

Complex patterns of global spread in invasive insects: eco-evolutionary and management consequences

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Abstract	^		
	The advent of simple and affordable tools for molecular identification of novel insect invaders and assessment of population diversity has changed the face of invasion biology in recent years. The widespread application of these tools has brought with it an emerging understanding that patterns in biogeography, introduction history and subsequent movement and spread of many invasive alien insects are far more complex than previously thought. We reviewed the literature and found that for a number of invasive insects, there is strong and growing evidence that multiple introductions, complex global movement, and population admixture in the invaded range are commonplace. Additionally, historical paradigms related to species and strain identities and origins of common invaders are in many cases being challenged. This has major consequences for our understanding of basic biology and ecology of invasive		

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	insects and impacts quarantine, management and biocontrol programs. In addition, we found that founder effects rarely limit fitness in invasive insects and may benefit populations (by purging harmful alleles or increasing additive genetic variance). Also, while phenotypic plasticity appears important post- establishment, genetic diversity in invasive insects is often higher than expected and increases over time via multiple introductions. Further, connectivity among disjunct regions of global invasive ranges is generally far higher than expected and is often asymmetric, with some populations contributing disproportionately to global spread. We argue that the role of connectivity in driving the ecology and evolution of introduced species with multiple invasive ranges has been historically underestimated and that such species are often best understood in a global context.
Keywords (separated by '-')	Admixture - Bridgehead effects - Invasion genetics - Invasive species management - Multiple introductions
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Complex patterns of global spread in invasive insects: a eco-evolutionary and management consequences

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AQ1 Abstract The advent of simple and affordable tools 10 for molecular identification of novel insect invaders 11 and assessment of population diversity has changed 12 the face of invasion biology in recent years. The 13 widespread application of these tools has brought with 14 it an emerging understanding that patterns in biogeog-15 raphy, introduction history and subsequent movement 16 and spread of many invasive alien insects are far more 17 complex than previously thought. We reviewed the 18 literature and found that for a number of invasive 19 insects, there is strong and growing evidence that 20 multiple introductions, complex global movement,

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and population admixture in the invaded range are 21 commonplace. Additionally, historical paradigms 22 related to species and strain identities and origins of 23 common invaders are in many cases being challenged. 24 This has major consequences for our understanding of 25 basic biology and ecology of invasive insects and 26 impacts quarantine, management and biocontrol pro-27 grams. In addition, we found that founder effects 28 29 rarely limit fitness in invasive insects and may benefit populations (by purging harmful alleles or increasing 30 additive genetic variance). Also, while phenotypic 31 32 plasticity appears important post-establishment, genetic diversity in invasive insects is often higher 33 than expected and increases over time via multiple 34 introductions. Further, connectivity among disjunct 35 regions of global invasive ranges is generally far 36

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Keywords Admixture · Bridgehead effects · Invasion genetics · Invasive species management · Multiple introductions

47 Introduction

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48 A fundamental problem in invasion biology has long **4**9 been how to reconcile the likelihood of reduced 50 genetic diversity via founder effects with invasive 51 success across a range of habitats and niches in the 52 short and long term. Once a central "paradox" of the 53 discipline, researchers now understand that genetic 54 diversity has been historically underestimated in many 55 introduced species, while other invaders appear 56 remarkably tolerant to genetic uniformity and may 57 even benefit from periodic founder effects (Roman 58 and Darling 2007). Considerable work in the past few 59 decades has focused on understanding the role of 60 phenotypic plasticity in invasion success, mechanisms 61 of tolerance to low diversity and rapid evolution in 62 introduced populations-all of which appear to be 63 variously important in different systems to invasion 64 success (Lee 2002; Dlugosch and Parker 2008; 65 Whitney and Gabler 2008; Lawson Handley et al. 66 2011). There is also growing recognition that high 67 levels of genetic diversity can be preserved during 68 introduction and establishment (e.g., via high propag-69 ule number or multiple introductions) and that genetic 70 diversity can increase over time since establishment, 71 primarily due to subsequent introductions from the 72 native or adventive range (Kolbe et al. 2007; Keller 73 and Taylor 2010; Rius and Darling 2014; Gladieux 74 et al. 2015). A new paradigm emerging from this work 75 contends that global movement and spread for many 76 invasive alien species (IAS) is rapid and often 77 complex and that multiple introductions and migration 78 among disjunct parts of the adventive range are common. Thus, apparently disparate populations 79 80 across continents are effectively connected by gene

flow at ecologically relevant time scales. Such patterns81have important consequences from the perspective of82the evolutionary biology of alien populations that83researchers have only just begun to appreciate and84explore. The implications for IAS policy and management are also likely to be profound.86

IAS are a major threat to natural and managed 87 ecosystems worldwide. The rate of accumulation of 88 IAS continues to be very high in some parts of the 89 world (Aukema et al. 2010) and to increase in others 90 (Essl et al. 2015). Despite the laudable goal of 91 prevention and/or eradication of IAS, this is a hugely 92 difficult task, likely to be unsuccessful in the vast 93 majority of cases. In most situations, managing 94 95 invasive alien populations and controlling rates of spread are the only options (Pyšek and Richardson 96 2010). Effective management relies on a comprehen-97 sive understanding of ecological and evolutionary 98 patterns in IAS. We argue that this can only be 99 achieved by taking both a regional and global view 100 that explicitly considers patterns of movement within 101 and among regions in the context of adaptive evolu-102 tionary change. 103

The goals of this review are threefold. First, we 104 present representative examples from the growing list 105 of cases where global connectivity appears to be a 106 plausible model for understanding invasive success. 107 Second, we explore some of the potential conse-108 quences of rapid and complex patterns of spread and 109 the concomitant mixing of potentially divergent 110 genotypes on eco-evolutionary dynamics. Third, we 111 examine the ways in which cryptic movement and 112 complex spread may influence management in the 113 future. We do not attempt to recapitulate findings of 114 recent comprehensive reviews (Lee 2002; Dlugosch 115 and Parker 2008; Le Roux and Wieczorek 2009; 116 Lawson Handley et al. 2011; Rius and Darling 2014) 117 but rather build on a growing body of theory and 118 empirical evidence around globally distributed inva-119 ders to explore the potential fundamental shifts in our 120 understanding of invasion biology. 121

Patterns of global insect movement

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There is an accumulating number of examples where123the global movements of IAS are characterized by (1)124rapid spread from points of introduction via popula-125tion growth and natural dispersal; (2) frequent jump126

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127 dispersal to uncolonized, noncontiguous areas; (3) 128 multiple introductions from the native range; and (4) 129 frequent exchange among disjunct invasive popula-130 tions worldwide. In some cases, there is also evidence 131 for back-introduction from invasive populations into 132 the native range. The Sirex woodwasp, Sirex noctilio, 133 provides an excellent example of such complexity. 134 Since 1900, S. noctilio has invaded exotic Pinus 135 plantations in Australasia, South America and South-136 ern Africa and more recently (2005) into native and 137 exotic Pinus stands in North America (Slippers et al. 138 2015). Original hypotheses based on limited data 139 proposed a simple, stepwise route of introduction 140 between countries in the Southern Hemisphere (Slip-141 pers et al. 2001). However, a recent comprehensive analysis using mitochondrial cytochrome oxidase I 142 143 (COI) sequence and Simple Sequence Repeat (SSR) 144 data, as well as various population genetic tools [including Approximate Bayesian Computation 145 146 (ABC) analysis; Cornuet et al. 2008] revealed far 147 greater complexity in patterns of global spread 148 (Boissin et al. 2012). Two evolutionarily distinct 149 lineages of the wasp have spread widely, one of which 150 has a proximate origin in Europe while the origin of **15**1 the other is unknown. These lineages co-occur in some 152 regions including Chile and South Africa where they 153 interbreed, resulting in admixture. Most regions 154 appear to have received migrants from other invasive 155 populations (e.g., South America from Europe, Aus-156 tralasia and a population of unknown origin; South 157 Africa from South America and Australasia, etc.), 158 creating complex population admixtures of different 159 proximate sources, which may or may not represent 160 distinct lineages (but that differ at neutral markers). 161 Even North American populations, where the invasion 162 was most recently reported, appear to have experi-163 enced introductions from at least two sources (Berg-164 eron et al. 2011; Boissin et al. 2012; Castrillo et al. 165 2015). Interestingly, these analyses also suggest that Europe, where the wasp is native, has been invaded by 166 167 a lineage of unknown origin, possibly via an invasive population in South America (Boissin et al. 2012). 168

169 The complex pattern of spread and mosaic of 170 genetic mixing among invasive populations, as illus-171 trated by the *S. noctilio* example, is by no means 172 unique to that system. A quantitative review by 173 Dlugosch and Parker (2008) of recent population 174 genetic studies of plant, animal and fungal invasions 175 concluded that while most invaders experience a loss of diversity initially (i.e., years to decades post-176 establishment), diversity is often restored through 177 multiple introductions, increased populations sizes 178 (countering drift) and interconnectivity of popula-179 tions, and sometimes can even exceed that of native 180 source populations (e.g., Kolbe et al. 2004, 2007). 181 Interestingly, Dlugosch and Parker (2008) found a 182 U-shaped pattern in diversity loss over time; that is, 183 reductions in allelic richness are most severe at 184 intermediate time points post-introduction, perhaps 185 suggesting the importance of drift over founder 186 effects. A number of studies on invasive alien insect 187 populations also support the generality of the pattern 188 that diversity increases with time since introduction. 189 For example, in an extensive review of medfly 190 (Ceratitis capitata) studies, Malacrida et al. (2007) 191 found that multiple introductions consistently con-192 tribute to the maintenance or enhancement of genetic 193 diversity in this important global invader. Similar 194 processes have been described in invasive populations 195 of the Eucalyptus Bronze Bug, Thaumastocoris pere-196 grinus (Nadel et al. 2009), Harlequin Ladybird, 197 Harmonia axyridis (Lombaert et al. 2010), Red 198 Tomato Spider Mite, Tetranychus evansi (Boubou 199 et al. 2012), Eastern Subterranean Termite, Retic-200 ulitermes flavipes (Scaduto et al. 2012), mosquito 201 Aedes japonicas japonicas (Zielke et al. 2014), and a 202 number of other insect invaders (Table S1). The 203 changing nature of invasive alien populations caused 204 by multiple introductions over time highlights the 205 need to periodically reassess diversity in such popu-206 lations (something that is not currently being done 207 routinely for most invasive populations), especially in 208 light of the implications this can have for manage-209 ment, as discussed below. 210

Genetic diversity in invasive populations is not only 211 linked to multiple introductions, but can also result 212 from high propagule pressure, whether as a single 213 event or as a result of sustained pressure over time. For 214 example, Kerdelhué et al. (2014) showed that the 215 original introduction of the Maritime Pine Blast Scale, 216 Matsucoccus feytaudi, into southeastern France was 217 comprised of a very large number of individuals. 218 These introductions possibly occurred during World 219 War II due to large-scale wood movement. Conse-220 quently, the genetic bottleneck in these original 221 invasive populations appears to have been relatively 222 weak. Similarly, though the invasion of Drosophila 223 subobscura from Europe into South America was 224

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involved a less severe bottleneck (Pascual et al. 2007).
Low numbers of individuals arriving during the early
phase of invasion do not necessarily result in invasion
failure, however. For example, the recent colonization
of Western Europe by the Asian hornet, *Vespa velutina nigrithorax*, was initiated by the arrival in France of a
single multiply-mated female (Arca et al. 2015).

234 One of the outcomes of multiple introductions from 235 the native range of invasive insects is that globally, <mark>23</mark>6 populations of some invading pests can comprise two 237 or more distinct lineages, or even cryptic species 238 (Miura 2007). For example, in globally invasive 239 populations of a Eucalyptus leaf weevil (Gonipterus spp.), at least three distinct species have been found 240 241 with two species co-occurring in some regions without 242 the knowledge of the practitioners managing the pest (Mapondera et al. 2012). Here an incorrect name, 243 244 'Gonipterus scutellatus', has been applied to the 245 invasive pest for decades, becoming a serious imped-246 iment to management, including the selection of 247 specific biocontrol agents and understanding of invasion patterns. Invasive mites too, most notably erio-248 <mark>24</mark>9 phyoids, have regularly been found to comprise 250 multiple cryptic lineages and/or species (Carew et al. 251 2009; Skoracka et al. 2014) with closely related, **25**2 morphologically indistinguishable but molecularly 253 distinct forms that differ in important ecological 254 characteristics (particularly host range; Skoracka **25**5 et al. 2013), that co-occur in complex mosaics. The 256 degree to which the cryptic species and/or lineages 257 require more nuanced, targeted (or diversified) man-258 agement strategies is largely unknown. Cryptic forms 259 are at the very least a complicating factor for research 260 and management. The Gonipterus and eriophyoid 261 examples clearly illustrate how genetic tools can inform management but also highlight the desperate 262 263 need for adequate taxonomic systems to describe this <mark>26</mark>4 diversity. In many cases expertise to identify and 265 describe cryptic species or distinct lineages using 266 traditional tools simply does not exist. New ways to 267 systematically characterize and/or name biological 268 diversity that go beyond traditional taxonomic 269 approaches will have to be explored, particularly with 270 respect to microbes (Maddison et al. 2012), though 271 also for insects.

Apart from the complications arising from theexistence of different lineages in distinct parts of an

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invader's range (e.g., if management must be cus-274 tomized), the uniting or reuniting of previously 275 isolated populations or species can result in unique 276 combinations of alleles via hybridization or admix-277 ture, which can further complicate management 278 279 approaches. For example, the emergence of new genetic combinations resulting from uniting or reunit-280 ing separately evolving lineages has been shown for 281 the Urticating Pine Processionary Moth, Thaumetho-282 pea pityocampa. While the moth was considered to 283 have expanded naturally from southern Europe with 284 global warming, its northward spread now appears to 285 have been driven at least in part by long-distance 286 transport by humans of potted pine trees. As a result, 287 the northern front of the advancing distribution is 288 characterized by genetic admixture combining genes 289 of populations from different parts of Europe having 290 different primary phenologies (Kerdelhué et al. 2015). 291

The existence of globally distributed species is not 292 new, and in some cases appears to be largely 293 independent of modern trade (i.e., in highly dispersive 294 species with wide environmental tolerances, though 295 cryptic species also commonly occur in these groups; 296 Spellerberg and Sawyer 1999; Nelson 2002). Very 297 clearly, however, global spread is very strongly 298 influenced by the movement of our own species 299 (e.g., Liebhold et al. 2012; Santini et al. 2013). Based 300 301 on a recent spate of invasions of pests of agriculture, including forest plantations of pine and eucalypts 302 (particular the latter), it appears that many invasive 303 insects are reaching global status much more rapidly 304 than before (Hurley et al. 2015; Roques et al. 2015). 305 Species such as S. noctilio, Gonipterus spp. and 306 Ctenarytaina eucalypti (among others) that escaped 307 their respective native ranges in the late 1800s/early 308 1900s generally took between 50 and 100 years to 309 reach truly global distributions (i.e., presence on all or 310 most continents where hosts occur). Among more 311 recently emerging invasive insects, several have 312 achieved such distributions in little more than a 313 decade or less. For example, Leptocybe invasa, a gall 314 wasp on Eucalyptus, was first reported in Israel in 315 2000 (Mendel et al. 2004). At that time, this wasp was 316 completely unknown, but by 2008 it had spread 317 throughout the North and South America, southern 318 319 and southeast Asia, the Mediterranean and Africa in what appeared to be a more or less stepwise fashion 320 (Nugnes et al. 2015). L. invasa spread has been 321 exceptionally rapid, but several other pests of 322

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323 Eucalyptus (e.g., Glycaspis brimblecombei, Ophe-**32**4 limus maskelli and Thaumastocoris peregrinus) are 325 currently spreading globally with similar pace. This 326 phenomenon has been seen in a number of insects 327 from diverse taxonomic lineages, as well as across hosts, herbivorous feeding guild, and life histories (Hurley et al. 2015). While some recently emerging **33**0 pests that exhibit rapid spread could be specifically and idiosyncratically linked to pathways that permit it (Paine et al. 2010), Roques et al. (2015, this issue) showed that this faster spread constitutes a general **33**4 phenomenon for invasive insects since the mid-1990s, for Europe at least.

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336 There is widespread agreement that increasing 337 global connectivity, in particular the growing volumes and rates of movement of goods and people, is the 338 339 most important factor influencing the increase in the 340 number of invasive insects and micro-organisms **3**41 (Fisher et al. 2012; Garnas et al. 2012; Liebhold 342 et al. 2012; Boyd et al. 2013; Santini et al. 2013; Roy 343 et al. 2014). Garnas et al. (2012) highlight the complex <mark>34</mark>4 interplay between factors that influence the global 345 movement of pests, leading to the rapid attainment of 346 global distributions and 'pest homogenization' on crop <mark>34</mark>7 and forestry hosts. Apart from trade and the movement 348 of people, these include: (1) the global homogeniza-349 tion of host species (e.g., Eucalyptus that is increas-350 ingly becoming a global fiber crop; Hurley et al. 351 2015); and (2) the positive feedback between global 352 introduction and spread and subsequent invasion. This <mark>35</mark>3 latter phenomenon, where invasive populations act as 354 the source of further introductions, has been termed 355 the "bridgehead effect" and is increasingly seen as an 356 important driver of increasing rates of global invasive 357 species.

358 The "bridgehead effect" was first described by 359 Lombaert et al. (2010) in the context of the invasion of the Harlequin ladybird beetle (Harmonia axyridis), 360 361 where a highly fit invasive population in North <mark>36</mark>2 America appears to have acted as a source from which **36**3 further invasions into Europe, South America and 364 Africa originated. This event was particularly note-365 worthy as it follows on many years where beetles reared and repeatedly released in multiple regions 366 367 failed to establish and invade, and appears to have 368 resulted from population admixture (Facon et al. 369 2011). This phenomenon—where one or more inva-370 sive populations serve as a source or hub for further 371 global introduction-has also subsequently been described for many other insects (see Table S1) and 372 is evident in invasions of S. noctilio, L. invasa and 373 other insects given to global spread. A particularly 374 successful original invasion that serves as the source 375 of subsequent invasions could be the result of an 376 evolutionary shift in this population that increases its 377 invasive ability. Alternatively, such patterns could be 378 ascribed to a geographic or other advantage with 379 respect to human movement and trade (Garnas et al. 380 2012). Understanding the processes that influence 381 some populations to serve as sources of invasion while 382 others not is an important objective of future studies of 383 384 invasive insects.

The increased recognition of the complexity of 385 invasion patterns in insects (and other organisms) has 386 been driven in a large part by advances in the 387 availability of more powerful molecular markers and 388 analysis tools. In insects, mitochondrial COI sequence 389 data have long been used to trace the origin of invasive 390 populations. While useful and often very informative, 391 this tool is also plagued by problems, such as poor 392 amplification in some groups or the presence of 393 nuclear mitochondrial pseudogenes (numts) that can 394 cause an overestimation of diversity and otherwise 395 confound phylogenetic relationships if not detected 396 (Song et al. 2008; Haran et al. 2015). The ease with 397 which modern sequencing platforms allow the devel-398 opment of SSR markers (Santana et al. 2009) as well 399 as their power and repeatability for population genetic 400 analysis, has led to a dramatic increase in the use of 401 such approaches over the past decade. These same 402 advances in sequencing technology are now also 403 driving the increased use of single nucleotide poly-404 morphisms (SNPs) as preferred markers, particularly 405 at a whole genome or transcriptome level (Chown 406 et al. 2014). These genomic approaches to population 407 genetics not only vastly increase the power of the 408 markers available to describe patterns of diversity, but 409 also enable the study of the causes and consequence of 410 invasion at a population genetic level. These tools 411 have not yet been widely applied to invasive insects. 412

Apart from standard population genetic and phylo-413 414 genetic tools that have long been used to characterize molecular data from invasive populations, clustering 415 methods and likelihood-free ABC methods have in 416 417 recent years made it possible to evaluate among and quantify key parameters of increasingly complex 418 hypotheses about invasion routes, dubbed "scenarios" 419 (Miura 2007; Estoup and Guillemaud 2010). Two such 420

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421 tools that appear to be most widely used at present **42**2 (together with traditional tools) are STRUCTURE 423 (Pritchard et al. 2000) and DIYABC (Cornuet et al. **4**24 2008). In particular, DIYABC (as other model-based 425 ABC programs) makes it possible to combine molec-426 ular marker data with data about invasion history, <mark>4</mark>27 bottlenecks and historical population sizes. This 428 allows for quantifying the relative probabilities of 429 multiple complex scenarios in ways that were previ-430 ously not possible (see Table S1 for recent applica-<mark>43</mark>1 tions of DIYABC). These tools are responsible for **43**2 elucidating a number of the surprisingly complex <mark>43</mark>3 invasion routes described above. Interpretation of <mark>43</mark>4 results from analyses using STRUCTURE and ABC 435 (among other tools) can be challenging, especially in the face of imperfect knowledge of introduction dates 436 and incomplete and non-standardized sampling of some populations. Dlugosch and Parker (2008), however, point out that invasive populations are typically 'oversampled' and that in most cases the results should reflect a fairly accurate picture of the diversity and relations of at least invasive populations. There have also been some criticisms of ABC approaches on theoretical grounds that should be considered when using or interpreting these data (Robert et al. 2011).

446 Consequences of complex global movement **4**47 of invasive species

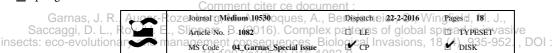
<mark>4</mark>48 The recognition that globally IAS are moving in **4**49 complex ways, that the number of propagules per 450 establishment event is often large, and that multiple **45**1 introduction events are common (sometimes from 452 disparate parts of the native or invasive range) has 453 broad consequences for predicted evolutionary trajec-454 tories of IAS (Lee 2002; Dlugosch and Parker 2008; 455 Wilson et al. 2009; Lawson Handley et al. 2011; Rius 456 and Darling 2014). In this section we focus on the <mark>45</mark>7 subset of invasive taxa that are adventive in at least 458 two or three disjunct regions and thus are currently-459 or have the potential to become-globally distributed, **46**0 and consider some of the consequences that such **46**1 patterns might have on fitness, local adaptation and long-term invasiveness. 462

463 Rates of secondary transfer to new areas and **46**4 migration between established populations increase 465 with the size and dispersion of the global adventive population. Thus, with each novel establishment 466

event, connectivity among regions increases and with 467 it the potential for the formation of novel genotype 468 assemblages in different regions (Fig. 1). Interestingly 469 (if intuitively), the probability of transfer to a new, 470 uncolonized region peaks then begins to decline once 471 half of the possible regions have been colonized, as the 472 opportunities for new establishments decline until a 473 species becomes cosmopolitan (Fig. 1, red line). This 474 contrasts starkly with the probability of movement of 475 individuals when secondary transfer among occupied 476 regions is included, which increases linearly with the 477 number of established regions (Fig. 1, blue line). The 478 479 fact that movement of individuals and propagules does not stop and in fact continues to increase once an area 480 has been invaded is perhaps an underappreciated 481 aspect of invasive species management. Unless there 482 are barriers to secondary introduction or spread, the 483 probability of admixture continues to increase and 484 remains high as species become globally distributed, 485 unless underlying pathways are disrupted (Garnas 486 et al. 2012). 487

Myriad direct and indirect effects of invasion have 488 been elucidated by researchers since Elton (1958) or 489 earlier and have been extensively reviewed (Liebhold 490 et al. 1995; Parker et al. 1999). However, the influence 491 of regional invasion on local and regional ecological 492 and evolutionary dynamics as well as on global 493 494 processes is perhaps less appreciated (Lee 2002; Lawson Handley et al. 2011). For example, the 495 phenomenon that "invasion begets invasion" is well 496 recognized, as reflected in emerging concepts such as 497 the bridgehead effect (Lombaert et al. 2010). Some 498 authors invoke rapid evolution in the adventive range 499 (e.g., selection for dispersal, for association with 500 human commerce or for other traits that enhance 501 fitness) as a key driver of the elevated probability of 502 503 subsequent transfer (Whitney and Gabler 2008). In some cases, this is surely true (Kolbe et al. 2007; 504 Turgeon et al. 2011). However, it is important to 505 recognize that these elevated rates are a property of 506 global population size and distribution and do not 507 require a specific mechanism to act when global 508 509 connectivity exists.

The increased potential for movement among 510 invaded regions brings with it a number of theoretical 511 possibilities for the mixing of genotypes or for the 512 sharing of acquired microbial associates and/or natural 513 enemies. Very high rates of secondary transfer could 514 have the effect of homogenizing populations and/or 515



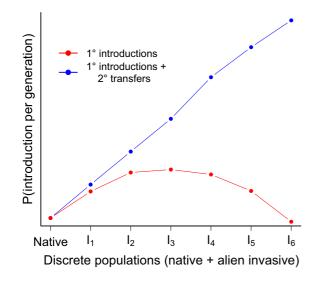


Fig. 1 Rates of transfer (P) to uninvaded regions (*red lines*) and to all regions irrespective of colonization status (*blue line*) based on simulation model employing a random transition matrix representing connectivity among region (n = 20,000). Note that when once half of the regions are colonized, the probability of populations reaching uncolonized regions decreases (to zero) while actual rates of transfer (and therefore the potential for transfer of cryptic genotypes or forms) continues to increase. It is likely that quarantine efforts would be abandoned once all six uncolonized regions (I_1 – I_6) are invaded while the movement of individuals continues. R code available upon request

516 communities across the adventive range, but this 517 seems unlikely given that introduction and establish-518 ment are still low-probability, chance events. Empir-519 ical evidence likewise supports the existence of 520 structure in the distribution of genotypes around the **52**1 world for many systems, rather than a pattern of global <mark>52</mark>2 panmixia (Sakai et al. 2001; Lombaert et al. 2010; **52**3 Boissin et al. 2012 and other examples discussed 524 above). Cases where haplotype diversity is low 525 typically arise from rapid spread of a genotype rather 526 than homogenization. Whether the creation of novel 527 assemblages via admixture is an important driver of 528 evolution (and perhaps of further rates and patterns of 529 spread) or whether genotype mixing is simply an <mark>53</mark>0 inevitable consequence of global invasiveness is a <mark>53</mark>1 key question with both practical and theoretical 532 considerations.

Admixture that brings together individuals and
genes from different source populations in the invasive range is now considered to be a common
phenomenon in invasive populations (Bossdorf et al.
2005; Wares et al. 2005; Rius and Darling 2014).

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However, understanding the importance of admixture 538 to evolution in the invasive range is not a simple 539 matter. The proposed roles of admixture include 540 promoting (1) genetic rescue of low diversity popu-541 lations (e.g., those at risk due to inbreeding or drift); 542 (2) adaptive evolution by increasing additive genetic 543 variance; (3) the aggregation of favorable traits or 544 gene combinations with possible effects on fitness; or 545 (4) disrupting local adaptation or creating mosaics of 546 maladaptation. Alternatively, admixture may have no 547 direct effects on population fitness or may be 548 confounded with correlated factors such as propagule 549 pressure that are difficult to tease apart (Rius and 550 Darling 2014). Finally, the effects of admixture may 551 be positive, negative or neutral depending on ecolog-552 ical context, the existence and outcomes of rapid 553 evolution in various parts of the invasive range, and/or 554 by the stochastic sampling of alleles via the processes 555 of both drift and secondary transmission. Some of the 556 hypothetical consequences of elevated propagule 557 pressure as well as different types of admixture are 558 559 highlighted in Fig. 2.

The role of genetic diversity

The importance of genetic diversity to population 561 success is so intuitive that it has become deeply 562 ingrained in the scientific literature. This is despite 563 myriad examples of widespread ecological success of 564 species that are either exclusively asexual, partheno-565 genetic, or have experienced severe bottlenecks post-566 introduction into a new range (Roman and Darling 567 2007). Two broad truths about the role of genetic 568 diversity and invasion success have emerged in the 569 past decades, as described in various examples above. 570 First, genetic diversity is not a prerequisite for the 571 establishment or spread of invasive organisms (e.g., 572 Keller and Waller 2002; Rius and Darling 2014; Arca 573 et al. 2015). Second, many invasive populations 574 exhibit high allelic diversity and are fully capable of 575 576 rapid adaptive evolution in the adventive range (e.g., Kolbe et al. 2004, 2007; Lawson Handley et al. 2011). 577

Key mechanisms

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The idea of diversity as a prerequisite for long-term579population growth and viability takes a few different580forms. First, there are direct effects on individual581

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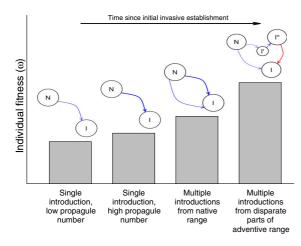


Fig. 2 Hypothetical consequences for mean individual fitness (ω) arising from common invasion scenarios. In these scenarios, the capacity for adaptive evolution in invasive populations is shown to increase (from *left* to *right*) with higher propagule number, where multiple introductions from the native range (*N*) result in simple admixture in an invasive range (*I*), and where admixture follows adaptive evolution in part of the global invasive range (*I*, *I'* and *I''*). Of course, not all empirical examples conform to this paradigm, and there are many counter examples. Still, these ideas are pervasive in the literature and warrant additional testing. Though not strictly necessary, scenario complexity may tend to increase as function of time since initial invasive establishment, indicated by the *black arrow*

582 fitness. Genetic diversity reduces inbreeding depres-583 sion, and in sexually reproducing individuals facili-584 tates the purging of deleterious mutations and the 585 decoupling of unfavorable gene combinations, particularly under bottlenecks of intermediate intensity 586 587 (Gleman 2003). Recent observational and experimen-588 tal evidence from the invasion of the Harlequin 589 Ladybird strongly suggests that moderate bottlenecks **59**0 can positively affect invading populations, in part by 591 increasing robustness to inbreeding (Facon et al. **59**2 2011). In contrast, levels of genetic diversity appeared **59**3 to play little or no role in the success of at least five **59**4 independent introductions of the Western Corn Root-595 worm from native North America into Europe (Ciosi 596 et al. 2008). In this case multiple introductions from 597 the same source pool have not resulted in admixture to 598 date but have led to the continental co-occurrence of 599 independent populations that are genetically distinct, 600 most likely as a result of drift.

The second main argument in support of theimportance of genetic diversity is that it enhancesthe capacity for adaptive evolution. Heritable genetic

variation is required for adaptation to novel or 604 changing conditions, which has been shown to occur 605 in a number of introduced species (Lee and Gelembiuk 606 2008; Whitney and Gabler 2008; Jones and Gomulk-607 iewicz 2012; Zenni et al. 2014; Tanaka et al. 2015). 608 Very often, IAS occupy a breadth of habitats and 609 niches, in many cases across broad geographic ranges 610 with divergent biotic and abiotic environments. Many 611 authors have taken this pattern as implicit evidence 612 that genetic diversity would at least benefit exotic 613 invaders if not represent a requirement for medium- to 614 long-term population success (Kolbe et al. 2004; 615 Roman and Darling 2007). However, phenotypically 616 plastic genotypes capable of coping with a variety of 617 conditions have been shown to be crucial to invasive-618 ness in many systems (Zepeda-Paulo et al. 2010; 619 Barrett 2015). In fact, phenotypic plasticity itself-620 once considered an impediment to adaptive evolu-621 tion-can mask cryptic diversity and promote the 622 emergence of novel traits, ultimately leading to an 623 increase in heritable genetic variation and to popula-624 tion and/or species divergence or local adaptation 625 (Hughes et al. 2008; Pfennig et al. 2010; Hughes 626 2012). Additionally, theoretical models demonstrate 627 that genetic bottlenecks have the capacity to increase 628 additive genetic variation in affected populations-629 either by "converting" epistatic into additive variation 630 via the fixation of some alleles due to drift (Goodnight 631 1988) or by increasing the frequency of rare recessive 632 alleles at loci where dominance effects occur (Robert-633 son 1952; Willis and Orr 1993). While some studies 634 are consistent with such predictions (Bryant and 635 Meffert 1993; Saccheri et al. 2006), on the whole 636 empirical evidence has been equivocal (van Heer-637 waarden et al. 2008; Jarvis et al. 2011; Dlugosch et al. 638 2015) and primarily derived from limited laboratory 639 studies. 640

Genetic effects of population size and population641growth642

Invasive populations tend to be characterized by high 643 population densities, rapid population growth, rapid 644 spread and broad geographic extent. Theory predicts 645 that population abundance and rates of expansion can 646 themselves influence the rates of loss, maintenance 647 and accrual of genetic diversity. For example, the total 648 number of mutations per generation and neutral 649 genetic diversity tend to scale linearly with population 650

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<mark>65</mark>1 size (Dlugosch et al. 2015). However, the relationship 652 between rate of evolution and effective population size 653 (N_e) is complex and difficult to predict in natural **65**4 systems given the opposing processes of drift and <mark>65</mark>5 selection. Theoretical and empirical studies tend to 656 support a negative relationship between population <mark>65</mark>7 size and rates of evolution (Lanfear et al. 2014), **65**8 though population expansion or contraction can tem-659 porarily increase these rates if some mutations are adaptive (Charlesworth and Eyre-Walker 2007; Lan-660 <mark>66</mark>1 fear et al. 2014). Thus, as invasive populations 662 increase rapidly post-establishment, rates of adaptive evolution may be elevated. However, this effect is 663 likely to be ephemeral in the absence of population 664 subdivision (which can allow small Ne to persist even 665 as global population size increases). Population struc-666 667 ture has been shown in a number of invasive insect species, especially in patchy environments (Villablanca et al. 1998), but its role as a driver of evolutionary change in rapidly spreading global invaders is far from established.

Genetic diversity and niche breadth

673 The idea of a positive relationship between niche 674 breadth and genetic and/or phenotypic diversity has 675 been around since at least Van Valen (1965). How-**67**6 ever, it has been notoriously difficult to establish 677 generality with respect to this phenomenon. Steiner 678 (1977) showed a moderate positive correlation <mark>67</mark>9 between average heterozygosity in Hawaiian Droso-680 phila species and host plant use (as well as elevation), though other authors have concluded that genetic 681 682 diversity is more strongly associated with habitat or 683 environmental heterogeneity (Pamilo 1988). In at least 684 one case, that of the globally invasive Argentine ant, 685 the loss of genetic diversity during invasion is cited as 686 one of the key elements promoting ecological success 687 (Starks 2003; Tsutsui et al. 2003). However, this <mark>68</mark>8 phenomenon may be unique to social insects and **68**9 therefore linked more to life history and patterns of **69**0 polygyny than to diversity within invasive populations <mark>69</mark>1 per se (Pedersen et al. 2006; Garnas et al. 2007).

<mark>69</mark>2 Many species appear capable of occupying a range **69**3 of habitats and climatic conditions despite single <mark>69</mark>4 introductions of only a few individuals or propagules. **69**5 For example, Drosophila subobscura populations in 696 the New World are estimated to have originated from **69**7 fewer than 15 individuals and have now spread to cover over 15 degrees of latitude in both the Northern 698 and Southern Hemispheres (Huey et al. 2000; Pascual 699 et al. 2007; Balanyà et al. 2009). In this case, despite a 700 strong bottleneck, there appears to have been strong 701 selection for chromosomal inversion frequency and 702 703 for wing size, both of which show a predictable latitudinal cline in the native range that has developed 704 independently in both northern and southern intro-705 duced populations. While the *D. subobscura* example 706 provides strong evidence of contemporary evolution in 707 low-diversity introduced populations-indeed some 708 of the fastest rates of trait evolution documented to 709 date in natural populations-the strength of the cline is 710 still considerably weaker than in native Europe. 711 Whether this reflects some consequences of reduced 712 diversity or simply the wider temperature range (and 713 variability) experienced by flies across their European 714 715 range, is not known. Additional chromosomal inversion types that correlate with climate regime are 716 present in Europe but have not yet been introduced 717 elsewhere. The idea that the arrival of one or more of 718 these types could enhance adaptive potential is an 719 intriguing possibility that cannot currently be tested. 720

Niche breadth may also expand in response to 721 relaxed interspecific competition, which along with a 722 loss of natural enemies, may facilitate the occupation 723 of a greater proportion of the fundamental niche. 724 725 However, the question of whether more generalized populations are themselves more genetically variable 726 has been elusive. There is a clear role for phenotypic 727 728 plasticity and/or selection for a generalized genotype, particularly in recently introduced populations (Rius 729 and Darling 2014). However, structured or diversified 730 731 habitat use does appear to arise as population niche breadth increases (Bolnick et al. 2007), though the 732 changes may or may not be heritable or even 733 genetically based (but see Pfennig et al. 2010). 734

Success of clonal invaders

735

736 Asexual organisms often have superior capacity for colonization and rapid spread, owing at least in part to 737 the ability of single individuals to start new popula-738 tions, the absence of a need for mate finding, and the 739 roughly twofold advantage in rates of population 740 growth (Maynard Smith 1978). There is some evi-741 dence, however, that habitat stability (i.e., low levels 742 of disturbance) and temporal instability (i.e., annual 743 crops which must be re-invaded each growing season) 744

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745 favor parthenogens (Hoffmann et al. 2008). For 746 example, a study of sympatric sexual versus asexual 747 populations of Rhopalosiphum padi (the bird cherry-748 oat aphid) showed that the diversity of host plants 749 utilized by the two forms differed significantly. 750 Isotopic signatures of asexual populations strongly suggested feeding on C₄ host plants (represented only <mark>75</mark>1 752 by maize in the region where the study was per-753 formed), whereas sexually reproducing individuals 754 primarily fed on C₃ plants, likely utilizing a far greater <mark>75</mark>5 diversity of grassland plants in the family Poaceae 756 (Gilabert et al. 2014).

757 A disproportionate number of IAS exhibiting low 758 genetic diversity are asexual, at least in aquatic 759 systems (Roman and Darling 2007). Many insects, even those for which recombination is common in the 760 761 native range, also show a tendency to switch to obligate or facultative parthenogenesis in introduced populations (Dybdahl and Kane 2005; Caron et al. 2014). Clonal lineages do exhibit some genetic variability, however, though inheritance and selection typically occur at the scale of the genome (rather than genes) in the absence of recombination. Most of this variation in asexual lineages probably derives from mutation, though gene duplication, chromosomal rearrangement and horizontal gene transfer (among other plausible mechanisms) can result in intraclone variability, including in insects (Lushai et al. 2003). In fact, evidence of within or among clone diversity in asexually reproducing organisms is accumulating. For example, Dybdahl and Kane (2005) found non-zero 776 heritabilities in important life history traits in a 777 parthenogenetic freshwater snail invader, though no 778 evidence of local adaptation was detected (suggesting 779 evolutionary potential but not necessarily that rapid 780 evolution had occurred). The same study also reported 781 evidence for phenotypic plasticity across elevations 782 but no all-purpose genotype (Baker 1965), which according to the authors predicts a flat reaction norm 783 <mark>78</mark>4 landscape across habitats.

785 Whether or not the success of clonal invaders bears 786 directly on the importance of genetic diversity and/or <mark>78</mark>7 admixture in non-clonal invaders is an open question. <mark>78</mark>8 In addition, there are contravening examples where 789 sexual invaders appear to displace ecologically sim-<mark>79</mark>0 ilar, asexual congeners (Auger-Rozenberg and Roques 791 2012). In the absence of horizontal gene transfer or **79**2 occasional or cryptic sex, there is no direct effect of 793 admixture in asexual organisms, as genomes do not 810

introgress. However, the concept of a true clonal 794 population has received criticism in recent years due to 795 high rates of intraclone variability, persistence of rare 796 genotypes and strong evidence for adaptive evolution 797 (Loxdale and Lushai 2003; Lushai et al. 2003). 798 799 Numerous asexual pests, for example, have evolved resistance to insecticides, including the spotted alfalfa 800 aphid, Therioaphis maculata in North America (Dick-801 son 1962). Populations of this insect currently com-802 803 prise numerous strains, including some with insecticide-resistance traits, despite apparently being 804 derived from a small asexual founder population 805 within a few generations (Lushai et al. 2003). In fact, 806 intraclone selection in obligate parthenogens appears 807 to be the norm across many groups, and in some cases 808 may be strong (Vorburger 2006). 809

Admixture and interspecific hybridization

Among the factors with the potential to influence 811 evolutionary trajectories in globally invasive popula-812 tions, perhaps the one most likely to be strongly 813 influenced by complexity in patterns of global spread 814 is admixture. Admixture refers to the genomic mixing 815 that results from the interbreeding of individuals from 816 distinct source populations or lineages. Secondary 817 contact outside the native range scales with the rate of 818 transfer among regions along with the number of 819 independent introductions outside the native range, 820 both of which are strongly influenced by growing 821 volumes of global trade. The importance of admixture 822 has historical precedent too and has been well 823 characterized with respect to the evolution of our 824 own species. Reconstructions of intraspecific admix-825 ture throughout human pre-history strongly suggests 826 that this has been common during range expansion and 827 secondary migration in humans, and very likely was an 828 important force favoring the sharing of favorable 829 alleles and for adaptive evolution (Hellenthal et al. 830 2014). There is also growing evidence that interspeci-831 fic admixture with Neanderthals was an important 832 833 source of adaptive variation for skin phenotype, and 834 perhaps other traits as well (Vernot and Akey 2014). Admixture has also been implicated in facilitating 835 range expansion under conditions of both current and 836 historical climate change in insects and other taxa 837 (Petit et al. 2003; Krehenwinkel and Tautz 2013). 838

Understanding how admixture influences fitness, 839 local adaptation and adaptive potential in invasive 840

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<mark>84</mark>1 species is not a simple task. First, multiple introduc-842 tions are a logical requirement for admixture in the 843 invasive range to occur (including for independently 844 introduced lineages which come into contact via <mark>8</mark>45 secondary spread). However, multiple introductions 846 can have direct effects on spread potential via elevated <mark>8</mark>47 propagule number, irrespective of source population 848 identity or differentiation. Second, while short-term 849 gains linked to heterosis-even if ultimately lost via 850 backcrossing-can be an important mechanism for <mark>85</mark>1 demographic rescue in small populations, such effects 852 might be easily confused with longer term benefits <mark>85</mark>3 linked to increased additive genetic variation (Rius 854 and Darling 2014). Admixture arising from the arrival 855 of novel alleles and gene combinations from secondary spread within and among regions can disrupt 856 857 locally adapted populations via gene swamping 858 (Verhoeven et al. 2011). Alternatively, admixture 859 can increase genetic diversity and adaptive potential, 860 or bring new "pre-adapted" traits with consequences 861 for fitness to established populations. In one case-862 that of H. axyridis-admixture is credited as a 863 principal cause in the creation of a bridgehead 864 population in eastern North America, which then <mark>86</mark>5 exported individuals with increased fitness and 866 propensity to invade to Europe and perhaps beyond 867 (Lombaert et al. 2010). A follow-up laboratory study 868 showed that key life history traits were changed in 869 favor of higher fitness in experimental crosses 870 designed to recreate observed admixture (between **87**1 the North American and biocontrol strains; Turgeon 872 et al. 2011). In the majority of cases where admixture 873 is implicated, however, little evidence exists that the 874 mixing of genotypes has had serious impacts on global invasiveness (Chapple et al. 2013; Rius and Darling 875 876 2014). In addition, several of the studies that have 877 detected positive effects of admixture attribute these to 878 short-term heterotic effects rather than gains in 879 additive genetic variation (Keller and Taylor 2010; <mark>88</mark>0 Keller et al. 2014), though this can still have important 881 long-term consequences.

882 Resource use and genetic diversity in insects

883 From the perspective of management of invasive pests,
884 particularly those under intensive management such as
885 in forestry or agricultural landscapes, a positive
886 correlation between admixture and invasiveness is not

the only way in which admixture could influence 887 relevant dynamics. To the degree that admixture 888 enhances fitness (e.g., via local adaptation or the 889 acquisition of favorable life history traits), impacts 890 equilibrium abundances and/or increases the propensity 891 892 for outbreak dynamics, such mixing could be very important. Perhaps more relevant in such systems, 893 however, is how admixture might influence either host 894 range or the capacity for adaptation to mitigation 895 strategies themselves. For example, the importation of 896 insecticide-resistance alleles has occurred via sec-897 ondary transfer in the peach potato aphid and has had 898 major consequences for growers in affected regions 899 (Margaritopoulos et al. 2009). 900

Biotypes and cryptic species

The increasingly widespread use of molecular tools 902 for species identification and the exploration of 903 population substructure has led to major increases in 904 the identification of cryptic species and/or biotypes 905 (Lawson Handley 2015). Biotypes are generally 906 considered to be population or lineages within a 907 species that differ in key traits. Often, biotypes are 908 asexual lineages and can differ in host preference (host 909 races), geography (geographic races) or other aspects 910 of life history, ecology or morphology. In addition to 911 differentiation in host (plant or insect) use, differences 912 in phenology among distinct types appear important to 913 maintaining separation. There are several examples of 914 915 the arrival of a genotype or species that is morphologically similar to individuals in an already invaded 916 917 area that has resulted in additional damage, increased 918 niche breadth, or that has confounded management (Perring 2001; Saltonstall 2002; Peccoud et al. 2008; 919 Garnas et al. 2012; Mapondera et al. 2012; Wenger 920 and Michel 2013; Shadmany et al. 2015). For example, 921 distinct host races of the pea aphid (Acyrthosiphon 922 pisum) feeding on pea and broad bean, alfalfa and red 923 clover in Chile are descended from biotypes in Europe 924 (rather than evolving in situ; Peccoud et al. 2008). 925 Thus it seems likely that multiple introductions of 926 927 host-adapted biotypes are responsible for the broad host range of this species rather than in situ evolution 928 in the invasive range. Similarly, some species of the 929 wheat curl mite ("Aceria tosichella complex") are 930 widely distributed with broad host range while others 931 are restricted and specialized (Carew et al. 2009; 932

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Skoracka et al. 2013, 2014). Other co-introduced
lineages (e.g., *S. noctilio*, *T. peregrinus*) do not appear
to differ markedly in host range, though more subtle
differences in preference cannot be excluded. Establishing the generality of biotype-specific host use in
invasive insects has major implications for quarantine
and pest management.

The Enemy Release Hypothesis is a central and well

940 Community sharing and symbiont transfer

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supported (if partial) explanation of the success of <mark>94</mark>2 943 invasive species (Roy and Lawson Handley 2012; 944 Heger and Jeschke 2014). However, when individuals from distinct source populations or lineages come 945 946 together, they rarely come alone. Invasive insects, for **9**47 example, bring with them a suite of obligate and <mark>94</mark>8 facultative symbionts, including mutualists, parasites **9**49 and commensals, some of which can have important <mark>95</mark>0 effects on fitness (Dillon and Dillon 2004; Moran <mark>95</mark>1 2007). In addition, there is growing evidence of **95**2 symbiont switching in novel communities (Werren et al. 2008; Taerum et al. 2013). For example, increased <mark>95</mark>3 <mark>95</mark>4 performance and the production of female-biased 955 offspring in Rickettsia-infected whiteflies (Bemisi 956 tabaci) provide a strong case for the role of a facultative **95**7 endosymbiont in the insect's invasion in California 958 (Himler et al. 2011; Lawson Handley et al. 2011). <mark>95</mark>9 Fungal symbionts once thought to be obligately asso-960 ciated with specific hosts have also been seen to change 961 in invasive populations. Populations of native Sirex <mark>96</mark>2 nigricornis in North America now regularly carry 963 Amylostereum areolatum, a fungal symbiont carried— **96**4 and putatively introduced—by the invasive S. noctilio, 965 and vice versa with the A. chailletii symbiont of S. 966 nigricornis (Hajek et al. 2013; Olatinwo et al. 2013; 967 Wooding et al. 2013). The fitness consequences of this switch are not yet known, but what is clear is that 968 969 secondary transfer of North American populations of S. **97**0 noctilio now carries additional risk. Given the ubiqui-**97**1 tous associations between insects and microbes, the co-**97**2 introduction and/or novel acquisition of microbial 973 associates by invasive insects may be quite common, **97**4 with impacts that are typically subtle or at least 975 overlooked. There are cases, however, where novel 976 associations acquired in a non-native range can have 977 truly devastating consequences (Hulcr and Dunn 2011; **97**8 Wingfield et al. 2015, this volume).

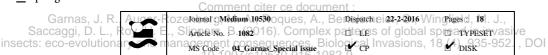
Implications of complex movement patterns for management	979 980
Quarantine and control	981

Controlling the movement of harmful or invasive 982 species is an incredibly complex task. Even for known 983 pests, restricting pathways and/or maintaining effec-984 tive quarantine requires constant vigilance as well as 985 cooperation from all relevant trade partners. Agree-986 ments such as those under the International Plant 987 Protection Convention (IPPC) aim to establish stan-988 dards to ensure fairness and technical soundness of 989 trade control measures, but competing interests, the 990 economic benefits of free trade and the sheer volume 991 992 of global shipping and transport make the prevention of primary or secondary pest establishment a daunt 993 ing task (Mumford 2002; Saccaggi et al. 2015, this 994 995 volume). Application of phytosanitary measures under these protocols, container inspection, and post-harvest 996 997 treatments (e.g., irradiation, heat, methyl bromide treatment, or exposure to high CO_2 or low O_2 998 concentrations) are often expensive and/or inade-999 quately applied, variably effective and inconsistently 1000 enforced (Liebhold et al. 2012; Haack et al. 2014; Roy 1001 et al. 2014; Eschen et al. 2015). Still, programs aimed 1002 at maintaining pest-free zones (PFZs) have been 1003 successful in some cases, such as for the medfly in 1004 Chile where consistent monitoring and regular erad-1005 ication efforts have prevented populations from gain-1006 ing a foothold since 1982 (Follett and Neven 2006). 1007

Given the difficulties of maintaining a PFZ or of 1008 preventing the establishment of known and unknown 1009 pests alike, it is not surprising that managing genotype 1010 or provenance-specific movement of established pests 1011 receives very little consideration. Once a pest has 1012 become firmly established, maintaining quarantine 1013 import restrictions is likely to be complicated by fair 1014 trade regulations (Mumford 2002). The one exception 1015 is for species where clear biotypes or strains can be 1016 identified, though this is the case for only a small 1017 subset of species. The arrival of new biotypes of the 1018 pea aphid to Chile increased the host range of the 1019 insect considerably, with major economic effect 1020 (Caron et al. 2014). 1021

So what of the knowledge that admixture, at least1022under certain circumstances, can influence invasive-1023ness or the capacity for adaptive evolution in intro-1024duced populations? In the face of massive economic1025

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1026 forces promoting free trade, it is unlikely that a purist 1027 strategy (such as banning or severely restricting trade 1028 among regions with different genotypes of the same 1029 pest) is feasible or even desirable. However, in a 1030 number of cases, ongoing vigilance may have prevented the movement of genotypes, biotypes or key symbionts, potentially avoiding further catastrophic effects of invasion. We advocate increased consideration of genetic and microbial diversity when implementing quarantine or the regulation of movement of globally established pests. It is critical for governments and regulatory agencies to recognize that the probability of movement of individuals increases significantly with global population size and with each region that is invaded. This is probably reasonably accepted with respect to the likelihood of new colonization events. However, greater recognition is needed that rates of secondary transfer increase and remain high even once a pest attains a global distribution (Fig. 1). This can have dramatic conse-1046 quences for evolutionary trajectories, and the long-1047 term efficacy of control methods is underappreciated 1048 at best.

1049 Prospects for the future

1050 Molecular tools have powerful potential for detecting 1051 the spread of pests and pathogens, but there are many 1052 challenges (Armstrong and Ball 2005; Bohmann et al. 1053 2014; Chown et al. 2014; Lawson Handley 2015). 1054 Environmental sampling, for example, is already being 1055 used to track the movement and spread of aquatic 1056 invaders via the detection of invader DNA rather than 1057 the species themselves (Jerde et al. 2011). Bulk 1058 screening of insect or microbial samples using mas-1059 sively parallel barcoding approaches could potentially 1060 be used to flag known invaders at ports of entry. Current 1061 limitations linked to cost, time and the availability of 1062 comprehensive barcoding databases of known pests 1063 present significant difficulties. However, there is little 1064 doubt that such technical barriers could be overcome 1065 with time and sufficient effort. In fact, there is scope for 1066 considerable automation of such screening, which 1067 would clearly be necessary given the volumes of trade 1068 in question. While at their core, inspection-based 1069 methods require a "blacklisting" philosophy where 1070 known pests are denied, such lists could be expanded to 1071 incorporate aspects of population-level diversity in the 1072 context of the known distribution of genotypes. In addition, enhanced databases together with advanced 1073 clustering algorithms should allow the flagging of 1074 species that are phylogenetically related to known 1075 invaders. Potentially harmful symbionts could also be 1076 readily detected in this way. 1077

Conclusions

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In this paper we examine and reflect on the growing 1079 evidence of complex patterns of global movement of a 1080 number of important invasive pests. One consequence 1081 of this complexity is widespread admixture and a 1082 general increase in genetic diversity over time. While 1083 the consequences of these patterns are not always 1084 clear, there is evidence that mixing of divergent 1085 lineages contributes to rapid evolution and to inva-1086 siveness and may seriously complicate management 1087 efforts. There are currently few, if any, effective 1088 mechanisms in place to systematically track genetic 1089 and evolutionary changes in populations at regional, 1090 national or international scale. There appears to be 1091 even less action with regard to policy to mitigate 1092 secondary spread between invaded regions despite 1093 clear evidence of its importance. Inclusion of such 1094 considerations within risk assessment protocols would 1095 1096 be a first step. The patterns and consequences high-1097 lighted in this paper will hopefully contribute to an urgent call for efforts to address these shortcomings. 1098

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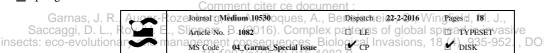
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