Ecological genetics of invasive alien species

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Abstract There is growing realisation that integrating genetics and ecology is critical in the context of biological invasions, since the two are explicitly linked. So far, the focus of ecological genetics of invasive alien species (IAS) has been on determining the sources and routes of invasions, and the genetic make-up of founding populations, which is critical for defining and testing ecological and evolutionary hypotheses. However an ecological genetics approach can be extended to investigate questions about invasion success and impacts on native, recipient species. Here, we discuss recent progress in the field, provide overviews of recent methodological advances, and highlight areas that we believe are of particular interest for future research. First, we discuss the main insights from studies that have inferred source populations and invasion routes using molecular genetic data, with particular focus on the role of genetic diversity, adaptation and admixture in invasion success. Second, we consider how genetic tools can lead to a better understanding of patterns of dispersal, which is critical to predicting the spread of invasive species, and how studying invasions can shed light on the evolution of dispersal. Finally, we explore the potential for combining molecular genetic data and ecological network modelling to investigate community interactions such as those between predator and prey, and host and parasite. We conclude that invasions are excellent model systems for understanding the role of natural selection in shaping phenotypes and that an ecological genetics approach offers great potential for addressing fundamental questions in invasion biology.

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Introduction

Ecological genetics, a field pioneered by EB Ford and his pivotal book of 1964 (Ford 1964), is the study of (1) evolution in modern-day populations, (2) the genetics of ecologically important traits, and (3) genetics in the context of interactions among organisms and between organisms and their environment. Although not directly discussed in Ford's book, all three of these definitions are highly relevant to the study of biological invasions, which are one of the greatest threats to biodiversity, agriculture, health and the global economy (Pimentel et al. 2001; Roy et al. 2011a). Integrating genetics with ecology in the context of biological invasions is indeed crucial, since the two are explicitly linked: ecological conditions in a new environment may be considerably different from the native range, and this can present major adaptive challenges for an invasive population (Reznick and Ghalambor 2001; Schierenbeck and Ainouche 2006; Ciosi et al. 2008). It is only in recent years that biological invasions have become regarded as "natural experiments", offering unique insights into ecological and evolutionary processes occurring in real-time (Lee 2002; Sax et al. 2007), and increasingly, understanding these processes is seen as crucial for implementing successful management policies.

Information on the demographic history and genetic make-up of an invasive founding population is critical for answering one of the most fundamental questions in invasion biology: what determines the success of invasive alien species (IAS)? In this case, an ecological genetics approach refers to the ecology of particular genotypes, and the role they play in adaptation to new environments, and ultimately invasion success. This question has already received considerable attention in the ecological and evolutionary genetics communities, and we are starting to uncover general insights (see below). In addition, genes (or more commonly, neutral molecular genetic markers) can be used as tools to study ecological processes such as colonization, dispersal or community interactions. While the field of "molecular ecology" has been established for decades, and there have been exciting new developments in both data generation (particularly from next generation sequencing, see "Appendix 3" section and Metzker 2010 for a recent review) and statistical analyses

(e.g. Approximate Bayesian Computational approaches, "Appendix 1" section; and landscape genetics, "Appendix 2" section) there has so far been relatively little uptake of these applications to studying invasive populations. Initial focus has been on determining the sources and routes of invasions, and the genetic make-up of founding populations, which is critical for defining and testing ecological/evolutionary hypotheses (Estoup and Guillemaud 2010, and see below). Now that considerable progress has been made in this area, we envisage a growth in the number of ecological genetics studies applied to IAS in the near future.

The aims of this paper are to (1) function as a review of ecological genetics in the context of IAS, (2) introduce new methods in the field and discuss how they can be applied to questions on invasive species, and importantly, (3) promote dialogue between ecologists and geneticists regarding fundamental questions in invasion biology. We begin with a review of recent progress in determining source populations and invasion routes, and advances in our understanding of the role of genetic variation in invasion success. We then focus on two areas that are beginning to be investigated in the context of ecological genetics of IAS: dispersal and community interactions.

Inferring source populations and invasion routes

Inferring source populations and invasion routes is a key first stage in invasion biology, with obvious practical applications for designing and implementing quarantine strategies, identifying natural enemies as potential biological control agents (Roderick and Navajas 2003), defining ecological characteristics of introduced populations to predict their spread (Kolar and Lodge 2001), and potentially direct the focus of conservation strategies. It is also a critical step for defining and testing ecological and evolutionary hypotheses and ultimately understanding the reasons for invasion success (see below, and Estoup and Guillemaud 2010). Historical and observational data on the spread of invasive populations is often sparse, but even when there is good documentary evidence, molecular genetic data can offer unique insights into the sources, routes and mechanisms of spread (e.g. Hoos et al. 2010; Lombaert et al. 2010, and see "Appendix 1" section and Fig. 1). However,

inferring routes using molecular genetic methods should supplement observational and historical records, not attempt to replace them. Indeed, when using an Approximate Bayesian Computational (ABC) approach ("Appendix 1" section), having observational data is a necessary requirement for defining a limited set of invasion scenarios that can be tested against each other statistically (Fig. 1).

Main insights from molecular genetic studies of invasion routes

Arguably the main insight from molecular genetic studies of invasion routes is that multiple introductions are commonplace, and go some way to explaining how populations of IAS overcome founder effects associated with colonization since they can lead to similar or even greater levels of genetic diversity in the invasive compared to native ranges (see below and e.g. thiarid snails, *Melanoides tuberculata* (Muller) (Sorbeoconcha: Thiaridae), Facon et al. 2003; anole lizards, *Anolis sagrei* (Cocteau in Duméril and Bibron) (Squamata: Iguanidae), Kolbe et al. 2004; western corn rootworm, *Diabrotica virgifera* (LeConte) (Coleoptera: Chrysomelidae), Miller et al. 2005; Ciosi et al. 2008; amphipods, *Gammarus tigrinus* (Sexton) (Amphipoda: Gammaridae), Kelly et al. 2006; and scotch broom, *Cytisus scoparius* (L.) (Fabales: Fabaceae), Kang et al. 2007).

A particularly interesting case is highlighted by the western corn rootworm, *D. virgifera*, which is native to Mexico and the east coast of North America, but was first observed near Belgrade in 1992, and is expanding in central and eastern Europe at a rate of 100 km per year. The expansion is essentially continuous, but there have been several isolated outbreaks peripheral to the main invasion front, which were thought to stem from a "leapfrogging" effect from the expanding eastern European population. Molecular genetic studies however revealed that this hypothesis was incorrect, and that most of the separate outbreaks result instead from repeated trans-Atlantic introductions (Miller et al. 2005; Ciosi et al. 2008). In contrast to most studies performed so far, *D. virgifera* shows higher genetic variation between invasive populations than within (Ciosi et al. 2008).

Molecular genetic studies have also revealed that invasions can lead to rapid adaptive evolution in spite
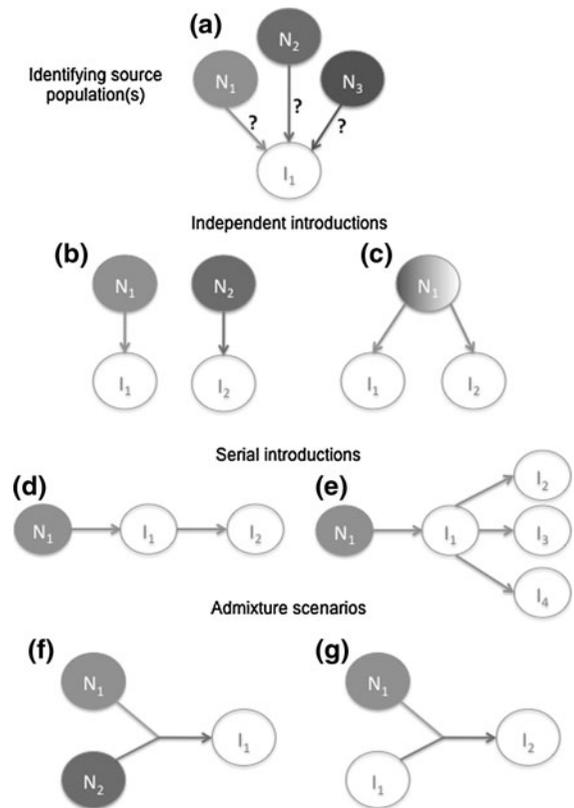
Fig. 1 Hypothetical scenarios of invasion routes that can be formally tested using DIYABC (Cornuet et al. 2008). *N* Native range populations, *I* invasive range populations, subscript numbers indicate different populations. **a** putative source populations of IAS can be identified. This is greatly facilitated if there is genetic differentiation (illustrated by different coloured shading) between source populations; **b** and **c** examples of independent introductions from the native range. In **b** native populations are genetically differentiated, whereas in **c** the native range is one panmictic population; **d** and **e** examples of serial introductions or stepping-stone colonisation events, where **e** corresponds to a "bridgehead effect" scenario, as seen in *H. axyridis* (Lombaert et al. 2010); **f** and **g** correspond to admixture scenarios between native populations, or between native and invasive populations respectively. The latter case is illustrated by *H. axyridis* in Europe, which results from a combination of European biocontrol stocks and invasive East USA individuals (Lombaert et al. 2010)

of strong bottlenecks (e.g. Amsellem et al. 2000; Dlugosch and Parker 2008), and that successful invasions may involve "bridgehead effects" in which widespread secondary invasions stem from a particularly successful invasive population (Fig. 1e) e.g. harlequin ladybird, *Harmonia axyridis* (Pallas) (Coleoptera: Coccinellidae), Estoup and Guillemaud 2010;

Lombaert et al. 2010). In *H. axyridis,* the recent burst of worldwide invasions followed a bridgehead scenario, with the invasive population in Eastern North America acting as a source population for colonists invading Europe, South Africa and South America (Lombaert et al. 2010). Although the bridgehead effect is a new concept in invasion biology, it is potentially a common phenomenon (for example it could apply to the invasions described by Downie 2002; Hänfling et al. 2002; Kolbe et al. 2004; Miller et al. 2005). There are important practical reasons for identifying bridgehead populations (Estoup and Guillemaud 2010). Invasive populations are generally thought to experience a lag phase between colonization and expansion, during which time they evolve adaptations that determine invasion success (Keller and Taylor 2008). Unless the native population is preadapted to become invasive, these adaptations must occur independently in the case of multiple independent introductions directly from the native area. During a bridgehead scenario however, the "evolutionary shift" occurs in a single introduced population, which makes this scenario parsimonious (Estoup and Guillemaud 2010). Identifying such populations should therefore be a high priority for preventing subsequent spread (Estoup and Guillemaud 2010).

In addition to information about the demographic history of invasive populations, recent analyses have provided insights into the genetic make-up of founding populations, and the role of genetic variation in invasion success. We now outline three key questions that can be addressed with this data: (1) what is the role of genetic diversity in invasion success (i.e. successful establishment and spread of an IAS), (2) does admixture during multiple introductions increase invasion success, and (3) does invasion lead to non-neutral evolution and novel adaptation?

The role of genetic diversity in invasion success

Genetic variability determines a population's capacity to adapt to new or changing environmental conditions (Fisher 1930; Sakai et al. 2001), and should therefore play an important role in determining its potential to become invasive (Lee 2002; Kolbe et al. 2004; Drake and Lodge 2006; Facon et al. 2006; Lavergne and Molofsky 2007; Roman and Darling 2007). Populations of IAS are traditionally thought to

have reduced genetic variation relative to their source populations, because of genetic founder effects linked to small population size during the introduction and establishment phases of an invasion. The low genetic variability associated with founder effects should, in theory, inhibit successful invasion, by limiting the population's ability to respond to selective pressures (but see Goodnight 1987, 1988). Moreover, small population size is predicted to increase the chance of inbreeding, which can result in exposure of deleterious recessive mutations in homozygous individuals. How invasive populations overcome the low variability associated with founder effects, and adapt to their new environments, was once regarded as a "paradox of invasion biology" (Roman and Darling 2007; Dlugosch and Parker 2008), but thanks to the considerable amount of molecular data that has now been collected to address this question, the paradox has essentially been put to rest.

Instead, data indicates that most invasions are not characterized by significant loss in neutral genetic diversity (see for instance Bossdorf et al. 2005), as typically measured using nuclear microsatellites or maternally-inherited mitochondrial DNA (mtDNA). Comparatively high neutral genetic diversity in invasive populations can be explained by multiple introductions, particularly when source populations are genetically divergent (e.g. Facon et al. 2003; Kolbe et al. 2004; Kang et al. 2007). However multiple introductions do not necessarily explain high genetic diversity (and evolutionary potential) in invasive populations (Lavergne and Molofsky 2007). For example, Eales et al. (2010) demonstrated, in an elegant study that illustrates the marriage between genetics and ecology, that high genetic diversity in an invasive population of anole lizards, *Anolis cristatellus* (Duméril and Bibron) (Squamata: Iguanidae), was a consequence of a single introduction event containing several genotypes. In this case the reproductive mechanism of the study species was also deemed important, since female anole lizards mate multiple times, and can store sperm from several males. This could have increased the number of genotypes above that of the number of founding individuals if the founding population included recently-mated females. Studies that compare levels of genetic diversity in multiple independent introductions in different locations of the same species are particularly useful, since these are equivalent to natural

biological replicates (Bossdorf et al. 2005), although note that this is tempered by difficulties of sampling introductions that fail to become invasive. In the case of *D. virgifera*, mentioned above, levels of genetic diversity differed considerably between the five independently introduced populations studied (Ciosi et al. 2008). When taken together with examples of successful invasions that are characterised by very low genetic diversity at neutral loci, this suggests that genetic variation is not an essential component of invasion success (Dlugosch and Parker 2008). The important point to make here is that there is a key difference between genetic variability at neutral molecular markers, which are irrelevant for selection and adaptation, and additive genetic variation, which is needed to respond to selection. Future studies need to focus on quantifying additive genetic variation (ideally in species characterised by multiple, independent introductions) to fully address the role of genetic diversity in invasion success.

Does admixture from multiple introductions increase invasion success?

As discussed above, multiple introductions are a common feature of biological invasions, but one major question that deserves attention is the role of intraspecific hybridization (i.e. "admixture") in invasion success. Admixture, like interspecific hybridization, can change the distribution of phenotypes in a population, and admixed individuals are able to outcompete their parental genotypes as a result of either heterosis effects or by creating new genotypes through recombination (Facon et al. 2005), or via phenotypic plasticity (e.g. Lavergne and Molofsky 2007). Both interspecific hybridization and intraspecific admixture are therefore important potential stimuli of invasion success (Lee 2002; Facon et al. 2005).

Admixture has been documented in invasive populations that stem from multiple introductions (e.g. Facon et al. 2005; Kolbe et al. 2008; Lavergne and Molofsky 2007), and may be driving invasion success in these examples. However, so far there have been few direct tests of this hypothesis. One direct and comprehensive test of the effects of admixture on invasive success was carried out in invasive parthenogenetic thiarid snails, *M. tuberculata,* using a combination of genetic analyses, laboratory experiments and field data (Facon et al. 2005, 2008). In the invasive range

(Martinique) five introduced asexual morphs from Japan, Indo-Malaysia and the Philippines are found, plus two sexual morphs produced locally through sexual reproduction. Sexual morphs exhibit novel combinations of traits that differ significantly from the parents (e.g. they produce larger but fewer offspring), suggesting non-additive interaction (heterosis) between parental genotypes, which allowed them to outcompete parents in natural habitats, and increase invasiveness, strongly suggesting their novel life-history strategies provided a strong selective advantage (Facon et al. 2005, 2008). Combining molecular genetic data on source populations, with field and quantitative genetic data, provided the first direct evidence that multiple introductions are primarily responsible for accumulation of adaptive potential in key ecological traits in this species (Facon et al. 2008).

The potential for invasion success to be increased by admixture was also recently tested in laboratory crosses between individuals from flightless biocontrol stocks and invasive European populations of the harlequin ladybird, *H. axyridis* (Facon et al. 2010). The authors tested the three criteria, outlined by Wolfe et al. (2007), that must be met for admixture to play a role in biological invasions, namely: (1) parental populations should be genetically differentiated from each other, (2) crosses should be possible between individuals from different parental populations and (3) admixed individuals should differ from their parents in life-history traits crucial to invasion success (e.g. fecundity, dispersal ability, parasite resistance etc.). All three criteria were met, and admixed individuals developed more quickly and were slightly bigger than parentals, indicating possible heterosis effects. This could have serious negative consequences for the native competitors and prey with which *H. axyridis* interacts. Admixture also increased genetic variance for survival during starvation periods, which could boost the efficacy of selection and give admixed *H. axyridis* an advantage during periods of famine. Evaluating whether effects of heterosis persist over several generations, and whether admixture occurs in the wild, are important avenues for future research in this area.

Does invasion lead to non-neutral evolution and novel adaptation?

Biological invasions happen over contemporary time-scales, and so, they can be viewed as windows

to observe evolution in action. Not surprisingly therefore, there is considerable interest in using invasions as model systems to better understand the role of natural selection and adaptation in shaping phenotypes (Keller and Taylor 2008). A comprehensive knowledge of sources and invasion routes is needed in this case to successfully disentangle the effects of demographic and stochastic events from selection. So far, although many examples of evolution during biological invasions have been described (see Whitney and Gabler 2008 for a review), it is not always clear whether changes in phenotypic and life-history traits during establishment and range expansion reflect adaptive evolution during the invasion process, or neutral changes linked to genetic drift (Keller and Taylor 2008). However, even in cases of clear adaptation, it is not always clear whether adaptation allowed the invasion, coincided with the invasion, or was a consequence of the invasion (Estoup and Guillemaud 2010). Indeed, not all invasions need adaptation. Again, investigations using independent introductions from separate locations should be fruitful here, and ideally they should include a subset of populations that have been introduced but have not become invasive (Estoup and Guillemaud 2010). If the same phenotype occurs in independent successful introductions, this is strong evidence that phenotypic evolution is adaptive rather than plastic (Keller and Taylor 2008).

Another approach that has been useful for investigating adaptation during invasions is to compare population differentiation at neutral molecular markers and quantitative traits (F_{ST} and Q_{ST} respectively, Keller and Taylor 2008). If adaptation occurs in the new environment, Q_{ST} is expected to be significantly greater than F_{ST}, in line with a response to selection (e.g. Lavergne and Molofsky 2007; Keller and Taylor 2008). For example, in invasive *A. cristatellus*, in Dominica, $Q_{ST} \gg F_{ST}$, and an altitudinal cline in scalation traits similar to those for related endemic species convincingly indicated that trait divergence in the invasive population was due to directional natural selection acting in just ten generations since introduction (Eales et al. 2010). This study demonstrates the combined power of using molecular genetic, ecological and experimental studies to fully explain observed phenotypes in introduced populations (Eales et al. 2010).

On a cautionary note, recent studies (e.g. Klopfstein et al. 2006; Excoffier and Ray 2008) have shown that a neutral phenomenon occurring during a population range expansion could be interpreted as a signature of positive selection. This phenomenon, coined "gene surfing", is due to strong genetic drift taking place in populations located on the edge of the expansion. Low-frequency alleles can thus surf on the wave of advance of a population range expansion, reaching high frequencies and spreading over large areas, leading to potentially large allele frequency differences between the source and the edge of the spatial expansion. This can be explored using simulations, and should be taken into consideration when investigating adaptation at range margins.

Dispersal

Dispersal is a key life-history trait of fundamental importance to invasion success since it influences the genetic and demographic structure of expanding populations and their ability to adapt to new environments. Although awareness of the crucial role that dispersal plays in biological invasions is increasing (Kokko and Lopez-Sepulcre 2006; Ronce 2007), so far few studies have actually tried to measure the dispersal ability of IAS, except in the context of biological control (but see below and Heimpel and Asplen 2011). This information is crucial for understanding and predicting spread of invasive species and biological control agents (Heimpel and Asplen 2011), as well as consequences of other global environmental change (Urban et al. 2008; Niitepõld et al. 2009). Since there is a direct, causal relationship between dispersal, gene flow and population structure, detailed analyses of genetic structure can be used to quantify "effective" dispersal (i.e. dispersal with breeding) in wild populations, and this approach can be particularly useful in species that are difficult to study using traditional mark-release-recapture experiments. Traditionally, methods were based on estimating the genetic distance between populations (i.e. F_{ST}), however in recent years, great progress has been made in individual-based methods to detect migrants, and in incorporating geographically explicit information (e.g. geographic features, habitat quality) into analyses in order to detect barriers to dispersal (i.e. landscape genetics, "Appendix 2" section). Here we identify and discuss two main objectives that we believe are particularly relevant: (1) studying

dispersal patterns (i.e. mechanism, rate, dispersal barriers) of IAS to learn more about their dispersal ability and predict future spread, which is also highly relevant in a biological control context (see e.g. Heimpel and Asplen 2011), and (2) using IAS as model organisms to increase understanding of the fundamental processes of dispersal and colonization.

Patterns of dispersal

Our ability to predict the spread of IAS is still limited, and in order to successfully do so, we need to understand the mechanisms underlying range expansion (e.g. Urban et al. 2008). The simplest model of range expansion is a random-diffusion process, often referred to as Fisher's "wave of advance" model, in which the range of an invading species is predicted to increase linearly with time (Fisher 1937; Skellam 1951). Although there are examples where this model applies (e.g. muskrat, *Ondatra zibethicus* (L.) (Rodentia: Cricetidae), in Europe, Skellam 1951; coypu, *Myocaster coypus* (Molina) (Rodentia: Myocastoridae), in the UK, Reeves and Usher 1989), other cases demand more complex range expansion models that include, for example, probability of long-distance dispersal (LDD) events (either by wind or human transport), which can accelerate the rate of range expansion as the length of the invasion front increases (Shigesada et al. 1995; Ciosi et al. 2010). A combination of both short and long distance dispersal (i.e. "stratified" dispersal) may be a common feature of invasions, and has already been described in several species of invasive insect (e.g. firethorn leaf miner, *Phyllonorycter leucographella* (Zeller) (Lepidoptera: Gracillariidae), Nash et al. 1995; gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae)*,* Sharov and Liebhold 1998; horse chestnut leaf miner, *Cameraria ohridella* (Deschka and Dimic) (Lepidoptera: Gracillariidae), Gilbert et al. 2004). This has important implications for control measures, which could be improved by preventing establishment of new focal populations or eliminating new ones rather than focusing on established invasion fronts (Moody and Mack 1988; Suarez et al. 2001).

The simplest models of range expansions are based on (1) the intrinsic growth rate and (2) a diffusion coefficient that assumes normally-distributed dispersal distances (Skellam 1951; reviewed in Suarez

et al. 2001), but in reality this assumption is often violated, and the utility of these models therefore limited, as a proportion of the population undergo LDD. Both rare LDD and stratified dispersal skew the distribution of dispersal distances so that distributions are often leptokurtic (i.e. normal with a narrow variance) rather than normal (Ibrahim et al. 1996; Suarez et al. 2001). LDD can increase invasion rate by an order of magnitude (Higgins and Richardson 1999) and even rare LDD events can result in conflicts between theoretical predictions and empirical data (Suarez et al. 2001).

Differentiating between different mechanisms of dispersal, and quantifying the rate and distance of LDD events is therefore essential for constructing accurate predictive models (Suarez et al. 2001). Unfortunately though, measuring LDD is not trivial because of the scarcity and unpredictability of LDD events (Gilbert et al. 2004) and so far few studies have quantitatively estimated its importance. Genetic methods offer some hope for determining dispersal mechanism and quantifying LDD since the process of expansion leaves unique genetic "signatures" in the population (Ciosi et al. 2010). A simple pattern of geographic "isolation-by-distance" (IBD), where there is strict agreement between pairwise genetic and geographic distances because gene-flow is predominantly via neighbouring populations, is expected under the wave of advance model (Slatkin 1993), whereas a weak pattern of IBD may reflect a more complex dispersal process. More sophisticated statistical frameworks are now in place to identify individual migrants ("Appendix 2" section). Of course, these methods are most powerful when used in conjunction with observational and/or historical records. A combination of these approaches was recently used to infer that the European outbreak of *D. virgifera* expanded its range via stratified dispersal (Ciosi et al. 2010).

The models of range expansion we have discussed so far assume that dispersal is through homogeneous environments or independent of the environment, which is likely to be an oversimplification. Environmental heterogeneity is expected to be an important determinant of range expansion, with invasions accelerating as individuals encounter favourable conditions, and decelerating as they reach less favourable environments (Urban et al. 2008). Heterogeneous environmental conditions can now be incorporated

into theoretical frameworks for predicting expansion (Hastings et al. 2005) and ecological and landscape variables (including spatial structure and metapopulation dynamics) can be explicitly linked to invasion rates (e.g. Facon and David 2006; Urban et al. 2008). For example, Urban et al. (2008) analysed invasion trajectories in invasive cane toads, *Bufo marinus* (L.) (Anura: Bufonidae), in Australia to determine whether range expansion accelerated, decelerated or was linear, and if certain environmental conditions influenced population growth. Cane toad invasion dynamics include both accelerating and decelerating range expansions, and sensitivity to temperature, topography, road networks and patch connectivity, indicating that environmental influences are essential for accurate theoretical predictions (Urban et al. 2008). Recently, spatially explicit models, developed using an ABC framework for investigating dynamics of invasions, have been applied to cane toads (landscape-ABC, Estoup et al. 2010). From these, it is evident that there was a small initial founder population, which was followed by a dispersal distance of 19 km generation^{-1} resulting in a spread of 50 km year^{-1}.

Understanding what constitutes a barrier or corridor to dispersal is critical for predicting and managing the spread of IAS. Recent developments in landscape genetics (see "Appendix 2" section) offer great promise for understanding how landscapes shape gene-flow, and identifying barriers and corridors to dispersal, but so far few studies of invasive species have taken advantage of them. However, in one notable exception, Zalewski et al. (2009) investigated genetic structure of invasive American mink, *Neovison vison* (Schreber) (Carnivora: Mustelidae) in Scotland, and identified genetic discontinuities consistent with the Cairngorn Mountains presenting significant barriers to dispersal. This work has important implications for mink eradication programmes. Barriers to dispersal can also take the form of more subtle landscape or environmental features, such as habitat type or temperature and/or humidity gradients. For example, in line with known ecology and habitat preferences, water and urban areas appear to act as substantial barriers to gene flow for fragmented populations of solitary bees, *Colletes floralis* (Eversmann) (Hymenoptera: Colletidae), whereas beaches, sand dunes and agricultural land facilitate gene flow (Davis et al. 2010). In another example, urban and rural developed land provided high landscape resistance for amphibians (Goldberg and Waits 2010). Information on which geo-climatic features increase population connectivity is being used to conserve fragmented populations, and to predict how species will respond to climate change, but is also useful for modelling the spread of IAS (e.g. Knowles and Alvarado-Serrano 2010; Sork et al. 2010).

Evolution of dispersal

Dispersal is not a fixed trait. Instead, it is an excellent example of a trait that can evolve in response to natural selection, and this is particularly evident during periods of range expansion (Kokko and Lopez-Sepulcre 2006; Ronce 2007), as exemplified by the evolution of longer legs in cane toads, *B. marinus*, which has facilitated rapid dispersal at the invasion front (Phillips et al. 2006). Strong selection is expected to favour increased dispersal at the expansion front since there are major fitness benefits to being among the earliest colonists of a new patch (Travis et al. 2009). This can create a positive feedback loop that can potentially accelerate the wave of expansion (Kokko and Lopez-Sepulcre 2006; Excoffier and Ray 2008). Travis et al. (2009) showed theoretically that accelerating invasion rates result from the evolution of density-dependent dispersal, even when costs associated with dispersal are moderate. Moreover, selection pressures for high dispersal must be very strong in order to overcome genetic drift and Allee effects in the small populations at the expansion front (Travis and Dytham 2002; Excoffier and Ray 2008). Understanding the evolution of dispersal (and density-dependent dispersal in particular, Travis et al. 2009) is essential for making accurate predictions about species range expansions (or contractions), particularly under current anthropogenic environmental changes (Kokko and Lopez-Sepulcre 2006). Studying dispersal evolution during biological invasions is not only necessary for predicting spread, but can also provide more general insights into the ultimate and proximate causes of dispersal.

Theoretical studies have generated clear, testable predictions about the evolution of dispersal during range expansions. For example, Travis and Dytham (2002) showed that range expansion is characterized by two distinct phases. First, populations at the invasion front should be characterized by an excess of

migratory individuals (relative to established populations) due to a selection advantage for founding new populations. Second, as more populations are established and the selective advantage to dispersal reduced, migration costs should select for lower dispersal (Travis and Dytham 2002). In a direct test of these predictions, Simmons and Thomas (2004) observed increased frequencies of dispersive, long-winged individuals in recently colonized populations of different species of bush cricket (Orthoptera: Tettigoniidae), relative to established core populations. However, within ten years after colonization, wing-morph frequencies stabilised, to resemble the core (Simmons and Thomas 2004). Such a trade-off between dispersal and fecundity has been investigated theoretically (Burton et al. 2010) and observed in several insect species (e.g. speckled wood butterflies, *Pararge aegeria* (L.) (Lepidoptera: Nymphalidae), Hughes et al. 2003; sand crickets, *Gryllus firmus* (Scudder) (Orthoptera: Gryllidae), Roff and Fairbairn 2007).

An obvious consideration is that for dispersal to evolve in response to natural selection, there must be underlying heritable variation in dispersal ability. This is illustrated beautifully in insects, where there is considerable evidence for additive genetic variance and high heritability in dispersal traits such as wing length and morphology, initiation and duration of flight, and production of enzymes linked to locomotion (e.g. several species of bush cricket (Orthoptera: Tettigoniidae), Simmons and Thomas 2004; sand crickets, *G. firmus,* Roff and Fairbairn 2007; and large milkweed bugs, *Oncopeltus fasciatus* (Dallas) (Heteroptera: Lygaeidae), see Roff and Fairbairn 2007 for review). Investigating the genetics behind these particular phenotypes is essential for a more mechanistic understanding of dispersal evolution, and for increasing the likelihood of predicting its rate (Travis et al. 2009). Studies of the *Glanville fritillary*, *Melitaea cinxia* (L.) (Lepidoptera: Nymphalidae), have been particularly enlightening in this regard. Butterflies from newly formed populations in the Åland archipelago have higher flight ability (accompanied by higher metabolic rate, Haag et al. 2005) and fecundity than those in established patches (Hanski et al. 2002). Moreover, dispersal ability is highly heritable (Saastamoinen and Hanski 2008) and associated with allelic variation at a single gene for phosphoglucose isomerase (PGI), a temperature-sensitive, glycolytic enzyme (Haag et al. 2005; Niitepõld et al. 2009). Individuals heterozygous at *Pgi* move longer distances at lower temperatures than homozygous individuals (Niitepõld et al. 2009). Although several studies have focused on PGI at the functional level (e.g. Watt et al. 2003; Wheat et al. 2006), to our knowledge this locus has not yet been investigated in the context of dispersal ability other than for *M. cinxia*. Although dispersal is without doubt a complex trait, under control of many genes, investigating whether allelic variation at *Pgi*, and selection acting on this locus, generally underlies enhanced dispersal ability during invasions, will be a worthwhile starting point.

Community interactions

Understanding the interactions between invasive alien species and other species within an invaded range is challenging but essential, particularly for quantifying effects on communities (Roy et al. 2009; Hesketh et al. 2010), and developing practical approaches to the management of IAS. Much of the current knowledge on community interactions stems from conventional laboratory and field studies, but there is a need to integrate theory with a multidisciplinary empirical approach. Species identification by molecular gut-content analyses is currently labour intensive, but is revealing unique insights into predator–prey relationships in the context of biological invasions (see Aebi et al. 2011). Recent developments in second and next generation sequencing offer considerable potential for investigating both predator–prey and host-parasite interactions, without prior development of species-specific markers (see "Appendix 3" section). This data can then be input into ecological networks, which represent the biotic interactions in an ecosystem, with species (nodes) connected by pairwise interactions (links), such as the quantitative food web illustrated in Fig. 2. Characterizing the structure of ecological networks is essential in the context of invasion biology to evaluate the impact of IAS on their prey, and to determine whether the invasive species themselves are parasitized or predated on. By quantifying the interactions within entire communities, it is possible to describe network structure and complexity as well as measure the responses of ecological systems to

environmental change. Recent advances in network ecology have been used to assess the impacts of (1) biological control on the wider insect community (Henneman and Memmott 2001), (2) habitat modification on host-parasite interactions and ecosystem services (Tylianakis et al. 2007), and (3) alien plants on plant-pollinator networks (Lopezaraiza-Mikel et al. 2007).

Below, we discuss how an approach based on molecular genetic data and ecological modelling could be used to investigate predator–prey and host-parasite interactions. It is important to note though that these two interactions could be investigated simultaneously. A combined molecular-ecological network approach would be particularly illuminating in the case of invasive generalist predators such as *H. axyridis* (see Aebi et al. 2011), which predate not only on aphids and other herbivorous pests, but also on beneficial insects within the same guild (i.e. a community of species that share the same host or prey). Laboratory experiments indicate that intraguild predation (IGP) by *H. axyridis* could be devastating to native coccinellids and other beneficial insects (e.g. Ware et al. 2008; Ware and Majerus 2008). Molecular gut-content analyses of *H. axyridis* have confirmed IGP in open field plots and in the wild (Chacón et al. 2008; Aebi et al. 2011), however whether IGP happens at an appreciable frequency in the wild is still subject to debate. Moreover, assessing rates of parasitism on *H. axyridis* (and other invasive insects) by native hymenopteran parasitoids as a natural form of pest control can be laborious using traditional laboratory rearing methods, and is

potentially biased (Henneman and Memmott 2001). Molecular genetic approaches ("Appendix 3" section) can overcome this problem and have the potential to provide rapid, highly-resolved data on predator–prey (e.g. gut-content analysis) and host-parasitoid interactions (e.g. host screening). They also have the advantage of being able to distinguish between morphologically indistinguishable species. However it should be noted that a molecular approach, when used alone, also has its drawbacks. For example, it may be difficult to detect encapsulated/undeveloped parasitoids, which are quite easy to detect with dissection, due to DNA degradation (Hoogendoorn and Heimpel 2002). The most powerful approach is therefore to couple molecular methods with conventional experimental and field survey methods, which together can assist in deciphering the dynamic relationships between species within ecological networks. From these networks it is then possible to assess the impacts of invasive insect infiltration on entire communities as well as exploring differences in network structure across the species range.

Predator–prey interactions

A number of studies have assessed the addition of alien species into a community using food web analysis (Henneman and Memmott 2001; Memmott and Waser 2002; Sheppard et al. 2004, and see Fig. 2). For example, Sheppard et al. (2004) examined the interactions between alien predators, introduced to Hawaii to control pest insects, and endemic

Fig. 2 Hypothetical quantitative food web showing the interactions between plants, herbivores and their predators/parasitoids. Each bar represents a species and bar width represents the species' abundance among all individuals sampled. The area of the triangles connecting trophic levels represents the relative number of higher-trophic-level species attacking the lower-level species
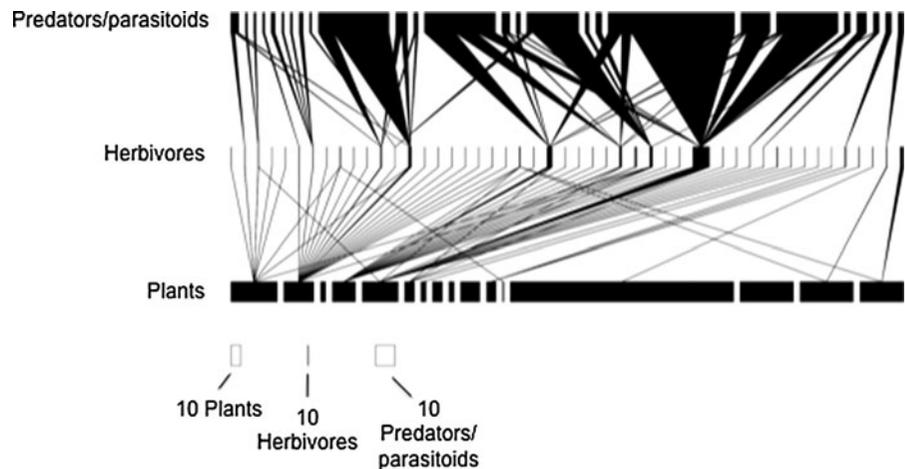
invertebrates (mainly Lepidoptera) within pristine upland habitats. Approximately 11% of the predators within the food web were alien to Hawaii (Sheppard et al. 2004). The findings of Henneman and Memmott (2001) were dramatic: 83% of Lepidoptera parasitoids, in a native forest on Kauai Island, were alien species introduced as biological control agents, and a further 14% were accidentally introduced adventive wasps (only 3% of the parasitoids were native). With the exception of these case studies, using networks to assess the impacts of invasive insect infiltration on communities is yet to be widely applied, partly due to problems of identifying cryptic interactions in the field. This could be overcome by employing molecular techniques more widely in network analyses, and recent advances in molecular gut-contents analysis have allowed unique insights (King et al. 2008).

A combined molecular-network approach could be particularly valuable for generating food webs to investigate the complex concept of invasional meltdown. Invasional meltdown describes the process by which an alien species facilitates invasion by another alien species by increasing the likelihood of its survival and/or the magnitude of its impact (Simberloff and Von Holle 1999). So, essentially, invasional meltdown is used to describe synergistic interactions among invasive alien species, which lead to accelerated and devastating impacts on native ecosystems. Invasional meltdown is a contentious theory (Simberloff 2006). It is a concept that is difficult to explore because, although many studies have examined individuals of one species providing a benefit to the establishment and spread of another, there is a scarcity of information on population impacts. The introduction of the yellow crazy ant, *Anoplolepis gracilipes* (Smith) (Hymenoptera: Formicidae), on Christmas Island and its interactions with native and alien scale insects (Hemiptera: Coccoidea) is considered to have led to major disruption of the community structure (O'Dowd et al. 2003). The complex set of interactions leading to invasional meltdown on Christmas Island requires understanding of the intricacies of the yellow crazy ant food web. The devastating alteration of the Christmas Island ecosystem is thought to be the only convincing example of invasional meltdown in action, however, more subtle effects through the infiltration of alien species into communities are widely reported. Interestingly, it has recently been hypothesized

that extensive invasional meltdown is occurring in North America involving eleven Eurasian IAS, including *H. axyridis,* with the presence of invasive soybean aphids, *Aphis glycines* (Matsumara) (Hemiptera: Aphididae) increasing regional abundances of other IAS (Heimpel et al. 2010). Exploration of this system with a molecular-network approach would be a particularly exciting avenue for further research.

Host-parasite interactions

Molecular genetic techniques are particularly useful for examining host-parasite interactions within a community context. Molecular markers can be used to identify species of parasite when morphological characters are limited, when there are problems identifying juvenile stages of the life cycle, or when the parasite is either cryptic or covert (Bonsall et al. 2005). By using current methods, which focus on species or genus-specific primers and target a particular species, it is likely that we are underestimating parasite diversity (Hesketh et al. 2010). It has been estimated that more than 1600 parasitic fungi attack beetles (Coleoptera), but studies generally focus on a few genera (Riddick et al. 2009). 454 sequencing or similar "metagenomics" approaches ("Appendix 3" section) offer powerful opportunities to detect and quantify all parasites present in a host community. This approach was recently used to identify Israeli acute paralysis virus as a potential agent of colony collapse disorder in honeybees, *Apis mellifera* (L.) (Hymenoptera: Apidae) (Cox-Foster et al. 2007), and to characterise microbes associated with the primary pest of bees, the ectoparasitic mite *Varroa destructor* (Anderson and Trueman) (Mesostigmata: Varroidae) (Cornman et al. 2010). In principle, the same approach could be used to characterize the community of parasitic organisms living within or on an IAS, and therefore to test the prediction of the enemy release hypothesis (Roy et al. 2011b) that there should be lower infection levels in alien populations compared to native populations of the same host species.

Enemy release is considered to be one of the mechanisms by which invasive alien species gain advantage in the invaded range. However, it is also probable that an alien species is host to pathogens that have not been experienced by species occupying the invaded range. "Pathogen spillover" refers to the transmission of disease from alien to native hosts

when a parasite hitchhikes with the invading species. So far, pathogen spillover has been given little consideration in the context of biological invasions, and studies have focused on disease outbreaks in wild populations, as a consequence of spread from infected domestic animals (e.g. pathogen spillover has been implicated in the decline of wild fish populations, Morton et al. 2004; and in pathogen transmission from commercial to wild bumble-bees, *Bombus terrestris* (L.) (Hymenoptera: Apidae), Colla et al. 2006). Investigation of pathogen spillover during invasions is warranted since this key process could exacerbate the effects of invasive alien species within a community, perhaps even contributing to invasional meltdown (Prenter et al. 2004; Colla et al. 2006). Such studies would benefit from the inclusion of molecular techniques, which provide the potential to rapidly screen invasive alien species for pathogens and to model the risk posed to native species.

Investigating the transmission dynamics of parasites using molecular methods is of vital importance for identifying potential biological control agents and for understanding the role of parasites in invasions. Parasites that are strictly vertically transmitted (i.e. from mother to offspring) are well suited as biological control agents, since there is low risk of host-switching to non-target species. Maternally-inherited endosymbiont bacteria, such as *Wolbachia* (Rickettsiales), are very common in insects (Hilgenboecker et al. 2008) and impose a range of consequences on their hosts' reproduction, including cytoplasmic incompatibility (CI), male-killing, and induced parthenogenesis (reviewed in Werren et al. 2008). Endosymbionts can also negatively influence other aspects of their host's biology, including life-span (McMeniman et al. 2009) and dispersal (Goodacre et al. 2009). CI-induction should facilitate *Wolbachia* invasion into wild host populations and may be a viable strategy to reduce pest populations (Zabalou et al. 2004) and pathogen transmission (McMeniman et al. 2009). For example, CI-*Wolbachia* has been proposed as a control agent against medfly, *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), (Zabalou et al. 2004), which is a major agricultural pest. In addition, life-shortening CI-*Wolbachia* was successfully introduced into *Aedes aegypti* (L.) (Diptera: Culicidae), the mosquito vector of dengue virus, and was maternally transmitted at high frequency (McMeniman et al. 2009). This offers hope

for reducing the impact of dengue fever, which has grown dramatically in recent decades (World Health Organisation). However, it is important to bear in mind that by increasing the proportion of females, and in some cases conferring substantial indirect fitness benefits to their female hosts (e.g. female neonate coccinellid larvae gain an indirect fitness benefit by consuming undeveloped eggs of their brothers, Hurst and Majerus 1993) these reproductive manipulators might actually facilitate host invasion (Hatcher et al. 1999; Galbreath et al. 2004). For example it was recently demonstrated, by an elegant series of experiments, that increased fitness and female-biased sex ratio linked to *Rickettsia* spp. nr *belli* likely facilitated invasion of the notorious sweet potato whitefly, *Bemisia tabaci* (Gennadius) (Hempitera: Aleyrodidae), in the USA (Himler et al. 2011). In addition, there is mounting evidence of extensive horizontal transmission of endosymbionts between different host species (reviewed in Werren et al. 2008). Investigations of parasite transmission dynamics are therefore essential in the context of biological invasions, and caution is needed before recommending reproductive parasites in biological control.

Finally, much can be learned about host-parasite interactions by comparing genetic structure in the interacting species. Host-parasite complexes can shed light on the interaction between gene-flow and the ability of natural selection to promote local adaptation (Criscione et al. 2005). It is also possible that the genetic structure of the parasite, or even just its distribution, could be used to help identify geographical origin of the host (Aebi and Zindel 2010). This approach might be particularly useful when there is low genetic structure of the host in its native range (and therefore reduced power to identify source populations). Again, for such an approach to be successful, parasite transmission must be strictly vertical.

Conclusions and perspectives

If EB Ford was alive to publish a new edition of "Ecological Genetics", biological invasions would surely constitute a significant component of his book. Studying ecological genetics of invasions is already allowing insights into the fundamental processes described in this review. We highlight two particular

areas of importance for future study. First, there is currently considerable focus in the ecological genetics community on studying adaptation in wild populations (see Stapley et al. 2010 for a recent review), and invasions are excellent model systems for understanding the role of natural selection in shaping phenotypes. Although technical challenges are still associated with next generation sequencing, rapid progress is being made. In particular, the RAD-tag method (Baird et al. 2008) allows an unprecedented number of genetic markers to be characterised and typed, offering a powerful means to identify loci contributing to adaptation during invasions (see Hohenlohe et al. 2010 for a recent application and Stapley et al. 2010 for a review). Second, the combination of molecular genetic techniques, particularly Roche/454-pyrosequencing or similar ("Appendix 3" section), and ecological network modelling offer great potential for quantifying predator–prey and host-parasite interactions between species in a community (Hesketh et al. 2010). This approach has particularly important implications for biological control—for example identifying previously uncharacterised natural enemies that could be potential biocontrol agents—and ultimately for addressing two of the most fundamental questions in invasion biology: (1) what is the impact of biological invasions on native, recipient species? and (2) does release from natural enemies increase invasion success? With the increasing potential to address these and other fundamental questions, the field of ecological genetics of invasive alien species has an exciting future ahead of it.

Appendix 1: Introduction to molecular genetic methods for inferring source populations and invasion routes

Two types of method have been used to make inferences concerning source populations and invasion routes: direct methods based on current and historical observations of IAS and indirect methods based on patterns in molecular data.

Direct methods are based on records of the presence and absence of invasive taxa. Routine controls carried out in airports and harbours by quarantine services and monitoring by environmental or agricultural agencies are particularly informative in this respect (Work et al. 2005). However, it is rarely possible to infer the routes of invasion with a high degree of precision by these direct methods. Indeed, given the low rates of establishment and expansion recorded for introduced individuals (Williamson 2006), there is no guarantee that the individuals intercepted would have spearheaded a successful invasion.

Indirect methods are based on the genetic patterns observed within and between populations at molecular markers. Traditional statistical treatments include the construction of trees from matrices of genetic distances between populations (e.g. Lozier et al. 2009; Thibault et al. 2009), parsimony networks (e.g. Voisin et al. 2005; Hoos et al. 2010) and the calculations of assignment likelihood (e.g. Genton et al. 2005; Ciosi et al. 2008). More recently, a number of studies have used clustering methods like those implemented in STRUCTURE (Pritchard et al. 2000). If the invasive population clusters clearly with one of the potential source populations, this is considered to provide fairly conclusive information about the origin of the invasive population (e.g. Marrs et al. 2008; Rollins et al. 2009). A shared ancestry of the individuals of invading populations with various populations from the native area is sometimes interpreted as evidence for an admixture origin of the invasive population considered, although it may also reflect the presence of unsampled sources, drift, or insufficient numbers of markers (Darling et al. 2008; Rosenthal et al. 2008). It is worth stressing that, although the abovementioned indirect methods have proved useful in many cases, they are all subject to two major limitations: (1) they poorly take into account the stochasticity of the demographic and genetic history considered and (2) they do not allow probabilistic estimations of competing introduction scenarios (e.g. Knowles and Maddison 2002).

Recently, a new indirect method called approximate Bayesian computation (ABC, Beaumont et al. 2002, implemented in DIYABC, Cornuet et al. 2008) has been proposed and used to draw inferences from molecular and historical data, about the complex evolutionary scenarios typically encountered in the

introduction histories of IAS (Fig. 1). General statistical features of ABC have been reviewed in two recent papers (Bertorelle et al. 2010; Csillery et al. 2010) and some practical aspects that are important when using this method to make inferences about invasion routes can be found in Estoup and Guillemaud (2010). Briefly, ABC is a model-based Bayesian approach in which the posterior probabilities of different models and/or the posterior distributions of the demographic parameters under a given model are determined by measuring the similarity between the observed data set (i.e. the target) and a large number of simulated data sets. ABC has four main advantages over the more traditional indirect methods described above: (1) it uses all the data simultaneously in inference, (2) it can be used to estimate probabilities, with confidence intervals for each of the scenarios compared (e.g. Cornuet et al. 2008, Fig. 1), (3) it allows the evaluation of the power of a given analysis on the basis of controlled simulated datasets (Cornuet et al. 2008; Guillemaud et al. 2010), and (4) it avoids the introduction of misleading biases, such as those due to unsampled populations (Guillemaud et al. 2010) or genetic admixture between multiple sources (Lombaert et al. 2010). ABC thus constitutes a real advance for inferring source populations and invasion routes.

Appendix 2: Introduction to molecular genetic methods for investigating dispersal

The rapidly developing field of landscape genetics aims to understand how population genetic processes are affected by spatial and temporal environmental heterogeneity, by integrating population genetics with landscape ecology and spatial statistics. Landscape genetics approaches enable two major insights into dispersal: first, individuals with multilocus genotypes that are representative of a population other than the one they were sampled in can be identified. This is a powerful way of identifying immigrants and therefore quantifying dispersal (e.g. Guillot et al. 2005a, b). Second, the pattern of spatial genetic structuring can be tested for correlations with landscape or environmental features, allowing identification of genetic continuity (or connectivity) between patches, or discontinuities resulting from

barriers to dispersal (see e.g. Balkenhol et al. 2009; Guillot et al. 2009; Storfer et al. 2010, for recent reviews).

Under a landscape genetics approach, the individual is the unit of study, and their exact geographic location must be recorded. Populations do not have to be identified a priori. Bayesian statistics are used to assign individuals to populations according to their multilocus genotypes, using software that employ clustering algorithms based on pre-defined population genetic models (e.g. STRUCTURE, Pritchard et al. 2000, see also "Appendix 1" section). In recent years, new technologies have greatly assisted marker development, vastly increasing the amount of data that can be collected, and decreasing the computation time required for data analysis. For example, new statistical approaches such as Discriminant Analysis of Principal Components (DAPC, Jombart et al. 2010), offer great potential for assigning individuals into clusters with minimal computing time when datasets are large, and when there is low population structure.

Isolation by distance tests (e.g. Mantel test) have long been used to identify correlations between genetic distance and environmental variables, but new statistical approaches are also being developed to model the relationship between genetic structuring and the environment, which allow inferences on the microevolutionary processes generating spatial genetic structure (see e.g. Guillot et al. 2009). Geographical information systems-based landscape analysis overlays landscape variables onto population genetic data to visualise patterns of genetic structuring (for example using ArcGIS or PATHMATRIX, Ray 2005), allowing environmental parameters likely to influence dispersal in heterogenous environments to be investigated. The spatial domain occupied by inferred clusters can be examined to identify dispersal barriers, using programmes such as GENELAND (Guillot et al. 2005b), and genetic diversity can be simulated, accounting for environmental and spatial heterogeneity, using software such as SPLATCHE (Currat et al. 2004). This latter approach has been modified to reconstruct invasion scenarios, investigating parameters such as dispersal distance and speed (Estoup et al. 2010). These types of simulations show how demographic processes interact with landscape features to determine spatial genetic structure (Epperson et al. 2010) and to

investigate how dispersal is affected not only by obvious geographical features (e.g. mountain ranges), but also by more subtle habitat characteristics (e.g. Davis et al. 2010). They therefore offer great potential for understanding dispersal ability, and ultimately, generating information that can be used to predict the spread of IAS.

Appendix 3: Introduction to molecular genetic methods for investigating community interactions

So far, molecular studies that have attempted to investigate the strength and structure of predator–prey and parasite-host interactions, within a community context, have primarily used standard PCR (e.g. Symondson 2002; Harper et al. 2005; Sheppard and Harwood 2005). The advantage of such markers is to be able to qualitatively evaluate specific interactions between a predator and its prey or a parasitoid and its host. On the other hand, developing species–specific molecular probes can be long and costly (see Aebi et al. 2011), and the development of species-specific markers to describe whole community's food web structure is impractical. Advances in second and next generation sequencing offer great promise as they do not rely on design of species-specific primers, are extremely sensitive, and could be used to create quantitative interaction networks. For example, Roche/454 massively parallel pyrosequencing offers considerable scope for investigating community interactions. By generating tags from 16S or 18S rDNA, data is generated for almost every organism in a sample to reveal previously uncharacterised aspects of the biological diversity (e.g. Dethlefsen et al. 2008). Datasets can then be compared to see how they differ in terms of composition. A particular advantage to this method is that many individual samples can be tagged, pooled, and sequenced in parallel (e.g. Meyer et al. 2008), and several populations can be investigated simultaneously (by "gasketing", i.e. splitting a 454 picotiter plate into several sections). This technique has already proven successful in assessing biological diversity in the ocean (e.g. Sogin et al. 2006; Huber et al. 2007), soil (e.g. Leininger et al. 2006), and in the human body (e.g. Dethlefsen et al. 2008). Of particular relevance, a metagenomic survey of 454 sequence data from 16S and 18S rDNA in honeybee, *A. mellifera* hives

uncovered presence of bacteria, fungi, parasites, metazoa, and viruses and found strong correlation between a particular virus and colony collapse disorder (Cox-Foster et al. 2007). A major challenge is to block amplification of the host DNA, but this can be achieved with the use of "blocking primers" (Vestheim and Jarman 2008).

Another challenge with this type of analysis is dealing with the volume of data generated. However, since metagenomics is an established method, several bioinformatics pipeline options already exist. For example, MG-RAST is a fully-automated service for annotating metagenome samples including phylogenetic classification (Meyer et al. 2008). MEGAN (http://ab.inf.uni-tuebingen.de/software/megan/welcome.html) and CARMA (http://www.cebitec.uni-bielefeld.de/brf/carma/carma.html) are also specific for metagenomics analysis to analyse large data sets and group operational taxonomic units (OTUs). Homology detection can be performed by comparing 16S and 18S sequences to reference databases such as SILVA (http://www.arb-silva.de/) using (for example) BLAT (BLAST-like alignment tool, Kent 2002) and OTUs defined based on multiple sequence alignment (Dethlefsen et al. 2008).

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