CHAPTER THREE

Invasions Toolkit: Current Methods for Tracking the Spread and Impact of Invasive Species

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Abstract

Biological invasions exert multiple pervasive effects on ecosystems, potentially disrupting species interactions and global ecological processes. Our ability to successfully predict and manage the ecosystem-level impacts of biological invasions is strongly dependent on our capacity to empirically characterize complex biological interactions and their spatiotemporal dynamics. In this chapter, we argue that the comprehensive integration of multiple complementary tools within the explicit context of ecological networks is essential for providing mechanistic insight into invasion processes and their impact across organizational levels. We provide an overview of traditional (stable isotopes, populations genetics) and emerging (metabarcoding, citizen science) techniques and methods, and their practical implementation in the context of biological invasions. We also present several currently available models and machine-learning approaches that could be used for predicting novel or undocumented interactions, thus allowing a more robust and cost-effective forecast of network and ecosystem stability. Finally, we discuss the importance of methodological advancements on the emergence of scientific and societal challenges for investigating local and global species histories with several skill sets.

1. INTRODUCTION

Through species extinction, immigration, displacement, and speciation, biodiversity is intrinsically dynamic. Species immigrate, shift the limits of their distribution, or go extinct, at various rates and spatial scales (Aguirre-Gutiérrez et al., 2016; Hoffmann and Courchamp, 2016; Jackson and Overpeck, 2000; Jackson and Sax, 2010; Savage and Vellend, 2015; Sax and Gaines, 2003). Over the last decade, unprecedented globalization and intensification of human activities have significantly accelerated the frequency and magnitude of biodiversity turnover (Barnosky et al., 2012; Vitousek et al., 1997). One of the most documented expressions of global anthropogenic forcing is the human-induced movement of nonnative species (Hulme et al., 2008; Levine and D'Antonio, 2003). This phenomenon usually refers to the voluntary or accidental introduction of taxa or genotypes far from their historical distributional areas as a result of trade, tourism, agriculture, or biological control programmes (e.g. Anderson et al., 2004;

Fisher et al., 2012; Geslin et al., 2017; Hulme et al., 2008; Levine and D'Antonio, 2003; Roy and Wajnberg, 2008). This introduction of nonnative species has increased by orders of magnitude since the 18th century (Grosholz, 2005).

Today, biological invasions appear as an important disruptor of biotic processes at a global scale, significantly contributing to the ongoing planetary-scale transition to a starkly different, unanticipated state (Barnosky et al., 2012; Vitousek et al., 1997). Major effects of nonnative species are changes in species diversity that could lead to impoverishment and homogenization of communities through the loss of phylogenetically or functionally unique species (Zavaleta et al., 2001). Growing evidence points out that effects of invasive species could also propagate across multiple organizational levels (e.g. Desprez-Loustau et al., 2007), thus affecting evolutionary trajectories and complex interactions within entire assemblages (Grosholz, 2002; Schlaepfer et al., 2005). All these observations have raised considerable concern about the impact of invasive species on global ecosystem functioning (e.g. Butchart et al., 2010; Hooper et al., 2005).

In order to prevent any adverse consequences of biological invasions, an efficient forecasting of their impacts is required in order to draw appropriate management actions. However, successful forecasts directly depend on our capacity to quantify such impacts in terms of biodiversity dynamics (Barnosky et al., 2012; Sala et al., 2000), evolutionary history (Sakai et al., 2001; Tayeh et al., 2015), or ecosystem functioning (Stachowicz et al., 2002) at relevant spatial and temporal scales (Fig. 1). Such an endeavour currently constitutes one of the biggest challenges in invasion ecology, still hindering our ability to prompt any general, evidence-based conclusions or management recommendations. Not only is the acquisition of large-scale empirical data methodologically demanding, but there is also a general lack of conceptual agreement upon how to define (Jeschke et al., 2014; Pyšek et al., 2012) or quantify (Hulme et al., 2013) the impact of invasive species.

First, studies explicitly measuring invaders' impact on components of ecosystem functioning are rare. Traditionally, studies tend to consider invader's establishment success as an approximation of ecological impact—in most cases, successful establishment is deemed equal to a necessarily adverse ecological impact. But in the rare cases in which functional consequences of biological invasions have been considered, nondesired ecological consequences are not necessarily the rule. Examples show that despite significant changes in the community composition and/or species richness they induce, biological invasions do not always lead to the loss of native species

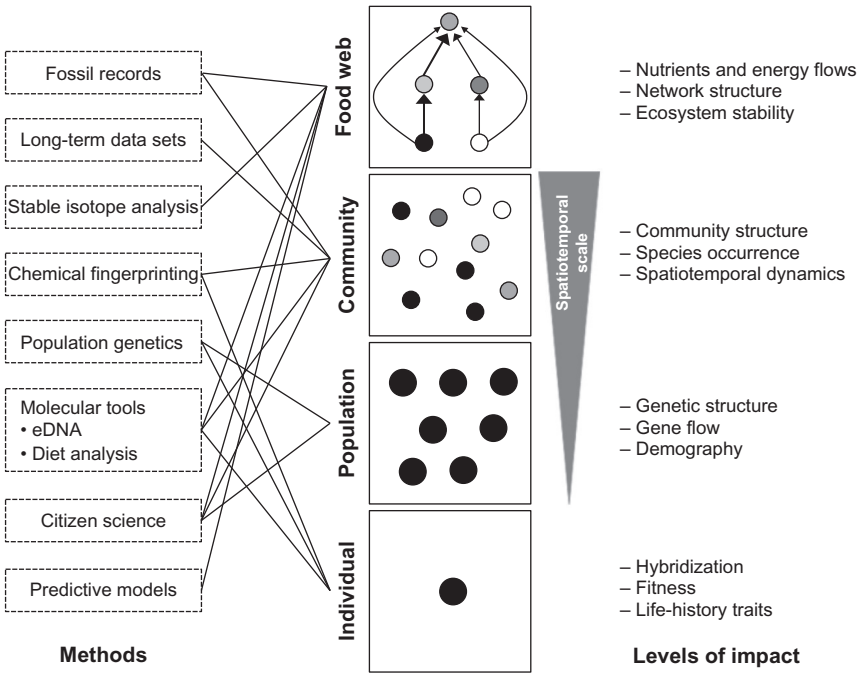

Fig. 1 Schematic overview of the utility of combining multiple methods for studying the distribution, the interactions, and the impact of invasive species at various organizational levels and spatio-temporal scales.

(Henneman and Memmott, 2001) or the disruption of local ecological processes (Carvalheiro et al., 2008). On the contrary, invasive species can actually be beneficial to local human populations (e.g. Pointier and Jourdane, 2000; Thomas et al., 2016b), suggesting that invasives' impact on ecosystem functions as a whole could be unexpected and complex to predict.

Second, the majority of studies chiefly focused on single cases (Hulme et al., 2013; Pyšek et al., 2012), usually considering only a single species within a very limited spatial and/or temporal range, preventing the incorporation of direct and indirect nonadditive effects, inherent in complex biological systems (e.g. Zavaleta et al., 2001). Moreover, they are inappropriate for establishing an explicit link or for predicting impacts on ecosystem-level processes and functions.

Network-based approaches recently emerged as a promising tool for predicting the impact of anthropogenic stressors on ecosystem function and stability (Bohan et al., 2016; Hines et al., 2015; McCann, 2007; Thompson et al., 2012). Patterns of species interactions within and among

trophic levels (i.e. network structure) are likely informative about mechanisms governing ecosystem-level processes. Such mechanisms comprise bottom-up or top-down trophic cascades (Pace et al., 1999; Polis et al., 2000), community assembly and species co-occurrence (Massol et al., 2017), competition (David et al., 2017), parasitism (Lafferty et al., 2008), or functional complementarity between species (Pantel et al., 2017; Poisot et al., 2013; Yachi and Loreau, 2007). All these mechanisms have been shown to control at least partly the rate of key ecological functions such as productivity (Jenkins et al., 1992; Paine, 2002) or nutrient recycling (Handa et al., 2014; Ngai and Srivastava, 2006), and prey attack rates (Peralta et al., 2014). Consequently, interaction networks provide a powerful framework incorporating both biological complexity and stocks and flows of ecosystem functions (Memmott, 2009; Thompson et al., 2012). Building upon network theory in invasion ecology thus opens an unprecedented opportunity to improve our current predictive capacity. From a management perspective, it is also a promising approach for the implementation of rules for management and restoration strategies (Memmott, 2009) with minimal management risks (e.g. Caut et al., 2009; Courchamp et al., 2003).

Growing evidence helps reinforce these assertions in the context of biological invasions. For instance, recent theoretical advances point out the importance of network-level attributes (e.g. trophic position and diet breadth) for predicting invasion success (Romanuk et al., 2009, 2017). Empirical evidence from plant–pollinator and plant–herbivore–parasitoid networks brings additional evidence regarding the importance of a network approach when dealing with community-level impacts of biological invasions (e.g. Albrecht et al., 2014; Carvalheiro et al., 2010; Geslin et al., 2017; Lopezaraiza-Mikel et al., 2007).

Finally, species interactions are subjected to constant change and evolution through time (Eklöf et al., 2012; Hairston et al., 2005; Montoya, 2007), with biological invasions being one important driver of such dynamic changes. Consequently, integrating temporal perspective into biological invasions studies is another important prerequisite for understanding the alteration of ecosystem functioning in response to these stressors (Brose and Hillebrand, 2016; Loreau, 2010). Indeed, when looking at ecological networks as a whole, a delayed response (i.e. a time lag) to perturbations can be expected, due to the ecological inertia. Only a temporal perspective could inform about the detection of tipping points—these critical states indicative of major changes in the system. However, integrating both biological complexity at multiple trophic levels and its dynamics in a realistic

ecosystem-level context could be challenging (e.g. Schindler, 1998). Especially, scalling up ecological observations could be resource-demanding resulting in a general lack of replication (e.g. Pocock et al., 2012) or in a general omission of many cryptic but important interactions (e.g. parasite or microbial communities; Amsellem et al., 2017; Médoc et al., 2017). Another major challenge relates to the general lack of "initial conditions" data, preventing a true analysis of impact.

Fortunately, during the last decade, ecologists experienced an unprecedented improvement of their methodological toolbox (summarized in Fig. 1). Thanks to methodological achievements, it is now possible to comprehensively estimate present and past biodiversity dynamics, while accounting for the numerous environmental and biological processes cited earlier. The most spectacular advance concerns the development of molecular techniques, which now allow sampling entire ecosystems or interaction networks in the form of minute amounts of ancient or modern DNA, present in the environment (eDNA; see Fig. 1). Indeed, DNA techniques offer an accessible, noninvasive, and cost-efficient tool for species surveillance, biodiversity assessment, or ecological network reconstruction. When combined with time-integrative environmental tracers, e.g., stable isotopes, molecular methods offer a powerful tool for revealing mechanisms behind energy transfer and ecosystem stability at various scales (Fig. 1). Other approaches, such as citizen sciences, are gaining important momentum and could provide valuable large-scale data about species distributions and interactions. If combined with new technologies (e.g. real-time video and GPS recording, real-time sequencing), citizen science promises to change the face of data collection and traditional ecological research as a whole. Palaeoecology and population genetics are tools that can essentially contribute to reconstructing past biodiversity dynamics, even in the absence of high-quality temporal data (Fig. 1). Finally, new modelling and statistical approaches, such as machine learning, can help optimize replicability and increase the current predictive power (Fig. 1).

In this chapter, we speculate that the inherent difficulties of collecting replicated system-level data could be significantly alleviated by mobilizing a full range of available techniques, tools, and models. The combination of multiple approaches should ensure replicable, high-resolution quantitative data, leading to a better understanding of how biological invasions affect ecosystem functioning and stability. Below we review current advances in the most popular methods in ecology and provide relevant examples of applications in the context of biological invasions.

2. DETECTING AND MONITORING SPATIOTEMPORAL CHANGES OF INVADERS AND INVADED COMMUNITIES AT DIFFERENT SCALES

One first prerequisite to any study on biological invasions is to disentangle native species from invasive species and determine when invasives were introduced. According to Webb (1985), clarifying whether a species is alien or native requires fossil and historical evidence and knowledge of its habitat, geographical distribution, cases of naturalization elsewhere, genetic diversity, reproductive pattern, and supposed means of introduction and therefore calls for large spatiotemporal perspectives. Since long-term, extensive monitoring data covering at the same time pre- and postsettlement stages have been rare, direct observation has been used in only a few studies. Current monitoring data series could be efficiently extended using retrospective approaches based on palaeorecords, museum specimens, and human historical records, while chronosequences (a series of study sites that differ primarily in the time since an event occurred, such as clearcutting, deglaciation, or species invasion) are another short-term approach to reconstructing long-term dynamics (Strayer et al., 2006).

2.1 Direct Methods for Reconstructing Past and Current Invasion History

2.1.1 Palaeogenetics and Fossil Records

Strayer et al. (2006) regretted that most studies on invasive species have been brief and lack a temporal context, with about 40% of recent studies that did not even state the amount of time that had passed since the invasion. Temporal records are crucial to detect, qualify, and explain invasion episodes. However, although palaeoecological approaches appear as the most straightforward way to complete observational data series, they have long been considered as too descriptive with little practical and conceptual applications. It is only very recently that several palaeoecological examples provided direct guidelines for the identification and management of invasives (Willis and Birks, 2006).

Lake and marine sediments preserve traces from the organisms living within the aquatic ecosystems and also act as accumulation basins for remains of organisms living in the surrounding terrestrial environments. Therefore, provided that sediment chronological accumulation is well preserved, the stratigraphical analyses of archived records can date how long a given species

has been present within a given geographical area (thus invalidating or confirming its native nature), and eventually providing a timing for the first species appearance (Willis and Birks, 2006). For instance, the status of the clubmoss (*Selaginella kraussiana*, Kunze) on the oceanic Azores archipelago has long been uncertain, although its introduction was hypothesized as consequent to the discovery and settlement of the Azores (van Leeuwen et al., 2005). Yet, high numbers of spores of this taxon were already present in the sediment cores from the two island lakes several thousand years before the Portuguese discovery and the Flemish settlement in the 15th century, invalidating the introduced status for *S. kraussiana* (van Leeuwen et al., 2005). In contrast, the nonnative nature of the toxic phytoplankton species *Gymnodinium catenatum* in the Northeast Atlantic (a species responsible for major worldwide losses in aquaculture as it induces risks of toxicity in shellfish feeding upon it) could have been confirmed in cyst records from dated sediment cores originating from the West Iberian shelf (Ribeiro et al., 2012).

For long time, the study of sediment records has been restricted to macroscopic remains, providing taxonomic information only for organisms, which produce fossilizing parts (spores and pollen from terrestrial plants, zooplankton carapaces or resting eggs, diatom frustules, phytoplankton cysts). Recent advances in the extraction and analyses of free DNA preserved in sediment archives have now almost infinitely extended the field of taxa for which the reconstruction of species dynamics over time is possible (Coolen et al., 2011; Domaizon et al., 2013; Giguet-Covex et al., 2014).

Information provided by palaeorecords goes far beyond the status of the suspected nonnative species or timing of introduction. It can efficiently document the colonization mechanisms, such as founding events, source of invasions, and invasion routes, and whether observed invasions result from single or multiple introduction events (as reviewed in Cristescu, 2015). It can also address other long-standing questions on whether invasive species are the triggering mechanism for ecosystem change, or merely opportunists taking advantage of environmental change caused by other biotic or abiotic factors (Lodge, 1993).

Most breakthroughs in the area of past invasion dynamics have been provided by emblematic examples of invasions by exotic freshwater zooplankton. Indeed, crustaceans from the order Cladocera possess traits such as long-term diapausing eggs and rapid parthenogenetic reproduction that make them efficient invaders of new habitats. Because diapausing eggs contain genetic as well as morphological information, zooplankton sediment egg banks also provide opportunities for studying the phylogenetic origin

and population size of founders (Duffy et al., 2000; Hairston et al., 1999; Mergeay et al., 2006), as well as population-level genetic consequences of natural colonization events (Alric et al., 2016; Brede et al., 2009).

A notorious example of the dispersive and invasive potentials of the cladoceran genus *Daphnia* comes from the "failed invasion" of Onondaga Lake, the United States (Duffy et al., 2000; Hairston et al., 1999). Palaeoecological studies of Onondaga Lake's egg bank revealed that it got simultaneously but transiently invaded (from the 1930s up to the 1980s) by two species of water flea (*Daphnia* spp.). *D. exilis* that exclusively occurs in temporary saline ponds in southwestern North America and therefore presented a range extension of 1000 km (Hairston et al., 1999), and *D. curvirostris*, an Eurasian species that has been only reported once before from North America, in extreme northwestern Canada (4500 km range extension for this species, Duffy et al., 2000). For both species, the low genetic diversity of the diapausing egg banks (allozyme diversity for Hairston et al., 1999, and genetic divergence on the 12S rRNA gene for Duffy et al., 2000) supported that dispersal resulted from an isolated event, most likely related to transport by industrial equipment. The transient settlement of both nonnative species pointed to invasibility being mediated by the lower water quality and increased lake salinity as a result of industry in the 1950s. Both invasive species disappeared as lake water quality improved ever since the 1980s (Duffy et al., 2000; Hairston et al., 1999). Most recent studies, however, highlighted that even transient invasions, resulting from time-restricted alterations of water quality (as for eutrophication and subsequent re-oligotrophication of deep European lakes), can result in irreversible changes in *Daphnia* genetic architecture via interspecific hybridization and introgression (Alric et al., 2016; Brede et al., 2009).

Mergeay et al. (2006) took palaeogenetic analysis one step further by reconstructing the invasion history of a single asexual American water flea clone (a hybrid between *Daphnia pulex* and *Daphnia pulicaria*) in Africa. They attributed the introduction of the water flea in Lake Naivasha to a single, accidental event sometime between 1927 and 1929. This period corresponded to the stocking of largemouth bass (*Micropterus salmoides*) from the United States. As a result of this concomitant introduction, authors showed that within 60 years the introduced water flea clone became the only occurring genotype, which displaced the genetically diverse, sexual population of native *D. pulex*.

The use of fossil data to address questions relative to invasions has been criticized because they do not necessarily provide accurate taxonomic

information (i.e. at the species level). But recent improvements in molecular analyses of preserved resting stages promise to overcome such limits (Hofreiter et al., 2015; Leonardi et al., 2016). There are also still-persisting doubts about long-range dynamics of fossil remains (Webb, 1985) due to time and space heterogeneities in remains production, transport, and archiving to the sediment. Consequently, the taxonomic composition of the palaeorecord does not necessarily reflect the actual taxonomic composition of past communities because mechanisms by which remains are produced, transported, and archived in lake sediment may vary between ecosystems but also with time for a single ecosystem. As a result, the detection of a species in a palaeorecord constitutes more robust information as the absence of detection could be also attributed to differential production, transport, or preservation of remains. Therefore, palaeorecords might be more adequate to invalidate rather than confirm the status of a nonnative species. Nevertheless, considering these limits, when combined with contemporary records, palaeodata offer a great but so far underexploited potential to document the status, the timing, and the mechanisms of successful invasions.

2.1.2 Historical Observations and Museum Records

Fossil records and palaeoecological samples provide important historical data for analyzing the long-term ecological impacts of biological invasions. However, geological records are usually not sensitive to short-term changes, and thus other methods are needed for documenting impacts over timescales of years to decades. Financial constraints typically limit the spatial scale and temporal scope of sampling in ecological studies, and this poses a challenge for collecting consistent ecological data over periods longer than the average duration of a funded research project (Dumbrell et al., 2016). Periodic natural history surveys and environmental monitoring efforts offer important exceptions to this rule (cf. Chauvet et al., 2016; Nedwell et al., 2016; Storkey et al., 2016).

Many long-term ecological data sets have been motivated by economic interests and were only later recognized for their ecological value. For example, the Continuous Plankton Recorder survey began as a project for understanding fish stocks throughout the world's oceans and now includes more than 200,000 samples spanning eight decades (Richardson et al., 2006). Inventories of Mediterranean fish biodiversity date back from 1800, but they have only recently been used to investigate how different environmental variables and fish functional and life-history traits could predict invasion success (Ben Rais Lasram et al., 2008).

Most data sets are more regional as they are motivated and funded by local economic interests, and these can be combined to examine larger-scale patterns of invasions. The Great Lakes of North America, for example, have a history of local monitoring projects funded by nearby state governments in the United States and nearby provincial governments in Canada. As a result, aquatic invasion in the Great Lakes basin has been relatively well characterized (Grigorovich et al., 2003). More recently, the RivFunction project funded by the European Commission provided a unique opportunity to demonstrate regional-specific impact on leaf litter decomposition following the establishment of various exotic woody species in freshwater streams across France and Great Britain (Chauvet et al., 2016). These records, often collected by government organizations, remain important data sources to track the timing and spatial extent of biological invasions.

In addition to environmental monitoring, natural history surveys have a long history in biology and are probably an underutilized resource in invasion biology. For example, there are approximately 3300 herbaria worldwide that contain an estimated 350 million specimens (and associated meta-data) extending back as over 400 years (http://sweetgum.nybg.org/science/ih/). Herbarium records have become an important data source for reconstructing the spatiotemporal spread of invasive plants as well as their pathogens and microbial associations (e.g. Lavoie et al., 2012; Ristaino, 2002; Yoshida et al., 2014, 2015). However, many of these invaluable resources are themselves threatened by financial cutbacks even as interest is building in natural history collections as an important link to the ecological conditions of the past.

In contrast to reconstructing the spread of invading species over space and time, identifying the ecological consequences of these invasions is much more complicated for at least two reasons. First, ecological impacts can be complex, involving multiple trophic levels (e.g. Pantel et al., 2017), but surveys tend to focus on specific taxonomic groups (e.g. birds, insects, plankton) rather than whole ecosystems. Second, any observable changes in community structure may appear to be driven by an invasion when both are in fact driven by another factor (e.g. human disturbance). In other words, it may be unclear whether invasive species are the "drivers" of ecological changes observed over time or merely "passengers" riding along a wave of other global change factors (Didham et al., 2005; MacDougall and Turkington, 2005).

Long-term surveys again provide a potential solution to the problems of ecological complexity and distinguishing "passenger" colonizing species

from invasive species driving ecological change. Ideally, such surveys would be conducted at multiple locations at time points preceding invasion by a species of interest. For example, long-term monitoring of plankton communities in Ontario lakes has proved fortuitous in providing baseline data for examining the ecological impact of *Bythotrephes longimanus*, an invasive zooplankton in both invaded and reference lakes (e.g. Palmer and Yan, 2013; Yan et al., 2002). Given that these lakes vary in chemistry, food web structure, and exposure to anthropogenic stresses including exposure to *B. longimanus*, it has been possible to show that this invader is indeed a major driver of changes to aquatic food webs.

2.1.3 Large-Scale Monitoring Through Citizen Science

Citizen sciences, where citizens take part in the data collection effort, have proven to be very efficient to monitor biodiversity over large scale and long term (Conrad and Hilchey, 2011; Couvet et al., 2008; Dickinson et al., 2010). With the development of such monitoring programmes, large data sets about species' spatial and temporal distributions, abundances, and traits are becoming available for a variety of taxa and regions. Such data sets offer promising opportunities to detect and monitor spatiotemporal changes in invasive species (Crall et al., 2010; Dickinson et al., 2010; Gallo and Waitt, 2011).

Data on species are usually collected by direct observations (vision, hearing) and, to a lesser extent, by indirect observations (traces, etc.). As for all sampling methods, they vary from unprotocoled observation reports such as single-species observations or species lists at a given times and places (e.g. http://ebird.org), to repeated standardized sampling of species abundance or species interactions within communities (e.g. http://vigienature.mnhn.fr). This variety usually goes with a trade-off between the amount of data collected and the level of constraints or skills required to collect data, and with data ranging from low to high precision (Purvis and Hector, 2000).

Citizen science monitoring programmes also collect data using digital technologies such as photographs (Stafford et al., 2010), camera traps (O'Brien et al., 2010), or sound recordings (Blumstein et al., 2011). These new recording methods benefit to biodiversity monitoring schemes by enabling a strong increase in the quantity and quality of the data collected. Such digital technologies are noninvasive, objective, and have minimal observation bias. In particular, some of these technologies can be coupled with automated signal recognition to allow species identification and individual count (Blumstein et al., 2011; Jeliazkov et al., 2016) that further

reduce both observer bias and the time spent on data analysis. Interestingly, such digital recordings also allow subsequent data validation by taxonomic experts and can be reanalysed later using novel techniques and novel knowledge.

The type of data set varies greatly and so does the type of questions that can be addressed. Large-scale standardized monitoring schemes of species assemblages have been shown highly relevant and powerful to quantify changes in community composition across space and time (for example, breeding bird surveys), and linking those variations to environmental variables to investigate the ecological mechanisms involved. Such highly standardized schemes may be less relevant to detect the first stages of an introduction or to survey the beginning of the expansion of an invasive species as the spatial resolution or coverage of such scheme may not be adequate. In that case, opportunistic data can be useful. Widespread Internet access has indeed favoured the development of several extensive inventory projects involving massive networks of volunteers who provide observations following relatively unstructured protocols (e.g. Gallo and Waitt, 2011; Roberts et al., 2007). If the increase in sample size presents several advantages, the use of such data requires great care and good knowledge of the limitations (bias) of the data (Kremen et al., 2011; Snäll et al., 2011).

Data from citizen science programmes are increasingly used to assess and predict the distribution of invasive species. In their review, Dickinson et al. (2010) present several examples of the use of citizen science data to track changes in the distribution of invasive birds in North America and Europe. Compared to traditional academic surveys, citizen science can appear as a cost-effective way to monitor the spatial distribution of invasive species (Goldstein et al., 2014), and they are now used for a variety of taxa, from plants (e.g. Blois et al., 2011) to insects (e.g. Kadoya et al., 2009), mammals (e.g. Goldstein et al., 2014), or fishes (e.g. Zenetos et al., 2013).

The use of species distribution models (SDMs) (Franklin, 2013) allows linking these distributional observations with environmental data, such as land use and climate data, to better assess mechanisms of invasion and predict invasion risk and future distribution (Barbet-Massin et al., 2013; Kadoya et al., 2009). Beyond the use of data collected in the invaded zone, there is a real interest to use the species distribution data in species native area to predict future distribution as including data from the entire (native and non-native) distribution of invasive species may help to better characterise its suitable habitat. This allows a better forecast of the potential for invasion in space and time, for example, under climate change (Beaumont et al., 2009).

Václavík and Meentemeyer (2012) using time series data on the invasion of a plant pathogen also showed that SDMs calibrated with data from later stages of the invasion performed better to estimate the potential range of invasive pathogen compared with those of the early stages of invasion.

Data from various citizen science programmes have been used to track the cascading effects invasive species have on the species of invaded communities. An important benefit of long-term monitoring of communities over large spatial scale is that they predate invasion, thereby allowing comparisons between invaded and uninvaded communities in space and time regardless of whether invasion events are predictable. Such comparison can provide almost "real-time" assessment of the impact of invasive species have on local communities.

Bird communities are among the first to be monitored by citizen scientists and clearly exemplify the benefits of such programmes (Dickinson et al., 2010). They can provide natural experimental set-up with contrasting situations to dissect the actual mechanisms, or interactions, linking invasive species to others. One good example is distinguishing between direct or apparent competition between house finches and house sparrows in North America by analyzing pattern of covariation in abundances among species (Cooper et al., 2007). Citizen science programmes also allow investigating how change in density of an invasive species can percolate to higher trophic levels within communities. Several cases highlighting the impacts invasive prey have on the density and distribution of local predators indeed come from the analysis of citizen science monitoring programmes (Barber et al., 2008; Koenig et al., 2013).

Such long-term monitoring programmes do also exist for other communities such as insects and have proven to be able to provide good quality data in a cost-effective way (Gardiner et al., 2012). For example, one of the rare well-documented cases of species decline following invasion comes from ladybird monitoring programmes in Belgium, Britain, and Switzerland, where several abundant local species have been shown declining after the arrival of *Harmonia axyridis* (Roy et al., 2012), a rapidly expanding invasive ladybird first introduced a biological control agent (Pell et al., 2008).

More recent programmes have taken advantages of new technologies available. For example, the programme eMammal in the United States uses camera traps to sample mammals over six contiguous states (McShea et al., 2016). Investigating the impact of domestic cats on wild fauna, they found that coyotes exclude domestic cats, and thereby protect natural areas by concentrating cat activity in urban areas where coyotes are rare (Kays et al., 2015).

Citizen science offers several advantages to monitor invasive species and invaded communities. If opportunistic data are useful to survey changes in distribution, the absence of information on effort developed and on its distribution in space and time limits the possibilities of using such data to survey changes in invaded communities. In contrast, in standardized monitoring programmes (using relevant sampling design in space and time), the potential bias can easier be detected and taken into account. The relevance of monitoring schemes to assess the state and trends of biodiversity across scales depends on both the quantity and the quality of data because the precision of estimates depends on the sample size (i.e. the number of sampling units available for estimation) and the natural variation of the measured parameter in time and space (i.e. variation within or among years, variation among populations or among habitats). A key issue is thus to increase the quantity and quality of locally collected data and to sustain the sampling effort through time (e.g. Dumbrell et al., 2016).

One way to increase data quantity is to try to increase the number of observers (e.g. the number of volunteers in citizen programmes), for example, by improving the communication about the existence and the general value of such programmes or by facilitating the participation with dedicated and user-friendly apps and websites. Regarding data quality, it is possible to reduce the observer error such as misidentification or poor species detection (Lotz and Allen, 2007; Strand, 1996; Thompson and Mapstone, 1997) through a better training of field staff and volunteers (Gallo and Waitt, 2011) and/or by using digital technologies (new recording methods and automatic recording devices). Finally, whatever the types of data used, citizen science data present analysis-related challenges (e.g. sampling bias, observer variability, and detection probability) that are not easily addressed with classical statistical approaches and implied the development of new approaches (Weir et al., 2005). Citizen science research has hence recently resulted in the development of new computational approaches for analysis of large, complex data sets (Bird et al., 2014; Isaac and Pocock, 2015; Kelling et al., 2009). New statistical models are developed to take into account the expertise of volunteers. For example, eBird project, which is one of the largest citizen science programmes in existence providing opportunistic data, allows birders to upload observations of bird species to an online database even if they have various levels of expertise. Modelling the expertise of birders improves the accuracy of predicting observations of a bird species at a site. Such models can also be used for predicting birder expertise given their history of eBird

checklists and identifying bird species that are difficult for novices to detect (Yu et al., 2010).

As in other fields, these approaches are revolutionizing the ways in which ecologists analyse large-scale patterns and visualize change at large geographic scales.

2.1.4 Molecular Techniques

Molecular techniques based on the detection of DNA directly from organisms or from their traces (i.e. environmental DNA, also known as eDNA) are rapidly popularizing among ecologists and managers as cost- and time-effective tools for reliable monitoring of nonnative species and/or their impact on native communities. Indeed, the development of molecular techniques gained an important momentum during the last decade through efforts to build standardized DNA sequence reference databases, protocols, and analytical pipelines (e.g. Armstrong and Ball, 2005; Boyer et al., 2016; Coissac et al., 2012; Eichmiller et al., 2016; King et al., 2008; Ratnasingham and Hebert, 2007; Valentini et al., 2009b), thus rendering the approach more accurate and more user-friendly. As a consequence, molecular techniques are now very broadly applicable and have been successfully employed for the detection of a growing number of invasive organisms from eDNA samples comprising vertebrates (Adrian-Kalchhauser and Burkhardt-Holm, 2016; Jerde et al., 2011; Piaggio et al., 2014; Secondi et al., 2016), invertebrates (Ardura et al., 2015; Goldberg et al., 2013; Tréguier et al., 2014), plants (Scriver et al., 2015), pathogens (Hall et al., 2016; Lamarche et al., 2015; Schmidt et al., 2013a,b), and even invasive genotypes (Uchii et al., 2016).

According to the degree of taxonomic precision and the level of a priori knowledge about the studied system, eDNA approach could encompass a range of distinct techniques, varying in their technical requirements (Table 1). For instance, a simple polymerase chain reaction (PCR) could be one very cost-effective tool for diagnosing a single-target species, either directly from collected specimens or indirectly from its traces (e.g. excreta, fur, skin, eggs, etc.; Naaum et al., 2014). This approach requires only the development of species-specific and sensitive enough primers, allowing the unambiguous detection of the target DNA, even in very low concentrations. PCR could also be tailored to very specific, allowing the differential detection of distinct social forms (e.g. the invasive fire ant *Solenopsis invicta*; Yang et al., 2009) or sexes (e.g. the feral fox *Vulpes vulpes*; Berry et al., 2007), within the same species. For an optimal protocol, targeting short fragments

Table 1 Summary of Major PCR Techniques Currently Used eDNA and Molecular Diet Analysis Studies

		Singleplex PCR		Multiplex PCR		Singleplex and Multiplex qPCR		
DNA Template	**DNA Revealing Technique**	**Single or Multiple Group-Specific or "Universal" primers**		**Multiple Species- or Group-Specific Primers**		**Single or Multiple Species- or Group-Specific Primers Fluorescent probes**		**No PCR**
Single whole specimen or eDNA	Gel electrophoresis	Presence/ absence of a species	Prinsloo et al. (2002); Ramsey et al. (2015)	Presence/ absence of a species	Thalinger et al. (2016)			
One known species		Prey attack rates	Boreau de Roincé et al. (2013); Gomez-Polo et al. (2015)	Prey attack rates	Hatteland et al. (2011); Pianezzola et al. (2013)			
		Parasitism rates	Agusti et al. (2005); Prinsloo et al. (2002)	Parasitism rates	Gariepy et al. (2005, 2008); Traugott et al. (2008)			
		Species taxonomical identity	Deng et al. (2015); Dupas et al. (2006)	Interaction network	Balmer et al. (2013); Sint and Traugott (2015)			
				Symbiont/ parasite community	Kurata et al. (2016)			
Single or multiple whole specimens or eDNA	Melt curves					Presence/ absence of one or several species	Domaizon et al. (2013); Tréguier et al. (2014)	
One or multiple known species						Prey attack rates	Gomez-Polo et al. (2015); Lundgren and Fergen (2011)	
						Parasitism rates	Liang et al. (2015)	
						Interaction network	Campos-Herrera et al. (2011); Lundgren et al. (2009)	

Continued

Table 1 Summary of Major PCR Techniques Currently Used eDNA and Molecular Diet Analysis Studies—cont'd

		Singleplex PCR		Multiplex PCR	Singleplex and Multiplex qPCR		
DNA Template	DNA Revealing Technique	Single or Multiple Group-Specific or "Universal" primers		Multiple Species- or Group-Specific Primers	Single or Multiple Species- or Group-Specific Primers Fluorescent probes		No PCR
					Diet	Bowles et al. (2011); Deagle and Tollit (2007)	
					Relative biomass[a]	Deagle and Tollit (2007); Takahara et al. (2012)	
Single whole specimen or eDNA	Sanger sequencing	Presence/ absence of a species	Adrian-Kalchhauser and Burkhardt-Holm (2016); Rougerie et al. (2011)				
One known or unknown species		Prey attack rates	Gorokhova (2006); Zarzoso-Lacoste et al. (2016)				
		Parasitism rates	Derocles et al. (2012); Traugott et al. (2006)				
		Species taxonomical identity	Kaartinen et al. (2010); Smith et al. (2011)				
		Phylogenetic signal	Kasper et al. (2004); Peralta et al. (2014)				
		Interaction network	Derocles et al. (2014); Peralta et al. (2014)				
		Diet	Wilson et al. (2009); Zarzoso-Lacoste et al. (2016)				

Multiple whole specimens or eDNA	High-throughput sequencing	Presence/absence of a species	Cannon et al. (2016); Zaiko et al. (2015b)	Presence/absence of one or several species	Andújar et al. (2015); Tang et al. (2015); Zhou et al. (2013)
Multiple known or unknown species		Prey attack rates	Mollot et al. (2014)	Prey attack rates	
		Parasitism rates		Parasitism rates	
		Species taxonomical identity[a]	Shokralla et al. (2015)	Species taxonomical identity	Gillett et al. (2014); Tang et al. (2015); Zhou et al. (2013)
		Phylogenetic signal[a]	See Lemmon and Lemmon (2013)	Phylogenetic signal	Andújar et al. (2015); Gillett et al. (2014)
		Interaction network	Ibanez et al. (2013); Mollot et al. (2014)	Interaction network	
		Diet	Boyer et al. (2013); Kartzinel et al. (2015)	Diet	Paula et al. (2015); Srivathsan et al. (2015, 2016)
		Relative biomass[a]	Murray et al. (2011)	Relative biomass[a]	Srivathsan et al. (2015); Tang et al. (2015); Zhou et al. (2013)
		Symbiont/parasite community	Gibson et al. (2014)	Symbiont/parasite community	Paula et al. (2015); Srivathsan et al. (2015, 2016)
				Intraspecific genetic variation	Srivathsan et al. (2016)

[a]Indicates cases where the validity of the data is debateable in the literature (e.g. quantitative estimates derived from sequence data or confident phylogenetic estimates from very short DNA fragments, targeted in metabarcoding studies).
Techniques are ordered according to the degree of a priori knowledge their require. The scope and the precision of generated data are provided. Empty cases indicate that no study using the corresponding technique is available to date.

of multicopy DNA is usually a leading choice as this optimizes the detection of rare, highly degraded eDNA molecules. Because of its simplicity, diagnostic PCR is implemented by a growing number of public agencies as an easily standardized tool for the routine surveillance of invasive species or for justifying the establishment of management actions. For instance, the Tasmanian government has adopted a sequential PCR approach (i.e. singleplex diagnostic PCR, followed by a Sanger sequencing) in the context of a programme aiming the eradication of the red fox from Tasmania (*V. vulpes*, Berry et al., 2007; Ramsey et al., 2015). Likewise, the State of Utah Division of Wildlife Resources in the United States is relying on PCR diagnostic as a monitoring tool of at-risk water bodies. Positive PCR detections are consequently used for the trigger off of appropriate management actions (for more details, see Darling and Mahon, 2011).

Multiple species- or group-specific primer pairs could be used together within a single PCR (multiplex PCR). This is a much more cost- and time-saving alternative to multiple separate singleplex PCRs, in cases where the simultaneous diagnosis of multiple species is required (e.g. Cooke et al., 2012; Láruson et al., 2012; Mackie et al., 2012; Nakamura et al., 2013). Multiplexed primer pairs usually need to target DNA fragments of contrasting lengths in order to allow the recovery of each taxon identity. Corresponding amplicons may or may not be Sanger sequenced for confirming species identity. Recent improvements in multiplexing protocols (Sint et al., 2012; Staudacher et al., 2016) as well as the availability of adapted reagents at very attractive rates (e.g. large choice of ready-to-use multiplex PCR commercial kits) could help achieving greater standardization, thus allowing comparison across multiplex PCR assays, regardless of the studied species or the target genes. For example, one interesting application of multiplex PCR is the concomitant detection and identification of invasive species and their symbionts or pathogens. Recently, Kurata et al. (2016) proposed a multiplex PCR approach for the diagnosis of *Bemisia tabaci* and its symbionts. Apparently, *B. tabaci* forms a species complex comprising several genetic groups that vary in their pest potential (pesticide resistance) and invasion impact (the ability to transmit pathogens to local crop plants), partly as a consequence of differences in the key symbionts each genetic group harbours.

PCR-based approaches could be complemented by a high-throughput sequencing of amplified DNA molecules (i.e. metabarcoding; Taberlet et al., 2012b). This approach allows the simultaneous taxonomic assignment of multiple species present in complex environmental samples (water, soil, faeces, gut contents, etc.), requiring no or little a priori knowledge about the

biodiversity under examination (Table 1). Two recent studies used this eDNA metabarcoding approach for assessing the whole biodiversity from marine and freshwater bodies—ecosystems for which traditional methods provide very limited insight. In both studies, the metabarcoding approach showed to be very successful in detecting rare, cryptic species that have been missed with visual surveys (Cannon et al., 2016; Port et al., 2016). More interestingly, Cannon et al. (2016) were able to successfully detect not only aquatic and semiaquatic taxa but also terrestrial species occurring nearby the riverbanks of the Cuyahoga River they surveyed. The DNA from the invasive Asian carp was also detected, while this invader was not known to be present in the Cuyahoga River. These encouraging results suggest that DNA metabarcoding could be a sensitive tool for monitoring present biodiversity, even in previously uncharacterized environments. When coupled with relevant estimates about temporal scales, the metabarcoding approach also allows reconstructing past biodiversity dynamics, based on sedimentary ancient DNA (e.g. Domaizon et al., 2013; Pansu et al., 2015a; Thomsen and Willerslev, 2015) or DNA trapped in deep ice cores (Willerslev et al., 2007). Metabarcoding approach based on ancient DNA helped thus reveal major and often unexpected shifts in plant and animal assemblages through large geological periods (e.g. Domaizon et al., 2013; Pansu et al., 2015a; Willerslev et al., 2014) as well as long-lasting impact caused by invasive species on native communities (Pansu et al., 2015b).

Furthermore, biodiversity estimates based on metabarcoding data have been shown to provide more accurate and, most importantly, auditable biodiversity estimates compared to traditional taxonomic surveys, strongly encouraging their use as source for policymaking and ecosystem-level management (Baird and Hajibabaei, 2012; Ji et al., 2013; Taberlet et al., 2012b; Valentini et al., 2016), so why not also as a management tool within the context of biological invasions? For instance, the two first ever studies using metabarcoding for detecting widespread invasive marine plankton species recommended a DNA metabarcoding approach, in combination with visual observations, for the routine surveillance of marine invasions (Zaiko et al., 2015a,b).

Probably the most promising application of PCR-based approaches is the possibility to derive quantitative estimation about the biomass or the density of the target species directly from the quantity of DNA retrieved from environmental samples (Rees et al., 2014). Currently, our understanding of such estimates comes mainly from aquatic ecosystems, where several studies found positive correlations between DNA concentration and biomass, density, and/or abundance (Erickson et al., 2016;

Pilliod et al., 2013; Takahara et al., 2012; Thomsen et al., 2012). The quantification of eDNA is usually achieved using a quantitative PCR (qPCR), allowing to infer the number of molecules present in the DNA template or the number of sequences yielded by high-throughput sequencing machines (Evans et al., 2016; Kelly et al., 2014).

Many of the methodological constraints associated with data production are now well documented (e.g. Pedersen et al., 2014). For example, the application of strict clean-lab procedures, including numerous negative and positive controls at each stage of the data production, is the very first step for achieving robust results. The use of sterile disposable labware and separate stations for pre- and post-PCR procedures is usually recommended (Cooper and Poinar, 2000; Pedersen et al., 2014). For palaeoenvironmental DNA analysis, particular care should be taken for avoiding contamination by modern DNA (e.g. Boere et al., 2011; Rizzi et al., 2012; Thomsen and Willerslev, 2015; Torti et al., 2015). Dealing with imperfect detection (Box 1) and PCR/sequencing errors in metabarcoding studies requires the incorporation of multiple technical and field sampling replicates (e.g. Roussel et al., 2015), as well as the use appropriate bioinformatic tools (Boyer et al., 2016; Schloss et al., 2011) and sequence analysis framework (De Barba et al., 2014).

The sole use of eDNA precludes obtaining information about the state of an organism, including its size, developmental stage, or state (dead vs alive). This implies a more close integration with other complementary techniques (traditional trappings or visual observations for example; Tréguier et al., 2014; Valentini et al., 2016). On the other hand, fast-growing advances in high-throughput sequencing, combined with functional analysis of gene expression, could appear as an excellent opportunity for building the next generation of eRNA molecular tools based on the analysis of the transcriptome from the very same environmental samples. For example, patterns of DNA methylation are now routinely used as marks of developmental history in animals (cf. Meehan, 2003) and could be adapted to meet the requirements of eDNA methods.

Some systems are faced with resolving more specific issues related to the spatiotemporal information delivered through eDNA. In lotic systems, for instance, effects of the downstream transportation and dilution of DNA need to be better accounted for in future studies (see Roussel et al., 2015). Understanding DNA degradability and turnover within water column and the soil is another important challenge for the monitoring of contemporaneous eDNA (cf. Turner et al., 2015; Yoccoz et al., 2012).

BOX 1 Dealing With Imperfect Detection in eDNA Studies

Imperfect detection is a common problem in ecological studies and refers to the uncertainty associated with the presence/absence of a species within a given environment or environmental sample (i.e. eDNA). It could be subdivided into two major types of errors: type I error is the detection of a taxon in the area where it is apparently absent (false positive); type II error occurs when a taxon fails to be detected, while it is actually present (false negative). This problem came into the spotlight recently in the context of eDNA and metabarcoding techniques as rapidly popularizing tools for biodiversity monitoring. Major concerns arose as the extreme (false positives) or the insufficient (false negatives) sensitivity of molecular tools could lead to an overinflation of degree of detection uncertainty. Moreover, because DNA techniques usually imply multiple steps—from field sampling/filtration to DNA extraction, PCR, sequencing, and bioinformatic analyses—the probability of false estimations could increase proportionally. As a potential way to minimize uncertainty in detection, the adoption of strict field and lab procedures preventing common sources of bias (e.g. contaminations, assay sensitivity, PCR and sequencing errors, etc.) has been proposed (e.g. Bohmann et al., 2014; Darling and Mahon, 2011). Among these procedures, multiple field, extraction, and PCR replicates as well as numerous positive and negative controls at each step of the processes are the rules. More recently, the importance of bioinformatic analyses, especially in the case of HTS approach, has been stressed for obtaining reliable species distribution data (de Barba et al., 2014). Such procedures showed to be satisfyingly efficient for preventing or managing false negative occurrences but do not really allow to account for false-positive detections. Furthermore, even minimized, a certain level of uncertainty persists and none of the above procedures could provide reliable estimations of detection probability or proportions of false detections. Fortunately, new statistical methods inspired by site occupancy models (SOMs) have been recently proposed (Ficetola et al., 2015; Schmidt et al., 2013a,b). SOMs and SODMs (for site occupancy detection models) have been adapted to meet assumptions of eDNA studies and could be calibrated using presence/absence data validated by multiple detection methods or by observations for closely related taxa (Lahoz-Monfort et al., 2016). SODMs can be used to estimate the proportion of samples where a species is present or the minimal number of samples/replicates necessary to obtain a confident detection estimates (within a defined confidence interval). SODMs appear as a promising tool to estimate detection and species distribution probabilities despite imperfect detection and might appear as a powerful unifying framework for eDNA analysis that needs to be further developed.

Finally, the metabarcoding approach implies the taxonomic identification of multiple unknown taxa by comparison with reference library of taxonomically annotated sequences. The fine taxonomic assignment of highly diverse and taxonomically difficult organisms (e.g. Tara Oceans, palaeoenvironments) could be challenging, simply by lack of comprehensive reference databases. On the other hand, the short DNA fragments targeted in metabarcoding studies with the objective to maximize the capture of highly degraded eDNA often preclude species-level taxonomic identification even in more common study systems. Additionally, a single short DNA metabarcoding sequence could be assigned simultaneously with different levels of taxonomic precision (due to sequencing/PCR errors) (Yoccoz, 2012), therefore contributing to inflate the uncertainty in biodiversity estimates derived from metabarcoding data. One possible way to deal with imperfect taxonomic assignments is combining metabarcoding and traditional field surveys, which could significantly improve the taxonomic resolution of detected biodiversity (cf. Yoccoz et al., 2012). However as visual surveys are not always feasible, another way to deal with the problem, besides the continuous completion of public databases, is to improve taxonomical assignments even in the absence of complete reference database. Several approaches have been proposed recently (e.g. Munch et al., 2008a,b; Zhang et al., 2012).

Molecular methods offer a large array of applications: from the detection and the accurate taxonomic assignment of single specimens at various life stages to the large-scale spatial and temporal monitoring of invading and invaded communities. One particular interest of using DNA techniques as monitoring tool for biological invasions is their capacity to detect cryptic and rare, low-abundance species with greater precision and minimal investment in taxonomic expertise and sampling effort (e.g. Ji et al., 2013; Yoccoz, 2012). The high taxonomic resolution, accessed through molecular data, could help identifying divergent taxa, even at the very early stages of genetic divergence. This information, combined for example with historical data about the origin or the time since introduction, could inform about ongoing events of speciation/diversification (Folino-Rorem et al., 2009) as well as about their prospective impact on local species (e.g. hybridization, competition, etc.). Molecular data can also help distinguishing between morphologically cryptic species and species exhibiting phenotypic plasticity for taxonomically relevant morphological characters (Folino-Rorem et al., 2009; Stoof-Leichsenring et al., 2012), which is one important prerequisite for identifying possible mechanisms of invasion success. DNA approaches

could also reveal coevolution patterns between taxa (e.g. host–parasite; Kyle et al., 2015). Moreover, as no diagnostic features are available for the large majority of the past and present biodiversity, DNA offers a unique opportunity to increase the number of species that can potentially be studied, including those retained in the sediment and permafrost records (Coolen et al., 2013; Domaizon et al., 2013) or in highly diverse microscopic soil or plankton communities (e.g. Tara Oceans; Karsenti et al., 2011). Specimens with imperfectly preserved morphology, old museum specimens, and different egg or larval stages are also accessible for diagnosis via DNA. This offers an unprecedented potential to analyse large-scale changes in the composition and structure of complex biological assemblages (Capo et al., 2015) and identify some general patterns. Beyond species distribution and genetic variation, molecular techniques could provide more functional insight of past and present communities, by targeting the expression of functional genes, such as the gene encoding for a cyanotoxin, which is produced by aquatic cyanobacterial communities (Savichtcheva et al., 2011). In turn, this allows a more direct estimation of a positive or negative impact within the invaded ecosystem. Other possible applications of DNA techniques for measuring the functional impact of biological invasions are discussed in Section 4.

Finally, the high sensibility of molecular techniques potentially allows the detection of nonnative species at the very early stages of the invasion process (i.e. at low species density), maximizing the chances for early intervention and successful management (e.g. Anderson, 2005). Therefore, DNA-based methods provide a robust and cost- and time-efficient methodological framework that has the potential to become the new institutional norm in terms of invasive species surveillance and management (e.g. Handley, 2015).

2.2 Indirect Methods for Reconstructing Past and Current Invasion History

2.2.1 Population Genetics

Studying invasions requires temporal data. These can be acquired by physically monitoring species abundances over time building upon long-term data sets or palaeorecords. However, good approximation of temporal data could also be derived from historical signatures in DNA, i.e., using population genetics. By studying intraspecific variability at presumably neutral DNA markers, one may infer the patterns of relatedness between current individuals. And these patterns of relatedness may inform on the recent past history of populations. Based on these principles, phylogeography, the use of

phylogenetic information in relation to geography (Avise, 2000), has been much used in the context of bioinvasions. For instance, phylogeography has proved powerful to detecting multiple introductions (e.g. Facon et al., 2003). The study of patterns of within-population diversity (i.e. allelic richness, heterozygosity, private variability) and the patterns of population differentiation are classically used to detect expanding populations, populations that have gone through a bottleneck event and identify populations that have been the source of bioinvasions. Once the empirical expertise acquired, this approach has been statistically formalized using various statistical methods; Approximate Bayesian Computation (ABC) is one such method (Beaumont, 1999). ABC methods allow confronting concurrent complex demographic and evolutionary scenarios to genetic data within a statistically grounded framework. In ABC the limiting step of very complex likelihood computations is replaced by a simulation procedure. The principle is to simulate numerous data sets under various considered scenarios and, for each scenario, under many different values of historical and genetic parameters (e.g. bottleneck intensity and duration, mutation rate, etc.). Scenario choice and parameter inference are then made by studying the frequencies of scenarios and the distribution of parameter values among the simulated data sets that are closest to the observed data (Beaumont et al., 2002). The similarity between simulated and real data is generally evaluated based on diverse summary statistics picked from the classical repertoire of diversity indices (allelic richnesses, heterozygosities, differentiation indices, etc.). ABC methods have already been successfully used to reconstruct the introduction pathways of several invasive species (e.g. Barrès et al., 2012; Dutech et al., 2012; Guillemaud et al., 2011; Miller et al., 2005).

In addition to reconstructing scenarios of invasion, population genetics may allow inferring demographic changes. Population declines and expansion, recent or more ancient, may in principle be detected and quantified using adequate molecular markers (Gilbert and Whitlock, 2015).

All these possibilities are however limited by the informativeness of molecular markers. The rate of evolution of markers makes them adequate to study processes that have occurred at a specific temporal scale. Slowly evolving markers (such as some mitochondrial sequences for instance) will be useful to reconstruct ancient phenomena. Recent demographic changes will only be detected with the help of very resolutive, thus very rapidly evolving markers (such as microsatellites). A precise inference of population demography therefore requires a dedicated development of markers with adequate resolution, large samples from several populations, and the use

of appropriate dedicated statistical inference methods. As a consequence, this type of approach has only been applied to species on a one-by-one basis. One can hardly imagine how it could be applied to networks of interacting species. But before discarding population genetics from the set of useful methods for network monitoring, one should consider the help of such methodologies in the absence of long-term abundance data (which is the case for a large proportion of nonnative species). With only contemporary samples and data, population genetics provides a window on past demographic changes. The ideal combined use of network analysis and population genetics could for instance consist in detecting keystone or indicator species of the networks and develop a dedicated population genetic approach for some of them.

A second case where population genetics has a natural place among the methods for monitoring invasions in networks is the one of rapidly evolving organisms, such as microbes. For organisms like viruses, bacteria, and many fungi, generation times are so short and populations so large that the timescales at which demographic and genetics processes occur could be confounded. Population genetics tools provide a direct access to demography. In the case of pathogens, this observation has led to the approach called molecular epidemiology. Classically molecular epidemiology uncovers invading pathogen strains in a network of resident, endemic. For instance, these invasive, epidemic strains can be associated with "star-like" networks of haplotypes, where a common haplotype is connected to numerous rare single locus variants (Achtman, 2008; Vernière et al., 2014). They may also be detected using phylogeny-based approach as a monophyletic clade emerging from the phylogenetic tree (Avise, 2000).

With the advent of high-throughput sequencing, population genetics can now be conducted on whole genomes (population genomics). The number of markers is no longer a limit and ample information on different temporal scales can be retrieved. Moreover, environmental samples such as faeces or gut contents could be used for inferring the genetic structure of interacting communities and monitor how it changes following invasion. This may consist, for example, in tracking the propagating effects of invading locus variants across trophic levels or quantifying the relative importance of intraspecific variability in key traits determining the degree of invasibility in local communities.

2.2.2 Chemical Fingerprinting

Preserved metabolically inert tissues such as skeletons or shells can be another valuable source for tracing back the establishment of a nonnative species and

possibly its geographical origin. By incorporating various chemical compounds from the environment, usually with a very low turnover, metabolically inert tissues "imprint" the more or less subtle variations in local chemistry over long time periods. Therefore, such tissues could be used as "environmental recorders" for tracking more or less accurately, any changes in habitat use by a species, throughout a lifecycle or across multiple generations. For example, the geochemical characterization of single or multiple trace elements (i.e. chemical fingerprinting) of preserved contemporaneous or historical tissues could be used for revealing the ancient geographic origin of an invasive species or for reconstructing transgenerational migration routes (e.g. Elsdon and Gillanders, 2003; Rubenstein and Hobson, 2004). This approach has shown to be particularly useful for retrospectively tracking migration routes and habitat use in teleost fishes because their otoliths (fish ear stones) grow continuously throughout the fish life cycle, with little or no reabsorption of material incorporated into their structure. Fish otoliths thus reflect the local chemical composition of water at the moment of the incorporation (Campana and Tzeng, 2000). For instance, lifetime variations in strontium (Sr) or strontium/calcium (Sr/Ca) ratios were frequently used for investigating fish migration patterns (e.g. Carpenter et al., 2003; Clarke et al., 2009; Tanner et al., 2011; Thorrold et al., 1997; Townsend et al., 1995) as they showed to be good proxies for environmental salinity (Campana, 1999). If different habitats with very similar microchemistry are to be discriminated, multielemental otolith fingerprints (i.e. the simultaneous analysis of multiple trace elements from the same tissue; Clarke et al., 2009; Forrester and Swearer, 2002; Mercier et al., 2011) could be used for increasing the resolution of analysis. Microchemistry fingerprinting could therefore be a powerful tool for tracking the arrival, and the life-history characteristics of nonnative species that are otherwise difficult to monitor (extinct, elusive, or small-sized invertebrates, aquatic organisms, etc., Carpenter et al., 2003; Zazzo et al., 2006). Moreover, because otoliths are usually well represented in fossil records (Nolf, 1994), the analysis of otolith trace elements could also be used for tracing past environmental changes, concomitant to the establishment of a nonnative species, thus providing functional understanding about prospective invasives' impact and environmental conditions that could have enhanced it (e.g. Jones and Campana, 2009). More recently, multielemental fingerprinting also showed to be a valuable tool for elucidating complex connectivity patterns among species as investigated by López-Duarte et al. (2012) in an impressive 12-year study.

Yet, for some trace elements, there could be great inter- and intraspecific variation for species originating from the same geographic locations that needs to be accounted for, especially in studies involving comparisons among multiple species (Sturrock et al., 2012). For example, factors such as temperature, age, or speed of growth have all been shown to influence elemental incorporation in fish otoliths (reviewed in Elsdon and Gillanders, 2003; Sturrock et al., 2012). Despite the existence of relatively well-characterized large-scale gradients in water chemistry, multiple confounding factors as local fine-scale heterogeneity or temporal variations in elemental composition for the same site could exist (Elsdon and Gillanders, 2004, 2006). This implies the collection of multiple samples per location and per time point for each site in order to obtain stable signatures. As for other approaches (e.g. molecular, stable isotopes) an experimental validation might be required in order to disentangle among intra- and interspecific variability, environmental heterogeneity, and methodological issues in detection (e.g. Elsdon and Gillanders, 2004). Finally, as indicated by López-Duarte et al. (2012), trace-elemental fingerprinting for multiple species could be costly and logistically demanding. The combination of different complementary methods (e.g. real-time species tracking or molecular markers; Cook et al., 2007) could provide more predictive power.

Alongside physical or molecular tracking methods, stable isotope ratios of oxygen ($\delta^{18}O$) and hydrogen (δD) are increasingly used for tracking species movement of terrestrial and aquatic organisms using their metabolically inert tissues (Gannes et al., 1998; Hobson, 1999; Rubenstein and Hobson, 2004). $\delta^{18}O$ and δD isotope ratios could be informative, for example, about the origin of an invasive or its migration dynamics across large, continental scales (Farmer et al., 2008). As such, $\delta^{18}O$ and δD isotopes could provide useful, complementary information to DNA-based population genetics tools in the case of recent introductions of species for which we lack samples from the geographical area of origin.

3. IDENTIFYING AND MONITORING ECOLOGICAL INTERACTIONS OF AND WITH INVASIVE SPECIES

3.1 Trophic Interactions

3.1.1 Stable Isotopes

Chemical elements with more than one stable isotopic form have been used as natural biomarkers in ecosystems. The two most commonly used

to address questions about feeding interactions are stable isotopes of carbon (^{13}C) and nitrogen (^{15}N). These two elements and their stable isotope compositions are necessarily acquired from an animal's diet and incorporated into that animal's tissues (DeNiro and Epstein, 1978, 1981). Primary producers can often be discriminated from their $\delta^{13}C$ (measured as the ratio of ^{13}C to ^{12}C relative to a reference standard) because of the strong imprint of photosynthetic modes on plants' $\delta^{13}C$. Thus, an animal's $\delta^{13}C$ composition can potentially identify the origin of the carbon in its tissues, which can be used to infer foraging location(s) and behaviours (Bearhop et al., 2004). For example, $\delta^{13}C$ naturally varies between the low trophic level organisms in the nearshore and offshore habitats of lakes (France, 1995), and the $\delta^{13}C$ composition of freshwater fish is used to estimate the relative amount of carbon derived from these habitats (e.g. Vander Zanden and Vadeboncoeur, 2002; Vander Zanden et al., 1999). On the other hand, an animal's $\delta^{15}N$ composition has been used as a surrogate for a continuous assessment of its trophic position within a food chain (as reviewed by Fry, 2006). Animals become progressively enriched in ^{15}N at higher trophic levels due to preferential retention of the heavier isotope during protein metabolism, which results in a stepwise enrichment of ^{15}N between consumer and resource.

The time frame to which stable isotope information is relevant in animal tissue directly depends on its turnover. For instance, once synthesized, the amino acids in feathers, scales, and hair are hardly remobilized. Their isotopic composition could be thought of as a documented record of their dietary past. In comparison, blood, muscle, or liver tissues have higher (albeit variable and possibly irregular) turnover rates that provide evidence of recent dietary history at varying time windows (Hesslein et al., 1993) or seasons (Perga and Gerdeaux, 2005). Not only can stable isotope measurements be taken from multiple tissues that provide dietary information at different timescales, but because some of these tissues can resist degradation (e.g. archived in collections of fish scales (Gerdeaux and Perga, 2006) or zooplankton exoskeleton extracted from sediment cores (Perga et al., 2010)), stable isotope analysis (SIA) has the potential to retrospectively reconstruct temporal changes in dietary characteristics of a given species/community, including before and after invasion. Sampling of feathers, blood, or fin clips can also be a good nonlethal alternative with the obvious advantage of sparing vulnerable populations of rare species (Kelly et al., 2006).

If the potentialities of SIA for questions related to invasions have been highlighted several times, these have been clearly underexploited so far.

They have yet proven invaluable to document invasive dietary position and niche width, how invaders might alter the overall food web structure, with subsequent consequences on key processes, such as nutrient cycling.

Being a complement rather than a surrogate to classical or molecular gut content analyses, SIA can evaluate on which local, native organisms an invasive one might potentially feed on. Because SIA is not time consuming, it allows repeatable comparisons between situations, documenting how the predation activities from the invasive species might change depending on the local availability of prey (Caut et al., 2008). Because SIA provides a time-integrated assessment of individual feeding habits, they also offer the option of quantifying the trophic niche of a species (Bearhop et al., 2004). This isotope-based life-history trait allows a good comparison of how nonnative and native species may compete, as shown for invasives as crayfish (Olsson et al., 2009) or fish species in UK waters (Britton et al., 2010).

The impact of an invasive species can expand beyond its own trophic level and consequently affect the overall food web structure. The seminal study by Vander Zanden et al. (1999) documented a reduced trophic position and a dietary shift from littoral to pelagic habitat in native lake trout (*Salvelinus namaycush*) in North American boreal shield lakes following the invasion by two nonnative predators, namely smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*). SIA also provides the opportunity to follow through long-term impact of invasive species at the food web scale. For example, the invading carnivorous Argentine ant (*Linepithema humile*) occupied a similar trophic level as ants in their native habitats. However, once established, the ants shifted to a lower trophic position as they consumed more plant material following severe reductions in native ant prey populations (Tillberg et al., 2007). Based on SIA, Inger et al. (2010) highlighted that the nonnative bream (*Abramis brama*) got caught in Lough Neagh food web, in which it sustains the river lamprey diets. Because SIA data have been piling up over the last decades, large meta-analyses allow testing for more generalistic patterns on the impacts of invasive within food web, as did Cucherousset et al. (2012), suggesting that invasions might promote a greater trophic variability within food webs.

Because primary producers' stable isotope composition is tightly connected to how carbon and nitrogen nutrients circulate within the given ecosystem, SIA may be able to address how these altered trophic interactions finally affect larger biogeochemical processes. A terrestrial example of this application is the study of Carey et al. (2004). They used SIA and

physiological measurements to document how carbon parasitism via arbuscular mycorrhizae may be an important mechanism explaining the success of spotted knapweed (*Centaurea maculosa*), out-competing its native prairie neighbours.

Nevertheless, other sources of variation, not specifically related to diet and trophic behaviour, could influence isotopic fractionation or data interpretation (reviewed by Boecklen et al., 2011; Vanderklift and Ponsard, 2003) and therefore need to be considered (Spence and Rosenheim, 2005). Most of these factors have already been well documented and could now be accounted for in many statistical methods (Kadoya et al., 2012; Parnell et al., 2013; Phillips and Koch, 2002; Phillips et al., 2014; Post, 2002; Post et al., 2007; Ward et al., 2011; Yeakel et al., 2011), while the integration of compound-specific stable isotope ratios (e.g. Chikaraishi et al., 2011, 2014; see also Traugott et al., 2013) could help improving the accuracy of stable isotope data. Finally, growing body of the literature advocates the incorporation of additional isotopic tracers (Jaouen et al., 2016; Vander Zanden et al., 2016), therefore opening perspectives to extend SIA to species with large diet spectra.

3.1.2 Molecular Techniques

DNA-based molecular methods for diet analysis emerge as a valuable complementary approach to SIAs. Not only do they provide the opportunity to get a detailed insight into the menu of a species, but also the taxonomic resolution of identified prey is increasingly improving with the swell of public reference databases. Historically, the use of molecular techniques for diet reconstruction derived from the enzyme-linked immunosorbent assays (ELISA) using monoclonal antibodies that react with an antigen of the target prey in a very specific manner (reviewed by Symondson, 2002). Although this technique has been progressively replaced by the PCR-based methods, monoclonal antibodies offer a range of advantages for tracking prey and parasitoid detection with high precision and sensibility (Greenstone, 1996; Stuart and Greenstone, 1990). The method can be specific enough to discriminate between the different developmental stages of the prey consumed (e.g. insect egg, larvae, or adults; Crook et al., 1996). Such high specificity greatly outperforms all currently available molecular techniques. Moreover, monoclonal antibodies could be designed in a way that increases prey detection success over time (e.g. Harwood et al., 2001; Symondson, 2002), thus maximizing prey detection especially in fast-metabolizing small-sized organisms. An additional advantage is that the probability of detecting secondary

predation with monoclonal antibodies (i.e. detection of a prey within the gut of the target prey organism under study) is very low (e.g. Harwood et al., 2001), compared to a PCR approach (e.g. Sheppard et al., 2005). Monoclonal antibodies thus offer interesting opportunities for characterizing trophic interactions of nonnative species. For example, this method showed very useful for detecting trophic linkages between two invasive insect species: the coccinellid *H. axyridis* feeding upon eggs from the leafhopper pest *Homalodisca coagulata* (Fournier et al., 2006). In a neat experimental study, Lundgren et al. (2013) used ELISA and showed that dandelion seeds (*Taraxacum officinale*, Asteraceae) marked with rabbit monoclonal antibody are consumed by a much broader community of arthropods in their nonnative range of distribution.

In general, monoclonal antibodies could be the easiest method for detecting very specific or unknown trophic linkages (e.g. different developmental stages) while allowing for without a priori screening of large number of predators. Yet, the monoclonal antibody approach is very limited for studying broad-spectrum diets, mainly because developing such a large array of distinct antibodies is prohibitively expensive. For more details see Symondson (2002).

Currently, PCR-based techniques are probably the most versatile and cost-effective molecular methods for the characterization of trophic interactions (Table 1). Indeed, PCR diet analysis could be seen as an alternative for assigning morphologically unidentifiable prey remains to specific prey organisms (e.g. Bartley et al., 2015; Kasper et al., 2004; Pérez-Sayas et al., 2015), bypassing most of the limitations of traditional visual surveys of feeding behaviour or gut content analyses (e.g. cryptic feeding, liquid prey, etc.). Singleplex diagnostic PCR, for example, could be one very cheap and robust approach for tracking the consumption of a target species by a wide range of predators. Egeter et al. (2015) used diagnostic PCR and demonstrated that the DNA of an endangered frog species could be detected in the stomachs and faecal pellets of a range of invasive rodents with PCR, showing overwhelmingly superior results compared to the traditional morphological identification of prey remains. Similar results were achieved in another recent study where the diagnostic PCR allowed higher detectability and more accurate taxonomic identification of ingested prey by invasive mammal species in French Polynesia (Zarzoso-Lacoste et al., 2016).

Besides predation, PCR methods are also a reliable tool for disentangling host–parasitoid interactions. Insect parasitoids (Hymenoptera, Diptera) are frequently introduced into new habitats as a part of biological control

programmes or could be efficient control agents of introduced species within their nonnative ranges. But parasitoids are also small-sized and a taxonomically challenging group. The monitoring of their trophic interactions by traditional rearing methods could therefore be laborious (Gariepy et al., 2008). As an alternative, Gariepy et al. (2014) combined a singleplex PCR and Sanger sequencing for detecting Scelionidae parasitoids within eggs of the invasive brown marmorated stink bug (*Halyomorpha halys*). The developed assay was sensitive enough to detect with 100% efficiency parasitoid DNA from parasitized eggs at different time periods (and as soon as 1 h after oviposition), and with lesser success from empty eggs after parasitoid emergence. When applied to field collected egg masses, the assay was also successful in identifying cases of hyperparasitism. This is one noticeable illustration of how eDNA (DNA shed on insect egg masses) could be used for retrieving trophic interactions without the physical disruption of local food webs opening promising avenues for the direct reconstruction of invaded food webs in a cost- and time-efficient way. One particularly revolutionizing application of PCR methods concerns planktonic assemblages, where the small size of the organisms involved usually precludes the use of other methods for quantifying predator–prey interactions (Maloy et al., 2013; Riemann et al., 2010; Sotton et al., 2014; Troedsson et al., 2009). For example, the presence of the toxic cyanobacteria *Planktothrix rubescens* in the gut contents of various zooplanktonic taxa (*Daphnia*, *Bosmina*, and *Chaoborus*) was estimated by qPCR, showing that these cyanobacterial cells constitute a part of food resource for herbivorous zooplanktonic taxa during metalimnetic cyanobacteria bloom periods (Sotton et al., 2014). As a consequence, zooplanktonic herbivores by diel vertical migration act as vectors of cyanotoxins by encapsulating grazed cyanobacteria and contribute to the contamination of zooplanktonic predators (Sotton et al., 2014).

More recently, the scope of PCR techniques for diet analysis has been significantly broadened by the development of the DNA metabarcoding as this approach introduces the possibility to examine the full diet spectrum of a species, while requiring very little a priori knowledge. DNA metabarcoding for diet analysis implies the use of general primers, for amplifying prey DNA from food remains, present in a dietary sample (e.g. gut contents or faeces). For dietary samples from unknown species, an additional set of species-specific primers could be used in order to confirm/reveal the identity of the target predator species (e.g. Shehzad et al., 2012). The use of unique identifiers ("tags") allows recovering data after sequencing from each individual consumer using bioinformatic approach (Binladen et al., 2007;

Boyer et al., 2016). DNA metabarcoding could be used for unravelling trophic interactions in herbivorous (Ait Baamrane et al., 2012; Ibanez et al., 2013; McClenaghan et al., 2015; Quéméré et al., 2013; Valentini et al., 2009a) and carnivore organisms (Boyer et al., 2013; Leray et al., 2015; Mata et al., 2016; Vesterinen et al., 2016). DNA metabarcoding for diet analysis has not been applied yet in the context of biological invasions but two recent studies indicate that this approach seems to be advanced enough to be applied within a more explicitly hypothesis-testing context. By combining SIA and DNA metabarcoding, Kartzinel et al. (2015) investigated the fine-scale trophic partitioning in a community of large mammalian herbivores, while Craine et al. (2015) showed how dietary changes, induced by climate warming, could potentially cause nutritional stress in native North American bisons (*Bison bison*).

Molecular techniques for diet analysis are one very promising tool and offer numerous research opportunities in invasion ecology and management. However, as previously mentioned, they are far from being perfect. For instance, Lundgren et al. (2013) noticed that the antibodies used for marking the sentinel prey for their ELISA analysis seemingly altered prey palatability and consequently food preferences of some predators, leading to biased estimations of prey attacks. They also found that marker (antibody) stability in the environment could be relatively short (90% of the marker was lost within 4 days), which could be an important source of misinterpretation, if not quantified prior the study. In PCR-based studies, the existence of multiple non-dietary sources of variation often preclude the comparison of dietary data obtained with multiple distinct primers, using different dietary samples or from different species. The existence of such bias ideally requires setting up complex multispecies, multifactorial experimental studies where the different sources of variation could be quantified at once, and hierarchized according to the relative importance of the bias they introduce. Experimental data could in turn be used for building general, corrective models similar to the species occupancy detection models (SODMs), which are currently used for optimizing the number of replicates necessary to minimize the probability of false positive or negative detections in eDNA studies (cf. Box 1).

When using DNA metabarcoding for a diet assessment, additional constraints apply. For example, as for eDNA biodiversity monitoring, highly conserved general primers are required to guarantee the successful amplification of multiple, phylogenetically diverse taxa (Taberlet et al., 2012b). In the case of carnivorous species that are closely related to their prey (e.g. a mammal predator consuming mammal prey), using general primers might

lead to the preferential amplification of the highly concentrated, non-digested predator DNA. In some cases, this could be avoided by specifically preventing the amplification of the predator/host DNA. Several methods for target DNA enrichment do exist (reviewed by O'Rorke et al., 2012), with the most popular including the use of predator-specific endonuclease restriction enzymes (Blankenship and Yayanos, 2005; Dunshea, 2009) or blocking primers (Deagle et al., 2009; Shehzad et al., 2012; Vestheim and Jarman, 2008). PCR techniques are also particularly prone to detecting secondary predation because of their high sensitivity (Sheppard et al., 2005). However, in some cases, secondary predation could be interpreted as an interesting opportunity for quantifying tri-trophic links or intraguild predation (Sheppard et al., 2005) from a single dietary sample. As for eDNA biodiversity monitoring, deriving quantitative information about ingested prey numbers or biomass remains challenging as biological processes like differential digestion rates or the different gene copy numbers between food species appear to distort relative species proportions (Deagle and Tollit, 2007; Deagle et al., 2005, 2010, 2013). However, recent findings encouragingly suggest that some sources of variation could be controlled for by using appropriate correction factors (Thomas et al., 2014, 2016a). Finally, another important yet unresolved methodological issue in diet analysis in general but particularly in the context of molecular techniques, as they are rapidly generalizing among ecologists, is the capacity to distinguish between active and passive predation (i.e. scavenging). Indeed, carrion could be a valuable and easily available resource and rates of scavenging are expectedly high (e.g. Foltan et al., 2005; von Berg et al., 2012), with significant but yet underestimated impact on food web dynamics (Wilson and Wolkovich, 2011). In terms of biological invasions, quantifying the rates of passive feeding is important in order to estimate realistic impacts on local food webs (e.g. Brown et al., 2015) or invasion success (e.g. Wilson-Rankin, 2015). However, experimental attempts to distinguish fresh from carrion prey with PCR techniques show that ingested decaying carrion prey is detected as efficiently as any of the fresh prey items offered (Foltan et al., 2005; Heidemann et al., 2011; Juen and Traugott, 2005; von Berg et al., 2012). As a possible solution, Juen and Traugott (2005) proposed the use of isoenzyme electrophoresis technique, which offers the opportunity to target specific enzymes, known to persist in dead corpses long after death, without being destroyed during the digestion process (i.e. have high retention times). To our knowledge, this approach has not yet been empirically tested. Another promising but still unexplored approach has been proposed by Wilson et al. (2010b).

Authors took inspiration from techniques used by forensic pathologists to determine the putative causes and time since death by relying on predictable changes in various physiological properties such as muscle pH and water loss rates. In an experimental setting focusing on the invasive predatory western yellowjacket (*Vespula pensylvanica*), Wilson et al. (2010b) showed that they were able to identify with 88% success which of the yellowjacket prey was carrion and which was killed by active predation, based on the physiological imprint of stress levels induced by predation. And even if this method has not been tested yet on prey subjected to digestion, it opens exciting new opportunities to explore in the near future.

Overall, molecular methods provide very straightforward presence/absence diet data. A semiquantitative approach is possible if the proportion of individuals positive for a given trophic link is considered. In such case, weighted trophic networks could be built and their properties examined. From the management perspective, molecular techniques could be useful for tracking dynamic changes in trophic behaviour following invasion as well as the successful integration of invasive species into local food webs (e.g. Gorokhova, 2006). Moreover, the growing numbers of empirical studies provide encouraging examples of how molecular diet analysis could possibly support decision making and management (e.g. Hatteland et al., 2011; Pianezzola et al., 2013). The best illustration for this comes from intensively managed agroecosystems, where in the context of biological control programmes, molecular methods could be a valuable tool for rapid large-scale-estimations of attack rates (e.g. Derocles et al., 2012; Traugott et al., 2008) as well as rates of incidental intraguild predation among predators (e.g. Davey et al., 2013; Traugott and Symondson, 2008). For example, multiplex PCR showed to be a valuable approach for identifying key predators and their attack rates on invasive slug species, which are important crop pests in Europe (Hatteland et al., 2011; Pianezzola et al., 2013). Bohan et al. (2000) further demonstrated that ELISA tests could be used for tracking dynamic predation of earthworms and slugs by a generalist carabid predator (*Pterostichus melanarius*). They showed that changing spatial associations between the predator and its prey were mostly driven by their respective density-dependent distributions rather than by agronomical factors such as crop or soil characteristics. By using diagnostic PCR for gut content analyses, Bell et al. (2010) extended this approach to a multispecies community of invertebrate predators and concluded that the relationship between predator–prey co-occurrences and feeding behaviour is fairly consistent across species, and therefore spatio-temporal community dynamics could be manipulated in order to optimize

pest regulation (in this case, slugs). Finally, DNA metabarcoding (Mollot et al., 2014; Vacher et al., 2016) has been successfully applied for characterizing the trophic behaviour of key arthropod pest predators, allowing for recommendations about relevant management practices aiming to enhance the biological control potential within arable fields.

3.1.3 Other Methods

For particular study questions, some nonconventional or less popular techniques could be a valuable source of trophic information. For example, Smith and Gardiner (2013) used video cameras for comparing field rates of egg predation between native and exotic coccinellid species. Sloggett et al. (2009) employed gas chromatography–mass spectrometry to track egg predation of native ladybird species *Hippodamia convergens* within the guts of exotic ladybird *H. axyridis*.

3.2 Mutualistic Interactions

There is now a vast body of literature investigating the impact of biological invasions on mutualistic networks (plant pollinators, seed dispersers) (Traveset and Richardson, 2006), but the majority of empirical data have been produced using direct observations (Giovanetti et al., 2015; Tiedeken and Stout, 2015) or experimental approaches (Chung et al., 2014; Russo et al., 2014), while tools such as molecular and SIAs have been still surprisingly underused. Studies suggest for instance the successful integration of invasive plant or pollinators within native interaction networks (e.g. Vilà et al., 2009) that could sometimes lead to important changes in the network structure and dynamics (Albrecht et al., 2014; Spotswood et al., 2012). However, it is still not clear if these changes are translated into functional impact, for example, in terms of gene or energy flow across and among trophic levels. For example, Bartomeus et al. (2008) showed that despite apparently high rates of pollen transfer between native and invasive plant species, the actual pollen deposition on native plants was really low. These findings highlight the importance of incorporating DNA and stable isotope analysis into the study of mutualistic networks, as they provide a direct and time-integrated measure of fluxes (energy, genes) and therefore of potential functional impacts following invasion. Such unique opportunity for gleaning both taxonomic and functional data at once offers an efficient and cost-effective methodological alternative for assessing the functional impact of invasive species that has the full potential to become a novel

paradigm for invasives' biomonitoring (e.g. Jackson et al., 2016). For example, a DNA metabarcoding could be a very straightforward approach for characterizing mutualistic networks. First, this type of interactions involves partners that are phylogenetically distantly related, thus facilitating the design of well-conserved, group-specific primers. Second, their DNA is more readily accessible as usually it is not degraded (compared to say prey DNA in antagonist interactions). Pollen DNA is generally of higher quality than digested prey items from faeces or gut contents, and there is no need for prior visual sorting or separation of pollen grains as for traditional palynology surveys (which could be time and effort demanding as well as subject to observer's bias; Richardson et al., 2015a,b). Moreover, molecular tools are much more sensitive in detecting rare, low-abundant plant species compared to visual observations (Richardson et al., 2015a,b). They are also suitable for detecting ancient pollen DNA in pollinators' crops from historical museum collections (e.g. Wilson et al., 2010a). The additional advantage of using highly sensitive detection techniques is the potential they open in terms of biodiversity monitoring as pollinators could be reliable "environmental recorders", thanks to their capacity to sample low-abundant nonnative plant species (Galimberti et al., 2014) that could be undetectable by other means. Moreover, several molecular markers for plants have already been developed, and their efficiency compared (e.g. Galimberti et al., 2014; Richardson et al., 2015a,b; Wilson et al., 2010a), which is a valuable resource allowing the design of further studies. Molecular data could also be complemented by SIA in order to reveal patterns of seasonal switching between an insectivorous and frugivorous diet in facultative pollinators (Frick et al., 2014), tracking community-level nutritious carbon pathways across heterogeneous habitats (Herrera Montalvo et al., 2013) or evidencing multiple hidden facilitative interactions between nonnative species, likely promoting invasion success (Lach et al., 2010).

Mutualistic interactions involving symbiotic bacteria or mycorrhizal fungi are another important type of facilitative interactions, and increasingly shown to influence life-history traits and fitness of nonnative species in invaded environments (e.g. Bogar et al., 2015; Himler et al., 2011). However, understanding direct and indirect effects of these symbiotic interactions on invasiveness requires the combination of multiples methods. First, bacteria or fungal symbionts are taxonomically challenging groups and most of them are not culturable. Second, because of the potentially intricate interactions between symbionts and their host, and/or environment, quantifying symbiont-related impacts might be delicate. Fortunately, in terms of

taxonomic diagnosis of multispecies symbiont communities, molecular techniques show encouraging results (e.g. Bansal et al., 2014; Cotton et al., 2015; Kurata et al., 2016; Thierry et al., 2015; Vasanthakumar et al., 2008) and should therefore be explored further in a more network-explicit context. For example, Hansen et al. (2007) found that the prevalence of secondary symbionts in the invasive psyllid *Glycaspis brimblecombei* was strongly correlated to parasitism rates by its main parasitoid, indicating that symbiont community could have multitrophic cascading effects.

3.3 Parasitic Interactions

The introduction of nonnative species in new habitats carries the risk of concomitant introduction of other "passenger" organisms such as parasites and various microbial pathogens. Such collateral introductions could significantly contribute to invasion success (Roy et al., 2012) or exacerbate impact on local communities, which usually lack suitable defences against exotic pathogens (Vilcinskas, 2015; Vilcinskas et al., 2013). Because of the disease risk collateral introductions involve, the characterization of parasitic interactions in invasive species is comparatively well documented. Particularly, molecular techniques have been a valuable diagnostic tool for detecting pathogens and their spread in a variety of aquatic and terrestrial invaders (e.g. Collins et al., 2014; Grabner et al., 2015; Lester et al., 2015; Spikmans et al., 2013; Vilcinskas et al., 2013). However, as for symbiont communities, the explicit consideration of nonnative parasite interactions within a multispecies network context is rare (Emde et al., 2014, 2016; Sato et al., 2011, 2012; Thieltges et al., 2013). A growing body of literature highlights the importance of integrating parasite interactions into ecological network models (Dunne et al., 2013; Lafferty et al., 2006). This is particularly relevant in the context of biological invasions, as nonnative parasites have been shown to mediate complex, unexpected changes in local interaction networks (Sato et al., 2011, 2012). One very neat example is the above-mentioned SIA study, showing the importance of carbon parasitism via arbuscular mycorrhizae as mechanism explaining the success of the invasive spotted knapweed (Carey et al., 2004). On the other hand, the ever-increasing power of HTS techniques allows the simultaneous detection of prey and parasite communities within the same individual sample (Berry et al., 2015; Srivathsan et al., 2015, 2016; Tiede et al., 2016). Additionally, HTS has the power to detect cases of coinfections by multiple pathogens within a single invasive host and has thus tremendous potential to reveal

complex indirect effects, alongside direct trophic impact, eventually promoting invasiveness (e.g. Lu et al., 2010; Zhao et al., 2013).

4. MEASURING THE IMPACT OF BIOLOGICAL INVASIONS ON ECOSYSTEM FUNCTIONS

Throughout the chapter, we already provided several examples how different techniques and methods can contribute to estimate the impact of invasive species—through changes in the local community composition and biodiversity, to ecosystem functions. In this section, and without providing too much methodological details, we try to put a specific focus on measuring impact on ecosystem-level processes. The need for broad-scale, ecosystem-level approaches for understanding and predicting biological invasions impact has been recognized more than a decade ago (e.g. Vander Zanden et al., 1999). However, assessing ecosystem-level processes is methodologically challenging, especially considering our constantly evolving perception of biological complexity. Still, the rising number of methodological opportunities brings the assessment and the integration of the ecosystem-level impact into tangible reach. For example, progress in molecular techniques has been paramount for the discovery of all the unseen biodiversity of microbial communities as well as their functional implications in ecological processes (Bik et al., 2012; Lansdown et al., 2016; Thompson et al., 2015). Molecular methods have been also essential in the characterization of past biodiversity dynamics, helping to understand general mechanisms behind long-term ecosystem functioning (Pedersen et al., 2014). This offers multiple opportunities for assessing and monitoring the impact of biological invasions. Accordingly, molecular techniques currently start playing a prominent role for estimating short-term or contemporaneous impact of invasion. For example, HTS allows the simultaneous diet assessment of multiple species, thus providing information about the degree of niche partitioning (e.g. Kartzinel et al., 2015) or habitat coupling (e.g. Soininen et al., 2014), both mechanisms playing an important role in ecosystem functioning and stability. Additionally, by yielding trophic data, molecular techniques allow the estimation of metrics indicative about the functional role and the degree of integration of an invader within the local interaction network. This is important as nonnative species have been shown to rapidly integrate into local ecosystems, sometimes as key network "hubs", establishing a high number of strong and weak linkages to local species (Aizen et al., 2008; Memmott and Waser, 2002; Vacher et al., 2010).

Consequently, if not properly quantified, their removal following (partly informed) management actions could cause unpredictable disrupting changes in local ecosystem functioning (e.g. surprise effect; Caut et al., 2009; Courchamp et al., 2003).

Finally, the fast-growing field of functional metagenomics—which seeks to connect an organism to its respective function in an environment—opens new so far unexplored opportunities. Methods such as metatranscriptomics (the analysis of the transcripts isolated from a community of organisms) and metaproteomics (the analysis of the protein profiles expressed by a community) are very complementary approaches to DNA sequence-based methods.

First, these methods allow the detection of a functionally active species that does not need to be characterized morphologically nor taxonomically. For example, a metatranscriptomics approach has recently been used for discovering functionally active viral natural enemies without the need to physically culture them and these viruses could be used for controlling nonnative species (Valles et al., 2012, 2013). Another possible application is the profiling of protein expression in natural communities and across environmental gradients in order to monitor how the community functional structure changes following invasion. This could be a powerful tool for monitoring invaded communities or/and invader's symbiont and parasite communities, helping to identify key genes determining invader's success and impact (e.g. Dlugosch et al., 2013; Scully et al., 2013). Second, particularly the metaproteomics approach allows the discovery of novel proteins/enzymes (and therefore ecological functions) that could not be predicted based on DNA sequences alone (Chistoserdova, 2009). As such, it has a promising avenue in discovering new functions that have not existed previously or have been disrupted by nonnative species.

In perspective, functional metagenomics might open an entirely new framework, where natural communities could be manipulated accordingly to the function that needs to be preserved/optimized. Consequently, management strategies will not aim in removing a certain species anymore but rather in optimizing its integration in local ecosystems, while minimizing its impact on ecosystem functioning. Nevertheless, the broad-scale ecological application of functional metagenomics is still in its infancy and further methodological challenges related to clonal library preparation, enzyme activity expression, or genome annotation need to be addressed (Chistoserdova, 2009; Lam et al., 2015). Moreover, as the function of great majority of genes is still unknown, predicting the function of newly discovered proteins is not always possible (Lam et al., 2015).

SIA is another practical method for measuring the impact of biological invasions on ecosystem functioning thanks to the synchronous and diachronous comparisons of ecosystems they allow. Its main advantage in this context resides in the existence of numerous data sets, already available worldwide. For example, Sagouis et al. (2015) used SIA data from the published literature for investigating the impact of nonnative fish species on the food web structure across 496 freshwater fish communities worldwide. For this study, historical collections of fish tissues, a part of long-term-monitoring programmes of the Laurentian Great Lakes, have been analysed with SIA over a period of more than 2 years in order to see how the introduction of nonnative species has influenced the local food web structure (e.g. Paterson et al., 2014; Rennie et al., 2009; Rush et al., 2012). The results show a profound impact of nonnative species on food web structure, energy flow, and stability within all these aquatic ecosystems, emphasizing importance of SIA as a sensitive approach in this context.

Additionally, recent development of new quantitative metrics for SIA, inspired by those used in functional ecology, might allow more efficient and comprehensive assessment of existing stable isotope data, thus providing new perspectives in terms of functional impact of invasive species (Cucherousset and Villéger, 2015; Layman et al., 2007).

5. USING EMPIRICAL DATA FOR IMPROVING OUR PREDICTIVE CAPABILITY THROUGH MODELLING AND MACHINE-LEARNING APPROACHES

We provided numerous arguments throughout this chapter about increasing capacity to produce large ecological data sets and large-scale environmental monitoring thanks to the emergence of a variety of complementary techniques. However, what has been missing, to date, are methods that could repurpose these data sets to build or reconstruct ecological networks that have not been empirically observed. Here, we present two major approaches for network reconstruction: predictive models and machine learning. The use of models predicting interactions between pairs of species or helping to construct interaction networks from massive amounts of correlative data (machine learning) can be useful tools for the assessment of the impact and potential success of exotic species. Combining these modelling approaches with new data acquisition protocols, such as the ones highlighted in the previous sections of this chapter, will pave the way for

more reliable and rapid assessments of invasion trajectories and impact on the ecosystem.

5.1 Predictive Models

5.1.1 Principle

Predicting novel interactions, i.e., interactions between species that have never been observed co-occurring in the same locations, is a challenge that has been tackled a few times, using different methods, in the past 10 years. For instance, Pearse and Altermatt (2013) have been among the first to propose a model to predict how native caterpillars might interact, through herbivory, with nonnative plants based on the phylogenetic proximity of native and nonnative plant species. One intrinsic difficulty associated with this type of model consists in defining a strategy to make efficient use of the available information, i.e., a statistical regression problem. In species interaction networks, information can come in different guises:

(i) one can make use of information on species traits, i.e., use information on the nodes of the networks to infer potential links based on existing links and node-related information of already known parts of the network. This is typically the approach followed when predicting food webs from the size of organisms (Gravel et al., 2013; Petchey et al., 2008);

(ii) one can make use of information on "distances" or "similarities" among species (i.e. dyadic or relational information among nodes) to infer their role in the network, e.g., by assuming that closely related species tend to interact in a very similar fashion due to phylogenetic conservatism or, on the contrary, tend not to share certain interaction partners given the competitive exclusion principle. Phylogeny is one obvious way of defining similarity in an eco-evolutionary context, but other means are available (e.g. distances in the space of carbon and nitrogen isotope ratios, or distances based on co-occurrence in different patches);

(iii) finally, one can make use of latent trait variables associated to nodes and/or to node relations. Latent traits or relations are, by definition, not measured per se, but can be estimated indirectly through data on the emerging network. When a two-way relation exists between latent traits and the probability of an interaction actually existing, i.e., when traits predict the interaction and the observation of interactions serves to infer the latent traits, then inference on latent traits in a "known part" of the network might help in predicting interactions in an "unknown" part of the same network. For instance, the methods developed by Allesina and Pascual (2008), Eklöf et al. (2013a,b),

Rohr et al. (2016), Williams et al. (2010), or Dalla Riva and Stouffer (2016) make use of latent traits that determine predator–prey interactions based on match–mismatch (e.g. Dalla Riva and Stouffer, 2016) or hierarchical relations (e.g. Allesina and Pascual, 2008; Williams et al., 2010), or even more complicated combinations such as match–mismatch and generalist–specialist information at the same time (Rohr et al., 2016).

5.1.2 Types of Models

Grossly caricaturing the current state of the art of models predicting interactions between pairs of species, we can classify them along two orthogonal axes: on the one hand, models can be based either on measured variables (in general, species traits such as body size or phenology) or on latent variables that are inferred from a "learning network" (i.e. part of the network to predict or a different one with some overlap of ecological communities); on the other hand, models can be divided based on their use of traits (be they measured or latent) through an "intervality" principle (as in the niche model), a "matching" principle (to interact, the vulnerability trait of the prey must closely match the foraging trait of the predator, e.g., Rohr et al., 2016), or a "generality" principle (species have different degrees, and so interact with different number of species, but somehow randomly; e.g. Pearse and Altermatt, 2013). Table 2 is an attempt at describing the various methods encountered in the literature. Except in the case of recent studies (Dalla Riva and Stouffer, 2016; Rohr et al., 2016), there are very few comparisons of the various models in terms of predictability or goodness of fit.

5.2 Machine Learning

5.2.1 Principle

At the core of network reconstruction is the idea that in the sample data there are the impressions of past interactions. Taxa that have interacted will have correlated values in the sample data, and there will be identifiable patterns or motifs between groups of interacting taxa. Such "ghosts of interactions past" can be searched for in the data and machine-learning methods used to reconstruct the ecological network in which they occurred (Vacher et al., 2016).

Network reconstruction has only a relatively short history in Ecology and has typically used either models based on finding using formal logic links in the data or mixed learning that combines statistical inference methods, such as Bayesian approaches, with logic to learn network structure. In one of the first applications of learning to network reconstruction in

Table 2 Summary of Existing Models Used to Predict Species Interactions

Paper	Type of Network	Information Used	Summary
Allesina and Pascual (2008)	All types	(Partial) network topology to obtain latent variables	The model predicts interactions using a minimal number of latent variables (the dimensionality of the model) using a variation of the food web niche model of Williams and Martinez (2000). Intervality in the initial niche model is broken when there is more than one dimension. Learning the model on part of the interactions may predict the other part using the latent variable estimated for each species.
Bartomeus (2013)	Plant–pollinator networks	Habitat (flower density, etc.) and plant species (flower morphology, etc.) covariates	Simultaneously estimate regression coefficients with measured covariates and detection probability for observed interactions. The associated hierarchical model can be used to predict novel interactions (or unobserved ones) based on covariates. Model selection is used to cut out unnecessary covariates from the regression.
Beckerman et al. (2006); Petchey et al. (2008)	Food webs	Body sizes, allometries	Using optimal foraging theory (i.e. the ratio of energy gained to time spent handling prey), the model generates probabilities for the various interactions to exist based on their profitability. The allometric version of the model makes use of the functional dependence between species sizes and handling time.
Dalla Riva and Stouffer (2016)	Food webs	(Partial) network topology to obtain latent variables	Network topology is used to obtain "latent traits" through a PCA-like approach, to summarize the position of species as preys and predators. Inferring traits can be performed on a partial network, thus allowing to predict interactions between certain species based on their interactions with others.

Dehling et al. (2016)	Plant–bird network (bipartite)	Various traits measured in both species groups	Each species of plant and bird is projected onto their respective functional space through a PCA. Each species is also projected onto the partner functional space through the centroid of its partner species. Procrustes rotation is used to find the morphism linking both functional spaces (i.e. to predict which functional position in birds matches with which functional position in plants).
Eklöf et al. (2013a,b)	All types	Different types of traits (phenology, size, habitat, etc.)	Interactions are predicted based on intervals of "matching traits" required by the focal species (e.g. a predator could only eat preys within a certain size interval, occurring over a certain habitat interval, during a certain phenology interval, etc.).
Gravel et al. (2013)	Food webs	Body sizes	The niche food web model of Williams and Martinez (2000) is the basis for a model of interaction prediction based on body sizes. Linear regression outputs, notably the coefficient of regression and the 95% quantiles, yield the variables used to fit the niche model.
Guimerà and Sales-Pardo (2009)	All types	Network topology	The model implements a series of stochastic block models (SBMs) to infer missing and spurious links within the observed network. At the end of the procedure, the model predicts interactions based on the SBM inference.
Ovaskainen et al. (2016)	Co-occurrence network	Measures of habitat characteristics (available resources), co-occurrence with other species	The model implements a co-species distribution modelling framework that makes use of both measured covariates and latent variables measuring species interactions.

Continued

Table 2 Summary of Existing Models Used to Predict Species Interactions—cont'd

Paper	Type of Network	Information Used	Summary
Pearse and Altermatt (2013)	Plant–herbivore network (bipartite)	Partial network topology, phylogenetic similarity among plants	The model to infer interactions "learns" on a part of the network is validated on another part and is used to predict novel interactions with exotic plants. The model is a generalized linear model that makes use of herbivore degree in the network and of phylogenetic similarity among plant species.
Rohr et al. (2010)	Food webs	Partial network topology, species body sizes	To explain interactions between species, the model makes use of body size and latent variables referring to vulnerability and foraging breadth, i.e., generality traits. Latent variables can in turn be correlated to other variables like phylogeny.
Rohr et al. (2016)	All types	Partial network topology	Latent trait variables are used to model interaction patterns. Two types of latent variables are used: matching traits and generality traits. The nested or modular nature of the network can be more efficiently captured by generality (respective matching) traits so that the estimation of the regression coefficients associated with these latent traits also informs on the position of the network along the nested-modular continuum.
Williams et al. (2010)	Food webs	(Partial) network topology to obtain latent variables, possibly using species size as a direct proxy for these variables	The model is the probabilistic version of the food web niche model of Williams and Martinez (2000). It can feed on either latent trait variables, which must be estimated from a part of the network, or species traits (such as size) that are suspected to drive the food web niche model.

ecology, Bohan et al. (2011) demonstrated that machine learning has the potential to construct realistic agricultural food webs, using a logic-based approach called abductive/inductive logic programming (A/ILP). A/ILP was used to generate plausible and testable networks from field sample data of the abundance of taxa (network nodes) alone. Importantly, this process did not just recover the obvious links that we already known from observation, but also suggested surprising and apparently illogical link. Spiders were consistently inferred by the machine learning as prey, despite being obligate predators. High probability links were also hypothesized for intraguild predation that might destabilize the network. Importantly, the learning reconstruction pinpointed a much lower number of test links necessary to validate the network than would have been required to build the network, using a classical approach, from scratch. A review of the literature revealed that many of the high probability links in the model had already been independently observed or suggested for this system. Moreover, the apparently illogical links to and the position of predatory spiders in the network were subsequently demonstrated to be correct using molecular testing for prey spiders in the guts of carabid beetles (Davey et al., 2013). This would suggest not only that learning and network reconstruction methods can produce plausible ecological networks (food webs) from sample data, but that by hypothesizing verifiable new links the learning is actually doing genuinely novel science.

5.2.2 Applications

Learning methods are being developed to reconstruct/hypothesize network interactions from the abundance patterns and additional background information, such as functional traits or meta-data associated with the samples (e.g. Bohan et al., 2011; Deng et al., 2012; Faust and Raes, 2012; Kurtz et al., 2015). Of enormous interest is the potential of HTS techniques as source for raw data for network reconstruction (Evans et al., 2016; Vacher et al., 2016). HTS platforms can generate several millions of DNA sequences for a few hundred dollars (Liu et al., 2012; Quail et al., 2012), and the price of this is reducing all the time. The approach is also quite general, allowing the characterization of DNA diversity using ostensibly the same methods across a broad range of complex environments (e.g. in air, soil, water, faeces, and gut contents, and on/in plant tissues, etc.), producing sample data containing many hundreds of taxa. Increasing numbers of these sequences can now be identified at the species level thanks to expanding

taxonomic databases (see Abarenkov et al., 2010; DeSantis et al., 2006; Kõljalg et al., 2005; Quast et al., 2013; Ratnasingham and Hebert, 2007).

Developments in the use of HTS data for reconstructing networks of ecological interaction have recently begun to be made. Vacher et al. (2016) described the reconstruction of a microbial network on the surface (phyllosphere) of oak leaves, using a mixed, statistical, and logical approach from pure HTS data on microorganism OTU co-occurrences. This network, which was studied to understand the behaviour of a pathogenic fungi, *Erysiphe alphitoides*, revealed striking patterns of connectivity once this pathogen has invaded the phyllosphere community. The pathogen was connected to the rest of the network through strong and negative links that suggested that *E. alphitoides* might be associated with the absence, and possible removal, of other microorganisms.

6. PERSPECTIVES AND CHALLENGES AHEAD

Conceptual and technical progress in terms of analytical methods over the last decade has been remarkable. To date, ecologists have a comprehensive toolkit for investigating, describing, and understanding biodiversity. We review a vast spectrum of methods covering most aspects of invasion ecology, and they all have their respective strengths and weaknesses. However, their full or partial combination constitutes a powerful synergy and offers the potential to revolutionise our understanding of biological invasions either by providing deeper insight into general ecological processes associated with invasion or by allowing the effective monitoring of their spread and impact. In this section, we try to provide some visionary insight into the future avenues that this potential offers in terms of methodological improvements but also some societal and conceptual challenges associated, for example, with the implementation of efficient management actions.

6.1 Methodological Challenges and Perspectives

6.1.1 Molecular Techniques

Increasing production of molecular and DNA sequence data will raise important challenges in terms of comparison and integration across studies. Currently, the majority of studies use a vast array of primers and protocols that are optimized for a specific question or model taxon but lack standardization in terms of detection sensitivity thresholds and/or taxonomic coverage. This means that merging disparate data from various studies could be questionable. A general methodological framework is imperative if we want to take full

advantage from molecular data advent. Nevertheless, the raising awareness about major drawbacks of molecular techniques has led to an increasing number of experimental studies aiming to document and quantify their effects on final estimates. Still, this increasing amount of information needs to be systematically incorporated into molecular data analyses. In this respect, molecular ecologists could find inspiring examples from stable isotope ecology for how complex confounding factors could be incorporated into data analyses. Encouraging efforts have been made recently in terms of the integration of false-positive/negative signals through the development of appropriate models (Box 1). The use of molecular tools is still taxon- and ecosystem-biased. For instance, the majority of eDNA studies cover aquatic environments and/or vertebrate species, while terrestrial and/or invertebrate and plant communities have been overlooked so far. Increasing the range of applications of molecular tools will not only provide more insights about methodological bias and limitations but will also create opportunities for methodological innovations and new research questions. Accordingly, more and more creative initiatives are emerging such as monitoring biodiversity through eDNA retrieved from air samples (Kraaijeveld et al., 2015; Taberlet et al., 2012a), or nationwide eDNA citizen science campaigns (Biggs et al., 2015), which will definitely broaden the scope of molecular tools. From this standpoint, the integration of molecular tools and citizen science offers tremendous potential in terms of biodiversity surveillance. Encouragingly, an increasing number of such of initiatives are being successfully launched (e.g. http://malaiseprogram.ca/; http://studentdnabarcoding.org/). The rapid development of portable, cheap HTS devices (Box 3) promises even more unexplored opportunities that could be harnessed in the context of biological invasions. For instance, significant improvements in cost might help bringing molecular tools closer to research and policymaking institutions in low-income countries, where invasives' pressure is probably the least documented.

In terms of network reconstruction, building large-scale ecological networks from molecular data is still anecdotal, given the huge potential offered by these techniques, especially with regard to plant–herbivore and plant–pollinator networks, where methodological constraints are relatively few. But we believe that the ever-increasing accessibility of high-throughput molecular techniques will promote their use by a wider community of ecologists, helping to take full advantage of these methods rapidly.

Finally, molecular methods have a promising future as a powerful tool integrating multiple organization levels. Very soon, it will be possible, with a single sequencing event, to collect information about species' distributional ranges, abundance, phylogeny, population and functional genetics,

BOX 2 Shotgun Sequencing for Biodiversity Assessment

Shotgun sequencing refers to the direct sequencing of genomic DNA. According to the matrix used to extract the DNA, shotgun sequencing has multiple applications. It could be used for whole genome sequencing when DNA is extracted from a specimen or for biodiversity assessment when DNA extraction is made from environmental samples. Considering the last case, this approach can bridge the main current limitations of DNA metabarcoding, namely PCR amplification bias (Coissac et al., 2016; Taberlet et al., 2012b; Zhou et al., 2013). Taking advantage of the unprecedented expansion of sequencing capacity provided by high-throughput sequencers, shotgun sequencing has the full potential to draw up new dimensions in biodiversity research (Papadopoulou et al., 2015). The direct sequencing of genomic DNA from bulk or environmental samples allows the parallel acquisition of a large array of genetic information including multiple mitochondrial, plastid, and nuclear markers, useful for robust and auditable taxonomic assignation and phylogenetic inference within a single sampling event (e.g. Gillett et al., 2014; Tang et al., 2015; Zhou et al., 2013), while available information could be used for inferring specimens' evolutionary history (Besnard et al., 2014), community assembly (Andújar et al., 2015), and diet or symbiont community (Paula et al., 2015; Srivathsan et al., 2015, 2016). Moreover, with the routine sequencing of genomes, scientists will no more be limited in their initial choice of loci. The same effort to build reference databases will provide, from the same specimens, markers useful for taxonomists, ecologists, and phylogeneticists, thus unifying their efforts for describing biodiversity (Coissac et al., 2016).

Shotgun sequencing could be realized directly from DNA extracts fragmented prior sequencing (i.e. genome skimming) or from DNA extracts that have been previously enriched using oligonucleotide probes or "baits" (for more details about the different DNA capture techniques, see Ávila-Arcos et al., 2011; Horn, 2012). While the genome skimming results in the low-coverage random subsampling of a small proportion of the total genomic DNA (Dodsworth, 2015), target enrichment consists in selectively targeting user-defined sequences across plastid or nuclear genomes (Ávila-Arcos et al., 2011). Because of their usually high-copy numbers, the nuclear ribosomal cistron, mitochondrial, and plastid genomes are fully sequenced with high sequencing depth. Most of the time, their complete sequence can be reconstructed/assembled from a genome skimming data set, while providing multiple useful markers for robust phylogenetic inference (Dodsworth, 2015). However, the large majority of reads belongs to the nuclear genome. Even if the data they provide cannot allow the assembly of full nuclear genomes, they can still provide some additional phylogenetic information. On the other hand, selective enrichment prior sequencing enables an increased sequencing depth and lower cost over regions of interest, very appropriate for large-scale biodiversity assessment via mass

sequencing of bulk samples. This is because the capture of desired genomic regions takes more advantage of the sequencing depth enabling the recovery even of low-abundant target taxa (e.g. Ávila-Arcos et al., 2011). The current cost per gigabase ranges between $40 (target enrichment; Zhou et al., 2013) and $80 (genome skimming; Coissac et al., 2016). But while the shotgun sequencing discovery of a single species within a bulk sample is estimated to about $20 (i.e. approximately the price of outsourced Sanger sequencing barcoding; Zhou et al., 2013), the preparation cost of high-throughput sequencing library is still relatively high, especially when it comprises only one specimen ($200; Coissac et al., 2016). This price excludes the cost related to computational power and data storage infrastructures. Therefore, further challenges include cost reduction as well as the development of appropriate bioinformatic tools for high-throughput genomic data analysis. Nevertheless, several recent projects demonstrated as a proof of a principle that upscalling the shotgun sequencing approach is feasible (Coissac et al., 2016; Ribeiro et al., 2012; Stull et al., 2013; Tang et al., 2015). The perspective of bringing high-throughput shotgun sequencing directly to the field via the portable MinION™ personal sequencing device (Box 3) is the very next step that will revolutionize the taxonomical and functional analysis of biodiversity.

symbiont and parasite communities, as well as its trophic interactions with other species (Table 1; Box 2; see also Barnes and Turner, 2016; Hajibabaei et al., 2007). This opens important perspectives for conceptual and analytical advancements in order to be able to integrate all these data in a common framework (cf. Kéfi et al., 2016).

6.1.2 Stable Isotopes

SIA is now a well-established and increasingly applied method in ecological studies, calling for a further expansion of the isotopic toolbox towards research questions incorporating more biological complexity and over larger set of spatiotemporal scales. The current development of new analytical frameworks and models (e.g. Healy et al., 2016; Phillips et al., 2014; Stock and Semmens, 2016; Yeakel et al., 2016) offers the possibility to derive an increasing spectrum of biological information from a limited number of isotopic elements including physiological, ecological, and environmental factors that shape the dynamics of the isotopic space. Therefore, it would

BOX 3 Oxford Nanopore MinION™

The MinION™ device is the first miniaturized portable real-time DNA sequencing device and also the first to offer no limits for the length of DNA fragments to be sequenced. The core of the MinION™ sequencer is a single-use flow cell composed by an array of protein nanopores, embedded in a synthetic polymer membrane and high-salt buffer. During the sequencing reaction, a voltage is applied across the membrane, which makes a current of ions to flow through the pores. The translocation of a single-strand DNA molecule through each pore disrupts the ionic flow in a sequence-specific manner. The signal (squiggle plot defined by the duration and the value of the disrupted current) is directly linked to the pattern of the DNA sequence present inside the pore (i.e. base calling). Each strand of a double-stranded DNA molecule is sequenced separately, but the two strands are needed for the base calling in order to generate one final consensus sequence (2D read). The running time for a single flow cell could be adjusted according to the need or the length of the DNA molecules but usually does not exceed 48 h, which corresponds to the maximal duration of the protein nanopore activity. Once all the pores have been deactivated, the flow cell needs to be replaced. For example, the R7.3 model of Nanopore Flow Cell available until mid-2016 has allowed the simultaneous read of up to 512 DNA molecules for an average of 115 million double-strand bases or approximately 20,000 reads (Ip et al., 2015). Considering this sequence yield and a minimal cost of $500 for a single flow cell, the current cost per gigabase could be estimated at about $5500. The required sequence coverage with the MinION™ will depend on two parameters: (i) the complexity of the target genome; (ii) the analytical method used. For example, a coverage of 29× was required to obtain the complete 4.6 megabases de novo assembled bacterial genome (Loman et al., 2015). However, at this stage of technological advancement, the amount of MinION™ generated data was still too low to allow the sequencing of large genomes.

Concerning the library preparation, various kits have already been released by Oxford Nanopore Technologies according to the nature of the DNA to be sequenced (e.g. amplicon, shotgun, or RNA sequencing). The price per kit varies between $400 and $500 and usually allows the preparation of up to six libraries. The minimum amount of DNA material required ranges between 20 ng and >1 µg, depending on the size of the DNA fragments to be sequenced, with usually, a higher DNA input improving the overall sequence yield. In terms of amplicon sequencing, between 12 and 96 distinct libraries can be pooled and sequenced at the same time, while the RNA sequencing requires the preliminary preparation of a complementary DNA.

The MinION™ device is connected to a laptop or a desktop computer through a USB connection. A control software, MinKNOW, allows the management of sequencing core tasks and related parameters during the sequencing run. At the end of the run, the base calling is activated through a cloud-based software Metrichor, provided by Oxford Nanopore. Raw sequencing data are first

uploaded on a cloud cluster and then downloaded and analysed as fast5 format data files on the local host computer. There are now several different bioinformatic tools and pipelines allowing the exploitation fast5 format data. Poretools (Loman and Quinlan, 2014) and poRe (Watson et al., 2015) are useful for converting and visualizing the raw data. MinoTour is a software for pre- and postalignment analysis of MinION™ sequencing data, and for determining sequence quality and error profiles. Some software packages were specifically developed to allow genome assembly that account for the high error rate of the raw data (currently >10%). These softwares include NanoCORR (Goodwin et al., 2015), NaS (Madoui et al., 2015), Nanopolish (Loman et al., 2015), and poreSeq (Szalay and Golovchenko, 2015), while the newest mapping algorithm for Nanopore sequencing reads, GraphMap, has been released this year (Sović et al., 2016). The first open-source base callers for Nanopore sequencing have also been released this year, DeepNano (Boža et al., 2016) and Nanocall (David et al., 2016).

In terms of applications, MinION™ was used for the real-time genomic surveillance in the resource-limited context of the Ebola virus outbreak (Quick et al., 2016). Several small bacteria and yeast genomes have been already sequenced, some combining MinION™ and Illumina data (Goodwin et al., 2015; Madoui et al., 2015; Risse et al., 2015), while other only relying on the MinION™ (Loman et al., 2015). MinION™ could find useful applications in metagenomics as well. It has been used for instance for identifying viral pathogens in complex clinical samples (Greninger et al., 2015), or unknown bacteria and viruses by amplicon sequencing (Kilianski et al., 2015). The characterization of highly diverse microbial community using the 16S rRNA gene is also possible (Benitez-Paez et al., 2016). Other applications include the analysis of methylated DNA bases (Simpson et al., 2016; Rand et al., 2016) or complementary DNA (Oikonomopoulos et al., 2016), while Li et al. (2016) proposed a pragmatic approach for circumvent the high single read error rate. Finally, the research group of Massimo Delledonne successfully used the MinION™ for sequencing the DNA of a wild frog species during a field expedition in Tanzania (https://publications.nanoporetech.com/2015/05/15/minions-and-nanofrogs/).

The newest flow cell models, R9 and then R9.4, were launched by Oxford Nanopore Technologies in May and October 2016, respectively. Their DNA base calling accuracy mostly depends on the speed of DNA translocation through the pores and the performance of the base caller itself. The R9 and R9.4 versions allow a faster translocation rate (up to 450 DNA bases per second instead of the 70 with the R7.3 version), and higher sequence yield with lower error rates (from >10% to ~5%), thus reducing the cost per Gb. An upcoming device called VolTRAX™—a palm-sized cartridge—promises for an automatized DNA library preparation without the need for human intervention.

This opens promising avenues for the adoption of the MinION™ device as a portable, versatile, diagnostic tool by practitioners and even citizen scientists in order to ensure the large-scale, real-time mapping of dynamical changes in biodiversity and species distributional ranges.

be possible to hierarchize the importance of individual vs community-level processes that determine the impact of invasives on food web structure and ecosystem functioning. If applied to data from fossil or museum records, this could be done in temporally explicit context in order to see how fine-scale variations in the functional or foraging diversity—based on individual isotopic signatures—correlate with the degree of invasibility in a given community or location. Furthermore, growing advancements in our understanding about the relative incorporation of dietary vs environmental sources of isotopic elements in animal tissues could allow in the near future to characterise both the diet and habitat of an individual by using compound-specific SIA from the same sample (e.g. amino acids; Fogel et al., 2016).

SIA could also benefit from a greater integration with molecular data. For example, the combination of SIA and DNA analysis could be particularly valuable for revealing the taxonomic identity, the ecological process, and the underlying functional impact of a nonnative species as elegantly demonstrated by Matsuzaki et al. (2010). On the other hand, techniques such as DNA/RNA-stable-isotope probing used in microbiology (Manefield et al., 2002; Neufeld et al., 2007; Radajewski et al., 2000), targeting the analysis of incorporated isotope-labelled specific compounds into nucleic acids using functional metagenomics, showed particularly valuable for characterizing the functional roles of a large array of unculturable microorganisms by revealing their unique biochemical pathways (e.g. Krause et al., 2010; Lueders et al., 2004). This type of methods could find multiple interesting applications in the context of biological invasions where the existence and the spread of cryptic invasive functions or genes within a given ecosystem could be characterized without the need to accessing the taxonomical identity of the invader. Finally, the development of artificial diet tracers, integrating the advantages of both DNA and stable isotope methods within a single analysis (e.g. silica particles with encapsulated DNA, Mora et al., 2015), could be an original and probably cost-effective alternative to the combination of multiple techniques. Further investigations will show how applicable is this approach in more realistic ecological context.

6.2 Perspectives and Challenges for Network Reconstruction

6.2.1 Interaction Network Models

The models presented under Section 5.1 aim either at reconstructing interaction networks from incomplete data or indirect evidence, or to predict

novel interactions between partners that have never been in contact before. In both cases, such models must deal with statistical issues linked to the amount of data and the number of parameters estimated used to make inferences—with big data, parsimony, and predictive power being serious issues (Giraud, 2014). In most cases, these models are also phenomenological in nature, i.e., they do not rely on a well-understood theoretical model, but rather make inferences based on correlations (Mouquet et al., 2015). As it has been the case for SDMs, phenomenological approaches have to evolve from comparisons of goodness-of-fit indicators to predictive power comparison and considerations about divergence of predictions among models (Araújo and New, 2007; Gritti et al., 2013; Peterson et al., 2011; Thuiller et al., 2008). While such comparisons have already been undertaken for some machine-learning approaches aimed at uncovering network structure from abundance data (Faisal et al., 2010), this has yet to be done on a systematic basis for models predicting novel interactions from the food web structure (but see Dalla Riva and Stouffer, 2016).

From a more biological point of view and again taking the example of SDMs, interaction network models will have to account for factors such as species evolution and dispersal between biogeographical units (Saltré et al., 2015; Thuiller et al., 2013). In the case of antagonistic interactions such as those between predator and prey or host and parasite, rapid coevolution through either frequency-dependent selection or an evolutionary arms race is expected, following Red Queen dynamics (Decaestecker et al., 2007; Gandon et al., 2008; Kerfoot and Weider, 2004; Salathé et al., 2008). Theoretical models investigating the evolution of plant defences have shown that, depending on plant dispersal rate and overall ecosystem productivity, one expects the evolution of little defence, specialized cheap defences, or high, costly defence (Loeuille and Leibold, 2008). Such considerations will have to be taken into account when modelling interaction networks on large spatial and temporal scales because they entail potential shifts in species role among interaction networks sampled at different times and locations (see also Poisot et al., 2012).

Theoretically linking interaction network characteristics to their invasibility and the potential impact of invaders is still in its infancy. While the amount of work linking network structure to network stability and robustness to species extinction is important (Allesina and Tang, 2012; Allesina et al., 2015; Astegiano et al., 2015; Dunne et al., 2002; Eklöf et al., 2013a,b; Goldstein and Zych, 2016; Kokkoris et al., 2002; Lehman and Tilman, 2000; May, 1973; Santamaría et al., 2016; Tang and

Allesina, 2014; Tang et al., 2014), similar explorations need to be conducted to link the network structure with invasion success and impacts, following the seminal work of Romanuk and colleagues (Romanuk et al., 2009; see also Romanuk et al., 2017).

6.2.2 Machine Learning

The future development of HTS-based reconstruction of networks has the potential to allow us to develop networks faster and more cheaply than previously, allowing comparison of networks across a great range of situations. Consequently, it becomes possible to imagine a situation where HTS methods may be used to sample ecosystems continuously, for the detection of invasions into reconstructed networks. Importantly, this would in addition probably be more sensitive than current methods of detecting invasion. To achieve this potential, however, it will be necessary to demonstrate clearly the methodological validity of network reconstruction from HTS data by: (i) identifying ecosystems with known and well-characterized networks; (ii) sampling these ecosystems using HTS; and (iii) reconstructing networks from the HTS sample data for comparison and testing them against the already existing networks.

6.3 Societal Challenges and Perspectives for Management

The development of new tools and the data acquisition they allow open multiple new challenges far beyond the sole area of scientific research. For example, throughout this chapter, we argued that a complete toolbox is an important prerequisite in biological invasions' management. Nevertheless, translating multiple type of data into decision-making programmes could be challenging as it requires a good understanding of the distinct advantages and disadvantages, as well as the level of uncertainty, associated with each method (Table 3). This is particularly relevant with regard to rising eDNA techniques for species surveillance, where a general, robust framework for data interpretation is still lacking. As advocated by Darling and Mahon (2011) an open and transparent discussion between multiple stakeholders will be necessary in order to negotiate the trade-offs between various sources of potential errors for each method and associated cost–benefits in terms of invasion management.

Another important challenge is related to the implementation of network perspective in management programmes (Kaiser-Bunbury and Blüthgen, 2015). Despite substantial advances in fundamental knowledge, it is still not clear how to use network theory for decision making as the

Table 3 Overview of the Advantages and Disadvantages Associated With the Different Tools and Methods Presented in This Paper As Well As Their Potential Applications in Invasion Ecology

Type of Method	Advantages	Disadvantages	Type of Information
1. Visual analysis of fossil records	• Easy and straightforward analyses • Cost effective	• Unsuitable for detecting the absence of a species • Not sensitive to short-term changes • Limited to organisms with fossilizing parts • Coarse taxonomic assignation	• Species occurrence • Passenger vs invasive organisms • Spatiotemporal changes in invasives distributions • Source of invasion • Invasion routes • Number of introduction events
2. Long-term data series	• Easy and straightforward analyses • Cost effective • Sensitive to short-term changes	• Few existing data sets • Limited to specific taxonomic groups • Drawbacks of long-term monitoring programmes (e.g. inertia, trade-offs on observed data, etc.)	• Passenger vs invasive organisms • Comparison of pre- and postinvasion • Spatiotemporal extent of invasions
3. Population genetics	• Historical inference from present-day data only	• Need for developing of markers with adequate resolution • Need for large samples from multiple populations	• Phylogenetic origin of the invader • Population size of founders • Population differentiation • Demographic changes • Genetic diversity • Hybridization events • Invasion routes and dispersal • Single vs multiple introductions
4. Citizen science	• Covers large spatiotemporal scales • Cost effective • Increasing number of taxa covered • Real-time monitoring of invasion	• Varying levels of protocol standardization • Need for simplified sampling designs and strong coordination • Need for advanced statistical tools	• Spatiotemporal changes in invasives distributions • Species occurrence • Community structure • Measures of individual traits • Predict invasion risk and future distributions • Comparison of pre- and postinvasion • Impact on higher trophic levels

Continued

Table 3 Overview of the Advantages and Disadvantages Associated With the Different Tools and Methods Presented in This Paper As Well As Their Potential Applications in Invasion Ecology—cont'd

Type of Method	Advantages	Disadvantages	Type of Information
5. Stable isotope analysis	• Easy and straightforward analyses • Rapid screening of large number of samples • Quantitative estimation of the proportional contribution of multiple prey • Time-integrative measure of diet	• Existence of multiple nondietary sources of variation • Limited to a narrow number of food sources	• Nutrients and energy flow • Trophic links • Food web structure • Trophic level • Habitat use • Invasion routes and dispersal
6. Chemical fingerprinting	• Fine-scale resolution of organism life history • Time-integrative measure of organism life history	• Need for very high precision • Need for (local) calibration	• Invasion routes and dispersal • Geographic origin of the invader • Habitat switch
7. PCR- and sequence-based DNA methods	• Versatile tool adaptable for different research questions and needs • Clues of species occurrence or interactions even when the species itself cannot be observed • Potentially large taxonomic coverage • The taxonomic specificity could be adjusted according to the research context • Rapid and cost-effective screening of large number of samples	• Sensitive to DNA-cross contamination • Sensitive to false positives and false negatives • Existence of multiple nondietary sources of variation • No quantitative estimation of the proportional contribution of prey	• Species occurrence • Predict invasion risk and future distributions • Trophic links • Food web structure • Predation and parasitism rates • Diet breadth • Impact on higher trophic levels
8. Predictive models	• Cost effective • Using different types of data	• Need for tailoring models based on available data • Possible indeterminacy (different possible mode is for the same observed data) • Possible diverging, nonrobust results (changing the model drastically change the predictions)	• Potential interactions between species • Inference of interaction networks from various data (traits, co-occurrence time series, etc.) • Changes in interactions due to invasion/environmental changes

choice of relevant metrics is potentially large. There is clearly need for more a posteriori validation (when practically feasible) of management impact in order to evaluate how invaded networks respond to different management scenarios (Courchamp et al., 2003). Beyond the financial arguments, getting prior feedback on management actions is important in order to prevent cascading "surprise effects" following management that could further jeopardize ecosystem functioning and services. So far such experimental validations are rare. Make a thorough use of above-mentioned set of surveillance techniques, as well as a closer collaboration between scientists and practitioners could help advancing in this direction (Kelly et al., 2014).

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GLOSSARY

Palaeoecology

Allozyme (alloenzyme) diversity Diversity of variant forms of an enzyme that are coded by different alleles at the same locus, as characterized by gel electrophoresis. A method (pre-next-generation sequencing era) to quantify genetic diversity.

Diatom frustules Hard and porous cell wall of diatoms, made of silica. They are preserved in the sediment and their typical morphological features can be used for taxonomic identification.

Metalimnetic cyanobacterial bloom Outbreak of cyanobacterial biomass occurring at the metalimnion depth, at the interface between the surface, warm and deeper, colder water layers of a lake.

Phytoplankton cysts Resting spores produced by some phytoplankton species. They are preserved in the sediment and their typical morphological features can be used for taxonomic identification.

Stratigraphic analysis Stratigraphy is a branch of geology, which studies rock layers (strata) and layering (stratification). It is primarily used in the study of sedimentary and layered volcanic rocks. A stratigraphic analysis focusses on archived components along a rock layer or sediment sequence as a way to go back in time.

Citizen science

Automated signal recognition Software based on classification algorithms used to identify digital records of species such as audio or pictures.

Detection probability Probability to detect a species when it is present. Such probabilities can vary among species, among environmental conditions of recordings, and among observers.

Fundamental niche The full range of conditions (biotic and abiotic) and resources in which a species could survive and reproduce.

Species distribution models (SDMs) Algorithms used to predict the distribution of species in space based on their known distribution in environmental space. The environmental space is most often characterized by climatic variables (e.g. temperature, precipitation), but can also include other variables such as soil type, water depth, and land cover.

Molecular ecology

Base-caller Algorithm that analyses the raw data produced by automated sequencers to predict the individual DNA bases.

Blocking primer This is a unique primer specifically designed to block the amplification of particular DNA sequences when universal primers are used in metabarcoding studies. Blocking primers are of particular interest for studies implying the HTS of ancient DNA or diet analysis to prevent the preferential amplification of modern or consumer DNA over target ancient or food DNA.

Diagnostic PCR A PCR assay that is used to test samples for the presence/absence of DNA from a single-target species or from a particular taxonomic group.

DNA template This is a matrix of DNA molecules that contains the target sequence the primers bind to.

Enzyme-linked immunosorbent assay (ELISA) This is an assay using an antibody specific to a particular antigen. The binding reaction between antigen and antibody is detected thanks to an enzymatic reaction provoking colour change in the assay substrate.

Environmental DNA (eDNA) This is related to the DNA molecules trapped in environmental samples like water, soil, or faeces.

Gel electrophoresis Method allowing the visualization of DNA fragments based on their size and charge. It implies the application of an electric field inducing negatively charged DNA molecules to move through a porous matrix (usually agarose gel). The method could be automatized and allow the simultaneous separation of multiple DNA fragments for multiple samples with great precision (e.g. capillary electrophoresis). The single-stranded conformation polymorphism (SSCP) is a particular case of electrophoresis, which allows separating DNA fragments that differ in their nucleotide sequence without sequencing (Sunnucks et al., 2000). The SSCP technique could offer a relatively simple and inexpensive alternative to sequencing in some cases (e.g. Varennes et al., 2014).

High-throughput sequencing (HTS) Technologies that parallelise the sequencing process by generate millions of sequences at the same time. There are several different high-throughput sequencing platforms, with currently the most popular being Illumina, Ion Torrent, and Oxford Nanopore. Regular updates about different platform specifications and cost could be found at http://www.molecularecologist.com/next-gen-fieldguide-2014/.

k-mers This is a term that refers to all the possible subsequences (of length k) from a read obtained through DNA sequencing.

Melt curves Analysis is used to determine the specificity and the sensitivity of a qPCR reaction. It refers to the temperature-dependent denaturation of the double-strand DNA measured by intercalating fluorescent probe.

Metabarcoding A method for the characterization of biodiversity recovered from complex environmental (soil, water, faeces, etc.) or bulk (Malaise traps) samples. It relies on simultaneous amplification of multiple species via PCR universal primers, high-throughput sequencing, and bioinformatic analysis.

Nested PCR It refers to a PCR reaction that involves two successive steps using the same or two different sets of primers, where the second step aims to amplify the PCR product of the first step. Nested PCR is used for amplifying secondary target gene regions or for enhancing the amplification of recalcitrant target regions.

Pair-end sequencing This is the high-throughput sequencing of both ends of the same target DNA fragment, allowing the high-quality alignment of sequence data.

Phylogenetic inference This refers to methods that provide estimates about phylogenetic (evolutionary) relationships among organisms based on observed heritable traits like morphology or DNA sequences.

Quantitative PCR (qPCR) Where the regular PCR primer set is combined with a specific fluorescent probe allowing a quantitative estimation of the number of molecules present in the template by comparison with a reference threshold.

Sanger sequencing This is a method of DNA sequencing developed by Frederick Sanger and colleagues in 1977. It refers to the selective incorporation of chain-terminating dideoxynucleotides by DNA polymerase during in vitro DNA replication, generating sequences between 100 and 1000 bp. In contrast to HTS, Sanger sequencing does not allow the simultaneous sequencing of multiple DNA molecules.

Sedimentary ancient DNA (sedaDNA) This is a metabarcoding method for the reconstruction of past communities and biodiversity dynamics based on ancient DNA trapped in sediments or ice cores.

Sequence reads These are millions of usually short DNA sequences, produced by high-throughput sequencing machines.

Singleplex/multiplex PCR A polymerase chain reaction (PCR) where one pair of primers is used to amplify one specific PCR fragment is called a singleplex PCR, whereas in multiplex PCR more than one primer pair is employed to simultaneously amplify several PCR fragments within one reaction.

Squiggle plot This is a graphical interpretation of the fluctuating electrical signals generated by the DNA translocation through the nanopore used in the MinION™ sequencing device.

Tag This is a unique short sequence added to the 5′-end of a primer allowing the downstream sequence sorting and sample assignation. Tags usually range between 8 and 12 bp. Samples with unique tags can be pooled and sequenced in the same sequencing run (=multiplexing). Sequences are later assigned to samples via bioinformatic pipelines.

Population genetics

Allelic richness This is the average number of alleles per locus. Allelic richness is used as a measure of population genetic diversity.

Approximate Bayesian Computation A class of model-based likelihood-free methods for statistical inference. Based on principles of Bayesian statistics, ABC algorithms provide a way to identify the models and model parameters that are most congruent with

data. To do so, they quantify the probability of the observed data under a particular model, that is, likelihood, and seek the model and parameters for which likelihood is maximal. But the likelihood function can easily be mathematically derived and numerically evaluated only for reasonably simple models. In ABC, the limiting step of very complex likelihood computations is replaced by an approximation of the likelihood, which is obtained by simulating (millions of) data sets under considered models and studying the distributions of models and model parameter values among the simulated data sets that are closest to the observed data using a regressive approach on summary statistics (Beaumont et al., 2002).

Genetic bottleneck A reduction in population effective size.

Haplotype This is a group of genes or alleles that progeny inherited from one parent.

Heterozygosity This is a measure of genetic variation within a population. Observed heterozygosity is defined as the percentage of heterozygous individuals per locus. Expected heterozygosity (also called gene diversity) is the expected number of heterozygotes given allele frequencies (Nei, 1987). Observed heterozygosity can only be computed for diploid genomes, while expected heterozygosity can always be computed.

Microsatellite A DNA sequence containing repeats of a certain motif (generally ranging from 2 to 5 base pairs). Microsatellites belong to the Variable Number of Tandem Repeats (VNTR) markers and also named short tandem repeats (STRs) or simple sequence repeats (SSRs).

Haplotype network A diagram representing genetic relationships between haplotypes. In a haplotype network, each haplotype is represented by a circle, with size proportional to the number of individuals belonging to that haplotype, connected to the most similar haplotype by a line. Each circle may be divided in slices of pie, in which the colour indicates sampling localities.

Neutral DNA marker A DNA sequence that is not subject to selection. Noncoding regions of DNA are traditionally supposed neutral, although for some of them, deleterious effects have been detected.

Private variability This is the part of within-population diversity that is unique to a given population. Private alleles are only found in one population.

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