Rothamsted Repository Download

A - Papers appearing in refereed journals

Morales-Hojas, R. 2017. Molecular ecology of insect pests of agricultural importance: the case of aphids. *Ecological Entomology.* 42 (Suppl. 1), pp. 18-27.

The publisher's version can be accessed at:

- https://dx.doi.org/10.1111/een.12445

The output can be accessed at: https://repository.rothamsted.ac.uk/item/84706.

Molecular ecology of insect pests of agricultural importance: the case of aphids

R A M I R O   M O R A L E S - H O J A S   Rothamsted Insect Survey, Rothamsted Research, Harpenden, U.K.

Abstract. 1. Ongoing environmental change is predicted to have a strong impact on biodiversity. Studies have already noted a range shift in many species as they track their favoured environments. A key challenge entomologists are facing is to understand how insect pest species are responding to this rapid environmental change, and molecular ecology has a central role to play in this task. In the present paper, I argue that molecular ecology has much relevance in relation to the monitoring of insect pests of agricultural importance, with a focus on aphids.

2. First, I examine how the combination of phylogeography and species distribution modelling can be a powerful approach to understanding species responses to climate change and to forecasting future distributions. Despite such a joint approach being increasingly used to understand these questions (e.g. in conservation biology), there are still very few studies that concern pest species of agricultural importance.

3. I then discuss how the use of samples from natural history collections represent an opportunity to directly observe the evolution of species, enhancing our knowledge of the evolutionary processes occurring at ecological time scales. I introduce the Rothamsted Insect Survey (RIS) sample archive and the central role it plays in the studies of pest species of agricultural importance.

4. Lastly, I assess how the advances in DNA sequencing technologies have allowed us to investigate genetic variation at the genome-wide level. Thus, they provide us with the opportunity of studying a variety of questions about the dynamics of pest insects that were previously impossible as well as unmanageable.

Key words. Agricultural landscapes, aphids, landscape genetics, migration, natural history collections, next generation sequencing, phylogeography, species distribution models.

Introduction

Climate exerts a strong selective pressure on organisms, and climatic alteration is seen as being largely responsible for the evolutionary and ecological processes that shape diversity (Parmesan, 2006). Ecosystems are changing fast as a result of the ongoing environmental change and species can respond to it by either tracking their most suitable environment (e.g. Austin & Rehfisch, 2005); by adapting to the new conditions by means of genetic changes (e.g. Umina *et al.*, 2005); or by means of phenotypic plasticity (e.g. Thackeray *et al.*, 2016). Those species unable to track their favoured climate or adapt to new conditions will most likely become extinct. Understanding how diversity has been shaped by past environmental change provides important clues to help forecast how species will

be affected by the ongoing climate change. Paleoecological data indicate that ecosystems are robust and dynamic, and the species extinction rate during past periods of rapid climate change has not been elevated (Blois & Hadly, 2009; Willis & MacDonald, 2011). Furthermore, these studies of fossil data have provided evidence for range shifts, adaptation to new environments, and ecological community shuffling. In light of this, similar responses are expected to occur as a consequence of the ongoing alterations. Several studies have shown that a large proportion of species in the temperate regions of the Northern Hemisphere are tracking their favoured environments by shifting their ranges northwards (Parmesan & Yohe, 2003; Root *et al.*, 2003; Chen *et al.*, 2011). However, these studies have also noted that the extent and rate of the range shifts vary among species. The observed differences in response have been attributed to particular intrinsic characteristics of the species such as their physiology, as well as to different ecological and environmental factors (Loxdale & Lushai, 1999). This lack

Correspondence: Ramiro Morales-Hojas. E-mail: ramiro.morales-hojas@rothamsted.ac.uk

of taxonomic consistency in the degree and direction of the response to environmental alteration highlights the importance of studying the effect of climatic factors at the species level and shows up the weakness of generalising to a higher taxonomic level. It also indicates a requirement to identify the common traits of species responding similarly, independently of their taxonomic classification, to be used as predictors to improve our understanding of how the global diversity is potentially going to be reshaped. Nevertheless, this task is proving difficult to achieve in practice (Angert *et al.*, 2011).

A key challenge is how to mitigate the negative consequences that will ensue from the ongoing rapid climate change. Central to this challenge are concerns about a potential increase in diversity and abundance of insect pests due to the alteration in weather patterns (e.g. Cannon, 1998). A key aspect that needs to be explored if we are to rationally manage insect pests and control their damaging effects on crops is how their distribution range is likely to be modified and identify the areas under risk of invasion concomitant with future climate projections. In this respect, phylogeography represents an important approach to understanding the distribution dynamics of species and the processes that underlie the geographic distribution of their genetic variation (e.g. migration, geographic barriers, etc.) (Marske *et al.*, 2013). It provides the means to investigate the consequences of past climatic events on species diversity and distribution, knowledge which can be used to forecast the potential response to the ongoing alterations. Our understanding of species response and the processes underlying it can be enhanced with the incorporation of historical samples to the phylogeographic analyses. Indeed, these samples provide direct evidence of the changes that occur within species or populations over time, which otherwise could only be inferred indirectly using present day samples (e.g. Fountain *et al.*, 2016; Holmes *et al.*, 2016).

Advancements in niche theory and modelling (Elith *et al.*, 2006; Chase, 2011) have generated an increasing interest in the use of Geographic Information Systems (GIS) to describe the factors that constitute a species environmental niche and use these to generate models of species geographic distribution (Kozak *et al.*, 2008; Alvarado-Serrano & Knowles, 2014). Species distribution modelling (SDM) or ecological niche modelling (ENM), which differ on whether the focus is on the geographic distribution or on the ecological factors that make up the species niche (Araujo & Peterson, 2012; Peterson *et al.*, 2015), use associations between known locations where a species is present and climate aspects to define a series of environmental conditions under which species are most likely to maintain viable populations. Such a climatic envelope is then used to generate a model of geographic distribution. These models are applied to address a variety of different questions [reviewed by Araujo and Peterson (2012)], including the prediction of species ranges and the identification of regions under the potential risk of invasion.

In the present paper, I make a case for a combined approach of distribution modelling and phylogeography to enhance our understanding of the distribution dynamics of insect pests and thus improve the forecasts of the future agricultural areas under risk. I focus mostly on aphids (Hemiptera: Aphididae), which comprise some of the most pernicious insect pest species (Van

Emden & Harrington, 2017). These have been predicted to increase in abundance (Cannon, 1998) due to their positive response to present and predicted climate change (e.g. Bell *et al.*, 2015; Sheppard *et al.*, 2016). Understanding the movement and distribution of aphids is fundamental to be able to plan sound control schemes that help rationalise the use of pesticides and reduce economic losses to the agricultural industry.

Understanding the distribution dynamics of insect pests

One challenge in the study of insect pests is the characterisation of the extensive cryptic variation (Loxdale *et al.*, 2016). Aphids, in particular, are rapidly evolving organisms that show great levels of variation that ranges from species complexes that comprise a number of sibling species to populations and lineages that differ in their host preference (see Blackman & Eastop, 2007; Loxdale & Lushai, 2007; Loxdale *et al.*, 2017). In some cases, like in the pea aphid *Acyrthosiphon pisum* Harris, there is an extensive variation in the host preference of different lineages within species (Muller, 1985a; Peccoud & Simon, 2010). These host races exhibit different levels of reproductive isolation as a result of local adaptation to the different hosts, which could eventually lead to an incipient speciation process (Ferrari *et al.*, 2006, 2008; Muller, 1985b; Peccoud *et al.*, 2009a). Other species, like the black bean aphid *Aphis fabae* Scopoli, are part of species complexes that include a number of closely related species and subspecies that are difficult to differentiate, independent of the degree of reproductive isolation they present (Coeur d'Acier *et al.*, 2004; Raymond *et al.*, 2001). Despite these taxonomic hindrances, the reliable identification of species and forms remains essential for the integrated management of pest insects and pest risk analysis. Microsatellite markers have been developed to identify species, host races, and reproductive modes within species (e.g. Simon *et al.*, 1999, 2001; Delmotte *et al.*, 2002; Caillaud *et al.*, 2004; Coeur d'Acier *et al.*, 2004; Wilson *et al.*, 2004); however, the new DNA sequencing technologies provide the means to identify genetic variation at a more detailed scale potentially helping uncover genetic variation at a finer scale. Furthermore, these technologies provide us with the opportunity to tackle the nature of clones (Loxdale, 2008).

Dispersal of pest species mediated by human trade or by climate change has resulted in economically- and environmentally-adverse impacts on the native biodiversity of the newly invaded regions. Defining the geographic distribution of pest species and the cryptic variation thereof is an essential step towards understanding and to some degree managing their movement and dispersal potential and, therefore, to reduce the damage they do to agriculture. Species distribution modelling (SDM) is increasingly being used to map the ranges of pest insects (e.g. Aragon *et al.*, 2010, 2013; Aragon & Lobo, 2012; Macfadyen & Kriticos, 2012; Kriticos *et al.*, 2015b; Godefroid *et al.*, 2016; Kumar *et al.*, 2016). As mentioned above, these models define the realised niche of species and by delineating the potential areas that have the required environmental conditions to maintain viable populations, they can be used to identify the areas under risk of invasion under present climatic

conditions (e.g. Wharton & Kriticos, 2004; Wang *et al.*, 2010; Aragon *et al.*, 2013; Kriticos *et al.*, 2015a,b; Kumar *et al.*, 2016). Nevertheless, many such studies that aim at identifying areas under risk of invasion do not forecast future distributions nor consider the potential effect of climate change on species ranges. In this respect, species distributions can be projected into a number of past and future climatic scenarios (e.g. IPCC) (Peterson *et al.*, 2002, 2008). These projections require the assumption that the environmental and biotic requirements of the species have not changed through time, what is known as ecological niche conservatism (Wiens & Graham, 2005; Wiens *et al.*, 2010; Peterson, 2011). Interestingly, the inferred models of past distributions provide a null hypothesis that can be tested using demographic reconstruction analyses that estimate the relative population sizes over time. This combined approach has proven a powerful tool to predict the response of species to the effects of environmental change, whether they will adapt to the new environmental conditions or shift their range tracking their preferred environment (e.g. Sillero *et al.*, 2014; Lagerholm *et al.*, 2017). Despite the evident potential of this combined approach, it is still rarely used to understand the distribution and adaptation capacity of insect pests. Studies of the SDMs of insect pests tend to be mostly concerned with the identification of potential areas of invasion, and usually do not include information about the phylogeographic history of the species or its geographic genetic structure (Aragon & Lobo, 2012; Aragon *et al.*, 2013; Godefroid *et al.*, 2016; Kumar *et al.*, 2016). Furthermore, when studying the spatial distribution and the factors that shape it, few studies acknowledge the genetic variation that occurs across a given species' geographic range, and that can affect the capacity of species to disperse to new areas. Incorporating genetic structure information, thus recognising the potential for local adaptation, into ENMs increases the accuracy of predictive models (Ikeda *et al.*, 2017). One study of agricultural pests that took into consideration the variability within species is that of Macfadyen and Kriticos (2012), who used distribution models to infer the potential geographic distribution of the bird cherry-oat aphid, *Rhopalosiphum padi* (L.), sexual and asexual lineages, independently. Modelling of these two life history types separately allowed the authors to confirm the *a priori* expectation that colder regions are more likely to be invaded by the sexual lineages of *R. padi*, depending on the presence of the overwintering host bird cherry, *Prunus padus* L. However, the study did not take into account the ongoing climate change and the SDMs were not projected using models of future climatic conditions. In addition, they did not test the hypothesis of niche conservatism, and thus it is not certain how the species and different reproductive lineages will respond to climate change. Equally, there are many studies on the phylogeography and population genetics of insect pests that do not include models of the species distribution (e.g. Llewellyn *et al.*, 2003; Peccoud *et al.*, 2009b; Lesieur *et al.*, 2016; Popkin *et al.*, 2017), limiting their capacity to understand the factors defining their ranges and the capacity to forecast the future distributions. It is important that these available approaches are employed in combination to provide better predictions for integrated pest management of aphids, or indeed any other type of pest organisms.

A relevant aspect of pest management is insect migration, which partly underlies the capacity of a species to disperse and ultimately helps shape its distribution. Migration and movement of aphids are difficult to study due to the small size of individuals, which makes them challenging to track by suction trapping (Harrington, 2014) and using the current radar technologies (Chapman *et al.*, 2003, 2011). However, advances in population genetics methods provide the analytical tools to infer the pattern and degree of migration between populations more precisely (e.g. Excoffier & Heckel, 2006; Knowles, 2009). Population genetics approaches have been used to establish the genetic structure and gene flow levels across populations of different aphid species, inferring in this way their migratory capacity. For example, *R. padi* and *Sitobion avenae* (F.), the grain aphid, were shown to have little genetic differentiation in the U.K. and France as a result of high levels of gene flow (Simon *et al.*, 1999; Delmotte *et al.*, 2002; Llewellyn *et al.*, 2003). As a result, the authors suggested that these species are long-distance migrants, which is in agreement with the large numbers that show up in traps [e.g. Rothamsted Insect Survey (RIS) suction-traps]. It is interesting to note that taxonomic classification does not condition the migratory capacity of a given species. For example, the genetic variation of the holocyclic blackberry-grain aphid, *Sitobion fragariae* (Walker), is structured at the local scale, which is indicative of restricted levels of gene flow across short distances in contrast to the closely related and predominantly anholocyclic *S. avenae* (Loxdale & Brookes, 1990). Although migration appears to be the main driver of the genetic distribution, the selection is also a relevant force that shapes the distribution of the different genotypes (e.g. Kasprowicz *et al.*, 2008; Gilabert *et al.*, 2015). Understanding the processes underlying the genetic distribution of aphids will allow us to monitor them better. For example, the currant-lettuce aphid, *Nasonovia ribisnigri* (Mosley), is very rarely observed in traps, whether suction or water traps. This argues that *N. ribisnigri* is not a highly migratory species, and therefore the surveillance of its migration should be done at a local scale rather than national. Studying the population genetics of the species will allow us to answer these questions and improve control of this pest (Loxdale & Lushai, 2007; Loxdale *et al.*, 2017).

The use of sample collections to understand ecological and evolutionary processes in agricultural landscapes

The availability of historical samples in museums and other collections allows the study of the evolutionary processes at an ecological timescale. Thus, patterns of variation in present-day samples can be used to infer changes that occurred in the past; however, samples from natural history collections provide the opportunity to study genetic and phenotypic changes in species directly. Thus, these type of samples are very valuable in ascertaining the effects of ecological or environmental events on the genetic variation of species (Mikheyev *et al.*, 2015; Carew *et al.*, 2016; Fountain *et al.*, 2016; Holmes *et al.*, 2016; Lagerholm *et al.*, 2017; Ruane & Austin, 2017). Collection samples within an agricultural landscape context represent

a unique tool to obtain a more comprehensive insight into the selective forces that shape pest diversity and distribution dynamics and, in this way deliver information that can be used to monitor better and control crop pests.

Despite the relevance of monitoring the movement and population dynamics of insects of economic importance, few countries have in place a system of surveillance and forecast. The RIS operates two networks of suction- and light-traps to monitor insects of agricultural importance across the U.K. (Storkey *et al.*, 2016). The suction-trap network currently consists of 16 suction traps across Great Britain that monitor the migration of small- to medium-sized insects at the height of 12.2 m (Fig. 1). The height of the traps was estimated as the logarithmic mean of aphid flight to optimise the collection of aphid species of agricultural importance (Taylor, 1974; Macaulay *et al.*, 1988; Bell *et al.*, 2015). This network was put in place in 1964, and the RIS hosts the longest running data sets of insect populations in the world (Harrington, 2014). The RIS provides essential information for early warning and prediction of aphid (and other organisms) migration and abundance. During spring and summer, the trap samples are collected daily and the catches sent to the RIS for taxonomic identification. The aphids are identified to species or species group (e.g. *A. fabae* sp. group) from the trap catches, counted, and recorded onto a database. The information about the counts of the different species of agricultural interest is circulated to the farming industry on a weekly basis. During late autumn and winter, when aphids have already migrated back to their overwintering primary host, traps are emptied weekly and the catches, if any, are identified to species and recorded onto the database. The use of these traps has allowed the identification of a very significant relationship between the winter temperature and the first-flight time of aphids and this allows the RIS to forecast when the different species will migrate from the winter host into the crops (Harrington *et al.*, 2007; Bell *et al.*, 2015). In addition, some of the aphid species collected in the traps are tested for plant virus presence (TuYV, BYDV, and BMV) and insecticide resistance status (Anstead *et al.*, 2008; Foster & Williamson, 2015). The network thus provides essential information about the risks that aphids pose and has allowed farmers to rationalise the use of insecticides (Harrington, 2014).

The long-term, standardised dataset held by the RIS is a very valuable resource to study ecological questions of insects. It has been used to understand the effect of climate change in the synchrony and phenology of aphid species (Harrington *et al.*, 2007; Thackeray *et al.*, 2010, 2016; Bell *et al.*, 2015). In these studies, analyses of time series data sets that included aphid and moth data, show that the phenology of organisms changes in the U.K. at different rates across taxonomic groups, hence revealing a potential disruption of habitats as a result of the mismatch. In addition, the factors that affect patterns of aphid flight (first flight, last flight, and duration of the flight season) and abundance in the U.K. were identified to be related to the North Atlantic current and winter temperatures (Thackeray *et al.*, 2010, 2016; Bell *et al.*, 2015). Other aspects that have been investigated using the RIS data are the trophic interactions of parasitoids and predators of aphid species. For example, using radar data for identifying ladybird flight and the RIS data on aphid abundance, the main factors affecting the migration

Fig. 1. Map of Great Britain showing the locations of the Rothamsted Insect Survey's suction traps. [Colour figure can be viewed at wileyonlinelibrary.com].

pattern of ladybirds were shown to be temperature and aphid abundance (Jeffries *et al.*, 2013). The effects of parasitism by hymenopterous parasitoids of aphids (e.g. braconids) are seen to function somewhat differently from predation by generalist arthropod predators such as ladybirds and spiders (Snyder & Ives, 2003). Analysis of samples from 1976 to 2013 from the RIS archive revealed a positive regulation of parasitoid braconid populations in response to their aphid host *S. avenae* (Perez-Rodriguez *et al.*, 2015). There was also a broad synchronisation of the migration time of the parasitoids and that of the aphid within a season.

The other available resource at the RIS is the sample archive. All the catches since 1974 have been preserved and are held at the RIS archive. Until 2003, aphid specimens were macerated in lactic acid before identification to enhance recognition of morphological features by clearing the majority of the body contents. The non-aphid samples between 1974 and 2003 were preserved in 70% ethanol and 5% glycerol. From 2003 onwards lactic acid was no longer used, and both aphid and non-aphid

samples were preserved in 95% ethanol and 5% glycerol. These samples are also a very valuable resource to study the action of evolution through time. For example, they have been used to understand demographic processes of aphids, and have been fundamental to investigate the dynamics of insecticide resistance in *Myzus persicae* (Sulzer) populations in Scotland (e.g. Fenton *et al.*, 2005; Kasprowicz *et al.*, 2008). They have also been used to study the population structure and migration patterns in aphid populations in the U.K. (e.g. Foster *et al.*, 2002; Llewellyn *et al.*, 2003; Malloch *et al.*, 2006).

The genomics revolution in molecular ecology

The development of the polymerase chain reaction (PCR) (Mullis *et al.*, 1986) brought about a transformative technical advance that served as the starting point of molecular ecology as a fully-fledged field. The use of allozymes as molecular markers to study population diversity led to the neutral theory of molecular evolution (Kimura, 1968; King & Jukes, 1969), and they enabled information on population genetic structure and dynamics of aphid species to be acquired (Loxdale *et al.*, 1985a,b). However, the development of the PCR meant that for the first time any genomic region could be amplified and the genetic diversity of field populations could be analysed using a larger number of samples than before. The significant advances in DNA sequencing technologies that we are currently experiencing are again providing a new thrust to the field of molecular ecology by allowing researchers to study many questions that were unmanageable before. Most importantly, the new tools allow the study of non-model species (Ekblom & Galindo, 2011). For example, it is now possible to study the responses to different environmental factors and identify the genetic bases of phenotypes by sequencing the transcriptomes of individuals, tissues or cells and analysing the genes expression levels (e.g. Nayduch *et al.*, 2014; Keeling *et al.*, 2016; Wu *et al.*, 2016; Yu *et al.*, 2016; Braden *et al.*, 2017). Similarly, they have also revolutionised the area of phylogeography and evolution allowing the discovery of genome-wide molecular markers that could not be used before to study genetic variation in natural populations. These genome-wide single nucleotide polymorphisms (SNPs) provide an excellent opportunity to have a precise population history and geographic structure of our species of study and for this reason it is widely used in phylogeographic and systematic studies (e.g. Misof *et al.*, 2014; Rasic *et al.*, 2014; Dussex *et al.*, 2016; Fountain *et al.*, 2016). These techniques will improve our knowledge of the population dynamics and the evolution of aphids, although their use within the agricultural landscape context is still in its infancy (Eyres *et al.*, 2016, 2017). It is expected that the availability of genomes of economically important species of aphids like *M. persicae*, *A. pisum*, *A. glycines*, *Diuraphis noxia* Kurdjumov and *Daktulosphaira vitifoliae* (Fitch) (Richards *et al.*, 2010; Nicholson *et al.*, 2015), and available in AphidBase (Legeai *et al.*, 2010), will encourage an increase in the number of studies using Next Generation Sequencing (NGS) techniques to investigate the molecular ecology of these organisms (Tagu *et al.*, 2010). The sequencing technologies have also improved our ability to understand ecological networks. In a recent, opinion paper, Evans *et al.* (2016)

proposed a new approach to study and define species interaction networks using a combination of nested tagging metabarcoding and network analysis to identify specific interactions between tree-herbivore-parasitoid food webs using the forest systems as a model. One of the advantages of using NGS methods versus the classic PCR approach is the possibility to process and analyse a larger number samples faster. A second advantage is that NGS allows identification of new interactions and new species as part of networks. A central question that remains to be answered is how stable are the associations between species through time and how environmental change modifies them. The new sequencing technologies and the use of collection samples (e.g. RIS archive) provide a unique opportunity to explore the evolution of associations at historical time scale (i.e. using specimens collected and stored since the 1960s) and to test how environmental change has modified species associations.

The emergence of the nanopore-based DNA sequencing platform, the minION (Oxford Nanopore Technologies, Ltd, Oxford, U.K.), is revolutionising the genomics field. It is a highly portable, USB-powered sequencing device that runs connected to a computer and provides long reads in real-time. The technology is very attractive as it can be easily deployed in the field under a diversity of conditions and it provides data in real-time that gives control of the sequencing experiment as it is running. One area of research where it is increasingly being used is in the metagenomics field. It was also successfully used in West Africa during the Ebola outbreak to characterise the evolution of the virus genome at the outbreak happened (Quick *et al.*, 2016). Similarly, it has been used in the Brazilian outbreak of the Zika virus to identify infections in remote areas and test mosquito populations for the presence of the virus (Faria *et al.*, 2016). This technology has, therefore, proven to be useful in a wide variety of field conditions and is potentially a very beneficial methodology to use in agriculture-related pest research. Given the characteristics of the minION and the uses where it has been shown to be useful, we are currently testing it at the RIS for identifying aphid pest species and the viruses they vector with the final goal of applying it in the field for crop protection.

Challenges of using NGS in molecular ecology

One fundamental aspect of molecular ecology studies is the need to reveal as much of the genetic variation as possible. This involves surveying nucleotide polymorphisms in the genome and estimate their frequencies within and among populations. An aspect that needs to be considered when inferring population parameters is the fact that allele frequencies are usually estimated using a sample set drawn from the larger populations. Therefore, the sampling strategy in terms of sample size and geographic range covered is critical and should be considered carefully. Ideally, sampling should be extensive to maximise the genetic diversity examined, but this is not always possible. Previous knowledge of the biology and natural history of the species of study (e.g. life history, population size, and structure etc.) and clear hypotheses of study help design the sampling strategy. For example, in the case of asexual aphids, sampling within the same or adjacent plants could lead to an underestimation of the genetic

diversity producing erroneous demographic parameters because a large proportion of the samples would represent the same asexual lineage. If there is no *a priori* knowledge, then it will be important to run preliminary analyses to assess the adequacy of the sampling strategy.

In addition to sample size and geographic cover, it is also fundamental to use an appropriate number of unlinked markers to obtain reliable estimates of genetic variation. The new sequencing technologies have facilitated the use of large numbers of genome-wide molecular markers allowing the inference of more robust population parameters. However, designing a comprehensive sampling scheme could imply a sequencing cost that can be prohibitive. To decrease these costs, different strategies have been developed to reduce the fraction of the genome that is sequenced in a large number of samples. These methods include exome sequencing (Ng *et al.*, 2009), RNA sequencing (Wang *et al.*, 2009), and restriction-site associated DNA sequencing (genotyping by sequencing – GBS, RADseq) (Baird *et al.*, 2008). Because such methods target different specific regions of the genome, the polymorphisms that result from experiments will be most useful for different questions. Thus, the method of choice should be carefully considered depending on the study question. These techniques can also be combined with pooling samples to reduce sequencing costs further. For example, 96–384 samples may be multiplexed to obtain a sequencing depth of 5× to 20× per tag. The number of pooled samples can be optimised depending on the intended number of tags, the coverage, and the size of the genome. At present, a GBS project for an organism with a genome size of ∼500 Mb and sequencing of around 100 000 tags (average 8× coverage) can be performed for approximately $30 per sample (based on a recent quotation for an aphid project). Thus, molecular ecology projects with a comprehensive sampling scheme are becoming more feasible.

The MinION (ONT) is a very promising sequencing technology, especially because its portability makes sequencing projects possible in the field. Nevertheless, the price of sequencing in the MinION ($900 per flow cell plus the cost of the required kits for the library preparation) can also be prohibitive if the intention is to sequence single individuals in a molecular ecology study. To reduce these costs, it is also possible to multiplex up to 96 samples and run them on a single flow cell, which equates the cost of a project to that using other sequencing technologies. One of the most promising uses of the MinION discussed above is its deployment in the field to identify pest species and viruses *in situ*. The positive ID of any species relies on their genome being available in the public databases, which is not the case for many of the species of agricultural interest (as with many other species). Thus, the use of a metabarcoding protocol along the lines of that proposed by Evans *et al.* (2016) to study ecological networks in combination with the MinION is at present the best way forward in pest surveillance.

Summary

1 The combination of phylogeography and species distribution modelling in an agricultural context will improve our forecasts of the global risk that insect pests pose to agriculture in the near future. It is vital that insect pest research continues taking advantage of the methodological progress that these fields are experiencing. Mapping the potential global risk of pest establishment should take into account genetic diversity of species and the future climate projections. Another aspect to be explored within the agricultural context is the application of community phylogeography approaches (e.g. Hickerson & Meyer, 2008; Smith *et al.*, 2011; Stone *et al.*, 2012) to understand the dynamics of pests, the virus they vector, and hosts.

2 Crop surveillance is one aspect that can benefit greatly from improved methods of species identification. One of the most exciting advances in sequencing technologies is the development of fast, highly portable instruments that can be deployed to the field. Their use within an agricultural context may lead to a 'real-time' monitoring of pests and pathogens in crops. Work is in progress at the RIS to develop protocols specific for agricultural pest and pathogens.

3 Understanding ecosystem functioning is extremely relevant in agriculture (Wood *et al.*, 2015). The new sequencing technologies will play an important role in the identification of interactions between organisms that were unknown before. One vital application will be the identification of new viruses that circulate in insect pest populations and the description of these interactions. This field of research can potentially provide new ways of pest control.

4 Implementing insect monitoring schemes is essential to promote the early detection of pests and prevent outbreaks. However, insect surveys can also play a key role in understanding pest dynamics and evolution at ecological time scales. It is clearly important that we emphasise the value of the samples collected in such schemes to promote their preservation for future studies thereby.

References

Alvarado-Serrano, D.F. & Knowles, L.L. (2014) Ecological niche models in phylogeographic studies: applications, advances and precautions. *Molecular Ecology Resources*, **14**, 233–248.

Angert, A.L., Crozier, L.G., Rissler, L.J., Gilman, S.E., Tewksbury, J.J. & Chunco, A.J. (2011) Do species' traits predict recent shifts at expanding range edges? *Ecology Letters*, **14**, 677–689.

Anstead, J.A., Williamson, M.S. & Denholm, I. (2008) New methods for the detection of insecticide resistant *Myzus persicae* in the U K suction trap network. *Agricultural and Forest Entomology*, **10**, 291–295.

Aragon, P. & Lobo, J.M. (2012) Predicted effect of climate change on the invasibility and distribution of the Western corn root-worm. *Agricultural and Forest Entomology*, **14**, 13–18.

Aragon, P., Baselga, A. & Lobo, J.M. (2010) Global estimation of invasion risk zones for the western corn rootworm *Diabrotica virgifera virgifera*: integrating distribution models and physiological thresholds to assess climatic favourability. *Journal of Applied Ecology*, **47**, 1026–1035.

Aragon, P., Coca-Abia, M.M., Llorente, V. & Lobo, J.M. (2013) Estimation of climatic favourable areas for locust outbreaks in Spain: integrating species' presence records and spatial information on outbreaks. *Journal of Applied Entomology*, **137**, 610–623.

Araujo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. *Ecology*, **93**, 1527–1539.

Austin, G.E. & Rehfisch, M.M. (2005) Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global Change Biology*, **11**, 31–38.

Baird, N.A., Etter, P.D., Atwood, T.S., Currey, M.C., Shiver, A.L., Lewis, Z.A. *et al.* (2008) Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS ONE*, **3**, e3376.

Bell, J.R., Alderson, L., Izera, D., Kruger, T., Parker, S., Pickup, J. *et al.* (2015) Long-term phenological trends, species accumulation rates, aphid traits and climate: five decades of change in migrating aphids. *Journal of Animal Ecology*, **84**, 21–34.

Blackman, R.L. & Eastop, V.F. (2007) Taxonomic issues. *Aphids as Crop Pests* (ed. by H. F. Van Emden and R. Harrington), pp. 1–30. CAB International: Wallingford, UK.

Blois, J.L. & Hadly, E.A. (2009) Mammalian response to Cenozoic climatic change. *Annual Review of Earth and Planetary Sciences*, **37**, 181–208.

Braden, L.M., Sutherland, B.J., Koop, B.F. & Jones, S.R. (2017) Enhanced transcriptomic responses in the Pacific salmon louse *Lepeophtheirus salmonis oncorhynchi* to the non-native Atlantic Salmon *Salmo salar* suggests increased parasite fitness. *BMC Genomics*, **18**, 110.

Caillaud, M.C., Mondor-Genson, G., Levine-Wilkinson, S., Mieuzet, L., Frantz, A., Simon, J.C. *et al.* (2004) Microsatellite DNA markers for the pea aphid *Acyrthosiphon pisum*. *Molecular Ecology Notes*, **4**, 446–448.

Cannon, R.J.C. (1998) The implications of predicted climate change for insect pests in the UK, with emphasis on non-indigenous species. *Global Change Biology*, **4**, 785–796.

Carew, M.E., Metzeling, L., StClair, R. & Hoffmann, A.A. (2016) Detecting invertebrate species in archived collections using next generation sequencing. *Molecular Ecology Resources*. https://doi.org/10.1111/1755-0998.12644.

Chapman, J.W., Reynolds, D.R. & Smith, A.D. (2003) Vertical-looking radar: a new tool for monitoring high-altitude insect migration. *Bioscience*, **53**, 503–511.

Chapman, J.W., Drake, V.A. & Reynolds, D.R. (2011) Recent insights from radar studies of insect flight. *Annual Review of Entomology*, **56**, 337–356.

Chase, J.M. (2011) Ecological niche theory. *The Theory of Ecology* (ed. by S. M. Scheiner and M. R. Willig), pp. 93–108. University of Chicago Press: Chicago, USA.

Chen, I.C., Hill, J.K., Ohlemuller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.

Coeur d'Acier, A., Sembene, M., Audiot, P. & Rasplus, J.Y. (2004) Polymorphic microsatellites loci in the black Aphid, *Aphis fabae* Scopoli, 1763 (Hemiptera, Aphididae). *Molecular Ecology Notes*, **4**, 306–308.

Delmotte, F., Leterme, N., Gauthier, J.P., Rispe, C. & Simon, J.C. (2002) Genetic architecture of sexual and asexual populations of the aphid *Rhopalosiphum padi* based on allozyme and microsatellite markers. *Molecular Ecology*, **11**, 711–723.

Dussex, N., Chuah, A. & Waters, J.M. (2016) Genome-wide SNPs reveal fine-scale differentiation among wingless alpine stonefly populations and introgression between winged and wingless forms. *Evolution*, **70**, 38–47.

Ekblom, R. & Galindo, J. (2011) Applications of next generation sequencing in molecular ecology of non-model organisms. *Heredity*, **107**, 1–15.

Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Evans, D.M., Kitson, J.J.N., Lunt, D.H., Straw, N.A. & Pocock, M.J.O. (2016) Merging DNA metabarcoding and ecological network analysis to understand and build resilient terrestrial ecosystems. *Functional Ecology*, **30**, 1904–1916.

Excoffier, L. & Heckel, G. (2006) Computer programs for population genetics data analysis: a survival guide. *Nature Reviews Genetics*, **7**, 745–758.

Eyres, I., Jaquiery, J., Sugio, A., Duvaux, L., Gharbi, K., Zhou, J.J. *et al.* (2016) Differential gene expression according to race and host plant in the pea aphid. *Molecular Ecology*, **25**, 4197–4215.

Eyres, I., Duvaux, L., Gharbi, K., Tucker, R., Hopkins, D., Simon, J.C. *et al.* (2017) Targeted re-sequencing confirms the importance of chemosensory genes in aphid host race differentiation. *Molecular Ecology*, **26**, 43–58.

Faria, N.R., Sabino, E.C., Nunes, M.R.T., Alcantara, L.C., Loman, N.J. & Pybus, O.G. (2016) Mobile real-time surveillance of Zika virus in Brazil. *Genome Medicine*, **8**, 97.

Fenton, B., Malloch, G., Woodford, J.A.T., Foster, S.P., Anstead, J., Denholm, I. *et al.* (2005) The attack of the clones: tracking the movement of insecticide-resistant peach-potato aphids *Myzus persicae* (Hemiptera : Aphididae). *Bulletin of Entomological Research*, **95**, 483–494.

Ferrari, J., Godfray, H.C.J., Faulconbridge, A.S., Prior, K. & Via, S. (2006) Population differentiation and genetic variation in host choice among pea aphids from eight host plant genera. *Evolution*, **60**, 1574–1584.

Ferrari, J., Via, S. & Godfray, H.C.J. (2008) Population differentiation and genetic variation in performance on eight hosts in the pea aphid complex. *Evolution*, **62**, 2508–2524.

Foster, S. & Williamson, M. (2015) Investigating Pyrethroid Resistance in UK Cabbage Stem Flea Beetle Populations and Developing a PCR-based Assay for Detecting Turnip Yellows Virus in Aphids. AHDB Cereals & Oilseeds Report No. 552: Kenilworth, UK.

Foster, S.P., Harrington, R., Dewar, A.M., Denholm, I. & Devonshire, A.L. (2002) Temporal and spatial dynamics of insecticide resistance in *Myzus persicae* (Hemiptera: Aphididae). *Pest Management Science*, **58**, 895–907.

Fountain, T., Nieminen, M., Siren, J., Wong, S.C. & Hanski, I. (2016) Predictable allele frequency changes due to habitat fragmentation in the Glanville fritillary butterfly. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 2678–2683.

Gilabert, A., Dedryver, C.A., Stoeckel, S., Plantegenest, M. & Simon, J.C. (2015) Longitudinal clines in the frequency distribution of 'super-clones' in an aphid crop pest. *Bulletin of Entomological Research*, **105**, 694–703.

Godefroid, M., Rasplus, J.Y. & Rossi, J.P. (2016) Is phylogeography helpful for invasive species risk assessment? The case study of the bark beetle genus Dendroctonus. *Ecography*, **39**, 1197–1209.

Harrington, R. (2014) The Rothamsted Insect Survey strikes gold. *Antenna*, **38**, 159–166.

Harrington, R., Clark, S.J., Welham, S.J., Verrier, P.J., Denholm, C.H., Hulle, M. *et al.* (2007) Environmental change and the phenology of European aphids. *Global Change Biology*, **13**, 1550–1564.

Hickerson, M.J. & Meyer, C.P. (2008) Testing comparative phylogeographic models of marine vicariance and dispersal using a hierarchical Bayesian approach. *BMC Evolutionary Biology*, **8**, 322.

Holmes, M.W., Hammond, T.T., Wogan, G.O.U., Walsh, R.E., Labarbera, K., Wommack, E.A. *et al.* (2016) Natural history collections as windows on evolutionary processes. *Molecular Ecology*, **25**, 864–881.

Ikeda, D.H., Max, T.L., Allan, G.J., Lau, M.K., Shuster, S.M. & Whitham, T.G. (2017) Genetically informed ecological niche models improve climate change predictions. *Global Change Biology*, **23**, 164–176.

Jeffries, D.L., Chapman, J., Roy, H.E., Humphries, S., Harrington, R., Brown, P.M.J. *et al.* (2013) Characteristics and drivers of high-altitude ladybird flight: insights from vertical-looking entomological radar. *PLoS ONE*, **8**, e82278.

Kasprowicz, L., Malloch, G., Foster, S., Pickup, J., Zhan, J. & Fenton, B. (2008) Clonal turnover of MACE-carrying peach-potato aphids (*Myzus persicae* (Sulzer), Homoptera : Aphididae) colonizing Scotland. *Bulletin of Entomological Research*, **98**, 115–124.

Keeling, C.I., Li, M., Sandhu, H.K., Henderson, H., Yuen, M.M. & Bohlmann, J. (2016) Quantitative metabolome, proteome and transcriptome analysis of midgut and fat body tissues in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins, and insights into pheromone biosynthesis. *Insect Biochemistry and Molecular Biology*, **70**, 170–183.

Kimura, M. (1968) Evolutionary rate at the molecular level. *Nature*, **217**, 624–626.

King, J.L. & Jukes, T.H. (1969) Non-Darwinian evolution. *Science*, **164**, 788–798.

Knowles, L.L. (2009) Statistical Phylogeography. *Annual Review of Ecology Evolution and Systematics*, **40**, 593–612.

Kozak, K.H., Graham, C.H. & Wiens, J.J. (2008) Integrating GIS-based environmental data into evolutionary biology. *Trends in Ecology & Evolution*, **23**, 141–148.

Kriticos, D.J., Brunel, S., Ota, N., Fried, G., Lansink, A.G.J.M.O., Panetta, F.D. *et al.* (2015a) Downscaling pest risk analyses: identifying current and future potentially suitable habitats for *Parthenium hysterophorus* with particular reference to Europe and North Africa. *PLoS ONE*, **10**, e0132807.

Kriticos, D.J., Ota, N., Hutchison, W.D., Beddow, J., Walsh, T., Tay, W.T. *et al.* (2015b) The potential distribution of invading *Helicoverpa armigera* in North America: is it just a matter of time? *PLoS ONE*, **10**, e0133224.

Kumar, S., Yee, W.L. & Neven, L.G. (2016) Mapping global potential risk of establishment of *Rhagoletis pomonella* (Diptera: Tephritidae) using MaxEnt and CLIMEX niche models. *Journal of Economic Entomology*, **109**, 2043–2053.

Lagerholm, V.K., Sandoval-Castellanos, E., Vaniscotte, A., Potapova, O.R., Tomek, T., Bochenski, Z.M. *et al.* (2017) Range shifts or extinction? Ancient DNA and distribution molleing reveal past and future responses to climate warming in cold-adapted birds. *Global Change Biology*, **23**, 1425–1435.

Legeai, F., Shigenobu, S., Gauthier, J.P., Colbourne, J., Rispe, C., Collin, O. *et al.* (2010) AphidBase: a centralized bioinformatic resource for annotation of the pea aphid genome. *Insect Molecular Biology*, **19**, 5–12.

Lesieur, V., Martin, J.F., Weaver, D.K., Hoelmer, K.A., Smith, D.R., Morrill, W.L. *et al.* (2016) Phylogeography of the wheat stem sawfly, *Cephus cinctus* Norton (Hymenoptera: Cephidae): implications for Pest management. *PLoS ONE*, **11**, e0168370.

Llewellyn, K.S., Loxdale, H.D., Harrington, R., Brookes, C.P., Clark, S.J. & Sunnucks, P. (2003) Migration and genetic structure of the grain aphid (*Sitobion avenae*) in Britain related to climate and clonal fluctuation as revealed using microsatellites. *Molecular Ecology*, **12**, 21–34.

Loxdale, H.D. (2008) The nature and reality of the aphid clone: genetic variation, adaptation and evolution. *Agricultural and Forest Entomology*, **10**, 81–90.

Loxdale, H.D. & Brookes, C.P. (1990) Temporal genetic stability within and restricted migration (gene flow) between local populations of the blackberry-grain aphid *Sitobion fragariae* in South-East England. *Journal of Animal Ecology*, **59**, 497–514.

Loxdale, H.D. & Lushai, G. (1999) Slaves of the environment: the movement of herbivorous insects in relation to their ecology and genotype. *Philosophical Transactions of the Royal Society of London Series B: Biological Sciences*, **354**, 1479–1495.

Loxdale, H.D. & Lushai, G. (2007) Population genetic issues: the unfolding story using molecular markers. *Aphids as Crop Pests* (ed. by H. F. van Emden and R. Harrington), pp. 31–68. CAB International: Wallingford, UK.

Loxdale, H.D., Rhodes, J.A. & Fox, J.S. (1985a) Electrophoretic study of enzymes from cereal aphid populations 4 Detection of hidden genetic variation within populations of the grain aphid *Sitobion avenae* (F) (Hemiptera: Aphididae). *Theoretical and Applied Genetics*, **70**, 407–412.

Loxdale, H.D., Tarr, I.J., Weber, C.P., Brookes, C.P., Digby, P.G.N. & Castanera, P. (1985b) Electrophoretic study of enzymes from cereal aphid populations III Spatial and temporal genetic variation of populations of *Sitobion avenae* (F) (Hemiptera: Aphididae). *Bulletin of Entomological Research*, **75**, 121–141.

Loxdale, H.D., Davis, B.J. & Davis, R.A. (2016) Known knowns and unknowns in biology. *Biological Journal of the Linnean Society*, **117**, 386–398.

Loxdale, H.D., Edwards, O., Tagu, D. & Vorburger, C. (2017) Aphid genomics and its contribution to understanding aphids as crop pests. *Aphids as Crop Pests* (ed. by H. F. van Emden and R. Harrington), pp. 50–80. CABI: Wallingford, UK.

Macaulay, E.D.M., Tatchell, G.M. & Taylor, L.R. (1988) The Rothamsted insect Survey '12-metre' suction trap. *Bulletin of Entomological Research*, **78**, 121–129.

Macfadyen, S. & Kriticos, D.J. (2012) Modelling the geographical range of a species with variable life-history. *PLoS ONE*, **7**, e40313.

Malloch, G., Highet, F., Kasprowicz, L., Pickup, J., Neilson, R. & Fenton, B. (2006) Microsatellite marker analysis of peach-potato aphids (*Myzus persicae*, Homoptera : Aphididae) from Scottish suction traps. *Bulletin of Entomological Research*, **96**, 573–582.

Marske, K.A., Rahbek, C. & Nogues-Bravo, D. (2013) Phylogeography: spanning the ecology-evolution continuum. *Ecography*, **36**, 1169–1181.

Mikheyev, A.S., Tin, M.M.Y., Arora, J. & Seeley, T.D. (2015) Museum samples reveal rapid evolution by wild honey bees exposed to a novel parasite. *Nature Communications*, **6**, 7991.

Misof, B., Liu, S.L., Meusemann, K., Peters, R.S., Donath, A., Mayer, C. *et al.* (2014) Phylogenomics resolves the timing and pattern of insect evolution. *Science*, **346**, 763–767.

Muller, F.P. (1985a) Das problem *Acyrthosiphon pisum* (Homoptera: Aphidae). *Zeitschrift für Angewandte Zoologie*, **72**, 317–334.

Muller, F.P. (1985b) Biotype formation and sympatric speciation in aphids (Homoptera, Aphidinea). *Entomologia Generalis*, **10**, 161–181.

Mullis, K., Faloona, F., Scharf, S., Saiki, R., Horn, G. & Erlich, H. (1986) Specific enzymatic amplification of DNA in vitro: the polymerase chain reaction. *Cold Spring Harbor Symposia on Quantitative Biology*, **51**(Pt 1), 263–273.

Nayduch, D., Lee, M.B. & Saski, C.A. (2014) The reference transcriptome of the adult female biting midge (Culicoides sonorensis) and differential gene expression profiling during teneral, blood, and sucrose feeding conditions. *PLoS ONE*, **9**, e98123.

Ng, S.B., Turner, E.H., Robertson, P.D., Flygare, S.D., Bigham, A.W., Lee, C. *et al.* (2009) Targeted capture and massively parallel sequencing of 12 human exomes. *Nature*, **461**, 272–276.

Nicholson, S.J., Nickerson, M.L., Dean, M., Song, Y., Hoyt, P.R., Rhee, H. *et al.* (2015) The genome of *Diuraphis noxia*, a global aphid pest of small grains. *BMC Genomics*, **16**, 429.

Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology Evolution and Systematics*, **37**, 637–669.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.

Peccoud, J. & Simon, J.C. (2010) The pea aphid complex as a model of ecological speciation. *Ecological Entomology*, **35**, 119–130.

Peccoud, J., Ollivier, A., Plantegenest, M. & Simon, J.C. (2009a) A continuum of genetic divergence from sympatric host races to species in the pea aphid complex. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 7495–7500.

Peccoud, J., Simon, J.C., McLaughlin, H.J. & Moran, N.A. (2009b) Post-Pleistocene radiation of the pea aphid complex revealed by rapidly evolving endosymbionts. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 16315–16320.

Perez-Rodriguez, J., Shortall, C.R. & Bell, J.R. (2015) Large-scale migration synchrony between parasitoids and their host. *Ecological Entomology*, **40**, 654–659.

Peterson, A.T. (2011) Ecological niche conservatism: a time-structured review of evidence. *Journal of Biogeography*, **38**, 817–827.

Peterson, A.T., Ortega-Huerta, M.A., Bartley, J., Sanchez-Cordero, V., Soberon, J., Buddemeier, R.H. *et al.* (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.

Peterson, A.T., Stewart, A., Mohamed, K.I. & Araujo, M.B. (2008) Shifting global invasive potential of European plants with climate change. *PLoS ONE*, **3**, e2441.

Peterson, A.T., Papes, M. & Soberon, J. (2015) Mechanistic and correlative models of ecological niches. *European Journal of Ecology*, **1**, 28–38.

Popkin, M., Piffaretti, J., Clamens, A.L., Qiao, G.X., Chen, J., Vitalis, R. *et al.* (2017) Large-scale phylogeographic study of the cosmopolitan aphid pest *Brachycaudus helichrysi* reveals host plant associated lineages that evolved in allopatry. *Biological Journal of the Linnean Society*. https://doi.org/10.1111/bij.12869.

Quick, J., Loman, N.J., Duraffour, S., Simpson, J.T., Severi, E., Cowley, L. *et al.* (2016) Real-time, portable genome sequencing for Ebola surveillance. *Nature*, **530**, 228–232.

Rasic, G., Filipovic, I., Weeks, A.R. & Hoffmann, A.A. (2014) Genome-wide SNPs lead to strong signals of geographic structure and relatedness patterns in the major arbovirus vector, *Aedes aegypti*. *BMC Genomics*, **15**, 275.

Raymond, B., Searle, J.B. & Douglas, A.E. (2001) On the processes shaping reproductive isolation in aphids of the *Aphis fabae* (Scop.) complex (Aphididae : Homoptera). *Biological Journal of the Linnean Society*, **74**, 205–215.

Richards, S., Gibbs, R.A., Gerardo, N.M., Moran, N., Nakabachi, A., Stern, D. *et al.* (2010) Genome sequence of the pea aphid *Acyrthosiphon pisum*. *PLoS Biology*, **8**, e1000313.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C. & Pounds, J.A. (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.

Ruane, S. & Austin, C.C. (2017) Phylogenomics using formalin-fixed and 100+ year old intractable natural history specimens. *Molecular Ecology Resources*. https://doi.org/10.1111/1755-0998.12655.

Sheppard, L., Bell, J.R., Harrington, R. & Reuman, D.C. (2016) Changes in large-scale climate alter spatial synchrony of aphid pests. *Nature Climate Change*, **6**, 610–613.

Sillero, N., Reis, M., Vieira, C.P., Vieira, J. & Morales-Hojas, R. (2014) Niche evolution and thermal adaptation in the temperate species Drosophila americana. *Journal of Evolutionary Biology*, **27**, 1549–1561.

Simon, J.C., Baumann, S., Sunnucks, P., Hebert, P.D.N., Pierre, J.S., Le Gallic, J.F. *et al.* (1999) Reproductive mode and population genetic structure of the cereal aphid *Sitobion avenae* studied using phenotypic and microsatellite markers. *Molecular Ecology*, **8**, 531–545.

Simon, J.C., Leterme, N., Delmotte, F., Martin, O. & Estoup, A. (2001) Isolation and characterization of microsatellite loci in the aphid species, *Rhopalosiphum padi*. *Molecular Ecology Notes*, **1**, 4–5.

Smith, C.I., Tank, S., Godsoe, W., Levenick, J., Strand, E., Esque, T. *et al.* (2011) Comparative Phylogeography of a coevolved community: concerted population expansions in Joshua trees and four yucca moths. *PLoS ONE*, **6**, e25628.

Snyder, W.E. & Ives, A.R. (2003) Interactions between specialist and generalist natural enemies: parasitoids, predators, and pea aphid biocontrol. *Ecology*, **84**, 91–107.

Stone, G.N., Lohse, K., Nicholls, J.A., Fuentes-Utrilla, P., Sinclair, F., Schonrogge, K. *et al.* (2012) Reconstructing community assembly in time and space reveals enemy escape in a Western Palearctic insect community. *Current Biology*, **22**, 532–537.

Storkey, J., Macdonald, A.J., Bell, J.R., Clark, I.M., Gregory, A.S., Hawkins, N.J. *et al.* (2016) The unique contribution of Rothamsted to ecological research at large temporal scales. *Advances in Ecological Research* (ed. by A. J. Dumbrell, R. L. Kordas and G. Woodward), pp. 3–42. Academic Press, Oxford, U.K.

Tagu, D., Dugravot, S., Outreman, Y., Rispe, C., Simon, J.C. & Colella, S. (2010) The anatomy of an aphid genome: from sequence to biology. *Comptes Rendus Biologies*, **333**, 464–473.

Taylor, L.R. (1974) Insect migration, flight periodicity and boundary-layer. *Journal of Animal Ecology*, **43**, 225–238.

Thackeray, S.J., Sparks, T.H., Frederiksen, M., Burthe, S., Bacon, P.J., Bell, J.R. *et al.* (2010) Trophic level asynchrony in rates of phenological change for marine, freshwater and terrestrial environments. *Global Change Biology*, **16**, 3304–3313.

Thackeray, S.J., Henrys, P.A., Hemming, D., Bell, J.R., Botham, M.S., Burthe, S. *et al.* (2016) Phenological sensitivity to climate across taxa and trophic levels. *Nature*, **535**, U241–U294.

Umina, P.A., Weeks, A.R., Kearney, M.R., McKechnie, S.W. & Hoffmann, A.A. (2005) A rapid shift in a classic clinal pattern in *Drosophila* reflecting climate change. *Science*, **308**, 691–693.

Van Emden, H.F. & Harrington, R. (2017). *Aphids as Crop Pests*. CABI: Wallingford, UK.

Wang, X.Y., Huang, X.L., Jiang, L.Y. & Qiao, G.X. (2010) Predicting potential distribution of chestnut phylloxerid (Hemiptera: Phylloxeridae) based on GARP and Maxent ecological niche models. *Journal of Applied Entomology*, **134**, 45–54.

Wang, Z., Gerstein, M. & Snyder, M. (2009) RNA-Seq: a revolutionary tool for transcriptomics. *Nature Reviews Genetics*, **10**, 57–63.

Wharton, T.N. & Kriticos, D.J. (2004) The fundamental and realized niche of the Monterey Pine aphid, Essigella californica (Essig) (Hemiptera : Aphididae): implications for managing softwood plantations in Australia. *Diversity and Distributions*, **10**, 253–262.

Wiens, J.J. & Graham, C.H. (2005) Niche conservatism: integrating evolution, ecology, and conservation biology. *Annual Review of Ecology Evolution and Systematics*, **36**, 519–539.

Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V. *et al.* (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.

Willis, K.J. & MacDonald, G.M. (2011) Long-term ecological records and their relevance to climate change predictions for a warmer world. *Annual Review of Ecology Evolution and Systematics*, **42**, 267–287.

Wilson, A.C.C., Massonnet, B., Simon, J.C., Prunier-Leterme, N., Dolatti, L., Llewellyn, K.S. *et al.* (2004) Cross-species amplification of microsatellite loci in aphids: assessment and application. *Molecular Ecology Notes*, **4**, 104–109.

Wood, S.A., Karp, D.S., DeClerck, F., Kremen, C., Naeem, S. & Palm, C.A. (2015) Functional traits in agriculture: agrobiodiversity and ecosystem services. *Trends in Ecology & Evolution*, **30**, 531–539.

Wu, C., Crowhurst, R.N., Dennis, A.B., Twort, V.G., Liu, S.L., Newcomb, R.D. *et al.* (2016) De novo transcriptome analysis of the common New Zealand stick insect *Clitarchus hookeri* (Phasmatodea) reveals genes involved in olfaction, digestion and sexual reproduction. *PLoS ONE*, **11**, e0157783.

Yu, Q.Y., Fang, S.M., Zhang, Z. & Jiggins, C.D. (2016) The transcriptome response of *Heliconius melpomene* larvae to a novel host plant. *Molecular Ecology*, **25**, 4850–4865.