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

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47 **Introduction**

48 A fundamental problem in invasion biology has long
 49 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 propa-
 69 gule 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; Gladioux
 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
 79 common. Thus, apparently disparate populations
 80 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 man-
 agement 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 compre-
 hensive 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 evolu-
 tionary 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 conse-
 quences 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 Wieczorek 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 inva-
 ders 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 popula-
 tion growth and natural dispersal; (2) frequent jump

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323 *Eucalyptus* (e.g., *Glycaspis brimblecombei*, *Ophe-*
 324 *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
 328 hosts, herbivorous feeding guild, and life histories
 329 (Hurley et al. 2015). While some recently emerging
 330 pests that exhibit rapid spread could be specifically
 331 and idiosyncratically linked to pathways that permit it
 332 (Paine et al. 2010), Roques et al. (2015, this issue)
 333 showed that this faster spread constitutes a general
 334 phenomenon for invasive insects since the mid-1990s,
 335 for Europe at least.

336 There is widespread agreement that increasing
 337 global connectivity, in particular the growing volumes
 338 and rates of movement of goods and people, is the
 339 most important factor influencing the increase in the
 340 number of invasive insects and micro-organisms
 341 (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
 344 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
 347 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
 353 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
 360 the Harlequin ladybird beetle (*Harmonia axyridis*),
 361 where a highly fit invasive population in North
 362 America appears to have acted as a source from which
 363 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
 366 reared and repeatedly released in multiple regions
 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
 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 devel-
 opment 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 poly-
 morphisms (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 phylo-
 genetic 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 among and
 quantify key parameters of increasingly complex
 hypotheses about invasion routes, dubbed “scenarios”
 (Miura 2007; Estoup and Guillemaud 2010). Two such

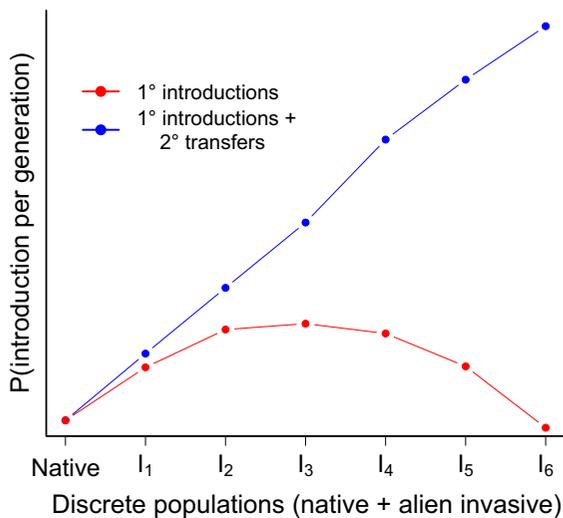


Fig. 1 Rates of transfer (P) to uninvaded regions (red lines) and to all regions irrespective of colonization status (blue line) based on simulation model employing a random transition matrix representing connectivity among region ($n = 20,000$). Note that when once half of the regions are colonized,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

communities across the adventive range, but this 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

- 651 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
654 systems given the opposing processes of drift and
655 selection. Theoretical and empirical studies tend to
656 support a negative relationship between population
657 size and rates of evolution (Lanfear et al. 2014),
658 though population expansion or contraction can tem-
659 porarily increase these rates if some mutations are
660 adaptive (Charlesworth and Eyre-Walker 2007; Lan-
661 fear et al. 2014). Thus, as invasive populations
662 increase rapidly post-establishment, rates of adaptive
663 evolution may be elevated. However, this effect is
664 likely to be ephemeral in the absence of population
665 subdivision (which can allow small N_e to persist even
666 as global population size increases). Population struc-
667 ture has been shown in a number of invasive insect
668 species, especially in patchy environments (Vill-
669 ablanca et al. 1998), but its role as a driver of
670 evolutionary change in rapidly spreading global
671 invaders is far from established.
- 672 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-
676 ever, it has been notoriously difficult to establish
677 generality with respect to this phenomenon. Steiner
678 (1977) showed a moderate positive correlation
679 between average heterozygosity in Hawaiian *Droso-*
680 *phila* species and host plant use (as well as elevation),
681 though other authors have concluded that genetic
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
688 phenomenon may be unique to social insects and
689 therefore linked more to life history and patterns of
690 polygyny than to diversity within invasive populations
691 per se (Pedersen et al. 2006; Garnas et al. 2007).
- 692 Many species appear capable of occupying a range
693 of habitats and climatic conditions despite single
694 introductions of only a few individuals or propagules.
695 For example, *Drosophila subobscura* populations in
696 the New World are estimated to have originated from
697 fewer than 15 individuals and have now spread to
698 cover over 15 degrees of latitude in both the Northern
699 and Southern Hemispheres (Huey et al. 2000; Pascual
700 et al. 2007; Balanyà et al. 2009). In this case, despite a
701 strong bottleneck, there appears to have been strong
702 selection for chromosomal inversion frequency and
703 for wing size, both of which show a predictable lati-
704 tudinal cline in the native range that has developed
705 independently in both northern and southern intro-
706 duced populations. While the *D. subobscura* example
707 provides strong evidence of contemporary evolution in
708 low-diversity introduced populations—indeed some
709 of the fastest rates of trait evolution documented to
710 date in natural populations—the strength of the cline is
711 still considerably weaker than in native Europe.
712 Whether this reflects some consequences of reduced
713 diversity or simply the wider temperature range (and
714 variability) experienced by flies across their European
715 range, is not known. Additional chromosomal inver-
716 sion types that correlate with climate regime are
717 present in Europe but have not yet been introduced
718 elsewhere. The idea that the arrival of one or more of
719 these types could enhance adaptive potential is an
720 intriguing possibility that cannot currently be tested.
- 721 Niche breadth may also expand in response to
722 relaxed interspecific competition, which along with a
723 loss of natural enemies, may facilitate the occupation
724 of a greater proportion of the fundamental niche.
725 However, the question of whether more generalized
726 populations are themselves more genetically variable
727 has been elusive. There is a clear role for phenotypic
728 plasticity and/or selection for a generalized genotype,
729 particularly in recently introduced populations (Rius
730 and Darling 2014). However, structured or diversified
731 habitat use does appear to arise as population niche
732 breadth increases (Bolnick et al. 2007), though the
733 changes may or may not be heritable or even
734 genetically based (but see Pfennig et al. 2010).
- 735 Success of clonal invaders
- 736 Asexual organisms often have superior capacity for
737 colonization and rapid spread, owing at least in part to
738 the ability of single individuals to start new popula-
739 tions, the absence of a need for mate finding, and the
740 roughly twofold advantage in rates of population
741 growth (Maynard Smith 1978). There is some evi-
742 dence, however, that habitat stability (i.e., low levels
743 of disturbance) and temporal instability (i.e., annual
744 crops which must be re-invaded each growing season)

- 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
 751 suggested feeding on C₄ host plants (represented only
 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
 755 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,
 760 even those for which recombination is common in the
 761 native range, also show a tendency to switch to
 762 obligate or facultative parthenogenesis in introduced
 763 populations (Dybdahl and Kane 2005; Caron et al.
 764 2014). Clonal lineages do exhibit some genetic
 765 variability, however, though inheritance and selection
 766 typically occur at the scale of the genome (rather than
 767 genes) in the absence of recombination. Most of this
 768 variation in asexual lineages probably derives from
 769 mutation, though gene duplication, chromosomal
 770 rearrangement and horizontal gene transfer (among
 771 other plausible mechanisms) can result in intraclope
 772 variability, including in insects (Lushai et al. 2003). In
 773 fact, evidence of within or among clone diversity in
 774 asexually reproducing organisms is accumulating. For
 775 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
 783 according to the authors predicts a flat reaction norm
 784 landscape across habitats.
- 785 Whether or not the success of clonal invaders bears
 786 directly on the importance of genetic diversity and/or
 787 admixture in non-clonal invaders is an open question.
 788 In addition, there are contravening examples where
 789 sexual invaders appear to displace ecologically sim-
 790 ilar, asexual congeners (Auger-Rozenberg and Roques
 791 2012). In the absence of horizontal gene transfer or
 792 occasional or cryptic sex, there is no direct effect of
 793 admixture in asexual organisms, as genomes do not
 794 introgress. However, the concept of a true clonal
 795 population has received criticism in recent years due to
 796 high rates of intraclope variability, persistence of rare
 797 genotypes and strong evidence for adaptive evolution
 798 (Loxdale and Lushai 2003; Lushai et al. 2003).
 799 Numerous asexual pests, for example, have evolved
 800 resistance to insecticides, including the spotted alfalfa
 801 aphid, *Therioaphis maculata* in North America (Dick-
 802 son 1962). Populations of this insect currently com-
 803 prise numerous strains, including some with
 804 insecticide-resistance traits, despite apparently being
 805 derived from a small asexual founder population
 806 within a few generations (Lushai et al. 2003). In fact,
 807 intraclope selection in obligate parthenogens appears
 808 to be the norm across many groups, and in some cases
 809 may be strong (Vorburger 2006).
- 810 Admixture and interspecific hybridization 810
- 811 Among the factors with the potential to influence 811
 812 evolutionary trajectories in globally invasive popula- 812
 813 tions, perhaps the one most likely to be strongly 813
 814 influenced by complexity in patterns of global spread 814
 815 is admixture. Admixture refers to the genomic mixing 815
 816 that results from the interbreeding of individuals from 816
 817 distinct source populations or lineages. Secondary 817
 818 contact outside the native range scales with the rate of 818
 819 transfer among regions along with the number of 819
 820 independent introductions outside the native range, 820
 821 both of which are strongly influenced by growing 821
 822 volumes of global trade. The importance of admixture 822
 823 has historical precedent too and has been well 823
 824 characterized with respect to the evolution of our 824
 825 own species. Reconstructions of intraspecific admix- 825
 826 ture throughout human pre-history strongly suggests 826
 827 that this has been common during range expansion and 827
 828 secondary migration in humans, and very likely was an 828
 829 important force favoring the sharing of favorable 829
 830 alleles and for adaptive evolution (Hellenthal et al. 830
 831 2014). There is also growing evidence that interspeci- 831
 832 fic admixture with Neanderthals was an important 832
 833 source of adaptive variation for skin phenotype, and 833
 834 perhaps other traits as well (Vernot and Akey 2014). 834
 835 Admixture has also been implicated in facilitating 835
 836 range expansion under conditions of both current and 836
 837 historical climate change in insects and other taxa 837
 838 (Petit et al. 2003; Krehenwinkel and Tautz 2013). 838
 839 Understanding how admixture influences fitness, 839
 840 local adaptation and adaptive potential in invasive 840

933	Skoracka et al. 2013, 2014). Other co-introduced	Implications of complex movement patterns	979
934	lineages (e.g., <i>S. noctilio</i> , <i>T. peregrinus</i>) do not appear	for management	980
935	to differ markedly in host range, though more subtle		
936	differences in preference cannot be excluded. Estab-	Quarantine and control	981
937	lishing the generality of biotype-specific host use in		
938	invasive insects has major implications for quarantine	Controlling the movement of harmful or invasive	982
939	and pest management.	species is an incredibly complex task. Even for known	983
940	Community sharing and symbiont transfer	pests, restricting pathways and/or maintaining effec-	984
941	The Enemy Release Hypothesis is a central and well	tive quarantine requires constant vigilance as well as	985
942	supported (if partial) explanation of the success of	cooperation from all relevant trade partners. Agree-	986
943	invasive species (Roy and Lawson Handley 2012;	ments such as those under the International Plant	987
944	Heger and Jeschke 2014). However, when individuals	Protection Convention (IPPC) aim to establish stan-	988
945	from distinct source populations or lineages come	dards to ensure fairness and technical soundness of	989
946	together, they rarely come alone. Invasive insects, for	trade control measures, but competing interests, the	990
947	example, bring with them a suite of obligate and	economic benefits of free trade and the sheer volume	991
948	facultative symbionts, including mutualists, parasites	of global shipping and transport make the prevention	992
949	and commensals, some of which can have important	of primary or secondary pest establishment a daunt-	993
950	effects on fitness (Dillon and Dillon 2004; Moran	ing task (Mumford 2002; Saccaggi et al. 2015, this	994
951	2007). In addition, there is growing evidence of	volume). Application of phytosanitary measures under	995
952	symbiont switching in novel communities (Werren	these protocols, container inspection, and post-harvest	996
953	et al. 2008; Taerum et al. 2013). For example, increased	treatments (e.g., irradiation, heat, methyl bromide	997
954	performance and the production of female-biased	treatment, or exposure to high CO ₂ or low O ₂	998
955	offspring in <i>Rickettsia</i> -infected whiteflies (<i>Bemisia</i>	concentrations) are often expensive and/or inade-	999
956	<i>tabaci</i>) provide a strong case for the role of a facultative	quately applied, variably effective and inconsistently	1000
957	endosymbiont in the insect's invasion in California	enforced (Liebhold et al. 2012; Haack et al. 2014; Roy	1001
958	(Himler et al. 2011; Lawson Handley et al. 2011).	et al. 2014; Eschen et al. 2015). Still, programs aimed	1002
959	Fungal symbionts once thought to be obligately asso-	at maintaining pest-free zones (PFZs) have been	1003
960	ciated with specific hosts have also been seen to change	successful in some cases, such as for the medfly in	1004
961	in invasive populations. Populations of native <i>Sirex</i>	Chile where consistent monitoring and regular erad-	1005
962	<i>nigricornis</i> in North America now regularly carry	ication efforts have prevented populations from gain-	1006
963	<i>Amylostereum areolatum</i> , a fungal symbiont carried—	ing a foothold since 1982 (Follett and Neven 2006).	1007
964	and putatively introduced—by the invasive <i>S. noctilio</i> ,	Given the difficulties of maintaining a PFZ or of	1008
965	and vice versa with the <i>A. chailletii</i> symbiont of <i>S.</i>	preventing the establishment of known and unknown	1009
966	<i>nigricornis</i> (Hajek et al. 2013; Olatinwo et al. 2013;	pests alike, it is not surprising that managing genotype	1010
967	Wooding et al. 2013). The fitness consequences of this	or provenance-specific movement of established pests	1011
968	switch are not yet known, but what is clear is that	receives very little consideration. Once a pest has	1012
969	secondary transfer of North American populations of <i>S.</i>	become firmly established, maintaining quarantine	1013
970	<i>noctilio</i> now carries additional risk. Given the ubiqui-	import restrictions is likely to be complicated by fair	1014
971	tous associations between insects and microbes, the co-	trade regulations (Mumford 2002). The one exception	1015
972	introduction and/or novel acquisition of microbial	is for species where clear biotypes or strains can be	1016
973	associates by invasive insects may be quite common,	identified, though this is the case for only a small	1017
974	with impacts that are typically subtle or at least	subset of species. The arrival of new biotypes of the	1018
975	overlooked. There are cases, however, where novel	pea aphid to Chile increased the host range of the	1019
976	associations acquired in a non-native range can have	insect considerably, with major economic effect	1020
977	truly devastating consequences (Hulcr and Dunn 2011;	(Caron et al. 2014).	1021
978	Wingfield et al. 2015, this volume).	So what of the knowledge that admixture, at least	1022
		under certain circumstances, can influence invasive-	1023
		ness or the capacity for adaptive evolution in intro-	1024
		duced populations? In the face of massive economic	1025

- 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 pre-
1031 vented the movement of genotypes, biotypes or key
1032 symbionts, potentially avoiding further catastrophic
1033 effects of invasion. We advocate increased consider-
1034 ation of genetic and microbial diversity when imple-
1035 menting quarantine or the regulation of movement of
1036 globally established pests. It is critical for govern-
1037 ments and regulatory agencies to recognize that the
1038 probability of movement of individuals increases
1039 significantly with global population size and with
1040 each region that is invaded. This is probably reason-
1041 ably accepted with respect to the likelihood of new
1042 colonization events. However, greater recognition is
1043 needed that rates of secondary transfer increase and
1044 remain high even once a pest attains a global
1045 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
1073 addition, enhanced databases together with advanced
1074 clustering algorithms should allow the flagging of
1075 species that are phylogenetically related to known
1076 invaders. Potentially harmful symbionts could also be
1077 readily detected in this way.
- Conclusions** 1078
- 1079 In this paper we examine and reflect on the growing
1080 evidence of complex patterns of global movement of a
1081 number of important invasive pests. One consequence
1082 of this complexity is widespread admixture and a
1083 general increase in genetic diversity over time. While
1084 the consequences of these patterns are not always
1085 clear, there is evidence that mixing of divergent
1086 lineages contributes to rapid evolution and to inva-
1087 siveness and may seriously complicate management
1088 efforts. There are currently few, if any, effective
1089 mechanisms in place to systematically track genetic
1090 and evolutionary changes in populations at regional,
1091 national or international scale. There appears to be
1092 even less action with regard to policy to mitigate
1093 secondary spread between invaded regions despite
1094 clear evidence of its importance. Inclusion of such
1095 considerations within risk assessment protocols would
1096 be a first step. The patterns and consequences high-
1097 lighted in this paper will hopefully contribute to an
1098 urgent call for efforts to address these shortcomings.
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