

Four priority areas to advance invasion science in the face of rapid environmental change

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1 **Four priority areas to advance invasion science in the face of rapid**

2 **environmental change**

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55

56 **Abstract**

57 Unprecedented rates of introduction and spread of non-native species pose burgeoning
58 challenges to biodiversity, natural resource management, regional economies, and human health.
59 Current biosecurity efforts are failing to keep pace with globalization, revealing critical gaps in
60 our understanding and response to invasions. Here, we identify four priority areas to advance
61 invasion science in the face of rapid global environmental change. First, invasion science should
62 strive to develop a more comprehensive framework for predicting how the behavior, abundance,
63 and interspecific interactions of non-native species vary in relation to conditions in receiving
64 environments and how these factors govern the ecological impacts of invasion. A second priority
65 is to understand the potential synergistic effects of multiple co-occurring stressors – particularly
66 involving climate change – on the establishment and impact of non-native species. Climate
67 adaptation and mitigation strategies will need to consider the possible consequences of
68 promoting non-native species, and appropriate management responses to non-native species will
69 need to be developed. The third priority is to address the taxonomic impediment. The ability to
70 detect and evaluate invasion risks is compromised by a growing deficit in taxonomic expertise,
71 which cannot be adequately compensated by new molecular technologies alone. Management of
72 biosecurity risks will become increasingly challenging unless academia, industry, and
73 governments train and employ new personnel in taxonomy and systematics. Fourth, we
74 recommend that internationally cooperative biosecurity strategies consider the bridgehead effects
75 of global dispersal networks, in which organisms tend to invade new regions from locations
76 where they have already established. Cooperation among countries to eradicate or control species
77 established in bridgehead regions should yield greater benefit than independent attempts by
78 individual countries to exclude these species from arriving and establishing.

79

80 **Key words:** biosecurity; climate change; ecological impact; invasive species; management; risk
81 assessment

82

83 **Introduction**

84 Invasion science – the systematic investigation of the causes and consequences of
85 biological invasions – is a rapidly evolving interdisciplinary field. Its explosive growth over the
86 past few decades mirrors societal concern over the upsurge in the global rate of invasions
87 (Seebens et al. 2017; Pyšek et al. 2020; Seebens et al. 2020) and reflects the fundamental and
88 applied importance of understanding how species spread into new regions, why some ecosystems
89 are more vulnerable to invasions, and what factors govern the impacts of non-native species. To
90 date, research addressing these issues has yielded valuable insights into the forces that structure
91 ecological communities, the relationship between diversity and stability, mechanisms of
92 adaptation and rapid evolution, causes of extinction and biotic homogenization, and the
93 connectedness between socioeconomic and ecological systems, among other phenomena
94 (Lockwood et al. 2013; Hui and Richardson 2019). More remains to be done to sharpen and
95 integrate these insights into predictive frameworks. In addition, pressure is increasing for
96 invasion science to adapt to emerging issues such as rapid advances in biotechnology,
97 accelerating global change, expanding transportation networks, abrupt landscape
98 transformations, and infectious disease emergence (Ricciardi et al. 2017; Nuñez et al. 2020).
99 Invasion science is a relatively young discipline (Ricciardi and MacIsaac 2008) that has
100 embraced diverse domains in ecology and cognate fields (e.g., population biology, biogeography,
101 evolutionary biology, paleoecology, physiology) and has formed linkages with disciplines related

102 to biosecurity – such as epidemiology, risk analysis, resource economics, and vector science
103 (Vaz et al. 2017). This multidisciplinary expansion reflects the increasing complexity of
104 biological invasions and their impacts (Richardson 2011; Pyšek et al. 2020).

105 Here, we consider how invasion science should adapt to the Anthropocene – an era of
106 burgeoning human influence, novel stressors, and rapid environmental change (Steffen et al.
107 2015; Waters et al. 2016). We are an international team of ecologists, with diverse and extensive
108 experience in biological invasions in many parts of the world. Our team gathered in September
109 2018 to consider emerging scientific, technological, and sociological issues which, if addressed,
110 should ensure that invasion science can more successfully contend with rapid global change.
111 Through consensus (see Supplemental Material), we arrived at four overarching issues, relevant
112 to a broad range of taxa, environments, and geographic regions, and which encompass some of
113 the most important challenges facing our field today (Figure 1).

115 **1. Predicting ecological impacts of invasions under rapid environmental change**

116 **1.1. The need for greater predictive power: Major advances and ongoing challenges**

117 *1.1.1. Environmental context-dependency of impacts*

118 While invasion science has made substantial progress in understanding how non-native
119 species arrive in new locations and establish self-sustaining populations (Catford et al. 2009;
120 Jeschke and Heger 2018), it has been less successful in forecasting when and where such species
121 will substantially affect their recipient environments (Ricciardi et al. 2013; Simberloff et al.
122 2013; Kumschick et al. 2015). Non-native species can affect ecological, economic, cultural, and
123 human health in diverse ways (Jeschke et al. 2014; Shackleton et al. 2018), but in this section we
124 focus on ecological impacts. Here, ‘impact’ is defined broadly as a measurable change to the

125 environment attributable directly or indirectly to the presence of a non-native species (Ricciardi
126 et al. 2013), and includes their effects on individual performance, population size and
127 composition of ecological communities of native species, which in some cases may be
128 irreversible (IUCN 2020).

129 Impact prediction is a long-standing, complex challenge. While rates of non-native
130 species introductions are increasing across regions (Seebens et al. 2017, 2020), impacts have
131 been recorded for only a small fraction of these species and the sites they invade (Ruiz et al.
132 1999; Ricciardi and Kipp 2008; Vilà et al. 2011; Hulme et al. 2013; Simberloff et al. 2013;
133 Evans et al. 2018b). It is generally assumed that most invasions have negligible environmental
134 consequences (Williamson and Fitter 1996), whereas a small proportion has significant and
135 sometimes enormous effects – an inverse magnitude-frequency distribution similar to that
136 associated with natural disasters (Ricciardi et al. 2011). However, uncertainty exists concerning
137 which cases truly reflect an absence of impact rather than a lack of study (Latombe et al. 2019).
138 Even well-known impacts exhibit substantial variation over time and space; invaders may remain
139 innocuous for years or even decades prior to becoming disruptive when, for example,
140 environmental change triggers a new impact (Crooks 2005; Coutts et al. 2018). The impacts of
141 any given invader can vary greatly among ecosystems (Strayer 2020) and across environmental
142 gradients within ecosystems (Kestrup and Ricciardi 2009; Stritar et al. 2010; Hulme et al. 2013;
143 Sapsford et al. 2020). Context-dependencies of invasion – that is, interactions among propagule
144 pressure, the traits of the invader, the composition of the recipient community, and the
145 physicochemical environment – have hardly been addressed by any formal body of theory, but
146 some overarching frameworks are now being explored (e.g., Cronin et al. 2015; Iacarella et al.
147 2015a; Dickey et al. 2020; Sapsford et al. 2020).

148 Coupled with the challenge of context-dependency is the sheer complexity of
149 mechanisms by which non-native species can interact with their environment (Ricciardi et al.
150 2013; Kumschick et al. 2015). Synergistic interactions, nonlinearities, time lags, threshold
151 effects, regime shifts, and indirect effects of non-native species are difficult to predict (Ricciardi
152 et al. 2013; Essl et al. 2015b; Kumschick et al. 2015; Aagaard and Lockwood 2016; Hui and
153 Richardson 2017; Strayer et al. 2017). Consequently, accurate risk assessment tools for sound
154 management decisions are still lacking.

155

156 *1.1.2. Temporal variation and time lags of impacts*

157 Factors affecting temporal variation in impact remain a major research gap, in large part
158 because of the vast majority of impact studies are conducted over very short time scales (Strayer
159 et al. 2006; Stricker et al. 2015). Time-since-invasion has been found to be an important correlate
160 of the ecological impacts of non-native species (Iacarella et al. 2015b; Evans et al. 2018a;
161 Zavorka et al. 2018), but time lags between establishment and peak impact have thus far evaded
162 prediction and are increasingly recognized as hindering risk assessment (e.g., Coutts et al. 2018).
163 Predictions of spatiotemporal variation in impact direction and magnitude could be improved
164 through experimental and theoretical investigations of the relationship between an invader's *per-*
165 *capita* effect and its abundance (Yokomizo et al. 2009; Cronin et al. 2015; Sofaer et al. 2018;
166 Bradley et al. 2019; Strayer 2020). We must also consider the influence of spatial scale on *per*
167 *capita* effects or impacts measured in small plots and mesocosms; attempts to extrapolate these
168 effects up to landscape scales relevant to management (e.g., by calculating the product of the *per*
169 *capita* effect, local abundance, and range size of an invader) might not adequately capture
170 changes to biodiversity, biotic interactions, and ecosystem function, and thus might

171 underestimate some large-scale consequences of invasion (Hawkins et al. 2015; Bernard-Verdier
172 and Hulme 2019; but see Dick et al. 2017b). Greater effort is required to test factors that mediate
173 indirect and multi-scale effects, particularly where an invader's impact is transmitted across a
174 suite of interacting species (Feit et al. 2018).

175 Conservation interventions and ecosystem management must contend with significant
176 time lags between the onset of the environmental stressors and the expression of invader impacts,
177 and forecasting such phenomena is plagued by context dependencies and non-linearities (Essl et
178 al. 2015b, c; Coutts et al. 2018). An understudied issue is how to recognize and manage the
179 interactive and cumulative effects of time lags in ecological responses to invasion. Delayed
180 biodiversity responses (e.g., dominance shifts, species turnover, metapopulation dynamics,
181 extinction debt) to anthropogenic stressors such as invasion can lead to abrupt shifts in
182 ecosystem functioning (Essl et al. 2015b) and underestimation of rates of contemporary
183 biodiversity change (Essl et al. 2015c). Given the management implications of this phenomenon,
184 ecological responses to compounded and cumulative stressors are becoming an increasing focus
185 of theory, experiments, and time series analyses (Foster et al. 2016; Candolin et al. 2018;
186 Kleinman et al. 2019; Shinoda and Akasaka 2020).

187

188 *1.1.3. Impacts on ecosystem processes*

189 Demand is growing for reliable assessments and predictions of the ecosystem-level
190 impacts of non-native species, especially those impacts that affect the provision of ecosystem
191 services in rapidly changing environments (Vilà and Hulme 2017). This need reflects the larger
192 challenge of understanding how ecosystem function is altered by the combined effects of species
193 gains (invasion, range expansion) and losses (extinction, range contraction), which are

194 simultaneously consequences and drivers of global change. With few exceptions (e.g., Mascaro
195 et al. 2012; Kuebbing et al. 2015), work on how these two forces affect ecosystem functioning
196 has developed largely in isolation (Wardle et al. 2011). Owing to this disconnect, ecologists are
197 unable to predict over the coming decades the net ecosystem consequence of these two opposing
198 forces – specifically, whether or not species that are gained at local scales through invasion will
199 affect ecosystem process rates in a comparable way to those native species that are lost.
200 Moreover, despite the many ecosystem impacts revealed thus far (Ehrenfeld 2010; Vilà et al.
201 2011; Simberloff et al. 2013), few types of ecosystems and invaders have been studied relative to
202 those that exist (Crystal-Ornelas and Lockwood 2020). It is likely that an enormous number of
203 non-native species have affected individual performance, population sizes, and community
204 structure, though direct and indirect effects on native species (e.g. via competition, herbivory,
205 predation, hybridization, and as diseases or their vectors), or by changing the physical, chemical
206 or structural characteristics of the environment (Blackburn et al. 2014; IUCN 2020), in ways that
207 have not been documented (Carlton 2009; Simberloff 2011). Ecosystem-level impacts must
208 remain a major focus, with researchers taking advantage of available technological tools (e.g.,
209 Asner et al. 2008). Further, research on how biodiversity loss affects ecosystem functioning must
210 be evaluated alongside effects of non-native species additions, to better understand how human-
211 driven species change will affect ecosystem processes across scales. For example, given that
212 community composition can influence biosphere-atmosphere exchange of greenhouse gases
213 (Metcalf et al. 2011), how non-native species influence processes that underpin this exchange
214 relative to native species extirpations can have significant, currently unrecognized consequences
215 for climate change.
216

217 **1.2. New and future challenges**

218 *1.2.1. Impacts of interventions for restoring ecosystem function*

219 Co-occurring environmental stressors are increasing pressures to use non-native species
220 for restoring ecosystem functions eroded by native species loss (Mascaro et al. 2012; Castro-
221 Díez et al. 2019). The notion of restoring ecosystems that have lost important species by
222 substituting non-native species to perform key functions traces back at least to the 1980s
223 (Atkinson 1988) and has seen growing interest in recent years (Seddon et al. 2014a; Galetti et al.
224 2017; Pires 2017). Of particular interest are proposals and ongoing projects to establish species
225 to replace seed dispersers of plant species that have lost their ancestral native mutualisms
226 (Seddon et al. 2014a; Galetti et al. 2017), and large herbivores and carnivores to fulfill lost
227 trophic linkages (Svenning et al. 2016). These efforts are often listed under the rubric of
228 *rewilding* (Lorimer et al. 2015; Svenning et al. 2016). Calls for active rewilding to restore
229 ecological processes (Perino et al. 2019) have primarily focused on the reintroduction of native
230 species, but some practitioners have advocated a ‘flexible’ approach to restoration that entails
231 using non-native species (Ewel and Putz 2004; but see Sotka and Byers 2019) as well as the
232 reintroduction of species into parts of their native range from which they have been absent for
233 various lengths of time.

234 As with translocation to accommodate climate change (see section 2.2.3), proposals for
235 translocations to restore ecosystem functions (e.g., IUCN 2013; Aslan et al. 2014) have been the
236 subject of substantial discussion of potential risks and benefits (Nogués-Bravo et al. 2016;
237 Rubenstein and Rubenstein 2016; Fernández et al. 2017; Pettorelli et al. 2018; Perino et al.
238 2019). Lunt et al. (2013) have compared possible risks and benefits of translocations to restore
239 ecosystem functions and translocations to address climate change, pointing to the possibility of

240 addressing both goals simultaneously. To employ proposed decision tools and adhere to the
241 International Union for Conservation of Nature (IUCN) guidelines, both advocates and critics
242 increasingly agree that progress is required on more accurate risk assessments and on
243 characterization, categorization, and quantification of the environmental impacts of
244 translocations (Jeschke et al. 2014), as has occurred with the EICAT framework (Blackburn et al.
245 2014; Hawkins et al. 2015; Evans et al. 2016), which has been adopted as an IUCN standard
246 (IUCN 2020), and similarly for socioeconomic impacts, as has begun under the SEICAT
247 framework (Bacher et al. 2018).

248 Conversely, other efforts to conserve native species or restore ecosystems involve non-
249 native species eradication. Such interventions should be preceded by a predictive risk
250 assessment of the indirect effects of invader removal (Bergstrom et al. 2009; Caut et al. 2009;
251 Ruscoe et al. 2011; Lindenmayer et al. 2017) and the legacy effects of invasion (Corbin and
252 D'Antonio 2012; Grove et al. 2015; Reynolds et al. 2017; Pickett et al. 2019). Eradication has
253 had demonstrable benefits to biodiversity (Baider and Florens 2011; Monks et al. 2014; Jones et
254 al. 2016), but targeting the removal of a single invasive species within an ecosystem that
255 contains several non-native species can be counterproductive. A predictive framework must
256 consider the topology of species interactions, both trophic and non-trophic, to determine when
257 single-species management may lead to unintended consequences (Glen et al. 2013; Ballari et al.
258 2016; Hui and Richardson 2019).

259

260 *1.2.2. Burgeoning novel organisms*

261 Escalating risks are associated with the intentional and unintentional release of novel
262 organisms (those with no analogue in the natural environment) through biotechnological

263 advances that create transgenic or genetically engineered organisms. For example, some
264 proposals for rewilding entail *de-extinction* – i.e., creation of various sorts of proxies of extinct
265 species for release to the wild. Versions of de-extinction are expected to become increasingly
266 feasible (Stokstad 2015; Shapiro 2017). The process involves either backbreeding (Stokstad
267 2015) or the reconstruction of the genome of an extinct species from recovered strands of DNA,
268 which can then be used either to modify or to replace the genome of a suitable living relative or
269 to genetically engineer embryos that can be implanted in a compatible host. Some
270 conservationists will advocate for such proxy species to be reintroduced to a suitable former
271 geographic environment (Seddon et al. 2014b), and perceived ecosystem management benefits
272 may arise from doing so (Church 2013). Environmental differences between contemporary and
273 historic habitats (Peers et al. 2016) might encourage further genetic manipulation to create better
274 adapted species. Depending on the length of time the proxy species has been extinct and the
275 method used to produce the proxy, introducing such entities to the wild is tantamount to
276 introducing a non-native species (IUCN 2013; IUCN/SSC 2016; Genovesi and Simberloff 2020),
277 an action that in the absence of predictive knowledge increases the likelihood of unintended
278 ecological consequences.

279 Advances in biotechnology will also facilitate the creation of self-replicating synthetic
280 cells designed for novel tasks such as contaminant remediation, carbon sequestration, and the
281 production of biofuels (Menetrez 2012; Azad et al. 2014; Singh et al. 2016; Dvorak et al. 2017).
282 As synthetic and transgenic organisms will contain combinations of ecological traits that are
283 unlikely to be encountered naturally, recipient communities will be evolutionarily naïve to these
284 organisms and could be predisposed to being altered by them (Saul and Jeschke 2015). Such
285 impacts could be subtle but far-reaching, as has been demonstrated for macroscopic transgenic

286 species (Post and Parry 2011; Vacher et al. 2011; Oke et al. 2013). Among the larger risks is the
287 capacity for such organisms to evolve in the wild and to exchange genes with other organisms
288 (Dana et al. 2012). Given the exponential growth of molecular technology, the rate of
289 development of such organisms could outpace progress in developing effective risk assessments
290 of their ecological effects. This issue emphasizes a need for greater integration of evolutionary
291 and microbial biology into invasion science, and for developing impact theory and risk
292 assessment methods that explicitly consider evolutionary change in both the invader and
293 interacting species.

294

295 **1.3. The way forward: a theoretical framework and tools for impact management**

296 *1.3.1. Developing and expanding a theoretical framework of impact*

297 To meet societal demands, invasion science must continue to build a body of theory for
298 understanding and predicting impacts from the level of populations to ecosystems (Ricciardi et
299 al. 2013; Blackburn et al. 2014; Bacher et al. 2018). Progress toward this goal requires that
300 hypotheses explicitly integrate abiotic and biotic context-dependencies, including biotic and
301 abiotic drivers of spatiotemporal variation in impact. This integration parallels and perhaps can
302 be informed by studies of how species loss affects ecosystem functioning in different
303 environmental contexts (Ratcliffe et al. 2017; Baert et al. 2018; Kardol et al. 2018). One example
304 of an integrative hypothesis is Environmental Matching (Ricciardi et al. 2013), which posits that
305 the *per capita* effects of an invader vary along environmental gradients such that they are
306 maximal where abiotic conditions more closely match the physiological optimum of the invader
307 (Kestrup and Ricciardi 2009; Iacarella et al. 2015a; Iacarella and Ricciardi 2015).

308 A second example that integrates context-dependence is the Ecological (or Functional)
309 Distinctiveness Hypothesis (Diamond and Case 1986; Vitousek 1990; Ricciardi and Atkinson
310 2004), which predicts that impact is most severe in communities missing species functionally
311 similar to the invader. This hypothesis is derived from two observed patterns with strong
312 empirical support. One such pattern is that a community's lack of eco-evolutionary experience,
313 or ecological naïveté, determines its vulnerability to non-native consumers, parasites, pathogens,
314 and competitors (Sih et al. 2010; Saul and Jeschke 2015; Davis et al. 2019; Nunes et al. 2019;
315 Anton et al. 2020). The second empirically supported pattern is that the largest community-level
316 and ecosystem-level impacts are generated by invaders that use key resources differently or more
317 efficiently than natives do and that can alter disturbance regimes, habitat structure, or food web
318 configurations (Vitousek 1990; Funk and Vitousek 2007; Morrison and Hay 2011). Given that
319 more closely related species tend to be ecologically similar (Burns and Strauss 2011), it follows
320 that phylogenetic distance, or simple taxonomic relatedness, is a proxy for functional
321 distinctiveness. Thus, an allied hypothesis predicts that invaders representing novel taxa, once
322 established in the community, are more likely to affect native populations negatively than
323 invaders that are taxonomically similar to natives in the recipient community (Ricciardi and
324 Atkinson 2004; Strauss et al. 2006; Davis et al. 2019). Despite longstanding recognition of eco-
325 evolutionary experience as a driver of impact, most risk assessments do not consider
326 evolutionary context. The consequences of the contemporary evolution of non-native species
327 (e.g., Bertelsmeier and Keller 2018), and the effects of invaders on the evolution of native
328 species, are underexploited but promising areas of research (Saul and Jeschke 2015; van Kleunen
329 et al. 2018) that point to the importance of integrating evolutionary biology in ways that enhance
330 the predictive power of invasion science.

331 Several distinct, and over a dozen overlapping, hypotheses explain invader impact
332 (Ricciardi et al. 2013), and additional hypotheses addressing invasion establishment success
333 could potentially be extended to understanding impact (Catford et al. 2009; Jeschke and Heger
334 2018). These hypotheses could be organized into a coherent body of impact theory by
335 eliminating redundancies and identifying commonalities (e.g., through consensus mapping of
336 hypothesis networks; Enders et al. 2020). We can envision a general predictive framework built
337 upon multiple axes that consider, among other things, 1) abiotic and biotic environmental
338 context; 2) functional distinctiveness between native and non-native species; and 3) time-since-
339 invasion (Figure 2). The generality of hypotheses needs to be tested within various ecological
340 and evolutionary contexts using, for example, spatially distributed experiments such as those
341 employed to examine plant responses to nutrient enrichment and exclosure of mammalian
342 herbivores (Borer et al. 2014). Experimental and survey designs that incorporate eco-
343 evolutionary context have rarely been applied to the study of non-native species (but see Wardle
344 et al. 2001; Colautti et al. 2014; Grimm et al. 2020). To address this gap, we advocate
345 comparisons of conspecific populations across invaded and native ranges, recognizing that
346 invasions and impact outcomes are population-level phenomena. Such experiments could be
347 coordinated by collaborative global networks (Packer et al. 2017), which are a potentially
348 powerful approach to understand the factors that govern large-scale variation in invader impact
349 across climatic gradients, disturbance gradients, biogeographic realms, and boundaries of
350 evolutionary significance.

351 Moreover, scientists would profit by looking to other areas of ecology and evolution,
352 disease biology, and the social sciences, for theory that could potentially explain many
353 components of impact and seeking to integrate these approaches into invasion science. Several

354 classical ecological hypotheses, metrics, and concepts that have been tested in various contexts
355 relevant to invasions (e.g., theories addressing biological control, island biogeography, metabolic
356 scaling, resource utilization, competition) have arguably been underexploited by invasion
357 scientists. Experimental approaches that have sought to incorporate principles of trophic ecology
358 have revealed important patterns (Dick et al. 2017a, b; Cuthbert et al. 2018, 2020). For example,
359 prey switching (frequency-dependent predation) is a classical concept that has until recently been
360 virtually ignored by invasion science (Cuthbert et al. 2018, 2019). In recent years, the classical
361 functional response – the relationship between *per capita* consumption and resource density
362 (Solomon 1949; Holling 1959) – has been adapted and applied to forecasting and explaining
363 non-native species impacts through multispecies comparisons (Dick et al. 2017a, b; Dickey et al.
364 2018; Faria et al. 2019). The rationale for exploring these experimental approaches is that
365 invasion success and impact are often mediated by resource acquisition, a concept at the
366 foundation of many hypotheses in invasion science (Catford et al. 2009; Ricciardi et al. 2013;
367 Jeschke and Heger 2018) and that is relevant for both animals and plants (Rossiter-Racher et al.
368 2009; Ehrenfeld 2010). Indeed, several high-impact invaders have been found to be more
369 efficient at using limiting resources than their native and non-invasive counterparts (Rehage et al.
370 2005; Funk and Vitousek 2007; Morrison and Hay 2011; Dick et al. 2017a; DeRoy et al. 2020).

371 Broadening analyses to a more comprehensive community context could also help predict
372 impacts in different environmental contexts (Smith-Ramesh 2017). An underexploited approach
373 is to treat invaded communities as complex adaptive networks (Lurgi et al. 2014; Valdovinos et
374 al. 2018; Hui and Richardson 2019). Predictive information could potentially be gained from
375 modeling the dynamic responses of an ecological network, after developing appropriate metrics

376 of interaction strength, and thus identify resident species that are either facilitated or suppressed
377 by the invasion (Hui and Richardson 2019).

378

379 *1.3.2. Toward more comprehensive quantifications of invader impact*

380 There is growing interest in quantifying impacts beyond traditional ecological and
381 economic measures by using an ecosystem services framework that can capture information on
382 provisioning (e.g., food, timber, fuel), regulating (e.g., climate, floods, nutrient cycling) and
383 cultural services (Perrings 2010; Simberloff et al. 2013). For example, in highly-degraded
384 ecosystems some established non-native species may offer beneficial services to some
385 stakeholders (McLaughlan and Aldridge 2013), although any benefits of local cultivation of such
386 species must be weighed carefully against risks of further spread. Such accounting would also
387 need to consider negative impacts, which are diverse and substantive, on ecosystem services
388 (e.g., Walsh et al. 2016; Vilà and Hulme 2017; Milanović et al. 2020). However, at present we
389 know remarkably little about how even the most high-profile non-native species affect ecosystem
390 services (Vilà et al. 2010; McLaughlan et al. 2014), a problem related to the challenges of
391 evaluating ecosystem-level impacts (Simberloff 2011; Ricciardi et al. 2013). More reliable
392 quantification of potential ecosystem services of invasive species, coupled with a deeper
393 understanding of context-dependencies, would allow a more informed and comprehensive
394 impact assessment. To this end, the Millennium Ecosystem Assessment and, more recently, the
395 Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES), which have
396 examined how humans have altered ecosystems and these alterations have affected ecosystem
397 services and human well-being (Millennium Ecosystem Assessment 2005; Díaz et al. 2019),
398 could provide a suitable framework for developing protocols for risk assessment, perhaps

399 informed by the EICAT and SEICAT classification schemes (Hawkins et al. 2015; Bacher et al.
400 2018).

401 Comprehensive impact quantification is challenged by knowledge gaps that may render
402 risk assessments incomplete or misleading (Kumschick et al. 2015). One major gap is predictive
403 knowledge of the role of species traits, combinations of traits, and trait-environment interactions
404 in impacts, particularly at the ecosystem level. It is not clear under what situations the same
405 species traits that confer an ecosystem service can also damage an existing ecosystem service
406 (Vilà and Hulme 2017) or contribute to an ‘ecosystem disservice’ – properties or functions that
407 are disadvantageous to humans (Milanović et al. 2020). Another major context-dependency that
408 could distort risk assessment of a given invader is the presence of other invaders. Predictions, as
409 well as post-hoc assessments, are potentially hampered by synergistic or antagonistic interactions
410 between invaders, including those that can contribute to invasional meltdown – in which one
411 invader facilitates another, leading to compounded impacts and potentially self-reinforcing
412 effects (Simberloff and Von Holle 1999; Ricciardi 2001; Green et al. 2011). Disentangling the
413 influence of various species involved in meltdowns requires detailed experimental planning (e.g.,
414 Braga et al. 2020), whereas invader interactions in multiple invaded ecosystems are generally
415 poorly studied (Kuebbing et al. 2013). It therefore seems likely that most synergistic effects go
416 unrecognized. Even where interactive effects do not occur, the cumulative effects of burgeoning
417 numbers of low-impact invaders on ecosystems have been virtually ignored. Approaches toward
418 quantifying and assessing the effects of multiple environmental stressors (Boyd et al. 2018;
419 Hodgson and Halpern 2018; Hodgson et al. 2019) could potentially be adapted for multiple
420 invading species and, furthermore, might be enhanced by efforts to collate experimentally-
421 validated invader interactions within global databases.

422

423 **2. Addressing the challenge of global environmental change in invasion science**

424 The second overarching issue is how invasion science can adapt to the onslaught of
425 global environmental changes presently altering the rates, dynamics, and impacts of invasions
426 through myriad drivers including climate change, overharvesting, extinction, pollution,
427 landscape transformation, and shifting trade patterns. Ecosystems are likely to become more
428 susceptible to invasions as these drivers degrade and modify food webs. For some native species,
429 global changes create physiologically intolerable or suboptimal conditions that lower relative
430 fitness (Catford et al. 2020) or provoke range shifts, further altering community composition and
431 susceptibility to invader impacts (Gallardo and Aldridge 2013; Wallingford et al. 2020).

432 Environmental change often affects native and non-native species differentially, modifying their
433 interactions and selection pressures through shifting abiotic and biotic ecosystem conditions
434 (Xiao et al. 2016; Meyerson et al. 2020; Stern and Lee 2020). This issue is well recognized and
435 has been widely investigated for several years, yet the need for research and management
436 solutions through the lens of invasion science is ongoing and increasing. Invasion science must
437 continue to develop an understanding of key issues regarding global environmental change
438 including interactions between invasions and other environmental stressors, climate adaptation
439 and mitigation strategies, and evaluating and managing species range shifts and translocations. In
440 this section, we primarily focus on climate change (Figure 3) but note that many other forms of
441 human-induced environmental change facilitate invasions and the relative dominance of non-
442 native species (Catford et al. 2014; Seabloom et al. 2015; Liu et al. 2017; Essl et al. 2019).

443

444 **2.1. Ecological synergies between invasions and climate change**

445 *2.1.1. Non-native species performance*

446 Species distributions worldwide are mostly determined by climate, tectonic movements,
447 and orographic barriers (Ficetola et al. 2017). Climate change will therefore have a major impact
448 on species range and distributions irrespective of whether species are native or non-native to a
449 particular region. However, differences in the magnitude of potential range shifts predicted for
450 non-native and native species will be determined by differences in their biology, such as
451 physiological tolerances and dispersal potential (Essl et al. 2019). The last decade has
452 accordingly seen major efforts to investigate the role of climate change in the introduction,
453 establishment, spread, and impact of non-native species (Hulme 2017).

454 Various meta-analyses have shown that non-native species often outperform and adjust
455 better than native species to a rapidly changing climate (Sorte et al. 2013; Oduor et al. 2016; Liu
456 et al. 2017). For example, hotter, drier environmental conditions enable non-native Asian tiger
457 mosquitoes to outcompete native tree-hole mosquitoes in the United States (Smith et al. 2015),
458 Eastern mosquitofish (*Gambusia holbrooki*) persist more successfully than native fish species in
459 France (Cucherousset et al. 2007), and non-native Monterey pine (*Pinus radiata*) to grow faster
460 than native conifers in Spain (Godoy et al. 2011). Warmer temperatures in freshwater
461 ecosystems will favor non-native species as these frequently have a greater heat tolerance than
462 related native species (Bates et al. 2013); similarly, in the Mediterranean Sea, increases in
463 temperature have facilitated the establishment of non-native tropical species (Raitsos et al. 2010).

464 A key element of climate change is an increase in the frequency and magnitude of
465 extreme climatic events, which can have greater effects on invasion than changes in average
466 conditions (Sheppard et al. 2012). Strong winds, floods, large waves, and storm surges can
467 transport organisms into new regions (Diez et al. 2012), as discussed below. Critically, extreme

468 climatic events like heat waves, fires, severe storms, droughts, and floods act as major
469 disturbances and will invariably destroy and damage resident native biota, reducing the uptake of
470 resources, and can also increase resource supply (Catford and Jones 2019). Such disturbances are
471 known to facilitate invasion (Davis et al. 2000), because many invasive species can take
472 advantage of fluctuations in resource availability caused by disturbances (Catford et al. 2012;
473 Singh et al. 2018). For example, European *Bromus* grasses that are highly invasive in North
474 America can exploit available soil moisture more efficiently and thus recover more rapidly than
475 native vegetation after drought (Harris 1967), enabling them to invade areas formerly dominated
476 by native woody species (Kane et al. 2011). Similarly, a non-native freshwater phytoplankton
477 species was able to invade and establish in a reservoir following the combined disturbance events
478 of macrophyte removal and extreme drought (Crossetti et al. 2019).

479

480 *2.1.2. Non-native species range shifts*

481 Shifts in temperature and rainfall patterns attributed to climate change can increase the
482 probability of establishment of non-native species, which were previously constrained by climate
483 (Walther et al. 2009; Hulme 2017) or climate-mediated interactions with native biota (Catford et
484 al. 2020). Increasing evidence indicates that non-native species tend to respond faster than native
485 species to climate change, with spread rates an order of magnitude higher than the velocity of
486 climate change (Hulme 2012). For example, non-native plants have expanded upwards in the
487 European Alps twice as fast as native species in response to warming (Dainese et al. 2017).
488 Nevertheless, climate change can lead to both increases (Kriticos et al. 2003; Barbet-Massin et
489 al. 2013; Gilioli et al. 2014) and declines (Bradley et al. 2009; Bellard et al. 2013; Xu et al. 2014)
490 in the geographical range of non-native species. A general finding is that, as a result of climate

491 change, the distribution range of non-native invertebrates and pathogens will expand, but range
492 contractions are mostly expected for non-native plants and vertebrates (Bellard et al. 2018). For
493 example, by the end of this century the suitable area worldwide for the red imported fire ant
494 (*Solenopsis invicta*) is predicted to be 21% greater (Morrison et al. 2014), whereas for the velvet
495 tree (*Miconia calvescens*) it is predicted that suitable habitat will be reduced in both its native
496 and introduced ranges (González-Muñoz et al. 2015). However, trends may differ between
497 terrestrial and aquatic environments. For instance, the warming of North American lakes is likely
498 to increase thermal suitability for southern species of fishes that could expand their distribution
499 poleward into non-native regions, potentially as far as the Arctic (Sharma et al. 2007; Della
500 Venezia et al. 2018).

501 Besides overall change in temperature and precipitation, extreme climatic events can also
502 help spread non-native species by overcoming dispersal barriers (Diez et al. 2012). For instance,
503 hurricanes promoted dispersal of non-native cactus moth (*Cactoblastis cactorum*) across the
504 Caribbean and into Mexico where it threatens native *Opuntia* species (Andraca-Gómez et al.
505 2015). Hurricane frequency was also positively correlated with the expansion of the non-native
506 grass *Phragmites australis* across wetlands along the Gulf Coasts of the USA (Bhattarai and
507 Cronin 2014). Likewise, flood events can increase pool connectivity and provide non-native
508 freshwater species access to newly inundated areas (Vilizzi et al. 2014). For example, floods
509 enabled the escape of cultured black carp (*Mylopharyngodon piceus*) in the Missouri River, US
510 (Nico et al. 2005), and tilapia cichlids in southeast Asia (Canónico et al. 2005) and have
511 facilitated the spread of zebra mussels (*Dreissena polymorpha*) in the Mississippi River
512 catchment (Tucker 1996). Nevertheless, the natural variability of climate makes it difficult to

513 attach high levels of confidence to some of the predicted changes, particularly those associated
514 with extreme weather events (Bellard et al. 2013).

515

516 2.1.3. *Novel interactions and per capita impacts*

517 Climate change will, in many cases, increase the introduction rate, establishment
518 probability, and spread rate of non-native species (Bellard et al. 2013), while simultaneously
519 facilitating extensive range shifts of native species (Inderjit et al. 2017; Pecl et al. 2017; Essl et
520 al. 2019), leading to novel ecological interactions and increased impacts. Range shifts are
521 expected to contribute to widespread biotic homogenization (where more species are shared
522 among communities) in some regions and the formation of novel communities in others (García-
523 Molinos et al. 2015). Diverse novel biotic interactions and assemblages will arise from divergent
524 responses of species and populations to climate change (Blois et al. 2013; Pecl et al. 2017). As
525 discussed previously, new biotic interactions often result in high impacts when resident species
526 have not co-evolved with newly arrived species (Ricciardi and Atkinson 2004; Cox and Lima
527 2006; Saul and Jeschke 2015). In some cases, range shifts of native species can cause impacts
528 similar to those involving non-native species (Sorte et al. 2013; Inderjit et al. 2017), although
529 impacts will be tempered by the eco-evolutionary experience of the resident species (*sensu* Saul
530 and Jeschke 2015). Few studies have addressed range shifts of native and non-native species as a
531 joint issue (Gallardo and Aldridge 2013; Sorte et al. 2013; Dainese et al. 2017; Inderjit et al.
532 2017; Singh et al. 2018).

533 While many studies have linked climate change to the spread of invasive species
534 (detailed above), the role of environmental factors in determining ecological impacts is
535 understudied (Dickey et al. 2020). Climatic conditions that shift towards the physiological

536 optimum of a non-native species could promote increased feeding rates, growth, or reproduction
537 that amplifies its competitive or predatory effects (Hellmann et al. 2008; Iacarella et al. 2015a).
538 For example, an invasive bryozoan is expected to have enhanced growth rates at warmer
539 temperatures in the Northwest Atlantic, with greater modeled impacts on kelp beds under future
540 climate conditions (Denley et al. 2019). Similarly, higher growth rates enable an invasive plant
541 to outcompete a native plant in China along higher latitudes in the field and at warmer
542 experimental temperatures (Wu et al. 2017). Predation rates of non-native species may also
543 increase when warming temperatures are within the physiological optima of the invader
544 (Iacarella et al. 2015a). For instance, the predatory response of an invasive freshwater amphipod
545 increases when exposed to elevated temperatures and infected by a common parasite (Lavery et
546 al. 2017). Given that non-native species are expected often to outperform native species in
547 response to environmental change, as discussed above, their competitive and predatory impacts
548 will likely also increase under these circumstances. A method has recently been developed that
549 incorporates the *per capita* and abundance effects of non-native species under altered variables
550 such as temperature, oxygen, salinity, and indeed any other variable in isolation or combination
551 (Dickey et al. 2020). This predictive method crucially also factors in the climate response of the
552 affected species (e.g., native prey), such that overall impact is holistically predictable. This
553 method is in its infancy and ground-truthing is now limited only by data (Dickey et al. 2020).

554

555 *2.1.4. Changes to ecosystem services and human well-being*

556 Research on the interaction between invasions and global environmental change is
557 essential to identify effects on ecosystem services and human well-being (Dukes and Mooney
558 1999; Walther et al. 2009; Pecl et al. 2017; Vilà and Hulme 2017). Although tools such as

559 SEICAT (Bacher et al. 2018) and INSEAT ('INvasive Species Effects Assessment Tool';
560 Martinez-Cillero et al. 2019) have been developed to classify non-native species within a
561 framework of ecosystem services and human well-being, these tools rely on expert elicitation as
562 there are still surprisingly few quantitative data on the ecosystem services effects of even the
563 most prolific invasive species. This is, in part, owing to the context-dependent impacts of
564 invaders (see section 1) and because environmental change can alter the balance of positive and
565 negative effects (McLaughlan et al. 2014). For instance, disturbed river banks and roadsides in
566 Africa favor proliferation of the invasive tree, *Prosopis juliflora* (Shiferaw et al. 2019), which
567 increases local income from wood sales but reduces habitat suitable for livestock and results in
568 lower income from cattle sales (Linders et al. 2020). The predicted future effect of interactions
569 among climate, socioeconomic factors, and invasions on plant biodiversity hotspots constitutes
570 the greatest threat in emerging economies located in megadiverse regions of the Southern
571 Hemisphere (Seebens et al. 2015). Invasions and climate change also pose a combined threat to
572 native species in protected areas and thus seriously compromise conservation of biodiversity and
573 ecosystem services (Gallardo et al. 2017; Iacarella et al. 2020). Interactions between invasions
574 and climate change will also affect human health; for instance, climate change models predict an
575 increase in the life-cycle completion rate and extended periods suitable for development of the
576 invasive mosquito *Aedes aegypti*, a vector of arboviruses including dengue, zika, and yellow
577 fever, resulting in accelerated invasion in North America and China (Iwamura et al. 2020).

578 To investigate the effects of invasions on ecosystem services and human well-being,
579 models should integrate interactions among several components of global change, not only
580 climate change (Walther et al. 2009). Furthermore, studies should also explore these interactions
581 in productive systems such as managed forests, agriculture, and aquaculture (Thomson et al.

582 2010; Ziska and Dukes 2014; Liebhold et al. 2017). A major concern for these resource sectors is
583 that drought, warming, and elevated CO₂ will affect the performance of non-native species (i.e.,
584 pests, pathogens, and weeds) in complex and currently unpredictable ways. Research on their
585 impacts requires, for example, quantifying not only how altered environmental conditions
586 change weed and crop performance in isolation, but the magnitude of weed-crop competition on
587 crop damage (Ramesh et al. 2017).

588

589 **2.2. Human responses to climate change that favor non-native species**

590 *2.2.1. Changes to invasion pathways*

591 Global change is also altering invasion risk by promoting new commercial trading routes
592 and corridors. Shifting global economic forces (e.g., tariffs, manufacturing trends, recession,
593 regional conflicts, climatic disasters) determine trade volume and thus the frequency with which
594 aircraft or oceanic vessels travel between airports or seaports (Seebens et al. 2015). Such shifts
595 drive temporal rates of species introduction and the range of taxa that invade (Levine and
596 D'Antonio 2003; Hulme 2015; Bertelsmeier et al. 2018). For example, commercial shipping at
597 polar latitudes of North America and Eurasia is either planned or already occurring, providing
598 novel opportunities for introducing non-native species to Arctic waters (Miller and Ruiz 2014;
599 Chan et al. 2019). The Southern Ocean is likewise becoming increasingly vulnerable to species
600 introductions owing to increased propagule pressure from vessel traffic and reduced physical and
601 physiological barriers (Aronson et al. 2015; Hughes and Ashton 2017; Smith et al. 2017;
602 McCarthy et al. 2019; Cárdenas et al. 2020). Such human responses to climate change (Figure 3)
603 are altering the origins, taxonomic identity, and rate of introduction of non-native species in

604 terrestrial, freshwater, and marine habitats worldwide (Seebens et al. 2015; Early et al. 2016;
605 Della Venezia et al. 2018).

606

607 *2.2.2. Climate adaptation: planting non-native species and adding infrastructure*

608 As governments increasingly develop adaptive strategies to address climate change,
609 many of these strategies are likely to entail using non-native species. Proposed interventions
610 include initiatives to develop agricultural or aquacultural enterprises to deliver carbon-neutral
611 energy sources (e.g., macroalgae and plants for biofuels) using known invasive non-native
612 species (Barney and DiTomaso 2008). Pressure is also increasing to develop new varieties of
613 pasture species that can better cope with changing climates, such as drought-tolerant and disease-
614 resistant species, many of which are non-native in the countries in which they are sold and
615 planted (Driscoll et al. 2014). Increased development of green roofs, vertical gardens, and water-
616 saving horticulture to mitigate effects of climate change (Perini and Rosasco 2016) carry the risk
617 of introducing non-native species by promoting drought-tolerant plants or breeding drought-
618 resistant varieties, cultivars, or hybrids. Similarly, many large-scale tree-planting programs have
619 not led to the replenishment of degraded forests with native tree species, but rather to
620 afforestation of non-forest land, including biodiverse grasslands, with monocultures of non-native
621 trees. Such efforts include massive tree-planting campaigns using non-native trees with the aim
622 of mitigating the impacts of climate change and for other poverty alleviation (Brundu et al.
623 2020). Such plantings might not help offset greenhouse gas emissions as much as expected,
624 owing to unforeseen fluxes and complex system dynamics (Covey et al. 2012; Luysaert et al.
625 2018; Popkin 2019). Indeed, inappropriate afforestation, especially in naturally treeless areas,
626 can have serious consequences for sustainable development, biodiversity conservation, and

627 ecosystem functioning (reviewed in Brundu et al. 2020). Furthermore, many species used in such
628 programs are highly invasive, which means that their impacts extend beyond areas identified for
629 afforestation (Brundu and Richardson 2016; Brundu et al. 2020).

630 Besides directly introducing species to sustain economic activities or to mitigate
631 emissions, governments at all levels are responding to environmental change by developing new
632 infrastructure. Strategies to combat sea-level rise have largely been addressed through
633 engineered solutions (armoring, raising road-beds, flood control structures). Each of these
634 adaptation strategies presents an opportunity for existing non-native species to expand their
635 range or impact and can create new suitable habitat for non-native species that arrive via ballast,
636 hull-fouling, or the marine aquarium trade (Bulleri and Chapman 2010). Offshore wind farms
637 also provide novel fouling habitats and ‘stepping stones’ for invasions (Adams et al. 2014; De
638 Mesel et al. 2015). Similarly, frequent droughts lead to efforts to provide secure water sources to
639 urban populations, including construction of dams, canals, and other water-diverting mechanisms
640 that can spread non-native species (Strayer 2010; Zhan et al. 2015; Gallardo and Aldridge 2018).
641 However, infrastructure developments can be designed to reduce their suitability as novel
642 habitats or invasion routes for invasions by non-native species, by minimizing environmental
643 disturbances or emulating natural habitats (Dafforn et al. 2015).

644

645 2.2.3. *Species translocations for conservation*

646 Conservation scientists have introduced species to locations outside their native range for
647 three main reasons: (1) to avoid extinction caused by an introduced species, often an introduced
648 predator; (2) to restore an ecological function (as detailed in section 1.2.1); or (3) to allow
649 species' ranges to keep up with climate change (Corlett 2016). Introductions to accommodate

650 global climate change have increasingly attracted attention. As early as 1985, conservationists
651 recognized that the climate of current species ranges will change so that locations with climate
652 similar to that of today may be distant or separated by inhospitable habitat; they proposed several
653 measures including direct human assistance in the form of translocation to suitable habitat
654 unoccupied by the species of interest when adequate autonomous movement seemed unlikely
655 (Peters and Darling 1985; Peters 1988; Davis 1989; Peters 1992). This proposal received little
656 interest for the next decade; a review of possible management responses to climate change listed
657 only 13 mentions of translocations (Heller and Zavaleta 2009). None of these acknowledged
658 possible negative effects of translocation. However, translocations had long been conducted in
659 the name of conservation, notably of species threatened by introduced predators (Seddon et al.
660 2012, 2014a). For instance, endemic New Zealand birds threatened by non-native rats and
661 mustelids had been translocated to predator-free islands since 1894, with many well-publicized
662 projects (Clout and Craig 1995; Seddon et al. 2012); occasional concern about such efforts had
663 been expressed on the grounds of potential unanticipated ecological impacts (e.g., IUCN 1987;
664 Conant 1988; Atkinson 1990; Craig and Veitch 1990; Towns et al. 1990).

665 Translocation as a management response to climate change began to gain substantial
666 attention with papers by McLachlan et al. (2007) and Hunter (2007), both raising the issue that
667 this constitutes introducing a non-native species, which in turn might lead to a damaging
668 invasion. Hoegh-Guldberg et al. (2008) produced the first decision tree for application of
669 potential translocations in response to climate change, but they, and Hunter (2007), suggested
670 that intercontinental introductions have proven far more likely to be damaging, whereas
671 proposed translocations for climate change would be more restricted. A broader and more
672 detailed criticism of climate change-motivated translocation (Ricciardi and Simberloff 2009a),

673 based on the possibility of non-target impacts, elicited an exchange with several respondents
674 (Ricciardi and Simberloff 2009b) and signaled a shift in the dialogue, with much more attention
675 paid to the possibility of unintended consequences by virtue of introducing new species. As such,
676 Richardson et al. (2009) expanded the decision-tree approach into a heuristic decision tool with
677 detailed considerations of both ecological and socioeconomic consequences of translocation or
678 failure to translocate; the difficulty lies in estimating the probability of various potential
679 outcomes (e.g., decline or loss of ecological functions in the recipient region) and quantifying
680 other risks, both ecological and socioeconomic, to inform comparisons and decisions. In the last
681 decade, translocation has received increasingly nuanced consideration of the relative risks and
682 virtues owing to the rapidly growing understanding of the enormous conservation challenge
683 posed by the scope and imminence of climate change and its likely effect on species ranges
684 (Hewitt et al. 2011; Thomas 2011; Schwartz and Martin 2013; Williams and Dumroese 2013;
685 Ricciardi and Simberloff 2014; Maier and Simberloff 2016; Simler et al. 2018).

686 The lines between translocation and biological invasion are becoming increasingly
687 blurred. Both events involve species expanding beyond their historical biogeographic ranges,
688 leading some authors to suggest that they differ only in public perception and value (Hoffmann
689 and Courchamp 2016; but see Ricciardi 2007; Wilson et al. 2016). In addition, views on how to
690 deal with the spectrum from ‘desirable’ self-migrating species, to translocations undertaken for
691 conservation (desirable to some, undesirable to others), to generally ‘undesirable’ biological
692 invasions, are yet to be reconciled. Further, determination of ‘non-native’, as defined by lack of
693 co-evolution with the invaded community (Ricciardi 2012), and ‘desirable’ or ‘undesirable’, as
694 defined by valuations of impact (Jeschke et al. 2014), will become increasingly challenging as
695 we seek to determine what to protect or manage in a shifting mosaic of species assemblages

696 (Gilroy et al. 2017; Hill and Hadly 2018). The current framework for managing non-native
697 species could yield protection of conservation-based translocated species despite potentially high
698 impacts, compared to management and mitigation of high-impact species that spread via self-
699 directed or direct, but accidental movement. Robust protocols for considering the entire range of
700 possible impacts of facilitated range shifts, as well as those of self-migrating species, must be
701 developed and integrated into policies and legislation with the engagement of stakeholders.

702

703 **2.3. Government responses and global efforts**

704 The global nature of biological invasions and their interactions with environmental
705 change can strain the capabilities of governments to anticipate and respond to invasions now and
706 into the future. As discussed in detail above, the ecology of invasions under climate change is
707 complicated. The directed asymmetrical movement of certain species poleward (Winter et al.
708 2014), and to higher elevations (Pyšek et al. 2011; Dainese et al. 2017), can point to systems
709 requiring early-detection monitoring or intervention. On the other hand, the effects of climate
710 change could play out neatly along latitudinal or altitudinal gradients (Hanberry and Hansen
711 2015). A key unknown is the relative importance of introduction enhancement (e.g., colonization
712 pressure, propagule pressure) from changing trade patterns versus the influence of climate
713 change factors in facilitating species' range changes. Policies that address invasions could also
714 be complicated by seemingly competing interests, including those associated with the economy
715 and trade versus biodiversity and human health. Despite devastating new species invasions and
716 pleas for a comprehensive approach to biosecurity, some countries, such as the United States,
717 have even recently reduced coordinated federal leadership and investments to address invasions
718 (Meyerson et al. 2019; Simberloff et al. 2020). Current coordinated global efforts to document

719 invasions and impacts include the Global Register of Introduced and Invasive Species (GRIIS)
720 and an invasive species assessment by the IPBES. These substantial undertakings will
721 undoubtedly deepen our understanding of invasion trends, impacts, and management, but neither
722 will result in policies to prevent species introductions that participating nations are obliged to
723 adopt. Rather, it remains the role of national and local governments to identify, fund, implement,
724 and enforce policies to manage invasions under changing conditions and, where possible, to
725 coordinate with other nations.

726

727 **3. Resolving the Taxonomic Impediment**

728 **3.1. The enduring problem of taxonomic identification**

729 The third overarching issue is our capacity to distinguish non-native from native species
730 accurately. Scientific understanding of the processes that control the diversity, abundance,
731 distribution, and impacts of non-native species ultimately depends on the quality of taxonomic
732 data. The steady global erosion in training and expertise in systematics means that invasion
733 science often lacks the taxonomic support to accurately identify many taxonomic groups in
734 terrestrial, freshwater, and marine habitats (Godfray 2002; and below). While this phenomenon
735 exists across biomes and taxa, the largest gaps in taxonomic knowledge are associated with some
736 of the most abundant species, including microorganisms and microfauna. Arguments (such as
737 those of Costello et al. 2013) that the field of taxonomy is robust appear to be based on, among
738 other fallacies, a misinterpretation that authorship inflation on taxonomic papers equates to an
739 increasing number of taxonomists (Bebber et al. 2013; Daglio and Dawson 2019).

740 Molecular tools have made remarkable progress and offer great promise for illuminating
741 the overlooked scale of biodiversity in all habitats (Hebert et al. 2003; Dinca et al. 2011). The

742 application of modern sequencing techniques often reveals a vast array of unknown and often
743 cryptic species. Srivathsan et al. (2019) report that of 7,059 specimens of flies (Diptera, family
744 Phoridae) collected in a single Malaise trap in Uganda over an eight-week period, MinION
745 sequencing revealed more than 650 largely or entirely undescribed species, exceeding the total
746 number of phorid taxa described for the entire Afrotropical region. Only one of these 650
747 species, however, has to date been formally described, based on morphological characters, as a
748 new species. Molecular techniques combined with advanced culturing methods have revealed an
749 enormous diversity of microbial taxa. Metagenomic sequencing of samples from only 68 ocean
750 locations revealed over 35,000 microbial ‘species’ (Sunagawa et al. 2015). Locey and Lennon
751 (2016) predict that the Earth may support as many as a staggering 1 trillion (10^{12}) microbial
752 species.

753 Nevertheless, the use of molecular technologies to identify taxa to the species level by
754 genetic fingerprinting or ‘barcoding’ has often proven to be an insufficient and unreliable
755 response to the taxonomic impediment. The panacea that simply sequencing specimens and
756 trusting that matching those sequences to databases will produce a reliable identification has
757 proven not to compensate for the growing gap in taxonomic expertise. Two principal problems
758 hinder molecular identifications: (1) accurate and complete barcoding of taxa across the
759 taxonomic spectrum, and (2) accurate and complete reference databases against which taxonomic
760 assignments are made (Harris 2003).

761 These problems are hindering the compilation of inventories of non-native taxa, even in
762 conspicuous and well-studied groups such as Australian *Acacia* species (Magona et al. 2018).
763 Taxonomic biases may result from the markers used (Clarke et al. 2014), while many species for
764 which sequences are obtained have no authenticated database reference (Briski et al. 2016).

765 Further, all new sequence entries should (but do not) require that the sequenced taxon has been
766 identified by a taxonomic expert based upon morphological evidence. Thus, a substantial fraction
767 of the species in these databases can be misidentified, at times egregiously so, potentially
768 producing erroneous matches that cannot be detected by non-specialists (Figure 4). For example,
769 DNA barcoding sequence information is missing from either the Barcode of Life Database,
770 GenBank, or both, for 60% of the 88 insect species listed in the Global Invasive Species
771 Database; 41% of the 88 species could be misidentified as another species, owing to
772 discrepancies between sequences and species identity (Boykin et al. 2012).

773

774 **3.2. Taxonomic impediments lead to under-estimations of invasion**

775 Without changes to ensure the development of broad taxonomic expertise, invasion
776 science will continue to underestimate, often substantially, the number (and also, therefore, the
777 impacts) of non-native species across all habitats, regardless of the surveillance and detection
778 program (e.g., De Barro et al. 2011). For example, Carlton and Fowler (2018) recently estimated
779 that non-native species are under-reported globally for the majority of marine taxonomic groups,
780 owing to a lack of widely available taxonomic expertise. Conversely, what has been initially
781 viewed as an invasion by one widespread species is sometimes later discovered to be a group of
782 similar species, some or all of which are restricted to their native ranges (Darling and Carlton
783 2018). More broadly, the inability to detect what could be the most common new invasions (by
784 species and genotypes) across terrestrial, freshwater, and marine habitats undermines ecosystem
785 management and biodiversity assessment, and our capacity to detect changes in ecosystem
786 structure and function.

787 The deficit of taxonomic expertise associated with microorganisms is especially
788 worrying. In general, species richness and density of organisms are inversely related to size. Not
789 only do small-bodied creatures dominate the world, but the magnitude of non-native species
790 transfers is often greatest for small organisms, many of which have life histories that facilitate
791 colonization (e.g., asexual reproduction; resting stages) (Ruiz et al. 2000). While invasions of
792 microorganisms are increasingly recorded (Seebens et al. 2017), the extent of these invasions,
793 and their impacts, remain poorly described outside of forestry, agriculture, and aquaculture
794 (Desprez-Loustau et al. 2007; Lohan et al. 2020).

795 Several marine disease outbreaks (such as those in oysters, sea urchins, and fishes) have
796 been attributed to non-native pathogens. For example, MSX is an oyster disease caused by a
797 protozoan (*Haplosporidium nelsoni*) that is native to Asia but was detected on the Atlantic coast
798 of North America in 1957. The native eastern oyster (*Crassostrea virginica*) proved highly
799 susceptible to MSX, leaving local populations substantially depleted from Chesapeake Bay to
800 Nova Scotia (Bushek and Ford 2016). The same is true for terrestrial and freshwater habitats
801 where non-native pathogens cause diseases such as ash dieback, crayfish plague,
802 chytridiomycosis, and sudden oak death (Skerratt et al. 2007; Grunwald et al. 2012; Roy et al.
803 2017). Many of these non-native pathogens spill-over, colonizing native host species in the
804 invaded range, whereas non-native hosts may harbor native parasites that then spill-back to
805 native hosts (Roy and Handley 2012; Blackburn and Ewen 2017). Both effects complicate
806 parasite identification (Morand 2017). Given recent work on the role of microbial communities
807 in ecosystem processes (Worden et al. 2015) and their importance in microbiomes, host-parasite
808 interactions (Egan and Gardiner 2016), and plant mutualisms (Traveset and Richardson 2014),
809 the potential importance of microorganism invasions is enormous. Thus, evaluation of

810 microorganism biogeography is a high priority if we are to understand the full scope and impact
811 of invasions in all ecosystems.

812

813 **3.3. Lack of taxonomic expertise limits our ability to test and develop invasion theory**

814 The taxonomic impediment also impairs our ability to evaluate and understand the
815 spatiotemporal dynamics of invasions and their impacts. Much of the theory and current
816 knowledge of invasion science has arisen from syntheses and analyses of secondary data drawn
817 from regional checklists and distribution atlases of floras and faunas (van Kleunen et al. 2015,
818 2019; Dyer et al. 2017; Pyšek et al. 2017). However, such checklists and databases can be
819 seriously compromised by the quality of species identifications (McGeoch et al. 2012).

820 Identifying plant hybrids, in particular, requires professional taxonomic expertise and is crucial
821 for management, given that hybridization often facilitates establishment (Yamaguchi et al. 2019)
822 and stimulates invasiveness, where the new taxon is more vigorous than either parent (Ellstrand
823 and Schierenbeck 2000; Vilà et al. 2000). An example is provided by *Fallopia taxa* (knotweeds)
824 in the Czech Republic, for which redetermination of plants in the field revealed
825 misidentifications for up to 16% of the records reported in the literature or deposited in herbaria
826 for *Fallopia japonica* and *F. sachalinensis*, and 20% of records of the hybrid *F. × bohemica*,
827 (Pyšek et al. 2001). Only after the complicated patterns of increased ploidy variation and rapid
828 post-invasion evolution in the invaded range of Europe were disentangled was it possible to
829 conduct ecological studies that revealed the elevated invasiveness of the hybrid compared to that
830 of the parents (Pyšek et al. 2003).

831 Other taxonomic challenges in plant invasion research include apomictic groups,
832 karyologically variable complexes, genera with specific reproduction systems, or those for which

833 horticulturalists have bred many cultivars and varieties (e.g., *Centaurea*, *Cotoneaster*,
834 *Heracleum*, *Lupinus*, *Myriophyllum*, *Phragmites*, *Rhododendron*, *Rubus*, *Spartina*, and *Tamarix*).
835 Some of those taxa are among the most widespread plant invaders, and ecological studies aimed
836 at understanding their invasion have profited substantially from detailed taxonomic knowledge
837 (Pyšek et al. 2013).

838

839 **3.4. Lack of taxonomic expertise limits our ability to manage invasions**

840 Taxonomic expertise is fundamental to management and policy efforts, from border
841 control to early detection (and both encouraging and justifying rapid response based on expert
842 identification) to post-invasion management. In several cases, misidentifications and failures to
843 recognize cryptic species complexes have delayed the discovery and introduction of suitable
844 biological control agents (Anderson and Wagner 2016). This is illustrated by biological control
845 of Cactaceae in South Africa that was delayed because the wrong species of herbivorous insect
846 was collected. After taxonomic problems were resolved and the appropriate insect was released,
847 the population of the non-native cactus declined (Paterson et al. 2011). Similarly, a carnivorous
848 beetle, *Laricobius naganoensis*, was inadvertently imported to eastern North America with a
849 closely-related species, *L. osakensis*, introduced from Japan to control an invasive insect – the
850 hemlock woolly adelgid. The U.S. Department of Agriculture subsequently permitted further
851 introduction of *L. naganoensis*, requiring no risk assessment or monitoring, simply because it
852 was too difficult to distinguish it readily from its congener (Leppanen et al. 2019).

853 Food security is also compromised by taxonomic problems. Inability to determine species
854 identity in imported live seafood can result in widespread substitution by cheaper species in
855 many countries, some of which include invasive non-native species. For example, in South

856 Africa several species of *Clarias* catfish are native to the continent and are used in aquaculture as
857 a local food source. However, the walking catfish (*C. batrachus*) – a southeastern Asian species
858 known to cause detrimental impacts where it has established – is prohibited for aquaculture. The
859 walking catfish is difficult to distinguish from its African congeners based on morphology alone,
860 making it an easy species to label inappropriately, import, grow, and sell (Grobler et al. 2015).

861 Equally worrisome is that, with the rapidity with which vectors and pathways are
862 changing in today's globalized economy, we may be unaware of – and unprepared for – many
863 future invasions. The widening gap between our desire to assess changing biodiversity and our
864 ability to identify species implicates all taxa in all habitats and thus compromises our evaluation
865 of the consequences of invasion. The need to narrow this gap through enhanced taxonomic
866 expertise is crucial if we are to keep pace with the constantly expanding numbers of non-native
867 animals and plants being introduced across the planet (Seebens et al. 2018, 2020).

868

869 **3.5. The way forward: Training the next generations of researchers to identify species**

870 The way forward requires a new international emphasis on the value of taxonomy. The
871 foundations of the scientific community's ability to recognize biodiversity, including the
872 presence and impacts of non-native species, have been crumbling for decades. Rebuilding these
873 foundations requires consensus that we need to do so, accompanied by agreement of the scale of
874 restoration required, a plan to undertake renovation, and the commitment and capital to see it
875 through. Each of these stages, except for commitment and capital, has been discussed
876 exhaustively to little avail. The challenge of old and oft-repeated clarion calls is that they fall on
877 deaf ears, or worse. And yet without this commitment, the global number of scientists who are
878 trained in the basics of taxonomy (including expert field identification) and possess skills in

879 measuring biodiversity will continue to diminish (Lücking 2020). Failures to identify organisms
880 correctly will lead to spurious conclusions in ecological studies and ultimately to inappropriate
881 and ineffective legislation, management, and policy (Pyšek et al. 2013). We note that recent
882 championing of *taxonomic sufficiency* or the Higher Taxon Approach, which is designed to
883 circumvent either the absence of, or the need for engaging, expert resources (de Oliveira et al.
884 2020; Gerwing et al. 2020), is inapplicable to invasion science – which requires the highest
885 quality and accuracy of species-level identification.

886 Thousands of protist, animal, and plant phylogenies produced every year contain
887 innumerable clades deprived of binomial nomenclature (Darling and Carlton 2018). Students
888 engaged in such work should be trained, supported, and encouraged to provide taxonomic
889 descriptions of clades as new species. The great satisfaction and pride of describing and
890 publishing new species, including the honor of choosing a name, could inspire a measurable
891 fraction of future generations of biologists and ecologists to become recognized taxonomic
892 experts while at the same time remaining experts in other specialties. A key advance will be the
893 dissolution of the enduring myth that simultaneously being an expert taxonomist and an expert
894 ecologist (or neurobiologist or molecular biologist) is impossible. Building pride in contributing
895 to global biodiversity knowledge is a critical step in addressing the taxonomic impediment in the
896 21st century. While we champion the rapidly growing concept of *integrative taxonomy* (Daglio
897 and Dawson 2019; Zhang 2020) – what Boxshall (2020) describes as the “reciprocal illumination
898 of morphological systematics and molecular sequence-based systematics” – we emphasize that
899 no integration is possible if only one partner is on the stage. The central role of taxonomists in
900 resource management, biodiversity conservation, and biosecurity must be affirmed (Hutchings
901 2020). The decline in funding and the startling erosion of taxonomic positions in museums and

902 other institutions must be addressed through novel collaborations, underscoring societal
903 significance.

904

905 **4. Enhancing international biosecurity and multi-stakeholder cooperation**

906 **4.1. Shifting international trade and travel patterns mediate invasions**

907 A final overarching issue is the need for invasion science to provide better guidance for
908 biosecurity programs, at both national and international levels. The suite of species transferred
909 between regions varies as global trade patterns wax and wane (Dyer et al. 2017; Seebens et al.
910 2018). An emerging example is the vast Chinese ‘Belt and Road’ initiative, which can potentially
911 elevate invasion risks greatly among the more than 120 countries through the development of a
912 series of land-based economic corridors between core cities and key ports (Liu et al. 2019).
913 Historically, changes to biosecurity policies that focus on specific pathways have been motivated
914 by the impacts of species arriving via those pathways, but the effectiveness of such reactive
915 approaches to policy development is hampered by long lags between the establishment of
916 pathways and the onset of invasion. Novel, forward-looking approaches to pathway risk analysis
917 are needed. For example, internet commerce of plants and animals is an expanding global
918 pathway that can radically transform the composition and introduction routes of species in trade
919 (Humair et al. 2015). Structural changes to the horticultural industry, such as the shift to off-
920 shore production, have major implications for plant health and trajectories of biological
921 invasions (Dehnen-Schmutz et al. 2010). Another emerging pathway is ecotourism; well-
922 meaning nature enthusiasts unwittingly introduce non-native species even to remote regions
923 (e.g., Nash 2009). Research is needed to develop educational and social engineering tools that
924 can be used to alter tourist behavior to reduce risks of future invasions.

925 Contemporary problems with non-native species reflect economic, societal, and trade
926 drivers and patterns that prevailed over the past few centuries (Essl et al. 2015a; Hulme 2015;
927 Dyer et al. 2017; Zieritz et al. 2017). This means that interventions to regulate pathways and
928 their effects on invasions are out of sync and that time horizons of decades must be considered in
929 strategic planning. The time lags inherent in many biological invasions imply that many
930 additional non-native species are destined to become established and cause problems in the
931 coming decades, even if biosecurity measures are radically improved (Essl et al. 2011). The
932 dimensions and implications of this invasion debt are yet to be clearly incorporated into strategic
933 biosecurity planning anywhere in the world (Rouget et al. 2016). To this end, Wilson et al.
934 (2018) included indicators pertaining to four components of invasion debt (introduction debt;
935 establishment debt; spread debt; and impact debt) among 20 indicators for reporting on
936 biological invasions at the national level. These indicators form the basis for regular reporting on
937 the status of biological invasions developed for South Africa – the first country to have instituted
938 such a comprehensive reporting protocol (van Wilgen et al. 2020). Uptake of such measures for
939 all countries is a priority.

940 Trends observed in past invasions, most of which have played out over the last five
941 decades, provide imperfect insights for planning of biosecurity interventions, since many aspects
942 of future invasions (e.g., taxa involved, pathways, drivers of progression along the introduction-
943 establishment-spread continuum, interactions between drivers) will differ from those of previous
944 invasions. Invasion science must develop more detailed understanding of how international trade
945 and travel are altered by national and international socioeconomic changes, and how these
946 changes in turn influence invasion trends (Hulme 2015). Such insights can greatly enhance the
947 development of scenarios and allow for improved risk categorization. A major priority for

948 invasion science is thus to advance beyond pattern recognition to embrace mechanistic socio-
949 ecological models; for example, the Global Trade Analysis Project model was used to assess the
950 economic and trade impacts of required phytosanitary treatments of wood packaging (Strutt et al.
951 2013), and it was later applied to estimate the ultimate economic benefits of this policy (Leung et
952 al. 2014). An improved understanding of the links between global socio-economic trends and
953 invasions will ensure more effective targeting of national and international biosecurity efforts.
954 Such knowledge is also needed to inform the development of incentives and educational tools to
955 alter the behavior of importers, travelers, and others whose activities pose significant invasion
956 risks (Colton and Alpert 1998; Perry and Farmer 2011; Springborn et al. 2016).

957

958 **4.2. Global cooperation among national biosecurity programs**

959 Most countries operate biosecurity programs that are designed to prevent the arrival,
960 establishment, and spread of non-native species inside their national borders (Meyerson and
961 Reaser 2002; Hulme 2011). In some cases, unexpected prioritization of biosecurity measures can
962 result from independent policy actions. For example, the EU Regulation (1143/2014) on non-
963 native species has resulted in stakeholders focusing on biosecurity programs that limit the export
964 of live animals and plants but which neglects new introductions. Moreover, contemporary
965 national biosecurity programs are generally designed to protect the interests of individual
966 countries (Black and Bartlett 2020), with relatively little consideration given to the ‘greater
967 good’ – i.e., protecting all nations from invasions. The mission of most national plant protection
968 organizations, for example, includes regulating imports that pose high risks of harmful
969 introductions, while simultaneously promoting exports from their own countries; scant attention
970 is given to minimizing risks associated with such exports (MacLeod et al. 2010). Cooperation is

971 urgently needed among countries to craft biosecurity programs that are more cost-effective than
972 those where countries act largely in isolation (Latombe et al. 2017). Despite long-standing calls
973 for a binding internationally convention on invasive alien species (Perrings et al. 2010; Stoett
974 2010), there has been no progress towards this goal in over a decade. Within individual
975 countries, there are often political and economic obstacles to adopting truly cooperative
976 biosecurity. Thus, rather than a top-down multilateral approach to regulation, it is likely that
977 closer integration of national biosecurity strategies will occur through a coalition of the willing.
978 A fine example is the Consultative Group on Biosecurity Cooperation established by Australian
979 and New Zealand ministers in 1999 under the terms of the Australia –New Zealand Closer
980 Economic Relations Trade Agreement. This group has led efforts to harmonize animal and plant
981 health measures affecting trade between the two countries as well as coordinating biosecurity
982 responses. The Plant Health Quadrilaterals is a strategic coalition composed of the national plant
983 protection organizations of Australia, Canada, New Zealand, and the United States that enables
984 the respective plant health and biosecurity officials to address plant health and biosecurity issues,
985 particularly as they affect international trade of plants, plant products, and other regulated
986 articles. In 2016, a similar quadrilateral group involving the same four nations was established to
987 coordinate efforts to address marine biosecurity. These coalitions do not have any regulatory
988 power, but through dialogue and cooperation they can address emerging issues in biosecurity in
989 an open and collaborative manner. For multilateral initiatives, a useful model for research on
990 cooperative biosecurity would be studies on cooperation between different countries to optimize
991 harvest from shared fisheries (Bailey et al. 2010). These studies apply game theory, which could
992 also be applied to biological invasions to explore how cooperative biosecurity might yield higher
993 benefits to all countries by collectively reducing the flow of species globally, rather than just

994 preventing invasions at the national level. Lampert (2020) applied a dynamic game-theoretic
995 model to identify a Nash equilibrium corresponding to optimal contributions that various
996 countries or other entities could adopt for managing invading species with shared adverse
997 impacts. This approach could be expanded to explore cooperation by countries to fund various
998 pre- and post-border biosecurity activities.

999

1000 **4.3. The role of the bridgehead effect in managing invasions**

1001 A key consideration driving the need for internationally cooperative biosecurity strategies
1002 is the tendency of organisms to invade new regions from locations where they have already
1003 established, a phenomenon referred to as the *bridgehead effect* (Lombaert et al. 2010;
1004 Bertelsmeier and Keller 2018) or ‘hub-and-spoke’ invasion topology (Carlton 1996). This
1005 phenomenon has been documented in historical global patterns of invasions for several plant and
1006 animal species (e.g., Bertelsmeier et al. 2018; Correa et al. 2019; Javal et al. 2019). The term was
1007 first coined by Lombaert et al. (2010), who used molecular analyses of the global spread of the
1008 harlequin beetle *Harmonia axyridis* and found that even though the species is native to east Asia,
1009 its invasions of Europe, Africa, South America and western North America all originated from
1010 eastern North America (Figure 5). Evidence exists that invasions from bridgehead regions may
1011 be promoted by genetic changes, demographics, or simply by the topologies of trade networks
1012 (Bertelsmeier and Keller 2018). More work is needed on the drivers of bridgehead dynamics to
1013 determine whether management-relevant generalizations exist.

1014 From the perspective of designing biosecurity programs, an important implication of such
1015 bridgehead dynamics is that benefits will accrue from preventing a species from establishing
1016 within a hub or bridgehead region – that is, an invaded location from which spread to other

1017 regions is more easily facilitated. Furthermore, cooperation among countries to eradicate or
1018 control species established in bridgehead regions could yield greater benefit than attempts by
1019 individual countries to exclude these species from arriving and establishing.

1020 The current unilateral approach that dominates national biosecurity has roots in the close
1021 relationship between trade and import quarantines; quarantine is an effective and important tool
1022 for excluding arrivals of new species, but there is a history of quarantine being abused to justify
1023 protectionist trade policies (Castonguay 2010). For example, the World Trade Organization
1024 (WTO) recognizes the International Plant Protection Convention (IPPC) as the authority for
1025 setting standards for plant quarantine, and the WTO uses its Appellate Body for settling
1026 quarantine-related trade disputes. However, while the IPPC identifies quarantine practices and
1027 harmonized standards that individual countries should follow, it generally does not implement
1028 actions to minimize the movement of species worldwide; however, the IPPC has developed a
1029 National Phytosanitary Capacity Development Strategy that facilitates investment by member
1030 countries in the development of biosecurity capacities in economically under-developed
1031 countries. Interdisciplinary research between invasion scientists and international trade
1032 economists is required to develop frameworks and justifications for globally collaborative
1033 biosecurity efforts (Horan and Lupi 2005). Among the topics this research could address is how
1034 countries with varying economic resources can share resources for preventing the global
1035 movement of non-native species (Early et al. 2016).

1036 This research could also focus on developing strategies to identify bridgehead regions
1037 and initiate cooperative biosecurity negotiations with governments responsible for such regions.
1038 Border inspection data provide information on the identity of the geographical sources of species
1039 arriving at ports and are thus valuable resources for identifying bridgehead regions (Bertelsmeier

1040 et al. 2018). Biosecurity agencies often consider inspection data as confidential (because of their
1041 possible significance in trade dispute litigation). Given the potential value of such data for
1042 identifying and delimiting bridgehead regions and global invasion risk (Turner et al. 2020), a
1043 challenge for invasion science is to ensure that such data are made more widely available and in
1044 a timely way to prevent regions that have received an invasive species from serving as sources
1045 for new invasions even before the bridgehead population has been discovered. Ultimately, such
1046 data sharing could help inform biosecurity practices in individual countries, thereby reducing
1047 risks of future invasions. The world has recently witnessed an unprecedented case of
1048 international sharing of spatiotemporal spread data for SARS-CoV-2 from its earliest stages,
1049 which should serve as an example for tracking other invasive organisms (Bertelsmeier and Ollier
1050 2020).

1051

1052 **4.4. Managing conflicting interests in biosecurity**

1053 A related problem is that of cooperative approaches to transboundary biosecurity. The
1054 establishment of non-native populations can span regions managed for varying purposes, often
1055 with conflicting priorities (Epanchin-Niell et al. 2010). Conflicts of interest frequently bedevil
1056 attempts to manage non-native species, especially when the focal species is simultaneously
1057 perceived as both beneficial and harmful by different sectors of society or in different areas of
1058 the landscape (e.g., van Wilgen and Richardson 2014). For example, the ornamental horticulture
1059 industry benefits from importing and propagating non-native plant species while its actions
1060 conflict with other societal segments (e.g., ranchers, farmers, conservation managers) who suffer
1061 from the impacts of plant invasions (Niemiera and Von Holle 2009). Invasion scientists must
1062 collaborate with economists and other researchers to devise approaches to engender cooperation

1063 among stakeholders who are differentially impacted by the same non-native species and to
1064 explore how to optimize diverse management interests. In responding to changing perceptions of
1065 non-native species, their impacts, and their value to society, invasion science is facing challenges
1066 similar to those confronting other disciplines including the medical profession with regard to
1067 how best to communicate information about risk (Alaszewski and Horlick-Jones 2003). Social
1068 science research must also develop effective strategies or models for systematic engagement of
1069 stakeholders seeking sustainable solutions to invasions (Shackleton et al. 2019).

1070 Conflicting interests among stakeholders that affect management of invasions sometimes
1071 manifest as ‘wicked problems’. These are characterized by diverse, opposing perspectives,
1072 objectives, and management goals that make them almost impossible to characterize or frame, let
1073 alone resolve, to the satisfaction of all stakeholders (Woodford et al. 2016). Woodford et al.
1074 (2016) suggest that systematic framing of ‘wickedness’ by mediators can lead to negotiated
1075 solutions – either by reaching agreement on the dimensions and implications of unavoidable
1076 conflicts, or by circumventing the conflict by seeking alternative management perspectives. To
1077 this end, Novoa et al. (2018) developed a 12-step process designed to place stakeholders at the
1078 center of the development and implementation of decisions relating to conflicts of interest in
1079 invasive species management. Fundamental requirements for achieving such aims are to 1)
1080 ensure that decisions and management actions are co-designed, co-produced, and co-
1081 implemented to promote social learning and provide feedback to stakeholders, and 2) increase
1082 levels of collaboration and partnerships beyond the natural sciences and academia (Shackleton et
1083 al. 2019). Further work is clearly needed to achieve integration of broad stakeholder engagement
1084 and co-operation in invasion research and management. Opportunities abound to apply existing

1085 economic theory on governing common-pool goods (Ostrom 2010) to solve problems related to
1086 the increasingly complex conflicts between stakeholders relating to invasive non-native species.

1087

1088 **Conclusions**

1089 Invasion science is an increasingly interdisciplinary field that addresses questions and
1090 hypotheses of fundamental and applied importance to ecology, conservation biology, ecosystem
1091 management and restoration, and biosecurity (Ricciardi et al. 2017; Pyšek et al. 2020). We have
1092 identified four overarching issues that are critically important for the field to further adapt to
1093 societal demands in the face of rapid global change. Reflected in these issues are burgeoning
1094 challenges posed by new sources and pathways (e.g. evolving trade routes and transportation
1095 systems) of invaders. Understanding and predicting invasions and their consequences are
1096 scientific endeavors, whereas managing them successfully largely rests with society; the former
1097 informs the latter, and both tasks are complicated by context-dependencies that are becoming
1098 increasingly significant as rapid environmental change ensues.

1099 Solutions to these challenges require innovations in theory and methods that potentially
1100 could be found through linkages with other disciplines. For example, factors promoting the
1101 emergence and spread of novel infectious disease could be better understood and managed
1102 through collaborative research involving medical science and invasion science, to the benefit of
1103 both fields (Nuñez et al. 2020). In addition, within the broad discipline of ecology there are
1104 disparate concepts and methods that have not yet been well integrated into invasion science (e.g.
1105 species interaction networks; Hui and Richardson 2019), or that are only now becoming broadly
1106 applied (e.g. the use of functional response metrics in risk assessment; Dick et al. 2017a, b;
1107 Dickey et al. 2020).

1108 New approaches are needed to forecast candidate invaders, probable invasion success,
1109 and consequent invader impacts under future terrestrial, freshwater, and marine conditions that
1110 have little or no analogue reference point in the past. A key growth point for the field would be
1111 to develop a better understanding of temporal invasion dynamics, including invasion debt and
1112 time lags. The concept of invasion debt (Essl et al. 2011; Rouget et al. 2016), in which invasions
1113 are the end result of processes currently at play (e.g., increasing propagule transport and
1114 introduction in the face of reduced environmental resistance) is analogous to the emergence of
1115 disease symptoms following viral or bacterial exposure resulting from lapses in hygienic
1116 measures or failed social behaviors. A more predictive understanding of invader impact could be
1117 advanced, in part, through research on interacting and cumulative time lags in biodiversity and
1118 ecosystem responses to invasions (Essl et al. 2015b, c).

1119 Fundamental taxonomic skills are essential for biosecurity and a deeper understanding of
1120 biogeography and evolutionary history – the foundations of invasion science. The application of
1121 invasion science to early detection is compromised without expertise suitable to identify non-
1122 native species rapidly. Misidentifications have and will lead to spurious conclusions in
1123 ecological studies and, ultimately, to inappropriate and ineffective management and policy, when
1124 such are called for. The necessary expertise could be cultivated through application and
1125 enhancement of infrastructure support (e.g. cyber-tools, specimen collections linked with
1126 permanent custodial care), and re-establishment of training of both classic and advanced
1127 taxonomic skills in biology programs.

1128 Finally, invasion science must address transcultural sociopolitical challenges including
1129 how best to communicate information and uncertainty about risk, how to engage diverse
1130 stakeholders who are differentially impacted by the same non-native species, and how to inform

1131 transboundary biosecurity policies. There is still much work required to harmonize the definition
1132 and application of biosecurity policies across different multilateral organisations such as the
1133 Convention on Biological Diversity, the International Plant Protection Convention and the World
1134 Organisation for Animal Health. Invasion science must continue to inform the rapidly evolving
1135 landscape of international biosecurity agreements designed to control pathways that create
1136 bridgehead populations, which can drive widespread invasions. International data-sharing will be
1137 needed to reduce invasion risk at regional and global scales. The remarkable example of the
1138 rapid cooperative sharing by most countries of spatiotemporal spread data for SARS-CoV-2 from
1139 its earliest stages should inspire global efforts to track other invasive organisms.

1140

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1156

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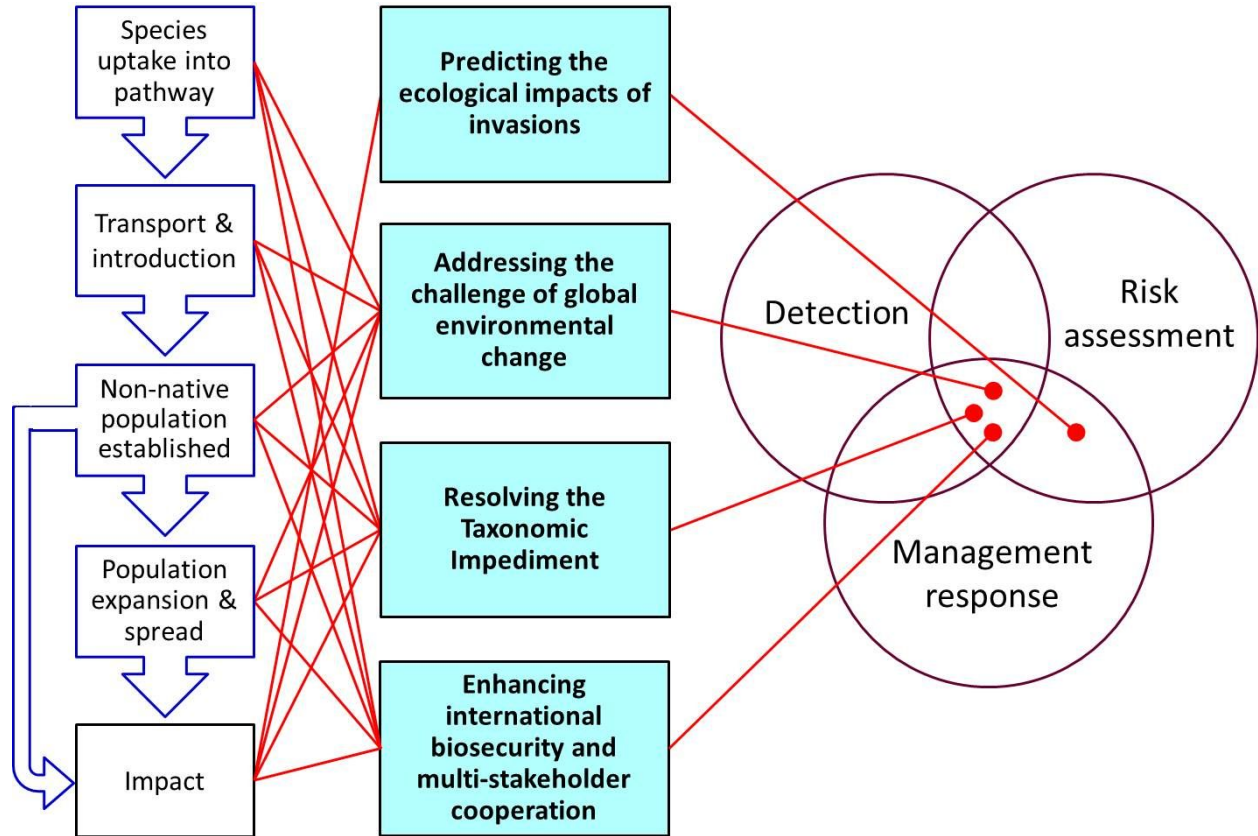


Figure 1. Four priority issues (center column) that must be addressed by invasion science to meet burgeoning challenges in an era of rapid environmental change. Through multiple connections, each issue is implicated in one or more stages of the invasion process (left column), as well as in the impact of the invader (which can occur at any stage from introduction to establishment to spread) and in the detection, risk assessment, and management response of invasion threats. For example, scientific understanding of the processes that control the diversity, abundance, distribution, and impacts of non-native species ultimately depends on the quality of taxonomic data; therefore, resolving the Taxonomic Impediment (the erosion of our capacity to recognize biodiversity and distinguish non-native from native species accurately) would enhance our ability to detect non-native species, assess their impacts, and respond to new invasion threats.

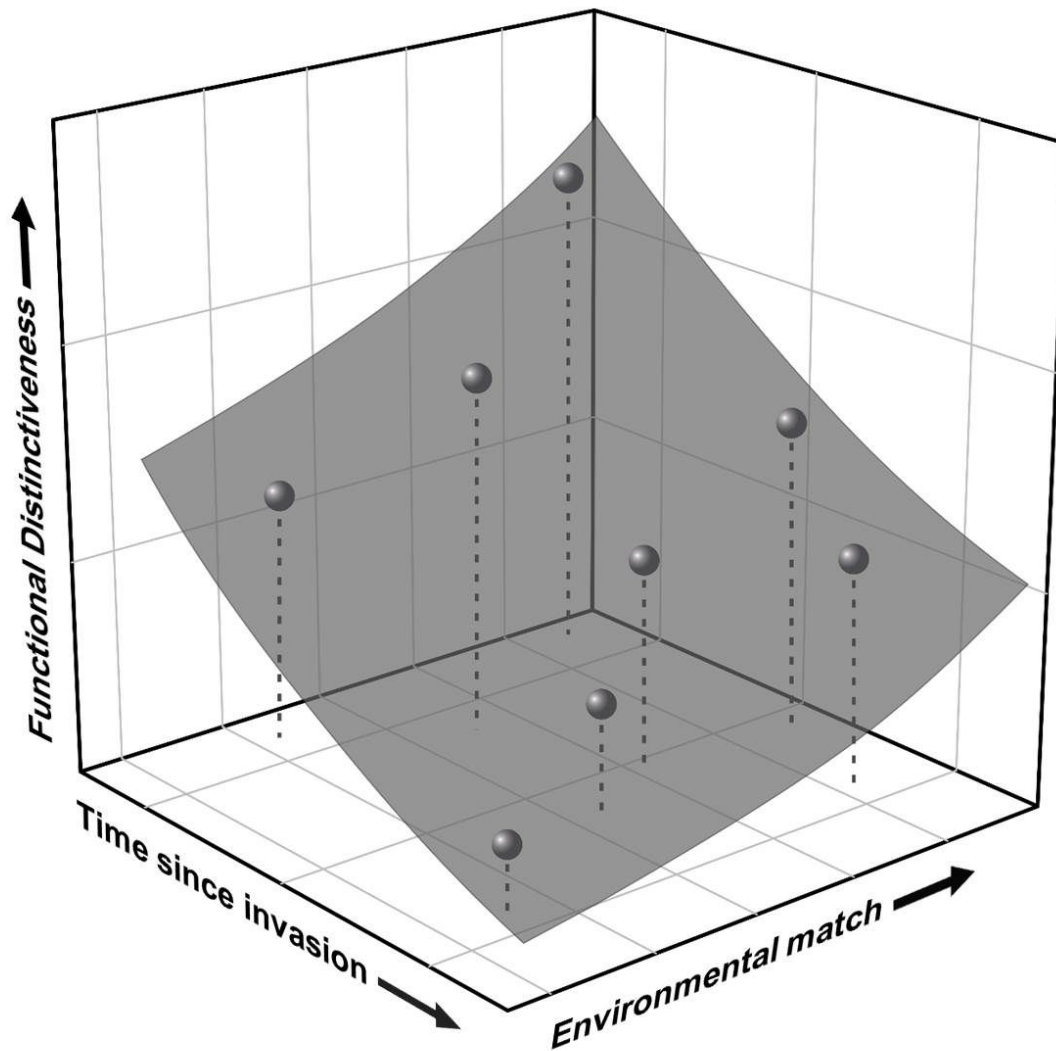


Figure 2. An example of integration of impact hypotheses. The 3-dimensional plot represents the predicted variation in an invader's ecological impact in relation to three factors, shown as axes: 1) the functional (or phylogenetic) distinctiveness of the invader among resident species; 2) the degree of environmental match – i.e., the inverse of the distance between mean abiotic conditions in the invaded environment and the invader's physiological optimum; and 3) time since invasion. Functionally novel invaders, especially those that exploit key resources, are

predicted to have greater impacts on the invaded ecosystem (Functional Distinctiveness Hypothesis). Invaders that are more physiologically matched to abiotic conditions in the invaded environment should have greater per capita effects (Environmental Matching Hypothesis). Further, in this example, impact is hypothesized to attenuate over time, based largely on the premise that given suitable time resident species (predators, prey, parasites, competitors) will adapt to the invader and dampen its influence. These factors are shown here to be mutually independent, but interactions are possible (e.g. physiological match may interact with time since invasion, owing to local adaptation or directional shifts in abiotic conditions).

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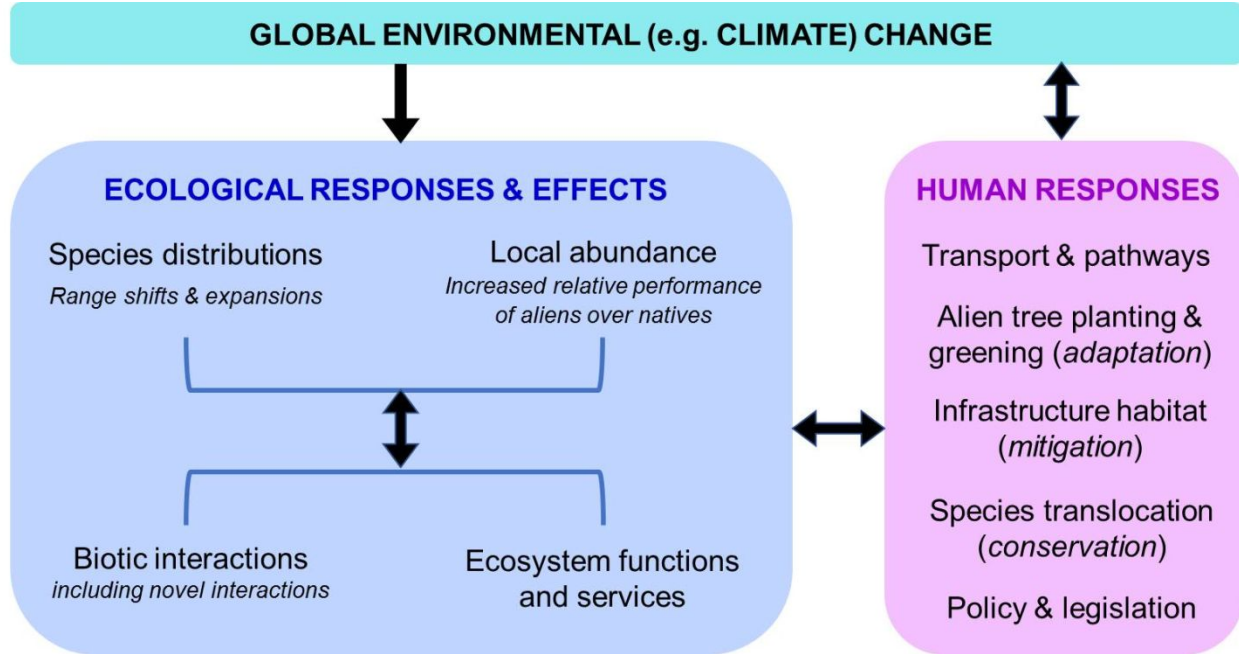


Figure 3. Global environmental change (in particular, climate change) directly and indirectly elicits ecological and human responses that promote invasions. Environmental change can trigger shifts in the distributions and abundances of native and non-native species, leading to novel biotic interactions and altered ecosystem functions and services, which can themselves prompt further ecological responses. Human responses include climate change adaptation and mitigation, as well as species conservation; many of the current human responses will likely facilitate invasions. These ecological and human responses also affect each other, compounding the direct impacts of environmental change.

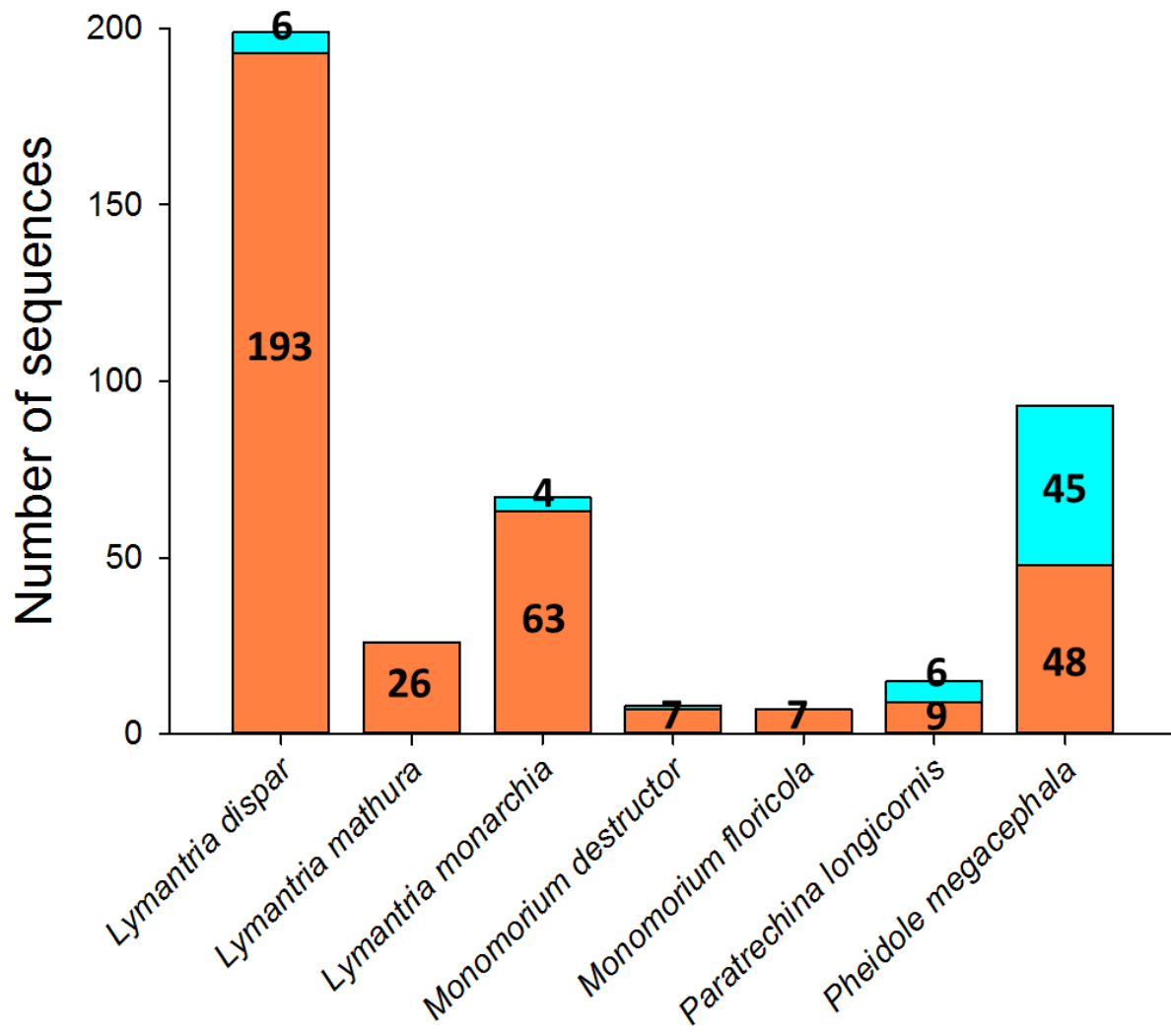


Figure 4. Examples of invasive insect species for which a discrepancy exists between the number of sequences available in GenBank v3.0 when using the two primary search query tools they provide: a taxonomy-based search of GenBank records (green) and a broader search using sequences or taxonomy of other publicly available data sources linked to GenBank (orange). Such discrepancies in search results across databases increase the risk that these species will be incorrectly classed as ‘unidentified’ when metabarcoding approaches are used to identify non-native insects. Data from Boykin et al. (2012).

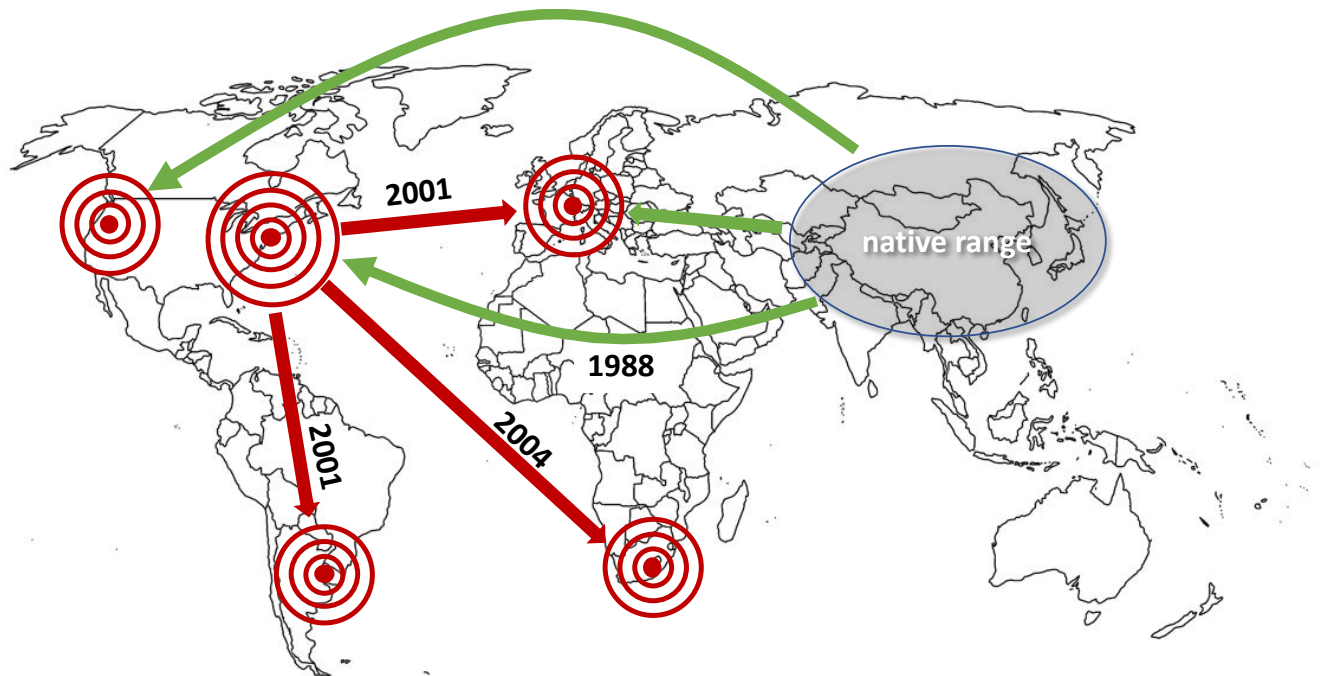


Figure 5. The Bridgehead Effect illustrated by the global spread of the Harlequin ladybird beetle *Harmonia axyridis*, based on genetic analyses by Lombaert et al. (2010). Intentional biocontrol introductions are shown in green, whereas accidental invasions are shown in red. In this example, most of the global spread of this species has originated from non-native populations established in Eastern North America, which has functioned as a bridgehead region (adapted from Lombaert et al. 2010).