Fig. 2).

1. 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

128 or invasion intensity a reliable predictor of seedbank density (Alexander and
129 D'Antonio 2003). These mismatches between what managers can see
130 aboveground, and what they cannot see belowground, have major
131 implications for control and restoration. They may cause managers to
132 underestimate the time and resources needed to control invasions fully, or to
133 abandon management efforts due to an unwarranted belief that control is
134 infeasible. Uncertainty about seedbanks can also result in inadequate
135 planning for invasive plant control after natural disturbances such as drought
136 or fires (Keeley et al. 2005; LaForgia et al. 2018). Before removing a
137 dominant invader, it may also be useful to know what native species are
138 present in the seedbank, if restoration will require reseeding, and if
139 secondary invaders are poised to emerge. Studies aimed at understanding
140 the high spatiotemporal variability of seedbank composition, and how it is
141 affected by variation in seed rain, seed dormancy/longevity, and
142 biotic/abiotic constraints on germination potential (see Online Resource 1),
143 would have immediate relevance to predicting the long-term impact of a
144 plant invasion and planning an appropriate management response, such as
145 topsoil removal or summer irrigation to flush the invasive seedbank (Funk et
146 al. 2015). Researchers could also usefully contribute to the growing body of
147 work on the responses of seedbanks to management intervention (Ma et al.
148 2015; Maclean et al. 2018).

149 Understanding differences in seed traits among invasive and native
150 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 (Richardson and Kluge 2008) or topsoil removal (Buisson et al. 2008).

2. 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

174 characterizations of modality such as wind vs. animal (Flores-Moreno et al.
175 2013; Pysek and Richardson 2007). Similarly, management-focused online
176 resources provide detailed references on dispersal for some widespread
177 invasive plants (e.g. *Bromus tectorum*), but considerably less for others (e.g.
178 *Bromus madritensis*, CABI Invasive Species Compendium, University of
179 California Weed Research and Information Center).

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

189 Still, academic research on spread can provide valuable management
190 guidance for some invasive species (Shea et al. 2010; Taylor and Hastings
191 2004). For example, models have been used to predict the effect of a
192 biological control agent on decelerating rates of plant spread (Jongejans et
193 al. 2008), which can be an important benefit of biological control even in
194 cases where eradication is not possible. Nevertheless, to date much of this
195 species-specific modeling concentrates on well-studied taxa such as
196 *Carduus*, *Cirsium*, *Cytisus*, or *Spartina*. Use of model species can facilitate

197 progress in theoretical understanding of dispersal and invasion, but may also
198 limit the diversity of data available to test for generalizable patterns (Bullock
199 et al. 2017; Tamme et al. 2014). A broader taxonomic focus would fill data
200 gaps critical to managers while facilitating studies that relate species traits,
201 such as seed and rhizome/stolon morphology, to dispersal and spread.

202 Beyond species-specific insights, research on spread can identify
203 intervention strategies and provide broad rules of thumb for management.
204 An example is Moody and Mack's classic 1988 paper, which used a simple
205 mathematical model to show that eradicating small outlying patches
206 (nascent foci) of invasive plants is more effective at slowing invasion than
207 chipping away at one large patch (Moody and Mack 1988). Studies using
208 more complex models have explored similar themes, demonstrating that
209 controlling the "tail of the distribution" (far-dispersing outlier individuals or
210 populations) is key to slowing invasion across a landscape (Lewis et al.
211 2016). Greater study of the role of extreme climate events, such as
212 hurricanes, in promoting rapid spread is also needed and could be combined
213 with modeling to help managers anticipate post-disturbance challenges in
214 their region (Diez et al. 2012).

215 Research on spread has two other practical applications. First,
216 researchers can identify processes or characteristics of invaders or sites that
217 influence spread, informing prioritization of resources, such as to early
218 detection and rapid response, and management efforts among species and
219 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 *Gallium mollago* 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.

235

3. 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

243 with limited distribution is far more cost-effective than waiting until such
244 species become widespread and abundant (Leung et al. 2002). That said,
245 the large scientific literature on key well-studied invaders has been used to
246 develop life-history generalities that can be applied to nascent invaders (e.g.,
247 Pysek and Richardson 2007).

248 Since Baker (1974) devised the list of characteristics that define an
249 ‘ideal weed’, ecologists have considered various aspects of species’ life
250 histories to determine their success as invaders. The most promising
251 generality is that, compared to non-invasive plant species, invaders often
252 grow faster (Dawson et al. 2011), reproduce earlier, produce smaller and
253 more numerous seeds (Rejmanek and Richardson 1996), are able to
254 capitalize on higher resource availability in disturbed habitats (Dawson et al.
255 2012), and spread through vegetative (clonal) propagation. While these
256 general guidelines can be used as a starting point, life history traits of native
257 and invasive species are context dependent, and land managers often lack
258 knowledge of basic ecology and life-history of problematic and nascent
259 invasive plants (Matzek et al. 2014). Ecologists are assembling trait
260 databases (e.g., TraitNet, TRY), and an increasing focus on capturing
261 intraspecific trait variation (e.g., Des Roches et al. 2018) may help managers
262 understand differential responses and impacts of specific invaders across
263 sites. Making these databases freely accessible, expanding coverage of
264 invasive species and traits, and updating them frequently to include nascent
265 invaders will enhance their utility for management.

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

280 Many barriers exist to collecting basic life history information,
281 particularly for nascent invaders. Notably, it can be difficult to secure
282 funding for species-specific, applied, or long-term monitoring projects. We
283 see many ways for academics to overcome these barriers, including seeking
284 smaller pools of funding (such as grants for undergraduate and masters
285 theses), incorporating basic life history data collection into undergraduate
286 lab curricula, contributing data to online databases or open-source
287 publication archives, and strengthening communication with managers by
288 attending or hosting workshops focused on local/regional invasive species

289 management (see *Closing the knowing-doing gap* below). Academics can
290 source valuable life history information from managers who regularly record
291 abundance data and treatment information on the properties they manage.

292

293 **4. Impacts of invaders**

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

310 Studies on impacts are also biased towards particular species,
311 functional groups, and biogeographic areas, greatly limiting their relevance

312 for management (Hulme et al. 2013). Many species that are considered
313 highly problematic by managers have been the subject of surprisingly few
314 studies on impacts (Hulme et al. 2013). For example, kudzu (*Pueraria*
315 *montana*) and Brazilian pepper (*Schinus terebinthefolius*) together have over
316 40,000 positive occurrence records online (eddmaps.org), and are the
317 subject of large-scale management efforts, but very little quantitative
318 information is available on their impacts (Hulme et al. 2013). Plant invaders
319 can occupy wide geographic ranges but, in most cases, the context
320 dependency of invader impacts is unknown (Hulme et al. 2013).

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

334 improve decision-making when prioritizing species for management (see
335 Online Resource 1).

336

337 **5. Response of invaders to climate change**

338 Climate change may alter the introduction, establishment, spread, and
339 impacts of invasive plants (Dukes and Mooney 1999; Hellmann et al. 2008),
340 with significant implications for management. The majority of studies to
341 date have focused on how rising temperatures and alteration of precipitation
342 patterns affect the survival, performance, and populations dynamics of
343 invaders (Sorte et al. 2013). Because invasive species can
344 disproportionately capitalize on greater resource availability following
345 disturbance, nutrient addition, or reduced competition, climate change may
346 increase their establishment (Sorte et al. 2013). Furthermore, higher inter-
347 and intra-annual variation in temperature and precipitation (Pendergrass et
348 al. 2017) may favor the establishment of invasive species, because many
349 invaders have broader climatic tolerances and higher phenotypic plasticity
350 than co-occurring natives (Davidson et al. 2011). Species distribution
351 modeling at the continental scale has predicted that many invaders will have
352 greatly expanded ranges under future climate conditions, but ranges also
353 may contract (see *Range and distribution of invasive species*). While these
354 model results are informative for management planning at the broadest
355 scales (i.e., statewide or nationally), there is an urgent need for downscaled

356 models that address the individual management unit (e.g., watershed,
357 region).

358 While the field of invasion ecology has seen great advances in our
359 understanding of how altered environmental factors influence establishment
360 and spread, many knowledge gaps remain. Invasive species may evolve in
361 response to environmental change on fast (~ five years) time scales (e.g.,
362 Nguyen et al. 2016), but our understanding of this phenomenon and its
363 effect on community-level processes over the long-term is limited. Research
364 has focused on how species will respond to changes in average climate (e.g.,
365 two degree increase in temperature, 50% reduction in precipitation) rather
366 than climate extremes. However, extreme climatic events (e.g., hurricanes,
367 floods, droughts) can enhance the transport, establishment, and impacts of
368 invasive species through various understudied mechanisms (Diez et al.
369 2012). There is also a need to understand how the resident community
370 responds to climate change, and whether it becomes more or less resistant
371 to invasion (Beaury et al. 2020; Haeuser et al. 2017).

372 While filling these knowledge gaps, researchers need to strengthen the
373 relevance of their research for management. Managers need information
374 that bears on prioritization (Beaury et al. 2020), particularly in areas where
375 climate change will have large impacts (e.g., island, estuary, and polar
376 ecosystems). Understanding how invasive species will shift range or change
377 in abundance with climate change will inform early detection and rapid
378 response efforts in new ranges, and allow managers to reduce focus on

379 invaders that may go locally extinct under new climate scenarios. Research
380 may also inform the choice and effectiveness of management techniques
381 (e.g., herbicides, biological control, altered disturbance regimes) under
382 future climate scenarios. For example, changes in several abiotic factors can
383 alter the fitness of biocontrol organisms and the phenological synchrony
384 between them and their target invaders (Seastedt 2015). Fire is used to
385 control invaders in some ecosystems (Pyke et al. 2010), but drier and hotter
386 conditions may create larger logistical challenges to prescribed fire. Finally,
387 restoration of native plant communities following invader removal has long
388 focused on re-establishing historical native communities, but other species
389 or genotypes may be needed for successful restoration under future climate
390 scenarios (Bucharova et al. 2019; Butterfield et al. 2017).

391

392 **6. Range and distribution of invasive species**

393 Prevention and early detection of invasive species are the most
394 effective forms of management (Westbrooks 2004). However, predicting
395 which species are likely to arrive, establish, and spread is a complex task
396 (Peterson and Vieglais 2001). Habitat suitability models leverage the known
397 distributions of species in their native and non-native ranges to characterize
398 essential niche dimensions and predict new areas of potential invasion
399 (Peterson and Vieglais 2001). These models largely rely on environmental
400 variables, such as climate, topography, land cover, and geology (Hirzel et al.
401 2006) and assume that local factors, biotic interactions, and demographic

402 processes are captured inherently by working at large scales (Gallien et al.
403 2010). The underlying assumption of this approach is that all species require
404 some level of environmental matching to shift ranges. Including the role of
405 human activities in introductions (i.e., socio-economic components; Bellard
406 et al. 2016) and species-specific demographic processes (Gallien et al. 2010)
407 can increase the accuracy of habitat suitability model predictions (Hirzel et
408 al. 2006).

409 Models that predict establishment risk are not good predictors of the
410 abundance of an introduced species or its ecological impact (Bradley 2013,
411 2016), which is essential information for land managers. Relying on climate
412 variables to define habitat suitability also increases uncertainty about
413 predicted future distributions because invasive species will likely respond to
414 climate change in complex ways that could either expand or contract ranges
415 (e.g., Bradley et al. 2009). Finally, realized niches in the native range may
416 differ from those in the introduced range, due to biotic constraints in the
417 former (Colautti et al. 2017) and evolutionary change of the invader in the
418 latter (e.g., Nguyen et al. 2016).

419 Despite recent developments in modeling and a focus on predicting
420 invasions, a knowing-doing gap exists between research and management in
421 this area (Sofaer et al. 2019). First, spatially explicit predictive models are
422 complex and increasingly focused on model validation and improvements
423 rather than species-specific recommendations for managers (although see
424 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 to prioritize 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).

7. 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 et al. 2008), or changes to disturbance regimes (Mack and D'Antonio 1998). These

448 mechanisms are not mutually exclusive; invaders may suppress natives
449 though multiple pathways simultaneously. However, in some cases native
450 species may reestablish in invaded communities (DeSimone 2011) or even
451 be facilitated by invaders (Rodriguez 2006). Improved understanding of
452 succession will help determine appropriate management and restoration
453 strategies for invaded communities (Sheley et al. 2006). For example, if
454 natives are able to reestablish in the presence of invaders, or if the
455 abundance of or negative impacts of invaders decline over time (Dostál et al.
456 2013), it may be possible to succeed with lower levels of intervention (and
457 less cost). On the other hand, if invaders exert a strong negative effect on
458 ecosystem processes or lead to a new stable state of the community, or if
459 native species are not available to colonize (Yelenik and D'Antonio 2013),
460 more active intervention would be required (Suding et al. 2004). Therefore,
461 researchers and managers should aim to understand whether and how
462 invaders limit recruitment of native species, whether they create strong self-
463 reinforcing feedbacks, and how effects might change over time

464 Invasive plant removal may yield positive results for native species but
465 invaders may have long-term legacy effects that hamper native community
466 succession (Corbin and D'antonio 2012). For example, some invasive
467 species increase soil N availability, and this effect can persist following
468 removal (Von Holle et al. 2013). This elevated N availability may reduce the
469 ability of mid- and late-seral species to establish, necessitating management
470 of soil N for successful restoration (Vasquez et al. 2008). To date, a limited

471 number of studies have examined legacy effects of plant invasions (Corbin
472 and D'antonio 2012; Grove et al. 2015). Future research should explore
473 potential legacies on biological, soil chemical, and physical properties of
474 ecosystems and how long these impacts persist.

475 The recovery of native plant communities following invader removal
476 may be limited by a depauperate native seedbank (see *Seedbanks*)
477 necessitating seed addition or transplanting nursery grown plants.

478 Conversely, native species recruitment may occur without intervention, and
479 in such cases passive restoration methods to further facilitate a desired
480 successional trajectory may be more cost-effective (DeSimone 2011). Other
481 important considerations are the mix of native species and the timing of
482 their addition. By planting diverse mixes of native species or native species
483 with similar functional traits to invasive species, practitioners may be able to
484 increase the biotic resistance of restored communities and limit reinvasion
485 (Byun et al. 2018; Funk et al. 2008). For example, in cheatgrass dominated
486 rangelands of Utah, planting native grasses along with native shrub species
487 increased restoration success compared to areas where only shrubs were
488 planted (Cox and Anderson 2004). However, such an approach should not
489 be assumed to always yield positive outcomes, and practitioners should test
490 the efficacy of different species mixes on the establishment of natives that
491 are the ultimate targets for restoration. For example, in coastal sage scrub
492 of southern California, Bell et al. (2019) found that seeding native annuals
493 along with native perennials did not limit the growth of invasive *Brassica*

494 *nigra* and negatively impacted the survival of perennial species. Identifying
495 general guidelines for the use of various restoration methods will require a
496 better understanding of seedbanks, dispersal potential, and which mixes of
497 native species will enhance resistance to reinvasion.

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

510

511 **Closing the knowing-doing gap**

512 So far in this paper, we have principally discussed research approaches
513 in invasion ecology that could provide information of relevance to
514 management. However, we have not addressed how ecologists practice
515 science. Indeed, throughout this paper we have tacitly supported the notion
516 that scientists decide what is important to study, produce information, and

517 then disseminate it for use by others, and that managers will adopt it if it is
518 sufficiently useful and relevant.

519 There are two problems with this notion. First, failure to select a
520 management-relevant topic of study, or a thematic gap, is but one way in
521 which the knowing-doing gap comes about (Habel et al. 2013). Focusing
522 here on what research topics are relevant to managers is unlikely to solve
523 the whole problem, as surveys of managers frequently show that their
524 biggest conservation challenges are fundamentally about social values,
525 funding, stakeholder conflicts, and commitment to the process (Braunisch et
526 al. 2012; Matzek et al. 2014; Moore et al. 2011). Researchers must also
527 address issues of working at management-appropriate spatial and temporal
528 scales (Bennett et al. 2012; Kettenring and Adams 2011), which may entail
529 sacrificing some control over experimental conditions. They must also
530 confront the challenge of translating research findings for managers and
531 finding settings in which to disseminate them (Enquist et al. 2017; Lavoie
532 and Brisson 2015). A large percentage of managers rely on their own
533 experiences and information rather than results from scientific research. For
534 example, one-third of 500 managers surveyed in California did not consult
535 the peer-reviewed literature (Matzek et al. 2014). However, when presented
536 with summarized scientific evidence, managers are more likely to adopt
537 effective management strategies (Walsh et al. 2015). Open-access papers in
538 journals focused on management or translational science (e.g., *Conservation*
539 *Science and Practice*, *Ecology and Society*) may be more accessible and

540 useful to practitioners. Research results presented at symposia and
541 workshops attended by managers, shared through conversations with
542 extension agents, or contributed to non-peer reviewed sources such as
543 websites (e.g., plants.usda.gov, calflora.net) and newsletters (e.g., statewide
544 invasive plant councils in the United States), are also more likely to reach a
545 management audience.

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

561 There are several concrete steps that academics can take to cultivate
562 academic-practitioner relationships and remove barriers to conducting

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

580 Additionally, researchers should consider how they incorporate applied
581 questions into their research programs. While this review has focused on
582 basic ecological research, there are many applied research areas that
583 urgently need to be addressed, such as the timing of treatment, negative
584 unintended consequences of management, herbicide effectiveness, and the
585 development of early detection tools (Matzek et al. 2015). It is beyond the

586 scope of this paper to review the need for research in these areas, but we
587 can close with the observation that improving this situation will require some
588 culture change within academia, particularly with respect to how
589 management-driven research is valued within the community. In addition to
590 encouraging academic institutions to provide recognition and career
591 advancement for early-career faculty who conduct translational science
592 (Hallett et al. 2017), researchers should emphasize the value of applied work
593 to editorial boards of journals and grant program officers.

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

608

609 **Conclusion**

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

620

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974

975 **Figure legend**

976

977 **Fig. 1.** A comparison of management priorities and published research
978 shows a mismatch for
979 specific topics in basic research. Negative values reflect
980 underrepresentation of topics in the literature compared to what managers
981 want. Sample sizes are $N = 122$ for manager-identified priorities and $N =$
982 243 for basic research papers. The survey was administered to managers in
983 California, which is ecologically diverse and presents a variety of
984 management challenges. Figure adapted from Matzek et al. (2015).

985

986 **Fig. 2.** The academic and management realms experience different
987 potential benefits from interacting with each other. Recognizing and valuing
988 the contrasting perspectives and goals helps to identify what academics and
989 managers respectively could gain from collaboration.

990

991 **Fig. 3.** Academic-manager partnerships can begin at any time in an
992 academic's career and can catalyze the exchange of information and
993 funding. In this case study, resource managers at Fort Lewis (Tacoma, WA,
994 now Joint Base Lewis-McChord) provided generous logistical support for a
995 graduate student conducting basic research on the invasive plant, Scotch
996 broom (*Cytisus scoparius*) (Parker 1997). When managers at Fort Lewis
997 needed help with a broom control problem ten years later, they called on the

998 student, who was now a professor at a research university. The researcher,
999 with collaborators and students, designed experiments together with
1000 managers, sharing results through regular in-person meetings and reports.
1001 Eventually they received National Science Foundation (NSF) funding to
1002 conduct additional basic research, using their collaborative work as
1003 preliminary data (e.g., Grove et al. 2019). As part of the Broader Impacts of
1004 their NSF grant, they helped plan and sponsor a networking workshop on
1005 broom control for nearly 300 resource managers from across Washington
1006 State. There are many potential variations of this partnership: graduate
1007 students may not continue in academia – many will cross over in career path
1008 to do applied invasion science – and several types of partnerships exist (e.g.,
1009 industry, non-profit organizations).