



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 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

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

Introduction

A fundamental problem in invasion biology has long been how to reconcile the likelihood of reduced genetic diversity via founder effects with invasive success across a range of habitats and niches in the short and long term. Once a central “paradox” of the discipline, researchers now understand that genetic diversity has been historically underestimated in many introduced species, while other invaders appear remarkably tolerant to genetic uniformity and may even benefit from periodic founder effects (Roman and Darling 2007). Considerable work in the past few decades has focused on understanding the role of phenotypic plasticity in invasion success, mechanisms of tolerance to low diversity and rapid evolution in introduced populations—all of which appear to be variously important in different systems to invasion success (Lee 2002; Dlugosch and Parker 2008; Whitney and Gabler 2008; Lawson Handley et al. 2011). There is also growing recognition that high levels of genetic diversity can be preserved during introduction and establishment (e.g., via high propagule number or multiple introductions) and that genetic diversity can increase over time since establishment, primarily due to subsequent introductions from the native or adventive range (Kolbe et al. 2007; Keller and Taylor 2010; Rius and Darling 2014; Gladioux et al. 2015). A new paradigm emerging from this work contends that global movement and spread for many invasive alien species (IAS) is rapid and often complex and that multiple introductions and migration among disjunct parts of the adventive range are common. Thus, apparently disparate populations across continents are effectively connected by gene

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

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

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

Patterns of global insect movement

There is an accumulating number of examples where the global movements of IAS are characterized by (1) rapid spread from points of introduction via population growth and natural dispersal; (2) frequent jump

dispersal to uncolonized, noncontiguous areas; (3) multiple introductions from the native range; and (4) frequent exchange among disjunct invasive populations worldwide. In some cases, there is also evidence for back-introduction from invasive populations into the native range. The Sirex woodwasp, *Sirex noctilio*, provides an excellent example of such complexity. Since 1900, *S. noctilio* has invaded exotic *Pinus* plantations in Australasia, South America and Southern Africa and more recently (2005) into native and exotic *Pinus* stands in North America (Slippers et al. 2015). Original hypotheses based on limited data proposed a simple, stepwise route of introduction between countries in the Southern Hemisphere (Slippers et al. 2001). However, a recent comprehensive analysis using mitochondrial cytochrome oxidase I (COI) sequence and Simple Sequence Repeat (SSR) data, as well as various population genetic tools [including Approximate Bayesian Computation (ABC) analysis; Cornuet et al. 2008] revealed far greater complexity in patterns of global spread (Boissin et al. 2012). Two evolutionarily distinct lineages of the wasp have spread widely, one of which has a proximate origin in Europe while the origin of the other is unknown. These lineages co-occur in some regions including Chile and South Africa where they interbreed, resulting in admixture. Most regions appear to have received migrants from other invasive populations (e.g., South America from Europe, Australasia and a population of unknown origin; South Africa from South America and Australasia, etc.), creating complex population admixtures of different proximate sources, which may or may not represent distinct lineages (but that differ at neutral markers). Even North American populations, where the invasion was most recently reported, appear to have experienced introductions from at least two sources (Bergeron et al. 2011; Boissin et al. 2012; Castrillo et al. 2015). Interestingly, these analyses also suggest that Europe, where the wasp is native, has been invaded by a lineage of unknown origin, possibly via an invasive population in South America (Boissin et al. 2012).

The complex pattern of spread and mosaic of genetic mixing among invasive populations, as illustrated by the *S. noctilio* example, is by no means unique to that system. A quantitative review by Dlugosch and Parker (2008) of recent population genetic studies of plant, animal and fungal invasions concluded that while most invaders experience a loss

of diversity initially (i.e., years to decades post-establishment), diversity is often restored through multiple introductions, increased populations sizes (countering drift) and interconnectivity of populations, and sometimes can even exceed that of native source populations (e.g., Kolbe et al. 2004, 2007). Interestingly, Dlugosch and Parker (2008) found a U-shaped pattern in diversity loss over time; that is, reductions in allelic richness are most severe at intermediate time points post-introduction, perhaps suggesting the importance of drift over founder effects. A number of studies on invasive alien insect populations also support the generality of the pattern that diversity increases with time since introduction. For example, in an extensive review of medfly (*Ceratitis capitata*) studies, Malacrida et al. (2007) found that multiple introductions consistently contribute to the maintenance or enhancement of genetic diversity in this important global invader. Similar processes have been described in invasive populations of the Eucalyptus Bronze Bug, *Thaumastocoris peregrinus* (Nadel et al. 2009), Harlequin Ladybird, *Harmonia axyridis* (Lombaert et al. 2010; Roy et al. 2016), Red Tomato Spider Mite, *Tetranychus evansi* (Boubou et al. 2012), Eastern Subterranean Termite, *Reticulitermes flavipes* (Scaduto et al. 2012), mosquito *Aedes japonicas japonicas* (Zielke et al. 2014), and a number of other insect invaders (Table S1). The changing nature of invasive alien populations caused by multiple introductions over time highlights the need to periodically reassess diversity in such populations (something that is not currently being done routinely for most invasive populations), especially in light of the implications this can have for management, as discussed below.

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

initiated by only a few founders, the subsequent (serial) introductions into North America apparently 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).

One of the outcomes of multiple introductions from the native range of invasive insects is that globally, populations of some invading pests can comprise two or more distinct lineages, or even cryptic species (Miura 2007). For example, in globally invasive populations of a Eucalyptus leaf weevil (*Gonipterus* spp.), at least three distinct species have been found with two species co-occurring in some regions without the knowledge of the practitioners managing the pest (Mapondera et al. 2012). Here an incorrect name, '*Gonipterus scutellatus*', has been applied to the invasive pest for decades, becoming a serious impediment to management, including the selection of specific biocontrol agents and understanding of invasion patterns. Invasive mites too, most notably eriophyoids, have regularly been found to comprise multiple cryptic lineages and/or species (Carew et al. 2009; Skoracka et al. 2014) with closely related, morphologically indistinguishable but molecularly distinct forms that differ in important ecological characteristics (particularly host range; Skoracka et al. 2013), that co-occur in complex mosaics. The degree to which the cryptic species and/or lineages require more nuanced, targeted (or diversified) management strategies is largely unknown. Cryptic forms are at the very least a complicating factor for research and management. The *Gonipterus* and eriophyoid examples clearly illustrate how genetic tools can inform management but also highlight the desperate need for adequate taxonomic systems to describe this diversity. In many cases expertise to identify and describe cryptic species or distinct lineages using traditional tools simply does not exist. New ways to systematically characterize and/or name biological diversity that go beyond traditional taxonomic approaches will have to be explored, particularly with respect to microbes (Maddison et al. 2012), though also for insects.

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

invader's range (e.g., if management must be customized), the uniting or reuniting of previously isolated populations or species can result in unique combinations of alleles via hybridization or admixture, which can further complicate management approaches. For example, the emergence of new genetic combinations resulting from uniting or reuniting separately evolving lineages has been shown for the Pine Processionary Moth, *Thaumethoea pityocampa*. While the moth was considered to have expanded naturally from southern Europe with global warming, its northward spread now appears to have been driven at least in part by long-distance transport by humans of potted pine trees. As a result, the northern front of the advancing distribution is characterized by genetic admixture combining genes of populations from different parts of Europe having different primary phenologies (Kerdelhué et al. 2015).

The existence of globally distributed species is not new, and in some cases appears to be largely independent of modern trade (i.e., in highly dispersive species with wide environmental tolerances, though cryptic species also commonly occur in these groups; Spellerberg and Sawyer 1999; Nelson 2002). Very clearly, however, global spread is very strongly influenced by the movement of our own species (e.g., Liebhold et al. 2012; Santini et al. 2013). Based on a recent spate of invasions of pests of agriculture, including forest plantations of pine and eucalypts (particular the latter), it appears that many invasive insects are reaching global status much more rapidly than before (Hurley et al. 2016; Roques et al. 2016). Species such as *S. noctilio*, *Gonipterus* spp. and *Ctenarytaina eucalypti* (among others) that escaped their respective native ranges in the late 1800s/early 1900s generally took between 50 and 100 years to reach truly global distributions (i.e., presence on all or most continents where hosts occur). Among more recently emerging invasive insects, several have achieved such distributions in little more than a decade or less. For example, *Leptocybe invasa*, a gall wasp on *Eucalyptus*, was first reported in Israel in 2000 (Mendel et al. 2004). At that time, this wasp was completely unknown, but by 2008 it had spread throughout the North and South America, southern and southeast Asia, the Mediterranean and Africa in what appeared to be a more or less stepwise fashion (Nugnes et al. 2015). *L. invasa* spread has been exceptionally rapid, but several other pests of

Eucalyptus (e.g., *Glycaspis brimblecombei*, *Ophelimus maskelli* and *Thaumastocoris peregrinus*) are currently spreading globally with similar pace. This phenomenon has been seen in a number of insects from diverse taxonomic lineages, as well as across hosts, herbivorous feeding guild, and life histories (Hurley et al. 2016). While some recently emerging pests that exhibit rapid spread could be specifically and idiosyncratically linked to pathways that permit it (Paine et al. 2010), Roques et al. (2016) showed that this faster spread constitutes a general phenomenon for invasive insects since the mid-1990s, for Europe at least.

There is widespread agreement that increasing global connectivity, in particular the growing volumes and rates of movement of goods and people, is the most important factor influencing the increase in the number of invasive insects and micro-organisms (Fisher et al. 2012; Garnas et al. 2012; Liebhold et al. 2012; Boyd et al. 2013; Santini et al. 2013; Roy et al. 2014). Garnas et al. (2012) highlight the complex interplay between factors that influence the global movement of pests, leading to the rapid attainment of global distributions and ‘pest homogenization’ on crop and forestry hosts. Apart from trade and the movement of people, these include: (1) the global homogenization of host species (e.g., *Eucalyptus* that is increasingly becoming a global fiber crop; Hurley et al. 2016); and (2) the positive feedback between global introduction and spread and subsequent invasion. This latter phenomenon, where invasive populations act as the source of further introductions, has been termed the “bridgehead effect” and is increasingly seen as an important driver of increasing rates of global invasive species.

The “bridgehead effect” was first described by Lombaert et al. (2010) in the context of the invasion of the Harlequin ladybird beetle (*H. axyridis*), where a highly fit invasive population in North America appears to have acted as a source from which further invasions into Europe, South America and Africa originated. This event was particularly noteworthy as it follows on many years where beetles reared and repeatedly released in multiple regions failed to establish and invade, and appears to have resulted from population admixture (Facon et al. 2011). This phenomenon—where one or more invasive populations serve as a source or hub for further global introduction—has also subsequently been described

for many other insects (see Table S1) and is evident in invasions of *S. noctilio*, *L. invasa* and other insects given to global spread. A particularly successful original invasion that serves as the source of subsequent invasions could be the result of an evolutionary shift in this population that increases its invasive ability. Alternatively, such patterns could be ascribed to a geographic or other advantage with respect to human movement and trade (Garnas et al. 2012). Understanding the processes that influence some populations to serve as sources of invasion while others not is an important objective of future studies of invasive insects.

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

Apart from standard population genetic and phylogenetic tools that have long been used to characterize molecular data from invasive populations, clustering methods and likelihood-free ABC methods have in recent years made it possible to evaluate and quantify key parameters of increasingly complex hypotheses about invasion routes, dubbed “scenarios” (Miura 2007; Estoup and Guillemaud 2010). Two such

tools that appear to be most widely used at present (together with traditional tools) are STRUCTURE (Pritchard et al. 2000) and DIYABC (Cornuet et al. 2008). In particular, DIYABC (as other model-based ABC programs) makes it possible to combine molecular marker data with data about invasion history, bottlenecks and historical population sizes. This allows for quantifying the relative probabilities of multiple complex scenarios in ways that were previously not possible (see Table S1 for recent applications of DIYABC). These tools are responsible for elucidating a number of the surprisingly complex invasion routes described above. Interpretation of results from analyses using STRUCTURE and ABC (among other tools) can be challenging, especially in the face of imperfect knowledge of introduction dates 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).

Consequences of complex global movement of invasive species

The recognition that globally IAS are moving in complex ways, that the number of propagules per establishment event is often large, and that multiple introduction events are common (sometimes from disparate parts of the native or invasive range) has broad consequences for predicted evolutionary trajectories of IAS (Lee 2002; Dlugosch and Parker 2008; Wilson et al. 2009; Lawson Handley et al. 2011; Rius and Darling 2014). In this section we focus on the subset of invasive taxa that are adventive in at least two or three disjunct regions and thus are currently—or have the potential to become—globally distributed, and consider some of the consequences that such patterns might have on fitness, local adaptation and long-term invasiveness.

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

event, connectivity among regions increases and with it the potential for the formation of novel genotype assemblages in different regions (Fig. 1). Interestingly (if intuitively), the probability of transfer to a new, uncolonized region peaks then begins to decline once half of the possible regions have been colonized, as the opportunities for new establishments decline until a species becomes cosmopolitan (Fig. 1, red line). This contrasts starkly with the probability of movement of individuals when secondary transfer among occupied regions is included, which increases linearly with the number of established regions (Fig. 1, blue line). The fact that movement of individuals and propagules does not stop and in fact continues to increase once an area has been invaded is perhaps an under-appreciated aspect of IAS management. Unless there are barriers to secondary introduction or spread, the probability of admixture continues to increase and remains high as species become globally distributed, unless underlying pathways are disrupted (Garnas et al. 2012).

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

The increased potential for movement among invaded regions brings with it a number of theoretical possibilities for the mixing of genotypes or for the sharing of acquired microbial associates and/or natural enemies. Very high rates of secondary transfer could have the effect of homogenizing populations and/or communities across the adventive range, but this

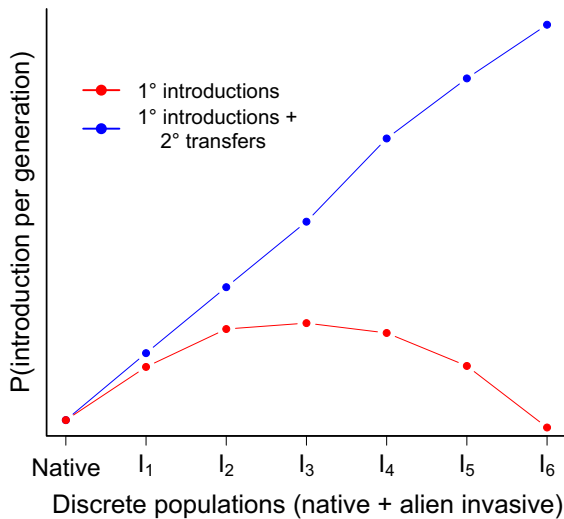


Fig. 1 Rates of transfer (P) to uninvaded regions (red lines) and to all regions irrespective of colonization status (blue line) based on simulation model employing a random transition matrix representing connectivity among region ($n = 20,000$). Note that when once half of the regions are colonized, 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

seems unlikely given that introduction and establishment are still low-probability, chance events. Empirical evidence likewise supports the existence of structure in the distribution of genotypes around the world for many systems, rather than a pattern of global panmixia (Sakai et al. 2001; Lombaert et al. 2010; Boissin et al. 2012 and other examples discussed above). Cases where haplotype diversity is low typically arise from rapid spread of a genotype rather than homogenization. Whether the creation of novel assemblages via admixture is an important driver of evolution (and perhaps of further rates and patterns of spread) or whether genotype mixing is simply an inevitable consequence of global invasiveness is a key question with both practical and theoretical 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). However, understanding the importance of admixture

to evolution in the invasive range is not a simple matter. The proposed roles of admixture include promoting (1) genetic rescue of low diversity populations (e.g., those at risk due to inbreeding or drift); (2) adaptive evolution by increasing additive genetic variance; (3) the aggregation of favorable traits or gene combinations with possible effects on fitness; or (4) disrupting local adaptation or creating mosaics of maladaptation. Alternatively, admixture may have no direct effects on population fitness or may be confounded with correlated factors such as propagule pressure that are difficult to tease apart (Rius and Darling 2014). Finally, the effects of admixture may be positive, negative or neutral depending on ecological context, the existence and outcomes of rapid evolution in various parts of the invasive range, and/or by the stochastic sampling of alleles via the processes of both drift and secondary transmission. Some of the hypothetical consequences of elevated propagule pressure as well as different types of admixture are highlighted in Fig. 2.

The role of genetic diversity

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

Key mechanisms

The idea of diversity as a prerequisite for long-term population growth and viability takes a few different forms. First, there are direct effects on individual fitness. Genetic diversity reduces inbreeding

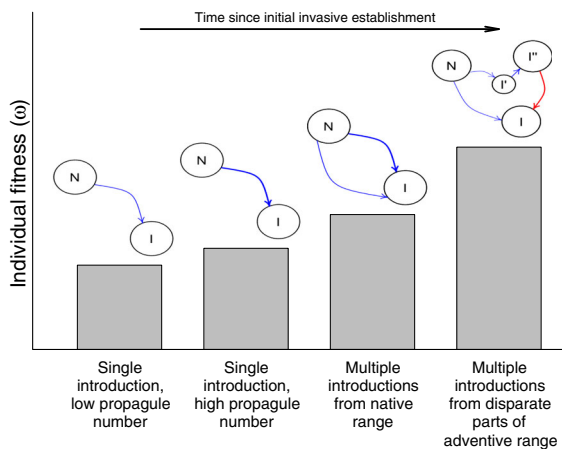


Fig. 2 Hypothetical consequences for mean individual fitness (ω) arising from common invasion scenarios. In these scenarios, the capacity for adaptive evolution in invasive populations is shown to increase (from left to right) with higher propagule number, where multiple introductions from the native 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*

depression, and in sexually reproducing individuals facilitates the purging of deleterious mutations and the decoupling of unfavorable gene combinations, particularly under bottlenecks of intermediate intensity (Gleason 2003). Recent observational and experimental evidence from the invasion of *H. axyridis* strongly suggests that moderate bottlenecks can positively affect invading populations, in part by increasing robustness to inbreeding (Facon et al. 2011). In contrast, levels of genetic diversity appeared to play little or no role in the success of at least five independent introductions of the Western Corn Rootworm from native North America into Europe (Ciosi et al. 2008). In this case multiple introductions from the same source pool have not resulted in admixture to date but have led to the continental co-occurrence of independent populations that are genetically distinct, most likely as a result of drift.

The second main argument in support of the importance of genetic diversity is that it enhances the capacity for adaptive evolution. Heritable genetic variation is required for adaptation to novel or

changing conditions, which has been shown to occur in a number of introduced species (Lee and Gelembiuk 2008; Whitney and Gabler 2008; Jones and Gomulkiewicz 2012; Zenni et al. 2014; Tanaka et al. 2015). Very often, IAS occupy a breadth of habitats and niches, in many cases across broad geographic ranges with divergent biotic and abiotic environments. Many authors have taken this pattern as implicit evidence that genetic diversity would at least benefit exotic invaders if not represent a requirement for medium- to long-term population success (Kolbe et al. 2004; Roman and Darling 2007). However, phenotypically plastic genotypes capable of coping with a variety of conditions have been shown to be crucial to invasiveness in many systems (Zepeda-Paulo et al. 2010; Barrett 2015). In fact, phenotypic plasticity itself—once considered an impediment to adaptive evolution—can mask cryptic diversity and promote the emergence of novel traits, ultimately leading to an increase in heritable genetic variation and to population and/or species divergence or local adaptation (Hughes et al. 2008; Pfennig et al. 2010; Hughes 2012). Additionally, theoretical models demonstrate that genetic bottlenecks have the capacity to increase additive genetic variation in affected populations—either by “converting” epistatic into additive variation via the fixation of some alleles due to drift (Goodnight 1988) or by increasing the frequency of rare recessive alleles at loci where dominance effects occur (Robertson 1952; Willis and Orr 1993). While some studies are consistent with such predictions (Bryant and Meffert 1993; Saccheri et al. 2006), on the whole empirical evidence has been equivocal (van Heerwaarden et al. 2008; Jarvis et al. 2011; Dlugosch et al. 2015) and primarily derived from limited laboratory studies.

Genetic effects of population size and population growth

Invasive populations tend to be characterized by high population densities, rapid population growth, rapid spread and broad geographic extent. Theory predicts that population abundance and rates of expansion can themselves influence the rates of loss, maintenance and accrual of genetic diversity. For example, the total number of mutations per generation and neutral genetic diversity tend to scale linearly with population size (Dlugosch et al. 2015). However, the relationship

between rate of evolution and effective population size (N_e) is complex and difficult to predict in natural systems given the opposing processes of drift and selection. Theoretical and empirical studies tend to support a negative relationship between population size and rates of evolution (Lanfear et al. 2014), though population expansion or contraction can temporarily increase these rates if some mutations are adaptive (Charlesworth and Eyre-Walker 2007; Lanfear et al. 2014). Thus, as invasive populations increase rapidly post-establishment, rates of adaptive evolution may be elevated. However, this effect is likely to be ephemeral in the absence of population subdivision (which can allow small N_e to persist even as global population size increases). Population structure 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

The idea of a positive relationship between niche breadth and genetic and/or phenotypic diversity has been around since at least Van Valen (1965). However, it has been notoriously difficult to establish generality with respect to this phenomenon. Steiner (1977) showed a moderate positive correlation between average heterozygosity in Hawaiian *Drosophila* species and host plant use (as well as elevation), though other authors have concluded that genetic diversity is more strongly associated with habitat or environmental heterogeneity (Pamilo 1988). In at least one case, that of the globally invasive Argentine ant (*Linepithema humile*), the loss of genetic diversity during invasion is cited as one of the key elements promoting ecological success (Starks 2003; Tsutsui et al. 2003). However, this phenomenon may be unique to social insects and therefore linked more to life history and patterns of polygyny than to diversity within invasive populations per se (Pedersen et al. 2006; Garnas et al. 2007).

Many species appear capable of occupying a range of habitats and climatic conditions despite single introductions of only a few individuals or propagules. For example, *Drosophila subobscura* populations in the New World are estimated to have originated from fewer than 15 individuals and have now spread to

cover over 15 degrees of latitude in both the Northern and Southern Hemispheres (Huey et al. 2000; Pascual et al. 2007; Balanyà et al. 2009). In this case, despite a strong bottleneck, there appears to have been strong selection for chromosomal inversion frequency and for wing size, both of which show a predictable latitudinal cline in the native range that has developed independently in both northern and southern introduced populations. While the *D. subobscura* example provides strong evidence of contemporary evolution in low-diversity introduced populations—indeed some of the fastest rates of trait evolution documented to date in natural populations—the strength of the cline is still considerably weaker than in native Europe. Whether this reflects some consequences of reduced diversity or simply the wider temperature range (and variability) experienced by flies across their European range, is not known. Additional chromosomal inversion types that correlate with climate regime are present in Europe but have not yet been introduced elsewhere. The idea that the arrival of one or more of these types could enhance adaptive potential is an intriguing possibility that cannot currently be tested.

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

Success of clonal invaders

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

favor parthenogens (Hoffmann et al. 2008). For example, a study of sympatric sexual versus asexual populations of *Rhopalosiphum padi* (the bird cherry-oat aphid) showed that the diversity of host plants utilized by the two forms differed significantly. Isotopic signatures of asexual populations strongly suggested feeding on C₄ host plants (represented only by maize in the region where the study was performed), whereas sexually reproducing individuals primarily fed on C₃ plants, likely utilizing a far greater diversity of grassland plants in the family Poaceae (Gilabert et al. 2014).

A disproportionate number of IAS exhibiting low genetic diversity are asexual, at least in aquatic systems (Roman and Darling 2007). Many insects, even those for which recombination is common in the 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 intracclone 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 heritabilities in important life history traits in a parthenogenetic freshwater snail invader, though no evidence of local adaptation was detected (suggesting evolutionary potential but not necessarily that rapid evolution had occurred). The same study also reported evidence for phenotypic plasticity across elevations but no all-purpose genotype (Baker 1965), which according to the authors predicts a flat reaction norm landscape across habitats.

Whether or not the success of clonal invaders bears directly on the importance of genetic diversity and/or admixture in non-clonal invaders is an open question. In addition, there are contravening examples where sexual invaders appear to displace ecologically similar, asexual congeners (Auger-Rozenberg and Roques 2012). In the absence of horizontal gene transfer or occasional or cryptic sex, there is no direct effect of admixture in asexual organisms, as genomes do not

introgress. However, the concept of a true clonal population has received criticism in recent years due to high rates of intracclone variability, persistence of rare genotypes and strong evidence for adaptive evolution (Loxdale and Lushai 2003; Lushai et al. 2003). Numerous asexual pests, for example, have evolved resistance to insecticides, including the spotted alfalfa aphid, *Therioaphis maculata* in North America (Dickson 1962). Populations of this insect currently comprise numerous strains, including some with insecticide-resistance traits, despite apparently being derived from a small asexual founder population within a few generations (Lushai et al. 2003). In fact, intracclone selection in obligate parthenogens appears to be the norm across many groups, and in some cases may be strong (Vorburger 2006).

Admixture and interspecific hybridization

Among the factors with the potential to influence evolutionary trajectories in globally invasive populations, perhaps the one most likely to be strongly influenced by complexity in patterns of global spread is admixture. Admixture refers to the genomic mixing that results from the interbreeding of individuals from distinct source populations or lineages. Secondary contact outside the native range scales with the rate of transfer among regions along with the number of independent introductions outside the native range, both of which are strongly influenced by growing volumes of global trade. The importance of admixture has historical precedent too and has been well characterized with respect to the evolution of our own species. Reconstructions of intraspecific admixture throughout human pre-history strongly suggests that this has been common during range expansion and secondary migration in humans, and very likely was an important force favoring the sharing of favorable alleles and for adaptive evolution (Hellenthal et al. 2014). There is also growing evidence that interspecific admixture with Neanderthals was an important source of adaptive variation for skin phenotype, and perhaps other traits as well (Vernot and Akey 2014). Admixture has also been implicated in facilitating range expansion under conditions of both current and historical climate change in insects and other taxa (Petit et al. 2003; Krehenwinkel and Tautz 2013).

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

species is not a simple task. First, multiple introductions are a logical requirement for admixture in the invasive range to occur (including for independently introduced lineages which come into contact via secondary spread). However, multiple introductions can have direct effects on spread potential via elevated propagule number, irrespective of source population identity or differentiation. Second, while short-term gains linked to heterosis—even if ultimately lost via backcrossing—can be an important mechanism for demographic rescue in small populations, such effects might be easily confused with longer term benefits linked to increased additive genetic variation (Rius and Darling 2014). Admixture arising from the arrival of novel alleles and gene combinations from secondary spread within and among regions can disrupt locally adapted populations via gene swamping (Verhoeven et al. 2011). Alternatively, admixture can increase genetic diversity and adaptive potential, or bring new “pre-adapted” traits with consequences for fitness to established populations. In one case—that of *H. axyridis*—admixture is credited as a principal cause in the creation of a bridgehead population in eastern North America, which then exported individuals with increased fitness and propensity to invade to Europe and perhaps beyond (Lombaert et al. 2010). A follow-up laboratory study showed that key life history traits were changed in favor of higher fitness in experimental crosses designed to recreate observed admixture (between the North American and biocontrol strains; Turgeon et al. 2011). In the majority of cases where admixture is implicated, however, little evidence exists that the mixing of genotypes has had serious impacts on global invasiveness (Chapple et al. 2013; Rius and Darling 2014). In addition, several of the studies that have detected positive effects of admixture attribute these to short-term heterotic effects rather than gains in additive genetic variation (Keller and Taylor 2010; Keller et al. 2014), though this can still have important long-term consequences.

Resource use and genetic diversity in insects

From the perspective of management of invasive pests, particularly those under intensive management such as in forestry or agricultural landscapes, a positive

correlation between admixture and invasiveness is not the only way in which admixture could influence relevant dynamics. To the degree that admixture enhances fitness (e.g., via local adaptation or the acquisition of favorable life history traits), impacts equilibrium abundances and/or increases the propensity for outbreak dynamics, such mixing could be very important. Perhaps more relevant in such systems, however, is how admixture might influence either host range or the capacity for adaptation to mitigation strategies themselves. For example, the importation of insecticide-resistance alleles has occurred via secondary transfer in the peach potato aphid and has had major consequences for growers in affected regions (Margaritopoulos et al. 2009).

Biotypes and cryptic species

The increasingly widespread use of molecular tools for species identification and the exploration of population substructure has led to major increases in the identification of cryptic species and/or biotypes (Lawson Handley 2015). Biotypes are generally considered to be population or lineages within a species that differ in key traits. Often, biotypes are asexual lineages and can differ in host preference (host races), geography (geographic races) or other aspects of life history, ecology or morphology. In addition to differentiation in host (plant or insect) use, differences in phenology among distinct types appear important to maintaining separation. There are several examples of the arrival of a genotype or species that is morphologically similar to individuals in an already invaded area that has resulted in additional damage, increased niche breadth, or that has confounded management (Perring 2001; Saltonstall 2002; Peccoud et al. 2008; Garnas et al. 2012; Mapondera et al. 2012; Wenger and Michel 2013; Shadmany et al. 2015). For example, distinct host races of the pea aphid (*Acyrtosiphon pisum*) feeding on pea and broad bean, alfalfa and red clover in Chile are descended from biotypes in Europe (rather than evolving in situ; Peccoud et al. 2008). Thus it seems likely that multiple introductions of host-adapted biotypes are responsible for the broad host range of this species rather than in situ evolution in the invasive range. Similarly, some species of the wheat curl mite (“*Aceria tosichella* complex”) are widely distributed with broad host range while others

are restricted and specialized (Carew et al. 2009; 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.

Community sharing and symbiont transfer

The Enemy Release Hypothesis is a central and well-supported (if partial) explanation of the success of invasive species (Roy and Lawson Handley 2012; Heger and Jeschke 2014). However, when individuals from distinct source populations or lineages come together, they rarely come alone. Invasive insects, for example, bring with them a suite of obligate and facultative symbionts, including mutualists, parasites and commensals, some of which can have important effects on fitness (Dillon and Dillon 2004; Moran 2007). In addition, there is growing evidence of symbiont switching in novel communities (Werren et al. 2008; Taerum et al. 2013). For example, increased performance and the production of female-biased offspring in *Rickettsia*-infected whiteflies (*Bemisia tabaci*) provide a strong case for the role of a facultative endosymbiont in the insect's invasion in California (Himler et al. 2011; Lawson Handley et al. 2011). Fungal symbionts once thought to be obligately associated with specific hosts have also been seen to change in invasive populations. Populations of native *Sirex nigricornis* in North America now regularly carry *Amylostereum areolatum*, a fungal symbiont carried—and putatively introduced—by the invasive *S. noctilio*, and vice versa with the *A. chailletii* symbiont of *S. nigricornis* (Hajek et al. 2013; Olatinwo et al. 2013; Wooding et al. 2013). The fitness consequences of this switch are not yet known, but what is clear is that secondary transfer of North American populations of *S. noctilio* now carries additional risk. Given the ubiquitous associations between insects and microbes, the co-introduction and/or novel acquisition of microbial associates by invasive insects may be quite common, with impacts that are typically subtle or at least overlooked. There are cases, however, where novel associations acquired in a non-native range can have truly devastating consequences (Hulcr and Dunn 2011; Wingfield et al. 2016).

Implications of complex movement patterns for management

Quarantine and control

Controlling the movement of harmful or invasive species is an incredibly complex task. Even for known pests, restricting pathways and/or maintaining effective quarantine requires constant vigilance as well as cooperation from all relevant trade partners. Agreements such as those under the International Plant Protection Convention (IPPC) aim to establish standards to ensure fairness and technical soundness of trade control measures, but competing interests, the economic benefits of free trade and the sheer volume of global shipping and transport make the prevention of primary or secondary pest establishment a daunting task (Mumford 2002; Saccaggi et al. 2016). Application of phytosanitary measures under these protocols, container inspection, and post-harvest treatments (e.g., irradiation, heat, methyl bromide treatment, or exposure to high CO₂ or low O₂ concentrations) are often expensive and/or inadequately applied, variably effective and inconsistently enforced (Liebhold et al. 2012; Haack et al. 2014; Roy et al. 2014; Eschen et al. 2015). Still, programs aimed at maintaining pest-free zones (PFZs) have been successful in some cases, such as for the medfly in Chile where consistent monitoring and regular eradication efforts have prevented populations from gaining a foothold since 1982 (Follett and Neven 2006).

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

So what of the knowledge that admixture, at least under certain circumstances, can influence invasiveness or the capacity for adaptive evolution in introduced populations? In the face of massive economic forces promoting free trade, it is unlikely that a purist

strategy (such as banning or severely restricting trade among regions with different genotypes of the same pest) is feasible or even desirable. However, in a 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 consequences for evolutionary trajectories, and the long-term efficacy of control methods is underappreciated at best.

Prospects for the future

Molecular tools have powerful potential for detecting the spread of pests and pathogens, but there are many challenges (Armstrong and Ball 2005; Bohmann et al. 2014; Chown et al. 2014; Lawson Handley 2015). Environmental sampling, for example, is already being used to track the movement and spread of aquatic invaders via the detection of invader DNA rather than the species themselves (Jerde et al. 2011). Bulk screening of insect or microbial samples using massively parallel barcoding approaches could potentially be used to flag known invaders at ports of entry. Current limitations linked to cost, time and the availability of comprehensive barcoding databases of known pests present significant difficulties. However, there is little doubt that such technical barriers could be overcome with time and sufficient effort. In fact, there is scope for considerable automation of such screening, which would clearly be necessary given the volumes of trade in question. While at their core, inspection-based methods require a “blacklisting” philosophy where known pests are denied, such lists could be expanded to incorporate aspects of population-level diversity in the context of the known distribution of genotypes. In addition, enhanced databases together with advanced clustering algorithms should allow the flagging of

species that are phylogenetically related to known invaders. Potentially harmful symbionts could also be readily detected in this way.

Conclusions

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

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