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Biological Invasion Theories: Merging Perspectives from Population, Community and Ecosystem Scales

Chabrerie O.[1], Massol F.[2], Facon B.[3], Thevenoux R.[4,5], Hess M.[6,7,8], Ulmer R.[1], Pantel J.H.[9], Braschi J.[6,10], Amsellem L.[11], Baltora-Rosset S.[1], Tasiemski A.[2], Grandjean F.[12], Gibert P.[13], Chauvat M.[14], Affre L.[6], Thiébaut G.[15], Viard F.[16], Forey E.[14], Folcher L.[4], Boivin T.[17], Buisson E.[6], Richardson D.M.[18] and Renault D.[15,19]

Affiliations

[1] Université de Picardie Jules Verne, UMR 7058 CNRS EDYSAN, 1 rue des Louvels, 80037 Amiens Cedex 1, France

[2] Univ. Lille, CNRS, Inserm, CHU Lille, Institut Pasteur de Lille, U1019 - UMR 8204 - CIIL - Center for Infection and Immunity of Lille, F-59000 Lille, France

[3] INRA, UMR PVBMT, Saint Pierre, France

[4] ANSES – Agence nationale de sécurité sanitaire de l'alimentation, de l'environnement et du travail, Laboratoire de la santé des végétaux - Unité de nématologie, F-35653 Le Rheu, France

[5] IGEPP, INRA, Agrocampus Ouest, Université de Rennes 1, 35650, Le Rheu, France

[6] Institut Méditerranéen de Biodiversité et d'Ecologie marine et continentale (IMBE), UMR: Aix Marseille Université, Avignon Université, CNRS, IRD, France

[7] Institut de recherche pour la conservation des zones humides méditerranéennes Tour du Valat, Le Sambuc, 13200 Arles, France

[8] NGE-GUINTOLI, Saint-Etienne du Grès, Parc d'activités de Laurade – BP22, 13156 Tarascon Cedex, France

[9] Department of Computer Science, Mathematics, and Environmental Science, The American University of Paris, 6 rue du Colonel Combes, 75007 Paris, France

[10] Naturalia-Environnement, Ingénierie en écologie, 20 Rue Lawrence Durrell, 84140 Avignon, France

[11] Université de Lille, UMR CNRS 8198—Evolution, Ecology and Paleontology, F-59650 Villeneuve d'Ascq, France.

[12] Université de Poitiers, UMR CNRS 7267 EBI- Ecologie et Biologie des Interactions, équipe EES, 5 rue Albert Turpin, Bat B8-B35, TSA 51106, 86073 Poitiers Cedex 09, France

[13] UMR 5558 CNRS - Université Claude Bernard Lyon 1, Biométrie et Biologie Evolutive, Bât. Gregor Mendel, 43 bd du 11 novembre 1918, 69622 VILLEURBANNE cedex, France

[14] Normandie Université, UNIROUEN, IRSTEA, ECODIV, 76000 Rouen, France

[15] Université de Rennes 1, UMR CNRS 6553 EcoBio, 263 Avenue du Gal Leclerc, CS 74205, 35042 Rennes Cedex, France

[16] Sorbonne Université, CNRS, UMR 7144, Station Biologique de Roscoff, Place Georges Teissier, 29680 Roscoff, France

[17] INRA, UR629 Écologie des Forêts Méditerranéennes, Centre de recherche Provence-Alpes-Côte d'Azur, CS 40509, 84914 Avignon, France

[18] Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, Matieland 7602, South Africa

[19] Institut Universitaire de France, 1 rue Descartes, 75231 Paris Cedex 05, France

Corresponding authors:

David RENAULT

Université de Rennes 1, UMR CNRS 6553 EcoBio, 263 Avenue du Gal Leclerc, CS 74205, 35042 Rennes Cedex, France

Email: david.renault@univ-rennes1.fr

Olivier CHABRERIE

Université de Picardie Jules Verne, UMR 7058 CNRS EDYSAN, 1 rue des Louvels, 80037 Amiens Cedex 1, France

Email: olivier.chabrerie@u-picardie.fr

Abstract

Biological invasions have reached an unprecedented level and the number of introduced species is still increasing worldwide. Despite major advances in invasion science, the determinants of success of introduced species, the magnitude and dimensions of their impact, and the mechanisms sustaining successful invasions are still debated. Empirical studies show divergent impacts of non-native populations on ecosystems and contrasting effects of biotic and abiotic factors on the dynamics of non-native populations; this is hindering the emergence of a unified theory of biological invasions. We propose a synthesis that merges perspectives from population, community, and ecosystem levels. Along a timeline of ecosystem transformation driven by non-native species, from historical to human-modified ecosystems, we order invasion concepts and theories to clarify their chaining and relevance during each step of the invasion process. This temporal sorting of invasion concepts shows that each concept is relevant at a specific stage of the invasion. Concepts and empirical findings on non-native species may appear contradictory. However, we suggest that, when mapped onto an invasion timeline, they may be combined in a complementary way. An overall scheme is proposed to summarise the theoretical dynamics of ecosystems subjected to invasions. For any given case study, this framework provides a guide through the maze of theories and should help choose the appropriate concepts according to the stage of invasion.

Keywords**:** non-native populations; geographic expansion; invasiveness; invasibility; dispersal; phenotypic plasticity; evolution; historical ecosystem; hybrid ecosystem; novel ecosystem

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I. Introduction

The number of invasive non-native populations, defined as organisms that are introduced to a region through human activity, establish self-perpetuating populations, and spread over substantial distances from introduction sites (Richardson, Pyšek & Carlton, 2011), is increasing globally (Seebens *et al.*, 2017). Biological invasions are now widely recognized as a major component of global change that can alter ecosystem functioning (Murphy & Romanuk, 2014; Mollot, Pantel & Romanuk, 2017), and redefine biogeography at a worldwide scale (Capinha *et al.*, 2015). Concomitantly, invasion biology has grown into one of the most vibrant fields of ecology (Simberloff, 2004; Simberloff & Vitule, 2014). The field has accumulated a multitude of hypotheses and theories (Catford, Jansson & Nilsson, 2009), some of which at first sight may appear to be redundant, complementary, or contradictory (Enders, Hütt & Jeschke, 2018). Despite attempts to develop a unified framework (Hallett, 2006; Catford *et al.*, 2009; Blackburn *et al.*, 2011; Dick *et al.*, 2017), the plethora of proposed concepts, theories, and definitions makes it difficult to navigate this theoretical maze. As a result, choosing and applying the appropriate theory to a given case of invasion represents a major challenge. Nowadays, despite strong connections between ecological and evolutionary concepts of invasion biology (Facon *et al.*, 2006; Vanderhoeven *et al.*, 2010), an integrated view of the spatio-temporal dynamics of the invasion process is still lacking.

Most of the theories proposed so far to explain invasions are useful, and valid, at least partly, for a given species (or group of species), habitat, invasion stage, spatial or temporal scale. Meanwhile, given the huge evolutionary and functional diversity that exists in the global invasive biota, a single model that describes or profiles a "good invader" or a "successful invader" is clearly an unrealistic aim (Facon *et al.*, 2006; Kueffer *et al.*, 2013). Moreover, divergences between empirical evidence are frequently reported, as are discrepancies between theories and observations (Jeschke, Pyšek & Richardson, 2012). Consequently, the main predictors driving differences in the magnitude of the invasion success in recipient communities and ecosystems are not understood in general.

Three challenging questions currently dominate the research agenda in invasion biology: (1) How can the exceptional success of some invasive populations in recipient environments be explained? (2) What effects do invasive populations have on local communities? (3) What will be the features of tomorrow's ecosystems? Work addressing these questions during the past two decades has mainly been focussed at population and ecosystem levels, with insights at the ecosystem level being increasing being sought when addressing these questions.

Here, we propose a synthesis that integrates perspectives on biological invasions at population, community and ecosystem levels to highlight the spatio-temporal and functional links between invasion theories at different stages of the introduction-establishment-naturalization-invasion continuum (*sensu* Richardson & Pysek, 2006). While studies are mostly taxon-focused, we include all potentially invasive populations in all groups, and their interactions. Along a theoretical timeline from the importation of propagules to the transformation of ecosystems and ecosystem services driven by non-native populations (Hobbs *et al.*, 2009; Richardson & Gaertner, 2013; Hobbs et al., 2014), we order concepts and theories related to invasions to picture their chaining and relevance during the sequential stages of the invasion process. Each concept and theory is

emphasized with a short name in bold and can be retrieved along the invasion timeline presented in Figure 1. In so doing, we organize the variety of concepts associated with invasion processes and incorporate them into an innovative spatio-temporal framework. Our invasion timeline, besides allowing the positioning of events that play out over a range of time scales such as spatial sorting, alteration of ecological interactions, or evolution, opens valuable research questions on the functioning and fate of future ecosystems and their underlying services. This perspective better captures the range of transformations occurring at population, habitat and ecosystem levels, their interconnections and feedback loops. In particular, it emphasizes the importance of the temporal dynamics of invasion processes and the unintended effects they may have on the rest of the ecosystem.

II. Introduction and establishment of non-native populations in historical ecosystems

(1) Pre-introduction events: the traits of non-native populations in their native ranges and transport

One of the first keys of the success of non-native organisms' integration into historical ecosystems may be found in the features of populations and environments in the native range of the species (Renault *et al.*, 2018).

Key adaptation events of non-native populations may occur at different steps of the invasion process (Rey *et al.*, 2012). Most studies focus on evolutionary changes that occur following introduction to the recipient habitat (i.e., post-introduction adaptation scenario, Lee, Remfert & Gelembiuk, 2003) or, more specifically at a primary site of invasion (Lombaert *et al.*, 2010). Adaptation events that take place before introduction within the native range of the invader (i.e. prior-adaptation scenario) are less often considered. However, a preselection of traits responsible for the invasive character of a non-native population may occur in its native area (**1: PRESE**, Fig. 1) (Rey *et al.*, 2012). This is particularly true when ecotypic variation exists in the native range. For instance, the invasion of Israel by the tropical ant *Wasmannia auropunctata* likely occurred after the sampling of a particularly cold-tolerant population at the southern limit of its native range (Rey *et al.*, 2012). In addition, multiple introductions from different source populations are expected to increase invasion probability, as reported in the green crab *Carcinus maenas* whose northward expansion in the eastern North America may have been facilitated by a second independent introduction of a presumably cold-adapted ecotype from Europe (Jeffery *et al.*, 2017; 2018).

Similar ecological niches, or at least similar climatic environments, occur in many parts of the world that have been connected through human-mediated transportation of species. In some instances, invasion may be facilitated by the introduction of organisms in regions displaying environmental characteristics, including climate, soil, disturbances, similar to those of their native range, as highlighted by Hufbauer *et al.* (2012). In this vein, a non-native population would be "pre-adapted" to environmental conditions of the recipient ecosystem (**2: PREAD**) (Mack, 2003; Vermeij, 1991). For example, in marine environments, ocean sprawl, i.e., the worldwide artificialization of coastal marine habitats, is a major driver of invasion success (Bishop *et al.*, 2017). This high prevalence of non-native organisms in artificial habitats, which are hubs and bridgehead for their future spread (**3: BRIDG**, bridgehead scenario/effect, Lombaert *et al.*, 2010), may presumably result

from adaptation to resist some particular abiotic factors typical of these habitats (such as pollutants, climatic conditions, availability of trophic resources), which evolved in their native range.

The continuing increase in the number of invasive populations worldwide (Seebens *et al.*, 2017) is strongly related to anthropochory (**4: ANTHRO**) through inter- and intra-continental exchanges (Perrings *et al.*, 2005). Populations are transported along commercial and touristic routes by aircraft, ships, cars or hikers. For example, invasion routes of the fruit fly *Drosophila suzukii* are closely related to fruit trade flows and pathways (Cini *et al.*, 2014); the invasion of European countries by the horse chestnut leafminer *Cameraria ohridella* was supported by flows of people, cars, trains and trucks (Gilbert *et al.*, 2004). The invasion of the Great Lakes drainage basin by numerous Ponto-Caspian species, such as *Dreissena* mussels, has been ascribed to ballast waters (Ricciardi & MacIsaac, 2000). A model based on observational data also showed that both shipping intensity and habitat match are good predictors of the risk of marine invasion (Seebens *et al.*, 2016).

Unbridled anthropochory can lead to the introduction of multiple populations (Fig. 1). This process increases propagule pressure and the probability of population establishment. The Propagule Pressure Hypothesis **(5: PROP)** (Simberloff, 2009), also known as "introduction effort" hypothesis (Blackburn & Duncan, 2001), combines the number of propagules introduced and the number of introduction events. It is recognized as a major universal determinant of establishment and further colonization success of non-natives. As such, this hypothesis is often seen as the "null model" when looking for determinants of species invasions (Colautti, Grigorovich & MacIsaac, 2006; Cassey *et al.*, 2018). Indeed, high propagule pressure increases the probability of persistence of the non-native populations by counteracting negative effects associated with small populations (mostly Allee effects), and helps increase genetic diversity, and thus adaptive potential of non-native populations.

(2) First contacts of non-native organisms with their recipient ecosystems

Non-native organisms can fail to integrate into the introduction area, partially succeed in integration, or become fully integrated and establish self-perpetuating populations. Williamson *et al.* (1996b) studied the proportion of imported species (including pests) achieving different levels of invasion success: 1 in 10 imported plants or animals subsequently appear in the wild (introduced or casual) into recipient communities. The same proportional rule prevails between introduced and naturalised populations, and between naturalised and invasive populations (**6: 3TENS**, the "*3 tens rule*"; Williamson, 1996a).

The causes of invasion failure are still poorly studied. In most cases, characteristics of individuals do not match with biotic and/or abiotic characteristics of the area of introduction (but see below **7: SINV**, **8: EINV** and **9: ELTON**). In some instances, non-native population characteristics and recipient environment characteristics may match only partially. In this case, the newcomer organisms face difficulties to fully ensure their fundamental biological functions. For instance, some non-native plants are unable to reproduce sexually in their invasion range (Lambertini *et al.*, 2010). Their proliferation is almost exclusively or totally ensured by clonal multiplication (**10: CLON**), at least in the early stage of the invasion process. Their sterility can be due to sub-suitable climatic conditions in recipient ecosystems (e.g. too cold to allow reproduction), to pollen sterility or auto-incompatibility, to the absence of cross-fertilization (low number of partner or dioecious species with only one sex introduced in the invasion range (Lambertini *et al.*, 2010), or to the absence of associated pollinators (Bufford & Daehler, 2014). Importantly, this apparent weakness of the lack of sexual reproduction may be converted into an advantage when

vegetative reproduction is more efficient than sexual one for invading recipient ecosystems (Lambertini *et al.*, 2010). Such clonal reproduction is frequent among non-native ornamental populations (Bufford & Daehler, 2014) and aquatic plants, and has been reported in both recent (*Elodea nuttalllii*, *Lagarosiphon major*; *Egeria densa*) and ancient *Vinca minor* (Darcy & Burkart, 2002; Čepková *et al*., 2016) plant invasions.

The successful integration of non-native organisms in the new area highly depends on their intrinsic characteristics, i.e. species invasiveness (**7: SINV**) (Pyšek & Richardson, 2007; Richardson & Pisek, 2006), and on the characteristics of the recipient environment, i.e. ecosystem invasibility (**8: EINV**) (Alpert, Bone & Holzapfel, 2000; Richardson, 2006). Invasiveness and invasibility usefully tease apart the determinism of species invasions. These concepts avoid dressing one-sided considerations that would assign the "invasive" attribute to a species regardless of the characteristics of the invaded habitat, or conversely attribute the feature "invasible" to an ecosystem regardless of the traits of potentially invasive organisms (Sol, Vilà & Kühn, 2008). A more synthetic view integrates the relationship between **SINV** and **EINV**. For instance, the framework proposed by Hui *et al.* (2016) considers the invasion fitness of an introduced population as a function of its trait value relative to the trait values of resident populations, or relative to the degree of trait saturation in the recipient community. Similarly, David *et al.* (2017) highlighted that the phylogenetic, functional, or ecological originality of an invading population relative to the recipient community can also affect the likelihood of its establishment success.

(3) Key determinants of species invasiveness

Species invasiveness (**7: SINV**) resides in (i) the performance, (ii) the originality and (iii) the plasticity of functional traits. Yet, the ability to predict which introduced populations will become invasive remains fuzzy (Mack *et al.*, 2000; Williamson, 2006; Romanuk *et al.*, 2009). Several authors have tried to resolve this question by asking whether invasive populations share biological traits and, in parallel, whether invaded habitats have similar features to ascertain which ones could be associated to ecosystem invasiveness **(8: EINV)** (Lonsdale, 1999; Kolar & Lodge, 2001; Romanuk *et al.*, 2017).

The functional traits that enable a non-native population to become a successful invader **(7: SINV)** are usually those that favour fast reproduction and dispersal to rapidly establish viable populations. Those traits are, for plants, high ploidy level and uniparental reproduction, and for plants and animals, high reproduction rate, high phenotypic plasticity, broad and flexible diet, reduced systemic inflammatory responses (Lee & Klasing, 2004), and a broad ecological tolerance that allow establishment and subsequent potential spread (Rejmanek & Richardson, 1996; Alpert, Bone, & Holzapfel, 2000; Kolar & Lodge, 2001; Pyšek & Richardson, 2007). The meta-analysis of van Kleunen *et al.* (2010) established that invasive plant species generally have higher values of performance-related traits (**11: HTRAIT**) characterizing physiology, leaf-area allocation, shoot allocation, growth rate, size, i.e. better values for many proxies of plant fitness, than non-invasive species do. However, several contradictory results of global analyses searching for important traits have been reported (Daehler, 2003; Leffler *et al.*, 2014). For Kueffer *et al.* (2013), conclusions about the invasiveness and impacts of a non-native species can be misleading without an understanding of the anthropogenic, ecological and evolutionary processes.

The Life History hypothesis (described as "Ideal Weed" in plant ecology) is directly related to the invasiveness concept and focuses on traits of non-native plant populations enhancing their establishment, spread and/or competitive abilities allowing to outcompete indigenous populations (Elton, 1958). Among these traits, in light of Baker's law (Baker, 1967), uniparental reproduction through, for instance, autonomous selfing or asexual reproduction is likely to be part of the invasiveness syndrome. Indeed, uniparental reproduction has consistently been reported in invasive terrestrial plants, across biogeographic regions and taxa (van Kleunen & Johnson, 2007; van Kleunen *et al.*, 2008), as an important trait for both establishment and spread (Pannell *et al.*, 2015). However, theoretical models on the evolution of dispersal and selfing in plants indicate that selfing in invasive species could only be expected under certain circumstances, not in general (Cheptou & Massol, 2009; Massol & Cheptou, 2011a, 2011b).

Compared with their native congeners, many non-native individuals possess original, species-unique traits, which can contribute to their invasion potential (**12: TRAIT**), i.e. no functionally equivalent trait is present among the species of the invaded ecosystem (Atallah *et al.*, 2014; Macel *et al.*, 2014). Individuals with novel life form arriving in a new environment have good chances to become invasive (Mack, 2003). In particular, a limited functional redundancy with native organisms enhances establishment success (Ordonez, Wright, & Olff, 2010; Divíšek *et al.*, 2018). Accordingly, the concept of limiting similarity (**14: SIMLIM**; Abrams, 1983) states that invasive populations will be unlikely to establish in a community dominated by functionally similar populations because of greater niche overlap (MacArthur & Levins, 1967; Funk *et al.*, 2008). Numerous studies have investigated the role of limiting similarity in invasion success, sometimes supporting (e.g. Dukes, 2001; 2002; Wang *et al.*, 2013), sometimes contradicting (e.g. Larson *et al.*, 2013; Yannelli *et al.*, 2017) the **SIMLIM** theory. For example, Dukes (2002) found the summer-active annual invasive forb *Centaurea solstitialis* to be most effectively suppressed by the presence of *Hemizonia congesta* ssp. *luzulifolia* which belongs to the same functional group. Conversely, Larson *et al.* (2013) showed that invasion success of the thistle *Cirsium arvense* was not affected by the presence of confamilial species, while early establishment of dissimilar guilds had negative effects.

Adaptive phenotypic plasticity, which confers high performance in a broad range of environmental conditions (Richards *et al.*, 2006), may also be key of establishment success, by allowing an invader to thrive in environmental conditions that only partially match those of its native area (see Renault *et al.*, 2018 for a review). According to the phenotypic plasticity hypothesis **(13: PLASTI)**, invasive organisms may have a greater plasticity in ecologically important traits as compared with non-invasive ones. In addition, populations of invasive species are expected to evolve greater plasticity in their invasive range compared to populations within the native range (Richards *et al.*, 2006). The phenotypic plasticity hypothesis has supporting examples (e.g. Davidson, Jennions, & Nicotra, 2011), but also counter-examples (e.g. Palacio-López & Gianoli, 2011). Fewer studies compared invasive and non-invasive populations, and most of these investigations concern plants. For instance, Lamarque *et al.* (2015) compared populations of *Acer negundo* and *Acer platanoides* from both their invasive and native ranges. These authors found that invasive populations of *A. negundo* expressed greater plasticity for diameter growth and phenological sensitivity, while no differences were observed between populations of *A. platanoides*.

According to (Lande, 2015) the discrepancy in the observed tendency can be explained by several parameters, including the type of plasticity (reversible vs. irreversible). Plasticity should theoretically be highly beneficial at the early stages of invasion, because of the probable costs of maintaining plasticity (van Kleunen & Fischer, 2005), and because it may allow for novel genetic variation to arise (Pigliucci, Murren, & Schlichting, 2006). A trait may then lose its environmental sensitivity, and therefore become stable to environmental changes by genetic assimilation (Pigliucci *et al.*, 2006). However, fluctuating environments are predicted to favour phenotypic plasticity, and this could explain the long-term persistence of plasticity in invaders of disturbed areas. The maintenance of adaptive plasticity could also be based on particular molecular genetic mechanisms, such as environmentally sensitive alleles, regulatory loci or epigenetic variation inducing environment-dependent expression patterns (Bock *et al.*, 2015; Estoup *et al.*, 2016; Gutekunst *et al.*, 2018).

Searching for lists of traits related to invasiveness, such as phenotypic plasticity or original traits, has often remained inconclusive (Mack *et al.*, 2000). These traits are only applicable to a few taxonomic groups (Kolar & Lodge, 2001) and are context-dependent (Leffler *et al.*, 2014). This extensive work on traits has revealed the large variety of invasive strategies, which depends on the temporal interaction of habitat characteristics and individual traits (Fig. 1). Importantly, the determinism and role of traits of invasive organisms change with the stage of ecosystem transformation, and this has been poorly considered so far. In historical ecosystems, trait characteristics of the newcomer (performance, originality and plasticity) have been acquired/preselected in their native areas. At this initial stage of invasion, trait originality seems to be a particularly important requisite, as the new populations need to make use of original niche and resources. Furthermore, trait plasticity enables invaders to enter and occupy disturbed and environmentally varying habitats across the globe.

(4) Biotic resistance as guardian of historical ecosystems

Ecosystem invasibility (**8: EINV**) is determined by abiotic (physico-chemical factors) and biotic components (e.g., local community composition, ecological networks, competition, predation). The biotic resistance of the recipient ecosystem partly explains the failure of many invasion attempts, previously described by the 3 tens rule (**6: 3TENS**). Some historic ecosystems are species-rich, stable and may hinder the infiltration and integration of new populations. Since Elton's hypothesis (**9: ELTON**), we know that species richness in a community partly explains its resistance to the arrival and integration of new populations, including non-native populations (Elton, 1958; Levine & D'Antonio, 1999). In theory, at least two different mechanisms can explain this pattern: either resource and niche availability decrease with species richness, or species-rich communities tend to comprise competitively superior species (Stachowicz & Tilman, 2005). Most experimental tests to date seem to favour the former interpretation, i.e. that species-rich communities are protected against invasion through a saturation of niches and a decrease in resource (Tilman, 1997; Stachowicz & Tilman, 2005; but see Hodgson, Rainey & Buckling, 2002 for an experimental counter-example involving species dominance in bacterial communities). Such a biotic resistance hypothesis assumes that the number of filled niches should be greater in a species-rich assemblage, which would also include a greater number of predators and competitors (Crawley *et al.*, 1999).

Both native plant species richness and functional group identity are important mediators of opportunities for the establishment success of an invasive population, as shown for the waterweed *Lagarosiphon major* (Petruzzella *et al*., 2018). The number of non-native populations in an ecosystem accumulates over time, and may also modify (increase or decrease) the biotic resistance of historical ecosystem. Previous invasions can increase invasion resistance for functionally similar invaders by removing the populations more sensitive to invasion (Rodriguez, 2001). Conversely, ingress of a non-native population may also open the door for further invasive ones, as suggested by the invasional meltdown hypothesis (**49: MELT**) which is discussed below. Stohlgren *et al*. (1999) showed that hot spots of plant diversity and biodiversity in general were successfully invaded by non-native plant populations in many landscapes in the USA, with a probable link with the degree of resource availability in native plant communities, independently of species richness. It was thus suggested that high species richness may not systematically support a complete use of all available resources, community stability, or resistance to invasion; conversely negative richness-invasibility correlations might not always be due to ecological processes but might instead be attributed to sampling effects (Wardle, 2001). Levine, Adler & Yelenik. (2004) also suggested that biotic resistance may have a stronger influence on the non-native populations, once established, than during their establishment (Levine *et al*., 2004), as exampled by invaded native fish communities in the USA (Carey & Wahl, 2010). Similarly, microcosm experiments by Dukes (2001) suggested that functional diversity is a better proxy of resistance against invasion, whereas species diversity is a good proxy of resistance against negative effects of the invader on the ecosystem, once established (Dukes, 2001).

Among the most important contributors of biotic resistance to invasions are the local native consumers / predators. Native consumers could prefer non-native over native prey, and may consequently limit invasions (Parker & Hay, 2005). The mechanism behind this susceptibility of non-native prey to native consumers may be the absence of shared evolutionary history. The increased susceptibility hypothesis (**15: ISH**; Colautti *et al*., 2004) posits that non-native prey have not experienced selection from these consumers and therefore lack effective defences.

Several theoretical studies have assessed species invasiveness and ecosystem invasibility from a food web perspective, mostly by using the niche model of Williams & Martinez (Williams & Martinez, 2000). Such work suggests that low-trophic level generalists are better invaders than specialists or higher-level consumers (Romanuk *et al*., 2009). Conversely, more densely connected food webs are more resistant to invasions (meeting Elton's hypothesis, but through the number of links rather than the number of species), but suffer larger extinction cascades when a successful non-native population invades (Romanuk *et al*., 2017). Food webs with more compartmentalization (where food webs are subdivided into groups of species that are more likely to interact with one another than with those outside the compartment) were also less susceptible to invasion (Krause *et al*., 2003). Finally, the theoretical study of Hui *et al.* (2016), based on the evolutionary food web model of Loeuille & Loreau (2005), indicates that the invasibility of recipient communities depends not only on their food web architecture, but also on the ecological characteristics and properties of the invading individuals.

(5) Invasibility of habitats and ecosystems

Many historical ecosystems show weaknesses and breaches ('invasion windows" sensu Johnstone, 1986) that are exploited by non-native populations at their establishment. The high invasibility of historic ecosystems, developed below, are mainly related to the use of niches neither exploited by local competitors nor defended by local enemies, such niches being more likely to occur in disturbed and heterogeneous sites.

In colonized habitats, non-native populations can potentially escape predators, pathogens, and parasites, which can be grouped under the general term "enemies" (Enemy Release Hypothesis, **16: ERH**; Keane & Crawley, 2002). This hypothesis predicts that a newly introduced invader establishes because of the lack of regulation by natural competitors and enemies (Williamson & Fitter, 1996; Keane & Crawley, 2002). For instance, using 26 host species of molluscs, crustaceans, fishes, birds, mammals, amphibians and reptiles, Torchin *et al*. (2003) found that introduced populations are less heavily parasitized than native ones. The absence of control by native enemies can in turn be partly explained by the Behavioural Constraint Hypothesis (**17: BCH**). **BCH** establishes that potential consumers and competitors need behavioural adaptations before recognizing and readily consuming or outcompeting an introduced population under natural conditions (Lankau, Rogers & Siemann, 2004). The absence of native "ecosystem guards" capable of slowing the progression of non-native population may increase the establishment success and geographic expansion in the invaded area.

According to the Empty Niche Hypothesis (**18: ENH**; Stachowicz & Tilman, 2005), unsaturated ecological niches are poorly occupied because of their short evolutionary history (e.g., recent volcanic islands), their climatic (glaciation-deglaciation in northern systems), geologic and topographic (isolation of mountain ecosystems) histories, or their degree of anthropogenic alteration. The establishment success of non-native populations relies on the assumption of niche differentiation with native populations, involving either the exploitation of unused resources (empty niche), or enhanced competitive ability to access a shared resource (niche replacement). The functioning of the less interactive populations within these types of communities has also been described by the neutral theory (**25: NEUTR**; Hubbell, 2001; Chave, 2004). This theory has been applied to invasions with contrasted successes (Fargione *et al.*, 2003; Herben *et al.*, 2004; Tilman, 2004), even though it represents an opportunity (**26: OPPO**) that may ease the integration of non-native populations (Chabrerie *et al.*, 2008).

The combination of the use of an empty niche and enemy-release opportunities (**18: ENH** and **16: ERH**) is likely to facilitate the establishment of non-native populations (Shea & Chesson, 2002). Both **ENH** and **ERH** invoke aspects of Charles Elton's hypothesis in seeking to explain the low biotic resistance of ecosystems. In this respect, insular ecosystems are particularly sensitive to the effects of invasion because they are often 'ecologically unsaturated', as depicted by the high number of non-native populations generally recorded on islands (Patiño *et al*., 2017). The high level of endemicity of island communities, which, in several instances, evolved under lower biotic pressures and in relative isolation as compared with continental communities, can make them more easily invaded by non-native populations. A famous example is the brown tree snake *Boiga irregularis* which decimated the avian forest community on Guam which was naïve to tree climbing

predators (Wiles *et al*., 2003). A plant example is the invasion of the non-native tree *Casuarina equisetifolia* on recent volcanic flows on La Reunion Island (Potgieter *et al.* 2014). Other examples are the ability of the invasive fruit fly *Drosophila suzukii* to use unripe and ripening fruits before the other drosophila feeding on ripe and rotting fruits (Poyet *et al*., 2014), or invasive seed wasps who have priority access to limited resources due to earlier phenology than their competitors (Gidoin, Roques & Boivin, 2015). Such cases point to invasive populations accessing unused or under-utilized resources or to gain competitive advantage to exploit shared and limited resources, leading to significant community-level impacts.

(6) Environmental heterogeneity and habitat disturbance favour invasibility

The environments in which invasions proceed are generally spatially and/or temporally heterogeneous in both their biotic and abiotic components. Environmental heterogeneity is likely to favour invasibility **(19: HETE)**, possibly promoting coexistence mechanisms between native and non-native populations and limiting the ecological impact of invaders (Melbourne *et al*., 2007). For instance, pulsed resources generate episodes of increased resource availability that can both increase niche opportunities and relax interspecific competition; this can favour the establishment of non-native populations and the ability of native population to persist in the presence of competitive invaders (Davis, Grime & Thomson, 2000; Shea & Chesson, 2002). The environmental heterogeneity hypothesis also encompasses the Fluctuating Resource Hypothesis raised by Davis *et al*. (2000). This hypothesis assumes that invasion success can be favoured if (i) some resources are not (much) used (unsaturated niche, low to absence of functional redundancy), or (ii) if there is a temporal or spatial increase in resource availability for an opportunistic invader (Thiébaut, 2005), either through increase of supply (eutrophication), or (iii) resource use decreases through, for example, the local extinction of a competitor (Sher & Hyatt, 1999; Davis *et al*., 2000). In many cases, this biotic and abiotic heterogeneity, which increases habitat invasibility, result from human-mediated disturbances.

Habitat disturbance (**20: DIST**) is globally recognized as an important feature of susceptibility to the installation and spread of non-native populations (Lozon & MacIsaac, 1997). Many easily invaded environments correspond to disturbed ones, especially on oceanic islands (D'Antonio & Dudley, 1995). Invasion frequency generally increases as levels of disturbance or ecosystem modification increases (Lonsdale, 1999; Richardson & Pysek, 2006), as habitat disturbances affects native population abundance and diversity, in turn favouring non-native populations (Didham *et al*., 2005). MacDougall & Turkington (2005) were among the first to empirically test the effects of habitat disturbance and invasive population abundance on native species declines using invasive grasses in fire-suppressed oak savanna of British Columbia. Other example includes the intensive grazing which exacerbated the dominance of the invasive annual grass *Bromus tectorum* in the endangered *Artemisia tridentata* big sagebrush ecosystems of the Intermountain West, USA, by disrupting key resistance mechanisms associated with bunchgrass abundance and composition (Reisner *et al*., 2013).

(7) Life history strategies of the colonizers along an invasion course

The constellation of human-modified sites provides an intercontinental network of disturbed niches that facilitates the installation of r-strategy non-native populations (**21: RSTR**). These r-strategist populations/species are likely to be replaced by more competitive populations/species in later stages of the invasion (Facon *et al.*, 2008). From this observation, two types of invasions can be distinguished: (i) early or "primary" invasions involving the appropriation of empty or poorly exploited niches and (ii) "secondary" invasions corresponding to the annexation of already occupied niches, possibly leading to competitive exclusion of taxa already present in those niches. Obviously, these two types of invasion are not expected to be associated with the same life-history strategies (Facon *et al.*, 2006). Primary invasions will more frequently be caused by r-strategist species (Davis, 2005) with a set of life-history traits that facilitate colonization e.g., small size, early reproduction, high fecundity, short-life expectancy. A good illustration has been highlighted by Rejmánek & Richardson (1996) who showed that pine species that invade habitats undergoing strong disturbances were mainly characterized by three r-selected traits, i.e., short juvenile period, light seeds, and short time intervals between breeding events.

On the contrary, secondary invasions will stem from K-strategist species with a set of life-history traits associated with competitive abilities, e.g., large size, late reproduction, low fecundity, long-life expectancy (**22: KSTR**). Two series of successive invasions, one concerning Tephritid flies in La Réunion island (Duyck *et al.*, 2007) and the other on Thiarid snails in Martinique island (Facon *et al.*, 2008), illustrate this process. In both situations serial replacements of taxa already present by better competitors occured in the same habitat. The key traits determining invasion success can be expected to shift during the course of an invasion (Sakai *et al.*, 2001). Specifically, features related to r-strategies will be advantageous in the initial phases of invasion that mostly occur in historical ecosystems. Traits related to K-strategies will be favored in the subsequent stages of the invasion, when the invader enters into competitive interaction with the already invaded community in hybrid and novel ecosystems. A meta-analysis in birds suggested that invasiveness cannot be solely explained by the r-K trade-off (Sol *et al*., 2012). A bet-hedging life history, characterized by delayed reproduction and longer lifespan, could be the best invasive strategy reducing (i) the risk of reproductive failure associated with maladaptation to a novel environment and (ii) population fluctuations (Sol *et al.*, 2012). It has been supported experimentally in an invasive ladybird by Tayeh *et al.* (2015), who highlighted that life histories can evolve rapidly within non-native populations, converging to a fine-tuned evolutionary match between the invader and the invaded environment.

(8) Low effects of non-native populations on native diversity in the early stages of introduction

At the onset of the invasion process, when the non-native population has been recently introduced into a historical ecosystem, its impact on community composition and ecosystem processes is usually superficial or even undetectable. This "ecological silence" accompanying the first stages of an invasion (latency period after introduction; **1: LATE**) could explain why the reality of the consequences of invasive species on their host environment was initially hotly debated (Gurevitch & Padilla, 2004; Asner *et al.*, 2008; Simberloff *et al.*, 2013). In the 1990s and early 2000s, a few studies demonstrated the effective impact of non-native plants on the diversity (especially species richness) of native plant communities (Costello, Lunt, & Williams, 2000). The relationship between the

richness of non-native species and that of native species could even be positive according to the spatial scale of observation (Sax, 2002; Byers & Noonburg, 2003) and the nature of the interactions between the native and the non-native species. For example, the presence of the invasive Water Primrose can have a positive effect on local diversity and ecosystem processes since the plant may act as a 'magnet' species facilitating pollinator visits to the native species *Lythrum salicaria* (Stiers, Coussement, & Triest, 2014).

Native and non-native species diversity are often positively correlated in large-scale studies, but negatively correlated in small-scale studies (Sax, 2002; Byers & Noonburg, 2003). Indeed, the same factors (light, degree of human-mediated modification of habitats, etc.) can have a positive effect on both non-native and native species, generating correlations between the diversity of the two groups of species, without the existence of strong causal relationships between native and non-native species diversity. The simple correlation between dominance of non-native populations and decline of native diversity does not constitute evidence that diversity changes are driven by non-native populations (Didham *et al.*, 2005).

III. Expansion of non-native populations and modifications of assembly rules in hybrid ecosystems

The main events characterizing the post-establishment stage of non-native populations are (i) their expansion, with a progressive adaptation to the environments encountered in their invasion area, and (ii) the modifications of assembly rules in hybrid ecosystems.

(1) Paradoxical success of genetically impoverished populations

Invasive populations are generally thought to be founded locally by a small number of individuals (Dlugosch & Parker 2008) representing a more or less reduced fraction of the genetic diversity of the source population (Nei *et al.*, 1975; Barrett & Husband, 1990). This population/genetic bottleneck leads to high inbreeding levels (**27: INBRE**) in introduced populations (Willi, van Buskirk, & Hoffmann, 2006). Furthermore genetic diversity is considered an important basis for the ability of populations to adapt to new environmental conditions (Fisher, 1930). From these two assumptions emerges the Genetic Paradox of Invasions (**28: GPI**): how do invasive populations adapt to the novel selective pressures encountered in the introduced area despite presumed reduced genetic diversity (Sax & Brown, 2000; Estoup *et al.*, 2016)? In this context, genetic analyses investigations first focused on comparing levels of genetic diversity between native and introduced populations (Bossdorf *et al.*, 2005; Dlugosch & Parker, 2008; Wares *et al.*, 2005). Many authors showed decreased levels of genetic diversity in the introduced populations compared with the native populations (Hagenblad *et al.*, 2015). However, reduced genetic diversity is not the rule in every environment. In particular, twenty years of genetic studies of introduced marine and aquatic populations have consistently reported similar or higher genetic diversity in introduced populations compared to their native counterparts (e.g., 76% of the European marine introduced species, Rius *et al.*, 2015). High propagule pressure from genetically diversified sources (**5: PROP**) can explain this pattern (Rius *et al.*, 2015, Viard *et al.*, 2016). Dlugosh *et al.* (2015) suggested that there is little explanatory power of the level of measured (and often neutral) genetic diversity on the introduction success. This does not imply that genetic variation is not important to consider,

because 1) admixture processes may create evolutionary novelties, and 2) neutral genetic diversity may not correspond to adaptive variations on traits that are relevant for invasiveness (Rius & Darling, 2014; Dlugosh *et al*. 2015; Viard *et al.*, 2016).

Genetic bottlenecks do not seem to constrain invasive success (Sax *et al.*, 2007), or even prevent rapid adaptive change (Prentis *et al*., 2008), as illustrated with the invasion case of *Drosophila subobscura* in Chile (Huey *et al.*, 2005). Severe genetic bottlenecks have been demonstrated for introduced populations worldwide. This is, for example, the case of the seaweed *Sargassum muticum*, for which 14 microsatellites failed to detect any genetic variation over >1200 individuals sampled from 46 locations over its Pacific and Atlantic introduction ranges (Le Cam *et al.*, 2019). In the same study, distinct introductions, but all accompanied by a severe genetic bottleneck, were then confirmed with ddRad-Sequencing. As pointed by Prentis *et al.* (2008), it is noteworthy that genetic bottlenecks can enable rapid adaptive change to occur (through the conversion of epistatic variance to additive variance for example (Whitlock *et al.*, 1995) or a complex interaction between inbreeding depression and recipient environment (Schrieber & Lachmuth, 2017). Alternative mechanisms such as phenotypic plasticity (**13: PLASTI**) could play a major role in the rapid adaptation of invasive populations as suggested for the parthenogenetic marbled crayfish (Gutekunst *et al.*, 2018).

The genetic (and ecological) paradox between inbreeding depression and adaptive success of non-native populations may also be solved by understanding the evolution of the mutation load during the invasion process. The mutation load is defined as the proportion by which the population fitness, or any other attribute of interest, is altered by recurrent mutation (Kimura, Maruyama & Crowe, 1963), and which constitutes a genetic burden. Consanguineous mating can purge a part of the mutation load and lethal mutations can also be purged in small populations (Glémin, 2003). Thus, small populations of non-natives, through the increase of consanguineous mating, may benefit from this purge of homozygous deleterious alleles (**29: PURG**) reducing their mutation load and promoting invasion, as it has been shown for the invasive harlequin ladybird (Facon *et al*., 2011).

(2) Evolution of traits in non-native populations

At early invasion stages, traits (variations in morphological, reproductive, life-cycle, physiological or chemical attributes) of individuals of non-native populations frequently differ from those of their congeners from the native range. Because they escape natural enemies in their invasive range (**16: ERH**), non-native populations can save the energy formerly used for defence, and reinvest it in growth, biomass, reproduction and competitiveness. This theory (Evolution of Increased Competition Ability, **30: EICA**) first studied in plants (Blossey & Nötzold, 1995) -and modified by Joshi & Vrieling (2005)- may partly explain the classic phenomena of latency during naturalisation (**23: LATE**), and the sudden explosion of invasive populations after environmental filtering during the expansion stage (Pyšek & Prach, 1993). This could also explain and reinforce the differences in performance commonly observed between native and non-native populations (Heberling & Fridley, 2013), or between different populations of non-native species differing by the time since their introduction (Boiché *et al.*, 2011). For example, Siemann & Rogers (2001) demonstrated

significant post-invasion genetic differences in the invasive tree species *Triadica sebifera*. Previously, Daehler & Strong (1997) showed a reduction of herbivore resistance in introduced *Spartina alterniflora* after one century. Through this increase in individual performances of non-natives, fundamental ecosystem processes, such as productivity, would be gradually ameliorated in space, but also in time through the extended phenology of leaf production among non-native populations (Fridley, 2012). The **EICA** hypothesis was also modified by taking into consideration the defence of invaders against novel enemies, such as pathogens, encountered in their new habitats (Müller-Schärer, Schaffner, & Steinger, 2004; Lee & Klasing, 2004). However, studies attempting to test the **EICA** or **refined EICA** (more efficient and less costly immune responses) hypotheses have reported mixed results (Zou, Rogers & Siemann, 2008; Cripps *et al.*, 2009; Diagne *et al.*, 2017).

(3) Unbridled dispersal at the invasion front

After a latency period **(23: LATE)** during naturalisation and release from natural enemies (**16: ERH**), non-native populations can expand rapidly their geographic range. In this process, dispersal ability crucially determines the speed at which colonisation of new habitats will occur (Renault *et al.*, 2018). Range expansion is often characterized by sequential founder events (Slatkin & Excoffier, 2012), resulting from short (stepping stone) or long-distance jumps. Individuals colonizing new habitats distant from the core population can have direct fitness advantages. Indeed, recently established individuals can benefit from decreased intra-specific competition pressure (Travis & Dytham, 2002; Burton *et al.,* 2010). Moreover, founder individuals, supposedly characterized by a majority of individuals with good dispersal abilities (Renault *et al.*, 2018), will share and transmit their genetic background at the invasion front (passive assortative mating). As this phenomenon repeats as the invasion front moves forward, dispersal traits should be enhanced at the leading edge of the range expansion, generating phenotypic differentiation between front and core individuals (Laparie *et al.*, 2013; Messager & Olden, 2019), and possibly breaking genetic covariation between dispersal and other traits encountered in native populations (Brown *et al.*, 2015). Behind the front wave and in core populations, higher population densities should favour competitive abilities of individuals, rather than biological traits enhancing their dispersal capacities (Burton *et al.,* 2010). The promotion of dispersal traits at the invasion front has been highlighted in the cane toad *Rhinella marina* rapidly invading the north-east coast of Australia (Phillips *et al.*, 2006; 2010), and this has led to the theory of spatial sorting (**31: SORT**; Shine *et al.,* 2011). Using such experimental evolution in replicated microcosm landscapes with different animal and plant models, several studies dissected which factors may drive the evolution of increased dispersal during range expansion and how this evolutionary shift may impact the ecological dynamics of invasion (Szucs et al., 2017; Weiss-Lehman, Hufbauer & Melbourne, 2017). All these studies end to the conclusion that at least five different processes may impact the evolution of the dynamics of range expansions: 1) novel selection pressures in the new habitat, 2) spatial sorting, 3) lower density at the expansion edge, 4) gene surfing, and 5) number and genetic background of the founders.

The consequences of range expansion for population dynamics and the potential of invasive species to encompass rapid range expansion and adaptation are now being extensively studied in theoretical and empirical works (Courant *et al.*, 2019; Morris, Börger & Crooks, 2019). Despite such

advances, our understanding of the processes generating phenotypic or genotypic variation in dispersal ability along the invasion gradient remains incomplete, especially under non-equilibrium conditions like range expansion and invasion (but see Phillips & Perkins 2019). Moreover, human-assisted dispersal events and multiple reintroductions impede our understanding of the actual expansion sequence. Spatial sorting should contribute to selecting dispersive phenotypes at the front (see Chuang & Peterson, 2016 for a review), the magnitude of this process being down-regulated by a range of life-history trade-offs that may either facilitate or constrain invasion success, with subsequent fitness consequences (*i.e.* constrained energetic outputs). While there are supporting evidence for this expectation (Schreiber & Beckman, 2019), some authors also failed in seeing reproductive consequences in the best dispersers (Tabassum & Leishman, 2018). This area of invasion science seems very promising. For example, genomic scanning methods provide the tools for discriminating evolutionary forces occurring on the genome (demographic events or genetic drift affect the whole genome, whereas selection acts on particular loci). However, in the context of range expansion, drift is expected to be strong in low-density invasion-front populations, allowing random alleles to arise from standing variation and reach high frequencies, thus displaying a positive selection-like signal (mutation surfing; Gralka *et al.*, 2016; Travis *et al.*, 2010). White *et al.* (2013) showed that this problem could be solved by sampling replicated invasion-front populations, as surfing produced by drift would result in independent allele 'selection' when adaptive trait promotion would affect the same loci.

In contrast with spatial sorting, which tends to accelerate invasion waves, the existence of an Allee effect (**32: ALLEE**) in invasive populations can dampen invasion speed. An Allee effect is characterized as positive density-dependence of population growth at low density. Many processes can cause Allee effects, e.g. mate finding, pollen limitation, or collective behaviours affecting organism fitness, and it is likely a general process among animal and plant taxa (and yet proper evidence of demographic Allee effect is rare (Gascoigne *et al.*, 2009; Kramer *et al.*, 2009). The link between Allee effects and invasion has been the subject of several studies (Taylor & Hastings, 2005; Grayson & Johnson, 2018). Allee effects may decrease the probability that an invader will get established; examples of this include the pinewood nematode *Bursaphelenchus xylophilus* and its vector the pine sawyer *Monochamus alternatus* (Yoshimura *et al.*, 1999) and the mass-attacking spruce bark beetle *Ips typographus* which had not established in North America in 2001 despite nearly 300 interceptions by US port inspectors since 1985 (Haack, 2001). Regarding the invasions that finally succeeded, such as the non-native vine *Vincetoxicum rossicum* (Cappuccino, 2004) or the smooth cordgrass *Spartina alterniflora* (Davis *et al.*, 2004), negative effects of low density may explain the lag time before invasion **(23: LATE)**. Evidence that Allee effects may slow spatial expansion has been gathered for the house finch *Carpodacus mexicanus* (Veit & Lewis, 1996) and for the gypsy moth *Lymantria dispar* (Tobin *et al.*, 2009); however, the dispersal capacities of introduced organisms may counteract Allee effects by increasing the chances of finding a mate, as reported in the house mice experimentally introduced on an island (MacKay *et al.*, 2019).

While a large class of models have found that the Allee effect can decrease invasion speed (Travis & Dytham, 2002), even to the point of countering spatial sorting (Shaw & Kokko, 2015; Shaw *et al.*, 2018), others have raised the possibility of peculiar phenomena taking place during

invasion. Such phenomena include patchy range expansion and the decoupling of persistence and spatial spread in predator-prey systems (Petrovskii *et al.*, 2005) or fluctuating invasion speeds when Allee effect is combined with negative density-dependence at large densities (Sullivan *et al.*, 2017). Recent innovative theoretical work on the dynamics of invasion waves has also shown that Allee effects might help maintain higher genetic diversity at invasion fronts (Roques *et al.*, 2012), partly because decreased invasion speed lowers the intensity of genetic drift (**INBRE**) at the front.

(4) Role shifting from non-native passenger to non-native driver of ecosystem changes

Given enough time, established non-native populations are likely to change assembly rules in their recipient community. Dominant invaders, through their activities, start modifying the ecosystem properties that pre-existed their introduction. Invaded ecosystems are thus progressively becoming 'hybrid' ecosystems (Mascaro *et al.*, 2013), with features intermediate between historical ecosystems comprising only native populations, and the ecosystems affected by non-native ones. The non-native populations go from the status of "passenger" **(24: PASS**; MacDougall & Turkington, 2005) to the status of driver of environmental changes. In the driver model (**33: DRIVE**; MacDougall & Turkington, 2005; Chabrerie *et al.*, 2008; White *et al.*, 2013), invasive populations affect local diversity by using ecosystem resources and space more effectively than native ones (Parker *et al.*, 1999). The dominant invaders subordinate native populations, which are thus limited or excluded by competition (MacDougall & Turkington, 2005). Because of the great transformations imposed to invaded ecosystems, these non-native species have been termed invasive engineers (**34: ENGE**; Cuddington & Hastings, 2004), drawing on the concept of ecosystem engineers proposed by Jones, Lawton, & Shachack (1994). Invasive engineers (or habitat modifiers, habitat formers or bio-constructors) are among the most ecologically influential forms of biological invaders. Such populations create, destroy or transform the invaded habitats, thereby affecting native organisms (Guy-Haim *et al.*, 2017). They sometimes trigger abrupt, and persistent changes in the structure and functioning of ecosystems akin to catastrophic shifts and alternative stable states studied in models of ecosystem functioning. The review by Guy-Haim *et al.* (2017), which focused on marine and estuarine environments, showed a wide variety of significant effects either positive or negative when considering studies separately, while concluding a small negative impact in their meta-analysis. Some studies show that the impacts of invasive ecosystem engineers depend on their density, and that at low density their effects can be positive (e.g. on soil microorganisms; Straube *et al.*, 2009).

(5) Expansion of non-native populations associated with novel biological weapons and defences

The "Novel Weapon Hypothesis" (**35: NWH**; Callaway & Ridenour, 2004; Vilcinskas, 2015) was formulated as an alternative explanation for the success of invasive populations. **NWH** posits that invasive populations may be equipped with new weaponry not detected or little used in the native range. In plants, numerous field and laboratory experiments have established the potential allelopathic effect of non-native populations on seed germination and direct inhibition of native plants (Thorpe *et al.*, 2009; Pinzone *et al.*, 2018). **NWH** also covers various invasive plant phytochemical activities, including anti-herbivore functions, as well as anti-fungal and anti-microbial effects (Schaffner *et al.*, 2011; Cipollini, Rigsby & Barto, 2012). This has been demonstrated with the phytotoxic disruption of *Alliaria petiolata* on native mutualistic mycorrhizal associations (Portales-Reyes *et al.*, 2015). However, **NWH** is compatible with the biotic resistance hypothesis (**9: ELTON**) insofar as invasive populations 'weapons' can sometimes be thwarted by defence mechanisms in native species (Barto, Friese & Cipollini, 2010), thus slowing their transformation

into hybrid ones. The **NWH** can be (i) the result of changes of biological characteristics in the invasive population between its populations of origin and its host range or (ii) existing traits related to negative interactions with its natural enemies in its native range against which native population of its invasive range are not adapted (Callaway & Ridenour, 2004; Yuan *et al*., 2013). In native plants, novel weapons of invaders are known to induce two responses: either (i) non-tolerance to the harmful allelochemicals due to the so-called "naïveté" observed with any antagonistic interactions (Schaffner *et al*., 2011; Carthey & Branks, 2012) or (ii) evolved tolerance to novel allelochemicals through natural selection (Callaway *et al.,* 2005).

The shifting defence hypothesis (**36: SDH**) differentiates between defences based on their effectiveness against specialist and generalist herbivores. It postulates that invasive plants may evolve towards new levels of chemical defence compounds in the invaded area for lack of their specialist herbivores **(16: ERH)**, but are now under attack by native generalist herbivores *(*Joshi & Vrieling, 2005; Doorduin & Vrieling, 2011). Hence plants shift towards less expensive qualitative defences (toxins) and fewer quantitative ones in the introduced range because digestibility compounds are costly to produce (Glawe *et al*., 2003). An example is the Eurasian native *Senecio jacobaea* which is an aggressive invader in North America, Australia, and New Zealand. The production of pyrrolizidine alkaloids was found to be higher in the invasive populations of *S. jacobaea* compared to native populations, which makes invasive populations better defended against the generalist herbivore *Mamestra brassicae*. Pyrrolizidine alkaloids and other toxic compounds levels were also found at higher concentrations in invasive individuals than in native individuals in a common garden experiment (Doorduin & Vrieling, 2011). If the defence chemicals against generalists are less expensive than the defence chemicals against the specialists, such an evolutionary shift in defence strategy in invasive populations may result in a net gain of resources for the plant, at the benefit of growth and reproduction (Joshi & Vrieling, 2005*)*.

Although **NWH** and **SDH** were first developed from work on invasive plants, they are also relevant for invasive animals. Some invasive insects harbour new chemical weapons by using molecules naturally present in the local resources of invaded ecosystems. This is the case of the non-native fruit fly *Drosophila suzukii* which is able to feed and use the toxic compounds of native plants present in its invasive range (Poyet *et al.,* 2015). This drosophila lays its eggs preferentially in a toxic substrate (containing atropine, a compound naturally present in the fruits of the native plant *Atropa belladonna*) in the presence of parasitoids (Poyet *et al*., 2017). Interestingly, the presence of atropine in the developmental medium confers a better resistance of *Drosophila* offspring against parasitoids, thus revealing the existence of a form of transgenerational medication in this species. This new weapon may result from a shifting defence mechanism as the toxic plants used by the invasive insects are present in their invaded area but absent in their native area.

In contrast to native populations, some introduced plants can benefit from improved mutualisms with soil microorganisms (especially symbiotic fungi), which will increase their performance (Enhanced Mutualism Hypothesis, **37: EMH**; Marler, Zabinski & Callaway, 1999; Reinhart & Callaway, 2006). According to the **EMH**, mutualism may be relatively more beneficial in novel ranges because the invasive population has escaped from the negative effect of natural enemies that may attenuate the positive effect of mutualists (mainly bacteria and fungi). For

example, neutral to negative impacts of soil biota were found for the populations of *Triadiaca sebifera* in their native range (China) whereas positive effects of soil biota were reported in a North American non-native range of the species. These positive effects were linked to the higher levels of arbuscular mycorrhizal fungi colonization and to the greater net benefits to the invader in North America than in China (Yuan *et al*., 2013). Importantly, one needs to assess individual interactions between microbial species and non-native macro-organisms to tease apart the importance of **EMH** from **ERH**. In contrast with the **EMH**, the Mutualism Disruption Hypothesis (**38: MDH**; Callaway *et al.,* 2008) predicts that invasive populations can also suppress soil mutualists in introduced ranges more aggressively than mutualists in their native ranges.

(6) Non-native species are playing with their natural enemies during the expansion stage

Despite the loss of their enemies (**16: ERH**), non-native populations may carry some of their parasites (12 to 50%) during the invasion process (Médoc *et al.*, 2017). Parasites may spread into new environment and infect local species, which is defined as 'spillover' (Daszak, Cunningham & Hyatt, 2000; Power & Mitchell, 2004). Non-natives may also catch and amplify a part of local parasites, then constituting reservoirs for parasite transmission and acting as hosts to ultimately release them into ecosystem, which is defined as 'spillback' (Kelly *et al*., 2009a). For example, the co-introduction of grey squirrels, *Sciurus carolinensis*, and the squirrel poxvirus from North America to the UK led to the pauperization of local red squirrel, *S. vulgaris* (Tompkins, White & Boots, 2003). Spillback can also induce untargeted metabolomics declines in native populations. For instance, the non-native grass *Avena fatua* amplifies and releases local viruses that are shared with the native grass *Elymus glaucus*, and then induce a population decrease of the latter species (Borer *et al*., 2007). These two phenomena are not exclusive and some cases report spillback and spillover processes (**38: SPILL**) occur on the same species. Weinstein & Lafferty (2015) relate that dog's nematodes in North America were found within local species (spillover) and conversely local nematodes from red wolf, *Canis rufus*, were found within domestic dogs, *Canis lupus familiaris*, and thus increase inoculum size by release through native hosts (spillback).

Spillover and spillback processes (**38: SPILL**) have an effect on host-parasite dynamics and thus on ecosystems dynamics (Kelly *et al*., 2009b; Lymbery *et al*., 2014; Amsellemen *et al*., 2017). Several parameters (climate, temperature, difference in virulence, accumulation capacity, connectivity of host, etc) could affect parasite prevalence over time and space via spillback and spillover (Clark *et al*., 2018). A parasite introduced in a new area under more favourable climatic conditions could lead to more generations per year and thus more infections of native populations. The virulence could also affect the intensity of spillback and spillover (Strauss, White & Boots, 2012). In the case of spillover, we expect that invasive populations could be already adapted to the associated parasite (Strauss *et al.*, 2012).On the other hand, local species are at best insensitive to parasites. Parasites may have different effects on their hosts, ranging from death to avirulence. They can modify the host behaviour and make it more likely to be predated. In some cases, all conditions seem to be in place for a spillback and/or spillover process but it was not observed (Folcher *et al.*, 2011). For now, some studies have explored the relationship between the phylogenetic proximity and the probability to share parasites but no clear patterns have emerged (Clark *et al.*, 2018; Strauss *et al.*, 2012; Streicker *et al.*, 2010).

In some cases, invaders may act as poor hosts for native parasites; in these circumstances, their density and risk of infection will decrease, a phenomenon referred to as the "dilution effect" (Kopp & Jokela, 2007; Kelly *et al*., 2009a). For instance, after the introduction of the non-native round goby, *Neogobius melanostromus*, the population of a local parasite, *Dilostomum* sp., declined. Invasive populations acted as a decoy for parasites and thus positively affected native fish which were less infected (Gendron & Marcogliese, 2017). These phenomena can be difficult to observe,

because either they occur too quickly (Dunn & Hatcher, 2015) or the origin of the parasite is unclear. Finally, spillback and spillover processes might be common and their effects on native populations may be absent or valuable (avirulence or symbiotic for example). In the future, new technologies, including next-generation sequencing, should be used to detect parasites and their origins (Mangla, Inderjit & Callaway, 2008; Wells *et al.*, 2015), and thus better detect the occurrence of spillback or spillover phenomenon. In parallel, modelling offers opportunities for elucidation of the effects of such processes on population dynamics and a better understanding of parasite assembly (Stauss *et al.*, 2012; Clark *et al.*, 2018), as exampled in a range of genera (Dunn & Hatcher, 2015). In general, when invasive species modify the community of parasites in their new areas, these can all gather in an "enemy alliance" (Strauss *et al.*, 2012) that affects the interactions between native and non-native populations.

(7) A delayed invasion but an invasion debt to be finally paid

The impact of invasive populations on recipient ecosystem is not immediate (**23: LATE**). Once a non-native is introduced in the historical ecosystem, its effects on natives may be delayed by the local biotic resistance (**9: ELTON**), the preponderant investment of introduced populations in dispersal efficiency (**31: SORT**), and the pace of adaptation of the non-native to its new environment (**29: PURG, 30: EICA**). The time lag between the introduction and the invasion stages can be very long (**23: LATE**), up to several centuries for some plant species (Groves, 2006). The **LATE** phenomenon was first observed for some weed species that are characterized by a time lag of more than 50 years between naturalization and a significant increase of their population. Groves (1999) first call them "sleeper weeds" (Groves, 1999). The term "invasion debt" (**40: DEBT**) was then used as a general term to describe the time-delayed invasion of populations that are already present in a region (Seabloom *et al.*, 2006; Essl *et al.*, 2011). This invasion debt is problematic because a low invasion level (*i.e.* a low number of introduced individuals) at a given time does not ensure the maintenance of ecosystem integrity in the future, even if no new individuals are introduced, thus masking the potential invasibility of ecosystems (Essl, Mang & Moser, 2012). However, the concept of invasion debt also provides a valuable metric that can be used to quantify the dimensions of future threats (Rouget *et al.*, 2016). By separating the invasion into components corresponding to different stages in the invasion process (introduction, establishment, spread and impact debts), Rouget *et al.* (2016) worked with 45 non-invasive *Acacia* species from South-Africa, and calculated that four could become established (establishment debt). The spread debt over a 20-year period varied from 0 (species unlikely to extend any further) to 10,000 km² for species with a large potential range. This corresponds to a current impact debt of 174 million US$ per species, which could increase to 500 million in 20 years if left unmanaged. In Europe, Haeuser *et al.* (2018) estimated the invasion debt of ornamental plant species by considering climate change. Modelling the effect of climate and species characteristics on naturalisation risk together with climate projections allows the forecasting of future threats and the implementation of proactive management of non-native populations. Preventing new introduction or managing current invasive populations does not eliminate the invasion debt, since debt already incurred will have to be paid in the future even if new introductions cease.

(8) Climate change as a major driver of non-native populations expansion

Climate change (**39: CLIM**) can alter the reproductive strategies of non-native plants, by promoting a shift from clonal spread to greater sexual reproduction as it was established for *Reynoutria* taxa in northern regions (Holm *et al.*, 2018). Changing climatic conditions can also facilitate the reproduction and subsequent establishment of non-native populations that have until now not been able to establish. Such successful non-natives may in the future encounter conditions more suitable for breeding and spread, as exampled by the tree *Schinus molle* in South Africa (Richardson *et al.*, 2010). Global changes may also facilitate the transport and arrival of new non-native populations (Gillard *et al.*, 2017). The review of Juroszek & von Tiedemann (2015) also established that disease risk is projected to remain unchanged or to be reduced in the future, mainly due to supra-optimal temperature conditions for the development of some pathogens during the growing season and/or reduced rainfall and leaf wetness, respectively. Climate change can exacerbate the impact of invasive populations on ecosystem through the disruption of the local species interaction networks. Specifically, warming alters plant-herbivore interactions by increasing ectotherm metabolism and growth rates (Miranda *et al.*, 2017), potentially leading to phenological mismatches between plants and pollinators, predators and prey, and pests and hosts.

IV. Rapid evolution of non-native populations and emerging properties in novel ecosystems

(1) Admixture and hybridization of non-native populations

Introduced populations may have been founded by different divergent lineages which were spatially isolated in the native species range. These introduced individuals with distinct genetic background may come into contact and reproduce; the result of this interbreeding between two or more previously isolated genetic lineages (in the native or in the introduced ranges) is called genetic admixture (**41: ADMI**). **ADMI** increases the overall genetic variance, generates heterozygosity and heterosis, and increases species fitness (Keller *et al.*, 2014; Lawson Handley *et al.*, 2011). **ADMI** can contribute to enhancing the spread and can facilitate the adaptation of introduced populations, as suggested for the green crab *Carcinus maenas,* following the independent introduction and hybridization between cold- and warm-adapted ecotypes (Jeffery *et al.*, 2018 and references therein). The same process may, on the other hand, also contribute to outbreeding depression, i.e. a decrease in average fitness. The role of admixture in biological invasions remains an open question and deserves further work (Rius & Darling, 2014).

In cases where populations were fully reproductively isolated, inter-specific hybridization and introgression (**42: HYBRID**) can occur, as shown in salamanders (Fitzpatrick *et al.*, 2010), marine mussels (Saarman & Pogson, 2015) or plants (Abbott, 1992; Petit *et al.*, 2004). Hybridization might benefit the non-native populations through adaptive introgression (Hedrick, 2013) (i.e. the introgression of adaptive alleles from native to non-native populations), and also threaten native populations (Todesco *et al.*, 2016). Using a modelling approach validated by data obtained in two *Cakile* species, Mesgaran *et al.* (2016) proposed that hybridization might also protect the non-native populations from genetic Allee effects. Importantly, hybridization can occur without introgression, as shown in bird species in the genus *Himantopus* (Steeves *et al.*, 2010) and in the tunicate *Ciona* spp. (Bouchemousse *et al.*, 2016). Both intra- and inter-specific hybridization (sensu lato) are important

mechanisms to consider as they could, among other things, counteract genetic depletion of founder events, and finally promote evolutionary novelties by breaking species boundaries (Harrison & Larson, 2014; Rius & Darling, 2014). From a genomic standpoint, rearrangements (**43: GENO**), like chromosomal inversions (Prevosti *et al.*, 1988) and polyploidization (**44: POLY**) have been reported in *Spartina* species where hybridization between native and non-native taxa produced offspring with a wide range of chromosome numbers and fertility levels (Ainouche *et al.*, 2009). In this context, the resulting complex evolution form, named *"reticulate evolution"* (**45: RETIC**) (Trewick *et al.*, 2004; Linder & Reiseberg, 2004), can occur in species with relatively close common ancestors (species of the same or a closely related genus). At long terms, these complex forms of evolution may result in adaptive radiation (**46: RADIA**) of introduced populations confronted to contrasted environments in post-invasion events {Carroll & Dingle, 1996). Finally, the selection resulting in evolutionary adaptations may possibly lead to speciation (**47: SPECIA**) in invasive species (Lee, 2002); thus the invasive species of today would be the native species of tomorrow.

In some cases, after a period of successful proliferation and expansion, an invasion may peter out, ending its race in an ecological and/or evolutionary dead-end (**48: DEAD**). This final and long-term invasion failure is different from the 3 tens rules (**6: 3TENS**) which corresponds to a short-term introduction failure due to a mismatch between the requirements of non-native populations (invasiveness) and recipient habitat characteristics (invasibility). The reasons for eventual long-term invasion failures are still to be studied. The trait performance or genetic diversity of the invasive population may decrease with time.

(2) New species, new rules, new properties, new ecosystems

The accumulation of non-native populations in a territory over time (Seebens *et al.*, 2017) inevitably leads to new interactions; these may be weak or strong, positive or negative (see **35: NWH** and **36: EMH**). In a few cases (10 of the 256 case studies reviewed in Simberloff & Von Holle, 1999), the establishment of newly introduced populations is facilitated by previously introduced species. This is the concept of invasional meltdown (**49: MELT**; Simberloff & Von Holle ,1999). This facilitation between former and recent invaders can be due to increased ecosystem invasibility, linked to reduced species diversity **(9: ELTON)**, or by environment transformation by ancient invasive populations **(34: ENGE)**. Through cascading effects, former invaders then increase the probability of survival of newly introduced ones as well as the potential magnitude of their impact on the ecosystems. This is the case of the American cherry tree, *Prunus serotina*, introduced to Europe near Paris in 1623 (Starfinger, 1997). This species hosts and feeds the larvae of the Asiatic spotted wing drosophila (*Drosophila suzukii*) in its fruits (Poyet *et al.*, 2014), a fly detected in 2008 for the first time in Europe (Asplen *et al.*, 2015). In the same geographic location, organisms from three regions (Europe, North America and Asia) have met (Poyet *et al.*, 2014). From a theoretical viewpoint, invasional meltdowns have been modelled in food webs, following the classic niche model, to assess the effect of non-native species coexistence (before the 'impacting' stage of invasion) on final invasion success (Pantel *et al.*, 2017): while coexistence of non-native populations is not necessary to obtain an increasing probability of invasion success with the number of species introductions, introductions of populations that have previously coexisted elsewhere increases the slope linking

the number of introductions to the fraction of successful invasions and thus make invasional meltdown more intense (Pantel *et al.*, 2017).

These recurrent international meetings of invasive populations over time produce novel combinations of non-native/native or non-native/non-native populations (**50: COMBI**) that are characterized by different biogeographic and evolutionary histories but complementary traits. Among these new combinations, new relationships between native and non-native populations can facilitate or impede the establishment of the non-native population (The New Associations Hypothesis **NASS**; Colautti *et al.*, 2004). Local adaptation of species in the native community or native-invasive coevolution can diminish the impact of invaders and integrate them into the native communities (Strauss, Lau & Carroll, 2006; Lankau, 2012). From these associations, new environmental conditions and new ecosystem functions may emerge while others disappear. A new ecosystem applied to invasions (Novel ecosystem concept: Hobbs *et al.*, 2006; Mascaro *et al.*, 2013; Richardson & Gaertner, 2013; **51: NOVEL**) is being created with emerging properties (Forsyth *et al.*, 2015; Kuebbing, Classen, & Simberloff, 2014) and with altered ecosystem services (Hobbs, Higgs & Harris, 2009).

Novel ecosystems are characterized by the unprecedented nature of their structure and composition and often by the irreversibility of the invasion. Indeed, the return to a previous state of the ecosystem or the total eradication of an established invasive population is almost impossible in practice. Beyond their ecosystem impact, some invasive populations redefine the dynamics of landscapes and constrain management habits (Chabrerie *et al.*, 2007). The multiplicity of potential combinations of species, previously unlikely and now possible, makes it difficult to predict what will be the ecosystem properties resulting from these association lotteries.

V. A functional perspective of invasions

A functional approach to ecosystem, based on the use of organism traits, would provide a better understanding of ecosystem changes following invasions (Drenovsky *et al.*, 2012; Liao *et al.*, 2008). A functional approach can help assess whether ecosystem states pre- and post-invasions are functionally homologous, and whether the services provided by ecosystems have changed (e.g. carbon storage, water quality). Several studies comparing coexisting native and invasive plant species have demonstrated differences between them in terms of functionally important traits (Baruch & Goldstein, 1999; Leishman *et al.*, 2007). Invasive populations, bearing new effect traits, will alter the functioning of recipient ecosystem, but up to now only few studies have linked these alterations to the trait sets of non-natives (Levine *et al.*, 2003). Using biological traits, allowing the computation of functional diversity indices at species and community scales, is a promising framework to understand changes in food webs and link ecosystem compartments such as below- and above-ground (Abgrall *et al.*, 2017; Moretti & Legg, 2009). Through adaptive changes of morphological (Atallah *et al.*, 2014) or behavioural traits, e.g. trans-generational medication (Poyet *et al.*, 2017), non-native populations can benefit from a wider range of resources (Poyet *et al.*, 2015) or better defend themselves than local populations and thus take precedence over them. However, native populations can also experience adaptive evolution in performance traits that mitigate the impact of non-natives (Mealor & Hild, 2007).

Since parasites (*sensu lato*, i.e. pathogens and true parasites) are involved in indirect interactions at all trophic levels, parasitic infections play a major role in invasion impact and success. Host-parasite interactions control and are controlled by the host immune response, and yet the immunology of invasions is still poorly known, with a clear imbalance in favour of theoretical rather than empirical studies (but see Vilcinskas, Mukherjee & Vogel, 2013). This observation is even more pronounced in invertebrate species, although it is now well established that invertebrates can acquire an immune experience from newly encountered microbes and transmit it to their offspring. Developing a framework for integrating ecology, microbiology, evolution and immunology to better understand the co-occurring spread of invasive species and their parasites would be useful. The main challenges in this regard are measuring a pertinent set of traits for the different biotic components of the ecosystem and discerning links between measured traits and ecological functions or processes.

VI. Conclusions and future directions

This review has explored theories and hypotheses aimed at elucidating aspects of biological invasions at the level of populations, communities and ecosystems. The resulting synthetic scheme (Fig. 1) summarizes the logical articulations between these theories along the invasion timeline, from establishment to expansion and then evolution of invasive populations. This scheme allows us to consider invasions from the perspective of both the non-native populations and the invaded ecosystem, and thus to highlight links between them. For instance, the grouping of **21: RSTR** and **20: DIST** hypotheses in Fig. 1 emphasizes the relation between the propensity of r-strategist species to be efficient invaders and the facilitation of such invasions by disturbances of ecosystems (Alpert, Bone & Holzapfel, 2000). Even earlier in the invasion process, the link between **7: SINV** and **8: EINV** hypotheses (Catford *et al.*, 2012) alludes to the constraints on invasive population traits due to their insertion into local food webs, e.g. foraging traits matching available prey characteristics (Baiser, Russell & Lockwood, 2010; Romanuk *et al.*, 2009).

Invasion theories can greatly benefit from a functional perspective (Pantel *et al.*, 2017). Studies on invasive plants have highlighted that taxonomic and functional diversities of the invaded community can have different effects on the success of potential invaders (Dukes, 2001). Functional overlap between the invading population and the ecosystem has been described as a potential explanation of invader's success, but this only applies in particular contexts according to the meta-analysis of Leffler *et al.* (2014). A better perspective can be achieved through elucidation of the actual roles of species, e.g. based on species diet (David *et al.*, 2017). For instance, the meta-analysis of Mollot *et al.* (2017) showed that invasive predators are more likely associated with decreases in species richness, independently of invaded habitat type, than are species in other trophic levels. Because functional traits and trophic characteristics are not always available in the literature, phylogenetic information has often been used as a proxy for, or as a predictor of, functional traits, with various degrees of success (Pearse & Altermatt, 2013; Tan *et al.*, 2015).

Considering the functional characteristics of invasive populations can also help assess, understand and predict their effects on ecosystem services. For instance, Geslin *et al.* (2017) reviewed the literature on the effects of widely introduced populations of crops and pollinating

insects on plant-pollinator interactions. One of their main conclusions is that domesticated insects generally occupy central positions in networks, and therefore probably compete with many other naturally occurring pollinators. In the case of the regulation of agricultural pests by predators, Jacquot *et al.* (2017) investigated the potential services and disservices of invasive ants in mango orchards, and they evidenced that distinct ant species had different effects depending on their omnivory and the trophic level on which they preferentially feed.

Going back to our timeline scheme (Fig. 1), the link between the various hypotheses and theories presented therein and the effects of invasive populations on invaded ecosystem services appears as a topic deserving further research. Whether a non-native population succeeds in a novel environment because it lacks its natural enemies (**16: ERH**) or because of too much disturbances of the invaded ecosystem (**20: DIST**) might provide clues as to what the effect of the non-native population might be on the functioning of invaded ecosystem and its services. The overall message from this review and the synthetic timeline scheme (Fig. 1) is that invasions do not occur in a vacuum and no single hypothesis is adequate to predict the likelihood of invasion, the resilience of particular ecosystems to invasion, the alteration to expect after the invasion, or the likely evolutionary aftermath to result from the integration of the invasive species.

Understanding biological invasions demands consideration of complex interactions between intrinsic species attributes, environmental attributes, and the effects of human actions (Thuiller *et al.*, 2006). However, this does not mean that it is not possible to forecast future trajectories of invasions (Bocedi *et al.*, 2014; Fournier *et al.*, 2019). We suggest that Fig. 1 can serve as a graphical model whose components can be used to construct more formal statistical models of population, community, or ecosystem dynamics in habitats where researchers are interested in predicting changes in response to non-native populations or the likelihood of particular habitats to host invasive species. The model parameters can be tuned using other examples of invasions in the same or similar taxonomic groups or habitat types, sources of uncertainty in the model can be assessed, and the models can be fine-tuned as more data becomes available in an iterative updating process (Dietze, 2017; Urban *et al.*, 2016).

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Figure 1

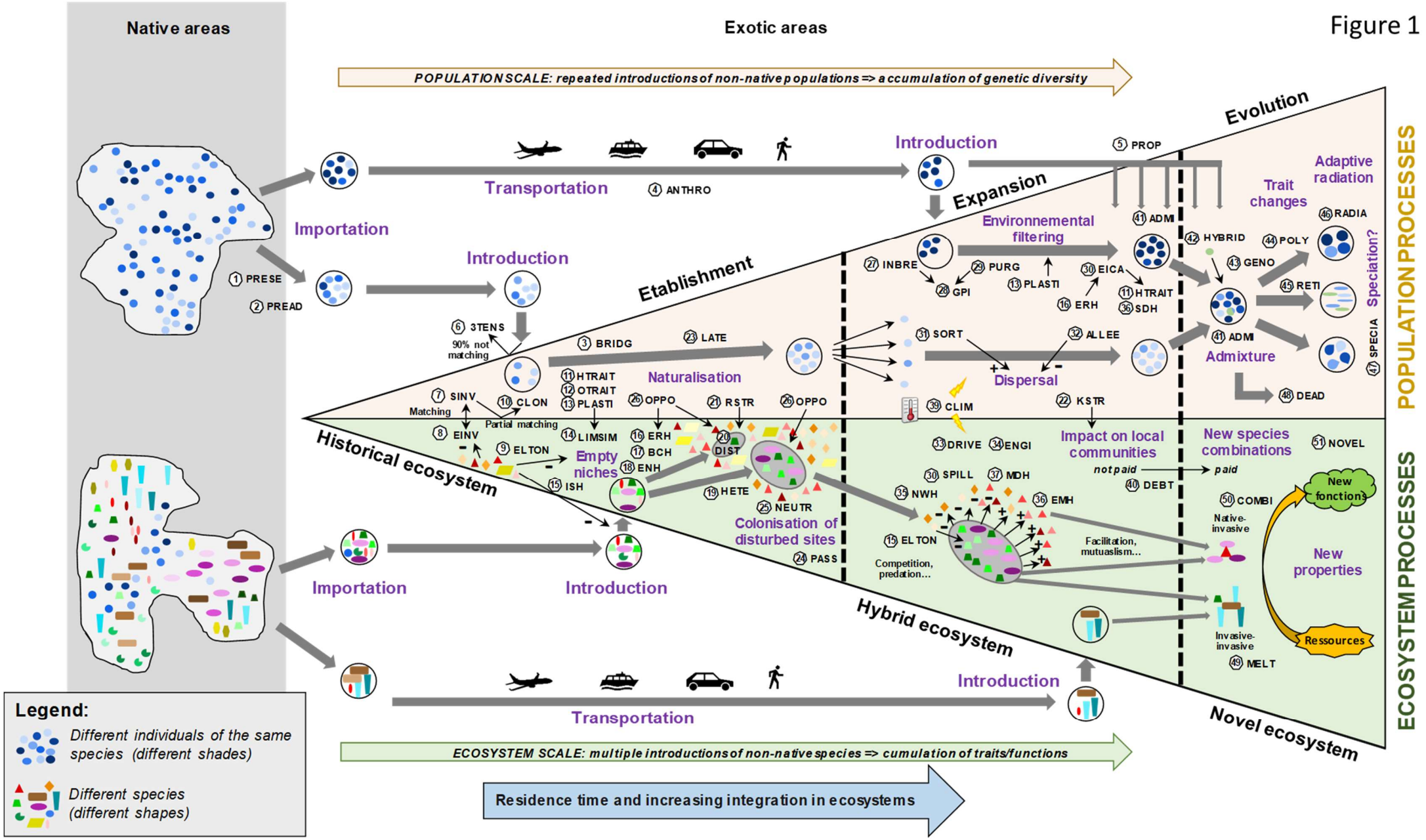

Native areas
Exotic areas
POPULATION SCALE: repeated introductions of non-native populations => accumulation of genetic diversity
Evolution
Introduction
5 PROP
Transportation
4 ANTHRO
Expansion
Importation
Introduction
Environnemental filtering
41 ADMI
Adaptive radiation
Trait changes
46 RADIA
42 HYBRID
44 POLY
43 GENO
45 RETI
Speciation?
47 SPECIA
1 PRESE
2 PREAD
Establishment
27 INBRE
29 PURG
28 GPI
13 PLASTI
30 EICA
16 ERH
11 HTRAIT
36 SDH
6 3TENS
90% not matching
3 BRIDG
23 LATE
31 SORT
32 ALLEE
Dispersal
41 ADMI
Admixture
48 DEAD
11 HTRAIT
12 OTRAIT
13 PLASTI
Naturalisation
26 OPPO
21 RSTR
26 OPPO
7 SINV
Matching
10 CLON
Partial matching
39 CLIM
22 KSTR
Impact on local communities
New species combinations
51 NOVEL
8 EINV
14 LIMSIM
16 ERH
17 BCH
18 ENH
20 DIST
9 ELTON
Empty niches
15 ISH
19 HETE
25 NEUTR
Colonisation of disturbed sites
24 PASS
33 DRIVE
34 ENGI
not paid
paid
40 DEBT
30 SPILL
37 MDH
35 NWH
36 EMH
50 COMBI
New fonctions
Native-invasive
15 ELTON
Competition, predation...
Facilitation, mutuaslism...
New properties
Ressources
Invasive-invasive
49 MELT
Historical ecosystem
Hybrid ecosystem
Novel ecosystem
POPULATION PROCESSES
ECOSYSTEM PROCESSES
Importation
Introduction
Introduction
Transportation
ECOSYSTEM SCALE: multiple introductions of non-native species => cumulation of traits/functions
Residence time and increasing integration in ecosystems
Legend:
Different individuals of the same species (different shades)
Different species (different shapes)

Figure legend

Figure 1: The invasion dynamics: hypotheses and concepts along the invasion timeline. Along the timeline, the above part of the scheme illustrates potential changes at the population scale of non-native populations. The bottom part describes concomitant transformations of ecosystem subjected to invasions.

Abbreviations of the concepts illustrated in figure 1 (bold characters):

1 PRESE: A "*preselection of traits"* responsible of the invasive character of an exotic species can occur in its native area (Rey *et al.*, 2012).

2 PREAD: "*Preadaptation*" (Mack, 2003): invasions may be facilitated by the introduction of organisms in regions displaying environmental characteristics similar to those of their native range. The recurrence of anthropogenic disturbance worldwide may also increase the frequency of contemporary adaptation to human-altered habitats (see also AIAI: "Anthropogenically Induced Adaptation to Invade", Hufbauer *et al.* (2012)).

3 BRIDG: Many invasions have stemmed not from the native range, but from a particularly successful invasive population, which serves as the source of colonists for remote new territories. This phenomenon was called the invasive bridgehead effect (Lombaert *et al.*, 2010).

4 ANTHRO: The ever-increasing frequency of invasive species all over the world (Seebens *et al.*, 2017) is strongly related to anthropochory through inter- and intra-continental exchanges (Perrings *et al.*, 2005).

5 PROP: The *"Propagule Pressure Hypothesis"* (Simberloff, 2009), also known as introduction effort (Blackburn *et al.*, 2011), combines the number of propagules introduced and the number of introduction events. It is recognized as a major determinant of establishment and further colonization success of invasive species.

6 3TENS: The "*3 tens rule*": Williamson & Fitter (1996) showed that there were statistical regularities to invasions: the statistical rule holds that 1 in 10 imported plants and animals appear in the wild (introduced or casual). The same proportional rule prevails between introduced and naturalised species, and between naturalised and invasive species (the "*3 tens rule*"; Williamson, 1996).

7 SINV: "*Species invasiveness"* resides in the performance, the originality and the plasticity of functional traits (Alpert, Bone & Holzapfel, 2000; Pyšek & Richardson, 2007; van Kleunen *et al.*, 2010).

8 EINV: *"Ecosystem invasibility"*: the successful integration of non-native organisms in the new area also depends on the characteristics of the recipient environment (Alpert, Bone & Holzapfel, 2000; Richardson & Pysek, 2006).

9 ELTON: According to "Elton's resistance hypothesis" (Elton, 1958; Levine & D'Antonio, 1999), a high local diversity reduces community invasibility.

10 CLON: Some exotic plants are unable to reproduce sexually in their invasion range (Lambertini *et al.*, 2010). Their proliferation is almost exclusively or totally ensured by clonal multiplication, at least in the early stage of the invasion process. This apparent weakness of the lack of sexual reproduction may be converted into an advantage in the case where vegetative reproduction is more efficient to invade recipient ecosystems (Lambertini *et al.*, 2010).

11 HTRAIT: Invasive plant species generally have higher values of performance-related traits characterizing physiology, leaf-area allocation, shoot allocation, growth rate, size, i.e. a better fitness than non-invasive plant species (van Kleunen *et al.*, 2010).

12 OTRAIT: Compared with their native congeners, the non-native species possess *"original, species-unique traits"*, which can contribute to their invasion potential. No functionally equivalent trait is present in the invaded ecosystem (Atallah *et al.*, 2014; Macel *et al.*, 2014).

13 PLASTI: According to the "*phenotypic plasticity hypothesis*", it is thus supposed that invasive species may have a greater plasticity in ecologically important traits than non-invasive ones, and populations of invasive species are expected to evolve greater plasticity in their invasive range compared to populations within the native range (Richards *et al.*, 2006).

14 LIMSIM: The concept of "*limiting similarity"* (Abrams, 1983) states that invasive species will be unlikely to establish in a community dominated by functionally similar species because of greater niche overlap (Funk *et al.*, 2008; MacArthur & Levins, 1967).

15 ISH: *"Increased Susceptibility Hypothesis"*: Native consumers may prefer exotic over native prey and consequently limit invasions (Parker & Hay, 2005). Exotic preys have not experienced selection from these consumers and therefore lack effective defences, as formulated by the Increased Susceptibility Hypothesis (Colautti *et al*., 2004).

16 ERH: *"Enemy Release Hypothesis"* (Keane & Crawley, 2002). By experiencing a decrease in regulation by consumers or other natural enemies, exotic species may rapidly increase in abundance and distribution.

17 BCH: The "*Behavioural Constraint Hypothesis*" establishes that potential consumers and competitors need behavioural adaptations before recognizing and readily consuming or outcompeting an introduced population (Lankau, Rogers & Siemann, 2004).

18 ENH: "*Empty Niche Hypothesis"* Invasive species may expand into new areas by filling an 'empty niche'; i.e. occupying previously unoccupied (or unsaturated) habitats or exploiting a resource unused by local species (Stachowicz & Tilman, 2005; Williamson, 1996).

19 HETE and **20 DIST:** Spatio-temporal environmental heterogeneity and disturbances can promote invasions (Melbourne *et al*., 2007).

21 RSTR and **22 KSTR**: "r-strategy" species (pioneers, opportunists, generalists) are favoured in early invasion stages and then competitively displaced by "K-strategists" in later stages (Facon *et al.*, 2008; Duyck *et al.*, 2007).

23 LATE: "*Latency period*" typically preceding population bloom of invasive species (Pyšek & Prach, 1993).

24 PASS: The correlation between dominance of invasive species and decline of native populations does not constitute evidence that ecological changes are driven by invasive species (Didham *et al.*, 2005). Indeed, habitat disturbances or fragmentation could have both detrimental impact on native population abundance and diversity while being beneficial for exotic species, then labelled as "passengers" of ecological change. This is the "*Passenger model"* (MacDougall & Turkington, 2005; Chabrerie *et al.*, 2008)

25 NEUTR: The *"Neutral theory"* (Hubbell, 2001; Chave, 2004), applied to invasions (Fargione *et al.*, 2003; Herben *et al.*, 2004; Tilman, 2004).

26 OPPO: "*Opportunist model"*. Non-interactive communities represent an opportunity (that may ease the integration of non-native species (Chabrerie *et al.*, 2008; White *et al.*, 2013).

27 INBRE: Initial genetic bottleneck of incipient invasion leads to high inbreeding levels in introduced populations (van Buskirk & Willi, 2006). Inbreeding may lead to both negative (inbreeding depression) and positive (purging) effects on the invasive success (see GPI and PURG).

28 GPI: *"Genetic Paradox of Invasions"*: how do invasive populations manage to adapt to the novel selective pressures encountered in the introduced area despite reduced genetic diversity (Sax & Brown, 2000; Estoup *et al.*, 2016).

29 PURG: The mutation load is defined as the proportion by which the population fitness, or any other attribute of interest, is altered by recurrent mutation (Kimura, Maruyama & Crowe, 1963). Consanguineous mating can "*purge a part of the mutation load"* and lethal mutations can also be purged in small populations (Glémin, 2003). Invasive species may benefit from this purge of homozygous deleterious alleles reducing their genetic/mutation load.

30 EICA: "*Evolution of Increased Competition Ability"* (Blossey & Nötzold, 1995): because they escape natural enemies in their invasive range, non-native populations can save the energy formerly used for defence and reinvest it in growth, biomass, reproduction and competitiveness.

31 SORT: Spatial sorting, selection of individuals with high dispersal ability at the leading edge of invasion (Shine *et al.* 2011).

32 ALLEE: "*Allee effect*" (Petrovskii *et al.*, 2005), occurring at the leading edge of invasion (Cappuccino, 2004; Davis *et al.*, 2004).

33 DRIVE: "*Driver model*": invasive populations affect local diversity by using ecosystem resources and space more effectively than native ones (MacDougall & Turkington, 2005; Chabrerie *et al.*, 2008; White *et al.*, 2013).

34 ENGE: Because of the great transformations imposed to invaded ecosystems, some non-native species have been termed "*Invasive engineers*" {Cuddington, 2004 #511}.

35 NWH: "*Novel Weapon Hypothesis"* (Callaway & Aschehoug, 2000; Callaway & Ridenour, 2004). Novel weapons may include chemical and biological weapons.

36 SDH: "*Shifting Defense Hypothesis*" {Müller-Schärer, 2004 #3552;Doorduin, 2011 #3553}.

37 EMH: "*Enhanced Mutualism Hypothesis*": in contrast to native populations, some introduced plants can benefit from improved mutualisms with soil microorganisms (especially symbiotic fungi), which will increase their performance (Marler, Zabinski & Callaway, 1999; Reinhart & Callaway, 2006).

38 MDH: The "*Mutualism Disruption Hypothesis*" predicts that invasive populations can also suppress soil mutualists in introduced ranges more aggressively than mutualists in their native ranges. (Callaway *et al.*, 2008).

38 SPILL: "*Spillover – Spillback*". Non-native populations may carry their parasites, infecting local species, ('spillover'), and may also catch and amplify a part of local parasites, then constituting reservoirs for parasite transmission and acting as hosts to ultimately release them into ecosystem ('spillback') (Dasak et al., 2000, Amsellem et al. 2017).

39 CLIM: Climate changes facilitate the arrival of thermophilic non-native species and exacerbate their impacts.

40 DEBT: Invasion debt describes the time-delayed invasion of populations that are already present in a region. This invasion debt is problematic because a low invasion level at a given time does not ensure the maintenance of ecosystem integrity in the future. This concept can help to quantify the future invasion risks (Rouget *et al.,* 2016).

41 ADMI: *"Genetic admixture"*, i.e. the result of interbreeding between two or more previously isolated populations within a species. It generates heterozygosity and heterosis increasing species fitness (Keller *et al.*, 2014; Lawson Handley *et al.*, 2011).

42 HYBRID: Interspecific "*hybridization*" between native and invading species (Abbott, 1992; Petit *et al.*, 2004)

43 GENO: "*Genomic rearrangements*", like chromosomic inversions (Prevosti *et al.*,1988) and polyploidy (POLY) can contribute to invasive species evolution.

44 POLY: "*Polyploidization*", i.e. genome duplication, in invasive species (Ainouche *et al.*, 2009).

45 RETIC: *"Reticulate evolution"*, a complex evolution form involving two genomic shocks: hybridization between evolutionary close native and invasive species (merger of divergent genomes),

and polyploidization (whole genome duplication) Ainouche *et al.*, 2009; Trewick, 2004). Reticulate evolution involving native and exotic species may lead to speciation (see the genus *Spartina*) through the creation of populations/species with various levels of polyploidy and various proportions of native and exotic genomes.

46 RADIA: "*Adaptive radiation*" in post-invasion events (Carroll & Dingle, 1996).

47 SPECIA: Selection resulting in evolutionary adaptations and possibly "*speciation*" in invasive species (Lee, 2002).

48 DEAD: In some cases, after a period of successful proliferation and expansion, the invasion is petering out and ends his race in *"an ecological and/or evolutionary deadlock"*.

49 MELT: The establishment of newly introduced populations is facilitated by previously introduced species. This is the concept of *"Invasional meltdown"* (Simberloff & Von Holle, 1999).

50 COMBI: "*New combinations*" between exotic-native species and between exotic-exotic species (see example in Poyet *et al.*, 2014). This includes new the "*New Associations Hypothesis*" **NASS** (Colautti *et al.*, 2004): the relationships between non-native and native species can facilitate or impede the establishment of the non-native species and influence the invasion success.

51 NOVEL: A new ecosystem with emerging properties (*"Novel ecosystem"* concept (Hobbs *et al.*, 2006; Mascaro *et al.*, 2013) applied to invasions (Richardson & Gaertner, 2013; Simberloff, 2015)) is created by the activity of the invasive species.