REVIEW

Biosurveillance of forest insects: part I—integration and application of genomic tools to the surveillance of non-native forest insects

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Abstract

Invasive species pose significant threats to forest ecosystems. Early intervention strategies are the most cost-effective means to control biological invasions, but are reliant on robust biosurveillance. State-of-the-art genomic approaches can provide an unprecedented opportunity to access detailed information on the invasion process and adaptive potential of invasive insects that pose an immediate threat to forests environments. Genomics can improve diagnostics of the invader and identify its route of invasion by determining the source population(s), assess its probability of establishment and patterns of spread, as well as provide evidence of adaptation. Applied biosurveillance efforts by plant health regulatory agencies will benefit substantially from the detailed insights that genomic data bring to our understanding of biological invasions.

Keywords Biological invasion · Biosecurity · Surveillance · Genomics · High throughput sequencing

Key messages

- Management and regulation of forest alien invasive species requires detailed knowledge about the biology and invasion history of invasive or non-native pests.
- Knowledge gaps in our understanding of biological invasion for many non-native pests include species identity, source, demographic history, and fitness.
- We highlight genomic tools and approaches that can be incorporated into biosurveillance programs to improve our understanding of biological invasions.
- Bioinformatic challenges exist when dealing with large volumes of genomic data, and approaches to identify fitness traits underlying "invasiveness" are still in their infancy.

- Uptake of genomic approaches in the study of forest invasive and non-native pests has been limited to date, but is on the verge of transforming the field of biosurveillance.

Introduction

Forests are a vital part of the global ecosystem and provide an array of economic and environmental benefits (Lugo 2015), but currently face unprecedented threats from invasive insects (Millar and Stephenson 2015; Trumbore et al. 2015). Forest invasive alien species (FIAS) are any species whose introduction threatens the capacity of our forest ecosystems to provide the economic, societal, and environmental services vital to our global well-being (Grebner et al. 2014). The number of new introductions and interceptions of FIAS is escalating at an alarming rate and is strongly correlated with a country's economic activity (DAISIE 2009). As the volume of trade is expected to increase in the foreseeable future (a result of bilateral and multilateral trade agreements and continued population growth), it is imperative that plant health regulatory agencies take advantage of technological advances to help mitigate the increased threat of invasive species and aid rapid intervention.

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Management of FIAS becomes increasingly difficult and expensive as invasives establish and reach high densities (Aukema et al. 2011). Thus, prevention, preparedness, and early intervention are the most cost-effective approaches to reduce the risk and impact of invasives (Leung et al. 2002; Lodge et al. 2006; Epanchin-Niell and Liebhold 2015). Biosurveillance is the process of gathering, integrating, interpreting, and communicating essential information about invasive pests and the risks they pose to the environment, economy, and human health. Biosurveillance informs early intervention strategies and should help decision-makers select among a range of management strategies, proven to be effective against already established pest populations (Chown et al. 2015; Fournier and Turgeon 2017).

Several risk factors, including the identity of the invader, source of the invasive population, probability of establishment, the invasion pathway, patterns of spread, and evidence of adaptation, are critical to reduce the inherent uncertainty in the assessment process and informing strategies for managing invasive species (Wittenberg and Cock 2001; Ibáñez et al. 2014). Since substantive resources are deployed to conduct biosurveillance activities, it is imperative that the techniques used to measure these risk factors maximize the knowledge gained and reduce uncertainty within biosurveillance efforts.

Recent genomic innovations have improved our ability to detect and identify potential non-native and invasive forest species, determine their sources, and assess the risk they pose to our forests (Chown et al. 2015; Cristescu 2015). Here we outline current advances in genomic technologies that can improve biosurveillance of FIAS. We present this review as two companion papers. In Part I, we focus on the use of genomics to improve data collection and response time for the biosurveillance of FIAS and highlight the common tools used to collect and analyze these data. Herein, we discuss available genomic resources and analytical frameworks needed to address problems related to invasion biology including: (1) species- and population-level identification, (2) determination of geographic origins and invasion pathways, (3) understanding movement and adaptations of populations, and (4) how to link genomic information to invasion-relevant phenotypes to inform risk assessment (Fig. 1). We conclude with a summary of the opportunities and future directions for genomic biosurveillance and current limitations to this framework, which is expanded in our second paper (Part II; Bilodeau et al. 2018) in relation to the adoption and implementation of genomic tools within a management framework.

Genomic biosurveillance of forest invasive species

A wide range of genomic approaches have been developed in the past decade (Fig. 1; Boxes 1, 2), providing a diverse toolkit to study FIAS (Cristescu 2015). Genome-wide data generated from high throughput sequencing [HTS, Box 1; formerly referred to as Next Generation Sequencing (NGS)] maximizes the resolution and statistical power with which we can examine the process of biological invasion. Although research on the genomics of invasive and non-native species is in its infancy, related studies have increased by 24% within the last 10 years (Fig. 2, "Appendix 1"). Genomic analyses appear to be gaining momentum in biological invasion research (Bock et al. 2015, Table 1). Here, we provide examples of how genomic data and statistical approaches can inform our understanding of FIAS identity, invasion source, spread pathways, history, and risk of establishment. Our aim is not to present an exhaustive list of studies, but to provide examples that demonstrate the breadth of knowledge that can come from genomic data. We hope that these studies serve as motivation to integrate genomic approaches into the study and management of biological invasions in the near future. We focus on five areas that represent key information needed to help counteract the invasion process: (1) pest identity, (2) invasion source, (3) invasion pathways, (4) history of the invasion, and (5) linking genotypes to phenotypes that characterize the invasion process (Fig. 1). Before we expand on these five research areas, we present a brief summary of the different genomic technologies that may be used to answer these types of questions.
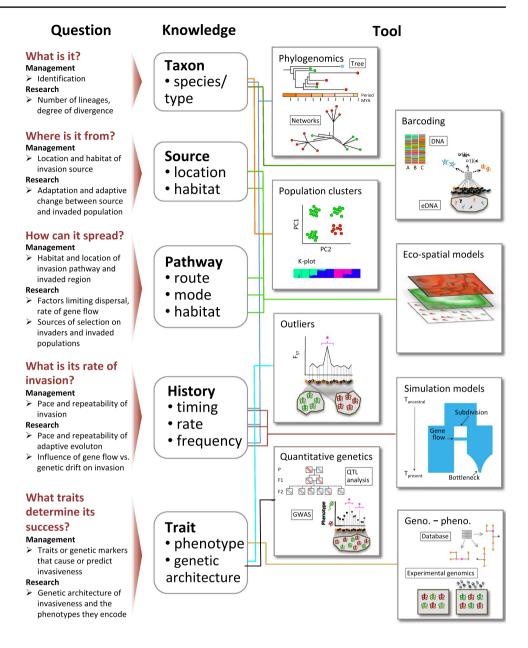
Genomic technologies

The past decade has seen unprecedented access to genomic tools and resources and a plethora of options are available for use (Alvarez et al. 2015; Cristescu 2015; Rius et al. 2015; Goodwin et al. 2016). We will focus on a subset of genomic approaches that can help us address key questions in the study and management of biological invasions (Fig. 1).

Whole genomes are the complete DNA blueprint of an organism. The availability of whole genome sequences (WGS) is foundational for effective use of genomics in the biosurveillance of FIAS. In the past, whole genomes were challenging to obtain for insects due to their genome size, small amounts of tissue, and lack of closely related species to aid assembly (Ekblom and Wolf 2014; Richards and Murali 2015). With continually decreasing costs, improved sequencing technologies, and more efficient assembly algorithms, genomic resources for insects are growing rapidly (González et al. 2018). Genomes are currently available for a small proportion of insect diversity (138 species, Yin et al. 2016), including five high-risk FIAS (Table 2). Since WGS serves as the foundation for much of the tool development needed for genomic-based biosurveillance, it is imperative to expand these resources

Fig. 1 Overview of questions related to biological invasion management or research. Questions can be classified into five broad categories: species identification (Taxon), population origin (Source), route of invasion (Pathway), invasion history (History), and traits of invasiveness (Trait). We link categories to popular tools that can use genomic data to address the questions of interest. Lines connecting Knowledge and Tools highlight the multidisciplinary approach needed to resolve the complex process of biological invasion. Tools are described in detail in Box 2

(e.g., Arthopods i5k Initiative, i5K Consortium 2013) to further describe and compare FIAS genomes and yield resources for downstream applications such as RNA-seq and functional genomics.

HTS techniques make it possible to obtain millions of markers spread throughout the genomes for a fraction of the cost compared to other techniques (Glenn 2011; Goodwin et al. 2016). HTS can be used in concert with other approaches that sample only a portion of the genome (e.g., microsatellites, mitochondrial DNA, restriction fragment length polymorphisms (RFLPs), amplified fragment length polymorphisms (AFLPs), and targeted sequencing, reviewed in Sperling and Roe 2009). Combining HTS with reduced genome sampling is a powerful approach that combines efficiency, low costs, and informative genome-wide data.

There are many ways to subsample the genome and leverage the power of HTS (Lemmon et al. 2012). A number of restriction enzyme subsampling approaches have gained widespread use (Andrews et al. 2016), including restriction site-associated DNA sequencing (RAD-seq, Baird et al. 2008) and genotyping-by-sequencing (GBS, Elshire et al. 2011). Collectively, these reduced representation shotgun sequencing approaches use restriction enzymes to fragment DNA into thousands of pieces and then use HTS to read a subset of the DNA fragments to capture genomic variation (single nucleotide polymorphisms, SNPs; small insertions/deletions, indels) (Altshuler et al. 2000; Campbell et al. 2018). These approaches can generate information about thousands of variants distributed throughout an insect's genome and serve as markers for the study of its population
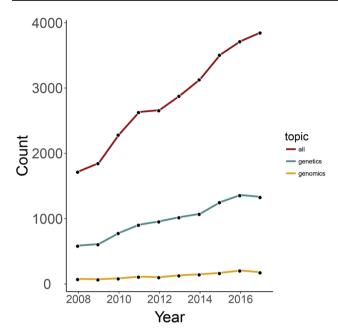
Fig. 2 Recent trends in the application of genetic and genomic approaches to biosurveillance of FIAS. Citation counts in each year are the total citations for the term "invasive." Search parameters are presented in "Appendix 1"

structure, or for performing genome-wide association tests involving informative phenotypic characteristics of the FIAS in question (Fig. 1).

Invasive species are, by definition, species capable of adapting to new environments. Gene expression patterns are heavily influenced by the environmental context experienced by the organism and vary across developmental stage and tissue type (Alvarez et al. 2015). The actively transcribed portion of the genome constitutes the transcriptome. Due to its high regulatory function, the transcriptome provides an invaluable complement to genomic data in the study of invasion biology as it provides insight into the interaction between an organism and its environment. HTS techniques, such as RNA-seq, provide novel ways to study transcriptomes in non-model organisms and, unlike microarrays or exome capture approaches, RNA-seq does not require a priori knowledge of a species' genome or expressed sequences. A major benefit of transcriptomic analyses also lies in the ability to establish gene expression "signatures" or profiles. Since these transcriptomic profiles are context dependent, they can be used to identify populations (via the generation of microsatellites, Duan et al. 2017) or physiological states of FIAS, which can help inform risk assessments. Transcriptomics can thus identify key processes or genes that help explain the adaptability of an invasive or non-native insect in its new environment (Alvarez et al. 2015). At least 30 transcriptomes from FIAS have been published (Table 3). Transcriptomic and the preceding genomic approaches are

dependent on high quality starting tissue (Todd et al. 2016), and obtaining properly preserved tissue for invasive species is necessary.

Identification: What is it?

Accurate identification of FIAS is an essential first step for early detection and subsequent management actions (Boykin et al. 2012). It ensures that regulatory agencies can respond appropriately before a FIAS establishes and spreads (Fig. 1: What is it?). Insects can be challenging to identify, given their diversity and variable morphology throughout their life cycle. Insects can be introduced at any stage of their life cycle, so detecting and identifying insects at any life stage is essential. Recent advances in DNA-based methods have significantly improved our ability to identify insect pests, particularly those that are difficult to distinguish using morphological characters alone. Molecular identification relies on the discovery and validation of marker genes with diagnostic signatures that can discriminate taxa. DNA barcoding is one widely used, simple, and powerful diagnostic method that relies on genetic variation in a standard universal gene to distinguish species through comparisons with a curated database (Hebert et al. 2003). This barcode approach successfully discriminated among members of *Lymantria*, a genus that contains several high-risk invasives including the Asian gypsy moth group (AGM; *Lymantria dispar asiatica, L. d. japonica, L. umbrosa, L. postalba, L. albescens*) and other threatening *Lymantria* species (*L. monacha, L. mathura, L. xylina, L. lucescens*). The polymorphisms contained in the genes used for DNA barcoding even allowed discrimination of individuals at the subspecies level (deWaard et al. 2010; Kang et al. 2015, 2017; Stewart et al. 2016). While this system shows great promise for single marker discrimination, DNA barcoding is not a panacea for identification of invasives. Lack of validated reference libraries, invariable, and conflicting genetic variation (i.e. gene tree—species tree conflicts) all contribute to shortcomings in this single marker approach (Collins and Cruickshank 2012; Dupuis et al. 2012).

Recent advances in HTS are making it clear that much more precise and accurate taxon identification is possible with genome-wide data, increasing confidence in identifications and overcoming a number of criticisms of single marker approaches (Dupuis et al. 2012). The development of a phylogenomics approach can clarify the evolutionary relationships of taxa and identify cryptic taxa (Fig. 1, Phylogenomics). Genome-wide approaches can identify hybrid or introgressed individuals that contain genomic regions from different parental species. Keena et al. (2008) and Picq et al. (2017) documented hybridization between subspecies of gypsy moth (*Lymantria dispar* spp.), although morphological detection of these hybrids was not possible.

Table 1 Survey of molecular studies that answer key questions about FIAS invasions

Scientific name	Common name	Molecular tool[a]	Knowledge	References
Coleoptera				
Agrilus planipennis	Emerald ash borer	mtDNA, AFLP, Msat	Source, history	Bray et al. (2011)
		RNA-seq	Trait	Mittapalli et al. (2010)
		Msat	Pathway	Keever et al. (2013)
		RNA	Trait	Rajarapu et al. (2011)
		RNAi	Trait	Rodrigues et al. (2017)
Anoplophora glabripennis	Asian long-horned beetle	mtDNA, Msat	Source	Carter et al. (2009)
		mtDNA	History, pathway	Javal et al. (2017)
		RNA-seq	Trait	Scully et al. (2013)
		SCAR	Taxon	Kethidi et al. (2003)
		Msat	Source	Liu et al. (2017)
Cerambycidae /Buprestidae	Wood-boring beetles	mtDNA	Taxon	Wu et al. (2017)
Dendroctonus ponderosae	Mountain pine beetle	AFLP, mtDNA	History	(Mock et al. 2007)
		Msat	History	Gayathri Samarasekera et al. (2012)
		RAD-seq	History	Dowle et al. (2017)
		SNPs	Pathway	Janes et al. (2014)
		mtDNA	History	Cullingham et al. (2012)
		SNPs	History	Janes et al. (2016)
		SNPs	History	Batista et al. (2016)
Dendroctonus valens	Red turpentine beetle	Msat	Source	Taerum et al. (2016)
		mtDNA	Source	Cognato et al. (2005)
Hylotrupes bajulus		mtDNA, Msats, SNPs SNPs SNOs	Pathway, history	Castalanelli et al. (2013)
Pissodes spp.	Pissodes weevils	mtDNA	Taxon, source	Wondafrash et al. (2016)
Polygraphus proximus	Four-eyed bark beetle	mtDNA	History	Kononov et al. (2016)
Xyleborus spp.	Ambrosia beetles	mtDNA, SNPs	History	Gohli et al. (2016)
Xylosandrus crassiusculus	Granulate ambrosia beetle	ddRADseq	History, pathway	Storer et al. (2017)
		mtDNA	Taxon	Landi et al. (2017)
Lepidoptera				
Cameraria ohridella	Horse-chestnut leafminer	mtDNA Msat	Source	Valade et al. (2009)
Hyphantria cunea	Fall webworm	Msat	History	Cao et al. (2016)
Lymantria dispar	Asian gypsy moth	mtDNA, RFLP	Taxon	Arimoto and Iwaizumi (2014, 2016)
		mtDNA	Taxon	deWaard et al. (2010)
		GBS–SNPs	Source	Picq et al. (2017)
		mtDNA, Msat	History, source	Kang et al. (2015, 2017)
		SNP	History, trait	Streifel et al. (2017)
		Msat, mtDNA	Taxon, history	Wu et al. (2015)
		mtDNA	Taxon	Djoumad et al. (2017)
		mtDNA	Taxon	Stewart et al. (2016)
Operophtera brumata	Winter moth	Msats, SNPs	Taxon	Havill et al. (2017)
		Msats, SNPs	History	Andersen et al. (2017)
		mtDNA	History	Gwiazdowski et al. (2013)
Thaumetopoea pityocampa	Pine processionary moth	AFLP, mtDNA	Pathway	Salvato et al. (2002)
		Msat	Trait, history	Santos et al. (2011)
		mtDNA, Msat	Taxon, history	Burban et al. (2016)
		RAD-seq-SNPs	History	Leblois et al. (2018)
Hemiptera				
Corythucha ciliata	Sycamore lace bug	RNA-seq	Trait	Li et al. (2016)
		mtDNA, Msat	Source, history	Yang et al. (2017)

Table 1 (continued)

Scientific name	Common name	Molecular tool[a]	Knowledge	References
		RNA-seq	Trait	Li et al. (2017)
Adelges tsugae	Hemlock wooly adelgid	mtDNA, Msat	Source, history	Havill et al. (2016)
Matsucoccus feytaudi	Maritime pine bast scale	Msat	Source, history	Kerdelhué et al. (2014)
Leptoglossus occidentalis	Western conifer seed bug	mtDNA, Msat	Source, history	Lesieur et al. (2018)
Thaumastocoris peregrinus		mtDNA, Msat	Source, history	Lo et al. (2018)
Hymenoptera				
Sirex noctilio	Sirex wood wasp	Msat, mtDNA	Source, history	Boissin et al. (2012)
Megastigmas schimitscheki	NA	Msat, mtDNA	Source, history	Suez et al. (2013)
		Msat, mtDNA	History	Auger-Rozenberg et al. (2012)

See Fig. 1 for details on knowledge

[a]*mtDNA* mitochondrial DNA, *RFLP* restriction fragment length polymorphisms, *SCAR* sequence characterized amplified regions, *GBS-SNPs* genotyping-by-sequencing-single nucleotide polymorphisms, *ISSR* inter simple sequence repeats, *Msats* microsatellites, *AFLP* amplified fragment length polymorphisms, RNA-seq RNA HTS sequencing

Table 2 Genomic resources for forest invasive alien insects: whole genomes

Species name	Common name	Genome size (MB)	Number of genes	Number of scaffolds	NCBI genome ID	References
Dendroctonus ponderosae	Mountain pine beetle	261	13,088	6520	11,242	Keeling et al. (2013)
Operophtera brumata	Winter moth	638	16,912	25,801	39,883	Derks et al. (2015)
Anoplophora glabripennis	Asian long-horned beetle	710	22,253	10,474	14,033	McKenna et al. (2016)
Thaumetopoea pityocampa	Pine processionary	537	29,415	68,292	344,465	Gschloessl et al. (2018)
Agrilus planipennis	Emerald ash borer	353[1]	18,543[1,2]	3988	12,835	Unpublished
Neodiprion lecontei	Red headed pine sawfly	237[1]	15,991[1,2]	4523	39,861	Unpublished

Genome-wide variation in the form of single nucleotide polymorphisms (SNPs) provides increased genome coverage that facilitated the detection of potential gypsy moth hybrids (Picq et al. 2017); some of the discriminant markers identified here were converted into diagnostic DNA assays (Stewart et al. 2016) to speed up and streamline detection of members of the *Lymantria dispar* complex. Identifying hybrid individuals could be important for risk assessments. This information can be very relevant to management decisions since the subspecies vary in their flight capacity and host range (traits). Another rapid diagnostic technology is loop-mediated isothermal amplification (LAMP). This method has recently been used for on-site diagnosis of agricultural pests of quarantine concern (Blaser et al. 2018). With LAMP, when DNA from a target pest is detected a visible change occurs in the sample due to the amplification of specific DNA targets at a constant temperature. Since LAMP can be conducted at a constant temperature, this eliminates the need for thermocyclers, which lends itself for use in field settings, such as ports of entry (Blaser et al. 2018).

FIAS may also carry invasive pathogens such as bacteria or other phytopathogens including fungi and oomycetes (Hendrickson 2002). For example, insects transmit pathogenic nematodes such as the devastating pine wood nematode *Bursaphelenchus xylophilus* (Dwinell 1997) and are responsible of the transmission and spread of Dutch elm disease (*Ophiostoma ulmi* and *O. novo-ulmi*) (Brasier and Buck 2001). These associated phytopathogens can lead to significant impacts on native forests (Loo 2009) or can influence the success of the invasive or non-native insect partner (Ryan et al. 2012; Slippers et al. 2015). Detection and identification of insect-vectored pathogens is an important step to managing their introductions and is greatly enhanced with genomic tools. Organisms also leave traces of their DNA throughout the environment. Environmental DNA (eDNA) sampled from air, soil, water, or bulk trap samples can be screened using HTS methods to improve detection rates and accelerate identification for potential pathogens (Abdelfattah et al. 2018; Comtet et al. 2015; Tremblay et al. 2017) (Fig. 1, eDNA, metabarcoding; Box 2). A HTS metabarcoding approach successfully quantified the microbial community of bark and ambrosia beetles and detected plant pathogens not known to be associated with these species (Miller et al. 2016; Malacrinò et al. 2017). Metabarcoding relies

Table 3 Genomic resources for forest invasive alien insects: transcriptomes

Species name	Biological context	RNA source	References
Coleoptera			
Dendroctonus ponderosae (Mountain pine beetle)	Pheromone biosynthesis	Fat body and midgut tissues from adult males and females treated with either methyl jasmonate or juvenile hormone	Keeling et al. (2016)
	Overwintering biology	Larvae sampled at four time points during overwintering	Robert et al. (2016)
	Pheromone biosynthesis	Fat body and midgut tissues from fed and unfed males and females	Nadeau et al. (2017)
	Detoxification of host compounds	Midgut and adhering fat body of emerged adults, treated with either JH or untreated; Adult antennae	Keeling et al. (2012)
	Olfaction	Antennae	Andersson et al. (2013)
Dendroctonus valens (Red turpentine beetle)	Olfaction	Antennae	Gu et al. (2015)
Ips typographus (European spruce bark beetle)	Olfaction	Antennae	Andersson et al. (2013)
Agrilus planipennis (Emerald ash borer)	Vision	Eyes	Lord et al. (2016)
	Development, digestion	Various stages: larvae, prepupae, pupae and adults; larval and adult midguts	Duan et al. (2015)
	Olfaction	Antennae	Mamidala et al. (2013)
	Host digestion, detoxification	3rd larval instar midgut and fat body	Mittapalli et al. (2010)
Anoplophora glabripennis (Asian long-horned beetle)	Olfaction	Male and female adults	Mitchell et al. (2017)
	Digestion	Larvae	Mason et al. (2016)
	Digestion	Larvae feeding on artificial diet or sugar maple	McKenna et al. (2016)
	Digestion	Larval midgut	Scully et al. (2014)
Monochamus alternatus (Japanese pine sawyer beetle)	Insecticide resistance	Multiple instars(?)	Lin et al. (2015)
	Insecticide resistance, immunity, digestion	Larvae	Wu et al. (2016) Zhou et al. (2017)
	Olfaction	Antennae	Wang et al. (2014)
	Antifungal response	Pupae exposed to fungal pathogens	Zhang et al. (2017)
Apriona japonica (Mulberry longhorn beetle)	Digestion	Larval guts	(Pauchet et al. 2014)
Megacyllene caryae (Hickory borer)	Olfaction	Antennae	Mitchell et al. (2012)
Tomicus yunnanensis (Pine shoot beetle)	Insecticide and environmental stress resistance	Adults	Zhu et al. (2012)
	Olfaction	Three developmental stages	Liu et al. (2018)
Lepidoptera			
Lymantria dispar dispar (European gypsy moth)	Response to *Bacillus thuriengensis* (Bt)	Midguts from Bt-infected and non-infected larvae	Sparks et al. (2013)
Lymantria dispar asiatica (Asian gypsy moth)	Development	Larval midgut and epidermis	(Xiaojun et al. 2017)
	Insecticide resistance	Larvae	Cao et al. (2015)
Lymantria dispar dispar *Lymantria dispar asiatica* *Lymantria dispar japonica* (Japanese gypsy moth)	Olfaction	Female antennae, larval head capsules	Clavijo McCormick et al. (2017)

Table 3 (continued)

Species name	Biological context	RNA source	References
Hyphantria cunea (Fall webworm)	Olfaction	Antennae	Zhang et al. (2016)
Thaumetopoea pityocampa (Pine processionary moth)	Virus infection	Larval head, gut, fat body and integument	Jakubowska et al. (2015)
	Envenomation by urticating setae	Larvae	Berardi et al. (2017)
	Phenology	Various stages from winter (WP) and summer (SP) populations	Gschloessl et al. (2014)
Hemiptera			
Corythucha ciliate (Sycamore lacebug)	Development	Nymphs, male and female adults	Li et al. (2016)

Box 1 Glossary

Adaptation One of the evolutionary forces related to a population's response to natural selection which favors phenotypes adapted to local conditions, hence also favors alleles underlying these successful phenotypes. Genomic regions/variants underlying strong local adaptation in a population are usually identified based on the detection of an unusually extended linkage disequilibrium (LD) pattern among the neighboring allelic variants (through hitchhiking) surrounding the beneficial variant observed in that genome region, called a selective sweep

Allele The variable state within a DNA sequence or locus

Evolutionary lineage A group of individuals possessing a shared evolutionary history

Genetic drift Changes in allele frequencies within populations due to random loss of individuals over time; greatest impact is in small populations where the loss of few individuals may result in proportionally large differences in allele frequency

Gene flow Movement of new genetic material into a population, introducing new alleles or altering the frequency of existing alleles within a population

Genetic marker A segment of DNA or protein that is variable among individuals and can be used to discriminate between them

Genomic architecture Defines the ensemble of genetic variants that defines the variability observed in a phenotypic trait (characteristic); a genetic architecture can be simple or polygenic depending on the trait

Genotyping-by-sequencing (GBS) A reduced representation library technique that uses restriction enzyme digestion to fragment genomic DNA and then sequences a specific size fraction using HTS (Elshire et al. 2011)

High Throughput Sequencing (HTS) Also called next generation sequencing. A collective group of genomic sampling technologies that uses high throughput, massively parallel sequencing platforms to simultaneously read DNA fragments from individual or pooled samples (Campbell et al. 2018)

Linkage disequilibrium (LD) Is defined as the non-random assortment of neighboring allelic variants found within a population (following many generations of mating/meiosis which is supposed to break down extended LD though genetic recombination); the overall extent of LD can be representative of a certain species, and is related to its life history; it is often determined by averaging over the LD patterns of multiple genes, while such estimate can differ from the genome-wide LD pattern that is now accessible through HTS approaches

Locus A specific location in the genome, such as the site of a gene or individual nucleotide within a chromosome

Metabolomics Quantification of the collective metabolic activity (biochemically active compounds) in an individual/species (the metabolome); usually, tissue-specific metabolic assessment is conducted; different types of metabolites require different chemical extraction methods from the target tissue and different analysis methods (LC-, GC-, MS-, NMR-based and coupled methods); thus, their assessment needs knowledge of their chemistry; metabolites are identified and quantified using available commercial standards

Natural selection The unequal transmission of gene variants ("alleles") across generations within a population due to their differential effects on lifelong reproductive success

Polymorphism A location in the genome that is variable (i.e., has more than one allele), e.g., biallelic and heterozygous locus (variant) in a diploid organism (alleles A/T) or occurrence of locus polymorphism assessed within a population (alleles A/A, T/T, A/T)

Proteomics Assessment of the ensemble of proteins' presence/activity (the proteome) in an individual/species; usually, tissue-specific protein assessment is conducted. Proteins are identified and quantified by mass spectrometry (MS) (Walther and Mann 2010)

Restriction site-associated DNA sequencing (RAD-seq) An alternative reduced representation library technique (Baird et al. 2008, see GBS above)

RNA sequencing (RNA-seq) HTS of the transcriptomic portion of an organism

Transcriptome Collection of expressed genes (i.e., those being activated) at a point in time and in a given condition, stage or tissue, which is measured by sequencing the cellular messenger RNA

Whole genome The complete, organized set of DNA for an organism

Whole genome sequencing (WGS) Sequencing, reading, and assembly of the complete set of genomic instructions that represent an organism

Box 2 Statistical tools for the analysis of genome-wide data

Most statistical approaches applicable to genome-wide data extend analytical approaches that were previously based on single or few genetic markers. Below, we briefly summarize several tools that can help answer key questions about the ecology and evolution of biological invasion (Fig. 1). There are key advantages when these approaches are used in conjunction with genome-wide data, but each approach comes with its own fundamental limitations or ongoing challenges

Phylogenomics: *Advantages* Phylogenomics uses genome-wide data to infer relationships among evolutionary lineages. This approach promises greater resolution compared to single-gene phylogenetics (Dupuis et al. 2012; Yang and Rannala 2017), avoiding the biased signal of individual markers that can arise due to differential patterns of inheritance (i.e., gene tree-species tree conflict, McCormack and Faircloth 2013). *Limitations* The benefit of enhanced phylogenetic signal can be compromised if it adds substantial noise or "non-phylogenetic signal" due to sequencing errors or mis-alignment. Additional noise may be introduced if genome-wide substitution mutations are incorrectly modeled in the data (Philippe et al. 2011; Philippe et al. 2017), leading to unresolved relationships or conflicts within the phylogenomic tree

Clustering: *Advantages* Genomic clustering methods are used to detect patterns of genomic variation across a set of individuals. Genomic variation may correspond to populations, ecotypes, or species. STRUCTURE is the most widely used method (Pritchard et al. 2000) and partitions genomic variation among a priori defined clusters. Principal components analysis (PCA, Novembre and Stephens 2008; McVean 2009) is an alternative, multivariate approach that reduces genomic variation to a limited set of axes that best represent the variation in the combined data. *Limitations* Strictly mathematical clustering approaches make no assumptions about the samples and so may neglect demographic or genetic features that affect population structure. Genetically explicit models attempt to capture those features, for example, by accommodating gene flow (Falush et al. 2003; Durand et al. 2009) or associations between linked loci (Lawson and Falush 2012). Genetic clustering analyses can be computationally intensive, particularly for large genomic data sets, although improvements in algorithm efficiency have made the analysis of large data sets more tractable (e.g., Raj et al. 2014). Finally, discrete clusters may not accurately describe genetic variation across a landscape if it is dominated by continuous processes such as isolation-by-distance (i.e., increasing genetic divergence among individuals with increasing distance between them). New methods are in development that try to evaluate which type of description is most appropriate for a given sample of individuals (Bradburd et al. 2018)

eDNA & Metabarcoding: *Advantages* Environmental DNA (DNA) and metabarcoding leverage HTS to perform biodiversity surveys using DNA in bulk samples such as soil, water, faeces, or air (Taberlet et al. 2012a) or a pooled sample of whole-organisms (Hajibabaei et al. 2011), respectively. A collection of standardized DNA fragments are extracted from the environmental or pooled samples and compared to a reference library for positive identification. Both methods provide an efficient method to survey the biodiversity of an ecosystem, and the resolution of these surveys has greatly expanded with genomic approaches. *Limitations* Successful metabarcoding and eDNA are dependent on validated reference libraries to positively identify individuals within a sample and these may be lacking for new invasive species. There are still challenges in terms of detection sensitivity (Taberlet et al. 2012b) given the variable, often degraded nature of DNA in the samples. Analyzing these data can also be computationally intensive, and streamlined bioinformatic tools are needed

Eco-spatial analyses: *Advantages* Eco-spatial analyses of population genomic data explore the relationship between genomic diversity and environmental variation, while controlling for the geographic location of those samples (Joost et al. 2007; Rellstab et al. 2015). This permits the identification of environmental factors that may influence the evolutionary history of populations while controlling for the effects of spatial proximity among individuals. *Limitations* Eco-spatial analyses face several statistical challenges. First, obtaining environmental data that represents the appropriate spatial and temporal scale for genomic data can be difficult (Schoville et al. 2012). Testing for associations between genomic variation and multiple environmental variables can limit the statistical power to detect a significant relationship. This issue, as well as the need to limit redundant information across strongly correlated (collinear) environmental factors often calls for selection of only a subset of factors or the reduction of the original variables to synthetic variables. Finally, estimating spatial effects among samples requires selecting a model of how spatial relationships are depicted (Lowry 2010)

Simulations: *Advantages* Simulations of population genomic history generate artificial population genomic processes through time, incorporating parameters for selection, drift, gene flow, population subdivision, or life history traits. Because models can be tailored to represent diverse invasion scenarios, they can supply customized null hypotheses about what genetic patterns would be expected from specific evolutionary histories, sources, or pathways of biological invasion. These null hypotheses can then be compared to observed data (Hoban et al. 2011). As a result, simulation models are gaining importance as an approach to test results or to explore assumption violations of other statistical methods. Genome-wide data can increase the simulation power by maximizing the genetic signal of a given lineage's evolutionary history, facilitating tests of relatively subtle or complex demographic scenarios. It also permits testing of heterogeneous processes across the genome (e.g., variation in recombination rate, mutation rate, or the strength of selection). *Limitations* For genomic data, this approach can be computationally intensive, limiting the diversity of evolutionary scenarios that can be explored. However, advancements in algorithm efficiency, statistical comparisons and computational approaches have improved access to a variety of simulations. Designing simulations has often required high-level programming, but user-friendly simulation software packages are now emerging that allow flexible parameter choice (Hoban 2014), as well as efficient workflows for model implementation and comparison

Box 2 (continued)

Association Studies: *Advantages* A variety of methods can be used to discover loci shaped by selection or associated with variation in key phenotypic traits. *Genome scans* identify loci that show large genomic differences between populations ("outliers," de Villemereuil et al. 2014; Hoban et al. 2016). Comparing sequence data near outlier loci to databases of gene function is one way to assess the potential functional significance of such candidate regions for selection. *Transcriptomics* (e.g., using RNA-seq) represents a method in which RNA is compared for differences in a trait of interest between populations, tissues, or environmental conditions. *Genome-wide association studies (GWAS)* involve directly correlating genome-wide variation with defined phenotypic variation (Goddard et al. 2016) potentially revealing one or more loci that are linked to a trait of interest. A related, complementary approach is *quantitative trait locus (QTL) analysis*, in which two phenotypically contrasting individuals are mated and the phenotype in their hybrid offspring is associated with the alleles inherited from each of the original parents (van Buijtenen 2001; Märtens et al. 2016). *Limitations* A dense sample of loci across the genome is required to find outliers. Furthermore, when outliers are detected they often do not show clear links to relevant phenotypes. Transcriptomic results are context dependent, potentially limiting their generality to other biologically relevant conditions. They also only target actively expressed parts of the genome, and so will miss non-expressed regions that may be under selection (e.g., regulatory regions). GWAS can return "false positive" loci if cryptic population or kin structure is not accounted for when testing for associations and requires large sample sizes to detect significant associations, especially if the tested trait is encoded by many loci of small effect. In this respect, QTL analyses have a statistical advantage over GWAS as they are initiated by crossing phenotypically contrasting parents. However, QTL analyses only reveal relatively large chromosomal regions associated with the focal trait. Furthermore, results from experimental crosses are limited by the Beavis effect whereby the QTL effects are overestimated, especially for small-effect QTLs, while the true number of QTLs is underestimated. These results are, in turn, dependent on sample size and heritability. Given the distinctive limitations of individual methods above, in practice two or more methods are often used concurrently

on polymerase chain reaction (PCR) to amplify a standard gene region (e.g., DNA barcode region), and this introduces PCR amplification bias, which results in downstream bias in community assessments (Papadopoulou et al. 2015). PCR-free approaches that use HTS to sequence whole mitochondrial genomes may provide more accurate assessments of diversity and biomass in environmental samples (Bista et al. 2018). The increased resolution provided by these HTS approaches improves biosurveillance detection power and helps clarify the risks posed by insect-vectored pathogens.

Sources and pathways: Where is it from and how does it spread?

Global movement of non-native pests is complex and mirrors the movement of goods and people (Garnas et al. 2016). Understanding the routes of introduction and sources of invasive populations is an important part of pest risk assessments. A pathway analysis focuses on assessing routes of entry and spread of an invasive species, as well as the likelihood of pest introductions at particular points of entry (Yemshanov et al. 2012). Population origin can also help guide the search for biological control agents that are adapted to similar climatic conditions as the invading species (Larson and Duan 2016).

Genomic data gathered from population samples can help improve our understanding of sources of FIAS and their pathways of entry (Fig. 1). Molecular markers derived from sequencing of genes such as mitochondrial DNA or by microsatellite genotyping have already highlighted the power of population genetics to detect migration (or the lack thereof) and assign individuals to source locations (Table 1,

Carter et al. 2009; Cao et al. 2016; Taerum et al. 2016). However, genome-wide scans promise to provide far greater resolution to these questions. For example, whole genome sequencing of humans in Europe led to the identification of distinctive profiles associated with their countries of origin—answering a question that microsatellites had previously failed to address (Novembre et al. 2008; Nielsen et al. 2017). Identifying source populations requires distinguishing populations in their native range with genomic variation, which requires comprehensive surveys of a specie's distribution. Inadequate sampling could miss cryptic diversity or admixed populations that are key sources for new invasive populations. Genomic data is further used to separate regions that evolve under neutrality and reflect differences in population history from those evolving under natural selection, which can be useful for studying adaptations and correlations between genotypes and traits (Fig. 1, Traits). Genome-wide data allow us to delineate groups or populations by clustering methods (Fig. 1, Population clusters) and identify individuals that share common ancestors and geographic origins. The mountain pine beetle (MPB, *Dendroctonus ponderosae*) is a destructive native pest of pines in North America, but has recently spread far beyond its native range into the northern boreal forest (Safranyik and Wilson 2006). This species is now considered invasive within the boreal forest (Nackley et al. 2017), and management of the invasive populations requires detailed knowledge on the invasion routes and spread patterns (Nealis and Cooke 2014). Genome scans were able to resolve MPB's origins in the native range and identify the route of spread through the Rocky Mountains (Janes et al. 2014). Furthermore, they showed that the invasive population of MPB was derived from multiple source populations, rather than a single source

population. Determining the geographic origins of invasives and detecting genomic mixing from multiple source populations have important implications on the ability for new populations to establish and persist in novel environments (Keller and Taylor 2010; Benazzo et al. 2015).

Population history: What is the history of invasion?

Genomics have the potential to reveal much more than the source and pathway of an introduction. Biological invasions progress through a series of stages: transport, colonization, establishment, spread, and adaptation (Blackburn et al. 2011; Brockerhoff and Liebhold 2017). These stages leave distinctive signatures in the genomic variation of a non-native population (Boissin et al. 2012; Chown et al. 2015; Cristescu 2015). Genome scans can be used to reconstruct the history of an invasion and help infer the size of the founding population, assess the demographic history of the invasive population, or identify signatures of adaptation to the new environment (Fig. 1, History, Trait) (Lawson Handley et al. 2011; Cristescu 2015). A powerful approach to reconstruct the invasion histories is through simulation models (Fig. 1. Simulation models). Simulation tools such as approximate Bayesian computation (ABC) can generate introduction and population history scenarios and compared then to the observed data to identify the best fit (Cornuet et al. 2008). This analytical approach resolved the complex global invasion history in the Sirex woodwasp (*Sirex noctilio*) using microsatellites and sequence data (Boissin et al. 2012). Most populations were mixtures of more than one source population, and some were founded by only a few individuals. Characterizing the nature of these founding populations improves our understanding of the invasion process and can have important implications for management strategies (Gray 2017).

Identifying signatures of adaptation in invasive or non-native populations provides key insight to the contemporary processes affecting these species (Colautti and Lau 2015). As we described earlier, MPB is a native pest of North American pine but is now considered invasive since it has expanded into forested regions that have not been historically attacked. Genome-wide data have shown signatures of adaptation in the invasive MPB populations, relative to populations within the native range (Janes et al. 2014; Batista et al. 2016; Lesieur et al. 2018; Lo et al. 2018). A number of genomic regions linked to cellular and metabolic processes showed selection in the northern invasive range of the MPB. Further work on MPB uncovered surprising genomic architecture underlying regional differences among MPB populations, suggesting an interplay between historical population structure and recent adaptations to local environmental conditions (Dowle et al. 2017).

Traits: What traits determine invasion success?

Natural selection—which will determine the outcome of a new introduction—acts on the phenotype, not the genotype; thus, genomic/trait association analyses must target phenotypes relevant to the establishment and success of an invasive species. Identifying the genomic markers for phenotypes that are relevant in FIAS invasions is an end goal for genomic-based monitoring and risk assessment. Host range characteristics or physiological constraints of a novel biotic and abiotic environment are phenotypes that are relevant to the likelihood, severity and spread rate of an invasion (Lehmann et al. 2015; Ju et al. 2017). The effects of these constraints will depend on the FIAS's physiological responses (i.e., its phenotype) and can be used to predict the range of environments where an invasive insect could establish and expand. These data provide a foundation for risk assessment and spread modeling. If these fitness- and outbreak-related traits are genetically based, then the genomic markers of the genotype will allow the phenotype—and therefore potential risk—to be predicted, even without the availability of live material.

Within a genotype, the range of physiological responses to environmentally relevant stimuli can be identified empirically or through association studies (Fig. 1, Geno-Pheno, Quantitative genetics) and used to inform risk models (Box 2). In contrast to correlative models that base predictions on current localities and environmental conditions (Battisti and Larsson 2015; Hill and Thomson 2015), mechanistic models quantify a pest's biology and derive their parameters directly from this phenotypic information to predict responses to novel environments, making them more robust to extrapolation (Maino et al. 2016). This mechanistic approach can provide insight into the appropriateness of the traits selected for modeling, the heritability of those traits and ultimately the probability of FIAS survival and establishment in novel environments.

In insects, some traits, such as flight speed (Lombaert et al. 2014), developmental thresholds (Jarošík et al. 2015), and cold tolerance (Lehmann et al. 2015) are clearly associated with invasiveness and may be useful in predicting some aspects of outbreaks (Philibert et al. 2011; Wu et al. 2015). Cold tolerance, for example, varies among populations (Kleynhans et al. 2014) and life stages (Boychuk et al. 2015), is a good predictor of native insect distribution (Rodriguez-Castañeda et al. 2017), and can determine invasiveness (Brightwell et al. 2010; Lehmann et al. 2015). While these physiological traits should have genomic signatures, these phenotypes are genetically complex, so identifying the genomic markers is not trivial (Hayward et al. 2014; Dennis et al. 2015; Cao et al. 2015). Further, the underlying molecular mechanisms that cause significant phenotypic shifts may not be reflected directly in the genomic sequence,

but through epigenetic modifications or phenotypic plasticity (Bateson 2015; Trucchi et al. 2016). Thus, the identification of genomic markers for these complex traits requires a good understanding of the physiology underlying the trait, the environmental conditions experienced by collected individuals, and the mechanisms causing its plasticity. This complexity represents a significant hurdle for these mechanistic models. Since our knowledge of these mechanisms is still sparse for most physiological traits relevant to FIAS (Han and Gatehouse 1993; Hayward et al. 2014), the identification of markers that are reliably predictive is challenging.

One approach to evaluate the risk of a certain FIAS is to measure these tolerances empirically at their extremes and use that information to predict boundaries for range expansion (Fahrner and Aukema 2018). This approach allows for an estimation of a "worst-case scenario" by testing the hardiest, most prepared individuals under the worst climatic conditions and provides environmental limits for modeling. Since we lack mechanistic-level resolution of the traits commonly associated with FIAS dispersal, assessments across multiple levels of biological organization are likely necessary to link phenotypes to their respective genomic variants. This systems-level approach, combining basic physiological measurements and various "-omics" techniques, is necessary to provide the context for the underlying life history traits of interest.

There are several genomic approaches to establish potential links between genomes and traits (Pardo-Diaz et al. 2015). First, genomic markers of a trait (e.g., flight capacity or cold tolerance) can be identified by mapping the patterns of trait inheritance within families derived from parental crosses that differed in the trait of interest (van Buijtenen 2001) (QTL analysis; Fig. 1, Quantitative genetics). This approach can be powerful since the traits in the crosses are controlled, and progenies have a shared genomic background but will segregate for the trait of interest (Keena et al. 2008). However, the results of this approach may not translate to wild populations and often fail to identify a precise locus or gene responsible for the trait (Storz et al. 2015). A second approach uses large sampling of natural populations that show variation for a trait and performs a genome-wide association study (Goddard et al. 2016) (GWAS; Fig. 1 Quantitative genetics). This approach has the advantage of sampling broadly in populations and increases the likelihood of identifying causative genes. A third approach is experimental and relies on the identification of candidate genes associated with traits based on gene expression patterns associated with a phenotype (e.g., genes expressed during cold treatment that can be linked to cold tolerance) (Pardo-Diaz et al. 2015). Clearly demonstrating the causative link between genotype and phenotype is not trivial (Storz et al. 2015) and will need to account for the allelic and environmental

variation experienced in natural populations, as well as substantive genomic resources which are generally lacking for most FIAS.

Expanding beyond genomics, additional approaches can be used to establish a link between genotype and phenotype. For example, the physiology of host use and overcoming host defenses is a key trait for FIAS invading new habitats. Invasive insects display a superior ability to exploit food resources and overcome host plant defenses, and these processes have been studied at the level of the transcriptome in mountain pine beetle, emerald ash borer and Asian longhorned beetle (Table 1). Improving our ability to predict invasive success in novel hosts would help assess risk of establishment and spread of FIAS. Transcriptomics has also been used to explore the sensory physiology for many invasive beetle species, as well as AGM (Table 1). Olfaction is the primary sensory process by which insects find host trees and locate mates. Transcriptomics can help discover genes involved in odor transport, neuronal signaling, and odor degradation and may give some important clues on its chemical ecology (Mitchell et al. 2017). Thus, transcriptomics is an accessible approach to understand the phenotype of invasive species.

In addition to transcriptomics, other approaches that target functional subsets of the genome, such as proteomics and metabolomics, have the potential to help bridge the biological gap between genotypes and phenotypes within FIAS (Box 2). These techniques can reveal systems-level resolution to physiological mechanisms of invasion-relevant traits, allowing for the assessment of phenotypes that would not have correlated signatures at the transcriptomic level. Metabolomics, for example, has been used to further characterize low temperature survival (Teets et al. 2012; Koštál et al. 2016), diapause (Zhang et al. 2013), and insect/plant interactions (Jansen et al. 2008). These "omic" approaches can also shed light on the roles that gut microbiota may play in the process of invasion or adaptation (Macke et al. 2017). While these methods are in their infancy with respect to FIAS research and management, their use in the field will grow as genomic resources for FIAS improve.

Conclusion

Invasion biology is fraught with uncertainty, but genomics provides a means to improve our understanding of the invasion process. Knowledge on species identity, colonization, spread, and adaptation can help reduce uncertainty and enhance early detection and intervention strategies, thereby contributing to protecting forests from invasive species and reducing their negative economic, social, and ecological impacts. Genomic biosurveillance has the capacity to deliver information that can transform invasive species risk

assessment and management. A number of molecular tools exist that accelerate species identification (e.g., DNA barcoding) and initial forays into invasion genetics hint at the potential for genomic approaches to advance biosurveillance and invasion science. The advent of HTS technologies takes this potential to a new level (Rius et al. 2015; Ricciardi et al. 2017). We can sequence or scan genomes from outbreak and survey samples to gain detailed biosurveillance information, adding new layers of information that were not previously attainable.

We have highlighted examples of how genomic tools can streamline identification, identify invasion pathways, resolve the complexity of spread and dispersal in invasive populations, and help predict the risk that new invasions pose to regional forests. The field of genomic biosurveillance is still in its infancy. The processing and analysis of genomic data is computationally intensive and requires access to bioinformatic expertise. These resources may be unattainable for many end users. We still lack reference genomes for most important forest pests, and the public databases are only sparsely populated with genomic resources. However, technological developments will rapidly change this situation as we have seen in human and public health genomics (Gardy and Loman 2017). The assignment of outbreak samples to sources is already operational in human pathogen outbreaks (Grubaugh et al. 2017). We envision that a similar framework for forest invasive species could be readily implemented, but increased investment in establishing foundational genomic resources for FIAS will be needed for the more challenging task of identifying the underlying traits or mechanisms that can help predict invasiveness.

For many invasive pests, identifying a single "invasiveness gene" is a simplistic goal, particularly given the numerous and complex nature of traits relevant to invasion (Goddard et al. 2016). As more genomic data become available, it will be possible to identify the genetic architecture of these traits, which may ultimately reveal genomic signatures relevant to invasion risk in FIAS. One of the biggest challenges is to match the increasing capacity in genomics with similar advances in phenomics or the study of phenotypic variability (Bateson 2015). Genomic data are most useful when linked to expressed phenotypes so that these traits can be predicted and placed into a spatially explicit risk assessment model.

Genomic surveillance tools are only truly transformative when they are fully implemented and deployed operationally within the plant health regulatory agencies. In Part II (Bilodeau et al. 2018), we examine how genomic biosurveillance can inform management and regulation of FIAS and identify the barriers to their use within this community. We highlight how our bioSAFE project (BioSurveillance of Alien Forest Enemies; https://biosafegenomics.com) can help overcome these barriers and link genomic and phenotypic characterization of invasive FIAS with biosurveillance activities of managers and regulatory agencies.

Author Contributions

All authors contributed to the development, writing, and editing of the following manuscript.

Compliance with ethical standards

Conflict of interest The author declares that they have no conflict of interest.

Human and Animal statement This article does not contain any studies with animals performed by any of the authors.

Appendix 1: Search parameters used in literature search for application of genomic statistical approaches in studies of biological invasion from 2008 to 2017

To assess the adoption of genomic data in research on biological invasions, we used Web of Science to search for articles published between 2008 and 2017 that used the term "invasive species" or "biological invasion*" in their titles, abstracts, or keywords. We compared this count to articles including those search terms while also referring to either genetic methods in general or to genomic methods in particular.

Web of Science search terms to identify studies employing any genetic methods:

TS = (invasive species OR "biological invasion*") AND TS = (gene* OR mitochondria* OR nuclear OR microtsatellite OR "simple sequence repeat" OR SSR OR "short tandem repeat" OR STR OR allozyme* OR genom* OR SNP OR GBS OR RAD OR RAD-Seq OR RADseq OR ddRAD OR AFLP OR RAPD OR RFLP OR transcriptom* OR exom* OR proteom* OR metabolom* OR "whole genome

sequencing" OR "whole-genome sequencing" OR WGS OR "expressed sequence tag*" OR EST OR "signature sequence tag*" OR SST).

Search term to detect studies employing genomic methods:

TS = (invasive species OR "biological invasion*") AND TS = (genom* OR SNP OR GBS OR RAD OR RAD-Seq OR RADseq OR ddRAD OR AFLP OR RAPD OR RFLP OR transcriptom* OR exom* OR proteom* OR metabolom* OR "whole genome sequencing" OR "whole-genome sequencing" OR WGS OR "expressed sequence tag*" OR EST OR "signature sequence tag*" OR SST).

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