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A niche perspective on the range expansion of symbionts

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ABSTRACT

Range expansion results from complex eco-evolutionary processes where range dynamics and niche shifts interact in a novel physical space and/or environment, with scale playing a major role. Obligate symbionts (i.e. organisms permanently living on hosts) differ from free-living organisms in that they depend on strong biotic interactions with their hosts which alter their niche and spatial dynamics. A symbiotic lifestyle modifies organism–environment relationships across levels of organisation, from individuals to geographical ranges. These changes influence how symbionts experience colonisation and, by extension, range expansion. Here, we investigate the potential implications of a symbiotic lifestyle on range expansion capacity. We present a unified conceptual overview on range expansion of symbionts that integrates concepts grounded in niche and metapopulation theories. Overall, we explain how niche-driven and dispersal-driven processes govern symbiont range dynamics through their interaction across scales, from host switching to geographical range shifts. First, we describe a background framework for range dynamics based on metapopulation concepts applied to symbiont organisation levels. Then, we integrate metapopulation processes operating in the physical space with niche dynamics grounded in the environmental arena. For this purpose, we provide a definition of the biotope (i.e. living place) specific to symbionts as a hinge concept to link the physical and environmental spaces, wherein the biotope unit is a metapopulation patch (either a host individual or a land fragment). Further, we highlight the dual nature of the symbionts' niche, which is characterised by both host traits and the external environment, and define proper conceptual variants to provide a meaningful unification of niche, biotope and symbiont organisation levels. We also explore variation across systems in the relative relevance of both external environment and host traits to the symbiont's niche and their potential implications on range expansion. We describe in detail the potential mechanisms by which hosts, through their function as biotopes, could influence how some symbionts expand their range – depending on the life history and traits of both associates. From the spatial point of view, hosts can extend symbiont dispersal range *via* host-mediated dispersal, although the requirement for among-host dispersal can challenge symbiont range expansion. From the niche point of view, homeostatic properties of host bodies may allow symbiont populations to become insensitive to off-host environmental gradients during host-mediated dispersal. These two potential benefits of the symbiont–host interaction can enhance symbiont range expansion capacity. On the other hand, the central role of hosts governing the symbiont niche makes symbionts strongly dependent on the availability of suitable hosts. Thus, environmental, dispersal and biotic barriers faced by suitable hosts apply also to the symbiont, unless eventual opportunities for host switching allow the symbiont to expand its repertoire of suitable hosts (thus expanding its fundamental niche). Finally, symbionts can also improve their range expansion capacity

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through their impacts on hosts, *via* protecting their affiliated hosts from environmental harshness through biotic facilitation.

Key words: biotope, colonisation process, ecological fitting, enemy release, environmental stability, host switching, metapopulation, niche construction, phoresy, symbiont organisation levels.

CONTENTS

I. INTRODUCTION

In the current world of globalisation and climate change, many species are expected to expand their distributional ranges due to the removal or displacement of dispersal and environmental barriers. Range expansion poses a number of ecological and evolutionary challenges, including (1) dependence on a complex interaction of processes ranging from individual dynamics to shifts in geographical distributions (Struve *et al*., 2010), (2) niche-based responses of the organism to the environment (Hutchinson, 1978; Chase & Leibold, 2003; Colwell & Rangel, 2009; Holt, 2009), and (3) movement throughout the biophysical space (Nathan *et al*., 2008). Range dynamics result from the interplay between niche and dispersal-related processes across different spatial and temporal scales (Pulliam, 2000; Colwell & Rangel, 2009; Hortal *et al*., 2010; Schurr *et al*., 2012; Godsoe *et al*., 2017). Recent efforts have advanced towards a synthetic, hierarchical view of range dynamics encompassing the interaction of processes that operate at different levels of biological organisation and, ultimately, determine range shifts (Yackulic & Ginsberg, 2016). Another promising research area under development is the integration of niche theory and range dynamics to understand how local-scale processes such as biotic interactions scale up to geographical ranges (Godsoe *et al*., 2017).

Symbionts are organisms that live on or within a host (Sapp, 1994). Symbiotic lifestyles are very successful life-history strategies, as evidenced by their wide representation across taxa and their multiple independent evolutionary origins (Poulin & Morand, 2004; Weinstein & Kuris, 2016). Indeed, symbionts comprise a substantial fraction of Earth's biodiversity. For example, parasites alone account for at least one-third of all animal and plant species, based on the most conservative estimates (Clayton, Bush & Johnson, 2015). In general, symbionts affect species interactions, coexistence and ecosystem dynamics (Hatcher, Dick & Dunn, 2006; Hatcher, Dick & Dunn, 2012*b*). When experiencing range expansion, symbionts influence invasions of many species and often threaten native biota through effects on their hosts (Dunn *et al.*, 2012; Strauss, White & Boots, 2012; Lymbery *et al.*, 2014; Traveset & Richardson, 2014). Obligate symbionts differ from free-living species in that they depend on strong biotic interactions with their hosts. This host dependence alters their levels of biological organisation (Poulin, 2007*b*; Tompkins *et al.*, 2011; Penczykowski, Laine & Koskella, 2015), and modifies the way they interact with space (Borer, Laine & Seabloom, 2016) and environment (Lymbery, 2015; Borges, 2017). Therefore, understanding their ecological dynamics involves studying processes at both among- and within-host scales (Mideo, Alizon & Day, 2008; Mideo *et al.*, 2011; Park *et al.*, 2013). Given that both spatial and niche processes are crucial for range dynamics, their alteration as a result of adopting a symbiotic lifestyle must have consequences on how an organism experiences range expansion. Here we aim at providing a comprehensive overview of the potential implications of having a symbiotic lifestyle for an organism's range expansion capacity. Previous reviews of symbiont dynamics do not embrace niche theory, usually adopt a host-centric perspective and are often exclusively focused on parasites and diseases (e.g. Hoberg & Brooks, 2008; Tompkins *et al.*, 2011; Telfer & Bown, 2012; Hatcher, Dick & Dunn, 2012*a*; Penczykowski, Laine & Koskella, 2015). Here, we present a symbiont-centred niche-based conceptual framework for range expansion of all symbionts (i.e. not restricted to parasites), and sensible to all the spatial and environmental particularities arising from living on or within hosts. The framework serves to describe the ways in which these distinctions from free-living forms may influence symbiont range expansion.

In this review we apply metapopulation concepts to describe a framework of organisation levels for symbionts that reflects the dependence of their range dynamics on lower-scale processes, especially those operating at the scale of either host individuals or land fragments inhabited by host communities. Following the generalised definition of biotope as 'living place' (Hutchinson, 1957), our framework defines the biotope of symbionts at two scales: host and land fragment. We classify range expansion mechanisms based on the key processes that may enhance biotope colonisation by symbionts. We characterise the dual nature of the symbiont's niche, whereby both host traits and the external environment can be relevant components. We suggest factors that may generate variation across symbiont–host systems in the predominance of one component over the other in governing the symbiont's niche. Then we show how the niche is linked to range expansion because it defines biotope suitability and ultimately occupancy. We emphasise the potential implications of using hosts as biotopes for the range expansion of some symbionts. For that, we introduce recent ideas about niche construction applied to symbionts (Buser *et al.*, 2014; Lymbery, 2015; Borges, 2017) to describe ways in which niche alterations driven by symbiont–host interactions could influence the symbiont's range expansion capacity. This is not a quantitative or analytical review about how to model range expansion – a topic already covered by other recent reviews (e.g. Schurr *et al.*, 2012; Yackulic & Ginsberg, 2016; Zurrell, 2017). Rather, we aim at addressing the more fundamental question of how ecological and evolutionary changes in the relationships between an organism and its biotope involving the niche can be related to large-scale geographical range dynamics. We adopt a conceptual niche-based approach to this question, applied to the specific case of range expansion processes experienced by organisms that are adapted to inhabit hosts.

II. DEPENDENCE OF RANGE DYNAMICS ON ORGANISATION LEVELS OF SYMBIONTS

Ecological processes are scale dependent (Allen & Starr, 1982). This is particularly true for range dynamics, which depend on lower scale occupancy dynamics through local colonisation/extinction processes that, in turn, are ultimately governed to some extent by habitat suitability (Hortal *et al.*, 2010; Struve *et al.*, 2010). Therefore, a comprehensive study of symbiont range dynamics should consider the cross-scale interactions between different levels of organisation, from individuals to geographical ranges (Tompkins *et al.*, 2011; Penczykowski, Laine & Koskella, 2015), all of which may influence the success of a symbiont throughout the range expansion process.

Different terminologies and concepts have been used to describe the levels of biological organisation of symbionts (summarised in Table 1). In parasitology, the set of conspecific symbionts inhabiting a host are called an infrapopulation. Then, the sum of all infrapopulations representing the pool of symbionts living on a community of available hosts is referred as population (Poulin, 2007*b*). Some authors described multiscale frameworks of parasite dynamics based on the organisation levels of hosts (Tompkins *et al.*, 2011; Penczykowski, Laine & Koskella, 2015).

Other researchers applied metapopulation concepts to symbiont dynamics in two different ways depending on the focal scale (Fig. 1). A metapopulation (i.e. population of populations) is a system of populations, sometimes called subpopulations, partially isolated due to habitat discontinuity, but connected to some degree by dispersal (see, e.g. Hanski & Gilpin, 1991). Therefore, metapopulation is a populational concept with a spatial component that may be defined in different ways depending on the scale of work, habitat structure, and the scaling of dispersal processes (in relation to habitat configuration). The 'host-as-patch'

Table 1. Different terminologies used to describe the levels of biological organisation in symbionts. Parasitologists define an infrapopulation as the subset of conspecific symbionts inhabiting a host individual, and a population as the set of symbionts living on a community of available hosts. A host-centric view considers that biological organisation levels of symbionts match those of their hosts. The land-patch metapopulation view of symbiont dynamics defines an interaction metapopulation as a host–pathogen association inhabiting fragmented patches following a metapopulation structure (i.e. fragmented populations connected by dispersal), which can adopt different spatial structures depending on the relative rates of host and pathogen dispersal. Finally, the host-as-patch view interprets host individuals as discrete habitat patches for symbionts, which harbour populations of symbionts within their bodies. A local metapopulation then is defined as the set of within-host populations inhabiting a community of available hosts interconnected by symbiont transmission among hosts. Thus, the host-as-patch view is focused on finer scales and interprets the patch differently than the land-patch view. The land-patch view defines the habitat patch as a fragmented land patch containing a symbiont–host association, thus strictly following the classical metapopulation concept, particularly in its treatment of patch as a land fragment (containing symbionts and their hosts). By contrast, the host-as-patch view interprets host individuals as discrete habitat patches inhabited by symbionts

	Scale			
Terminology	Within-host	Local	Regional	References
Parasitology	Infrapopulation	Population		Poulin (2007*b*)
Host-centric	Host individual	Host population	Host metapopulation	Penczykowski, Laine & Koskella (2015)
Land-patch		Local population	Interaction metapopulation	Thrall & Burdon (1997)
Host-as-patch	Within-host population	Local metapopulation		Grenfell & Harwood (1997)

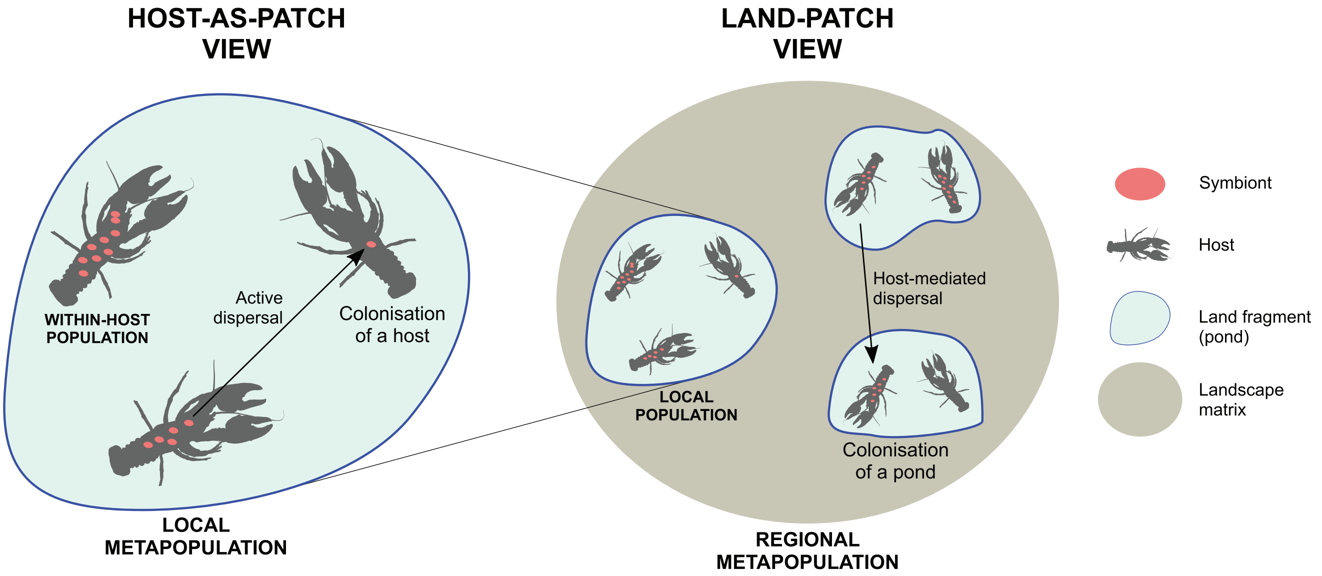


Fig. 1. Metapopulation views of symbiont dynamics. The host-as-patch view (left) interprets host individuals as patches, and defines a local metapopulation as the set of within-host populations of symbionts inhabiting a community of available hosts interconnected by symbiont dispersal through the external environment, or contacts among hosts. The land-patch view (right) considers land fragments as patches, and defines a regional metapopulation as the set of local populations of symbionts interconnected by dispersal.

metapopulation view describes local dynamics of symbionts within a community of hosts, whereby host individuals are conceived as patches that harbour populations of symbionts within or on their bodies, interconnected *via* dispersal among hosts (Grenfell & Harwood, 1997; Hanski, 1998; Holt & Barfield, 2006; Mihaljevic, 2012; Borer, Laine & Seabloom, 2016). Thus, because hosts act as discrete habitats for symbionts that aggregate them across space, the host-as-patch view suggests that living on hosts may involve drastic changes in the way an organism interacts with space locally. This local-scale perspective on metapopulations emphasises the role of interactions between intra- and inter-host processes in governing population dynamics of symbionts within a host community. It serves to understand the potential roles of host individuals in structuring populations and governing microhabitat suitability and local dispersal of symbionts, and how local-scale processes involving hosts as habitat units could influence range dynamics of symbionts.

Other authors applied the metapopulation concepts to investigate spatial structures of symbiont–host interactions at larger scales by considering land fragments as patches. They define an interaction metapopulation (Thrall & Burdon, 1997) as a host-symbiont association inhabiting fragmented land patches following a metapopulation structure (i.e.

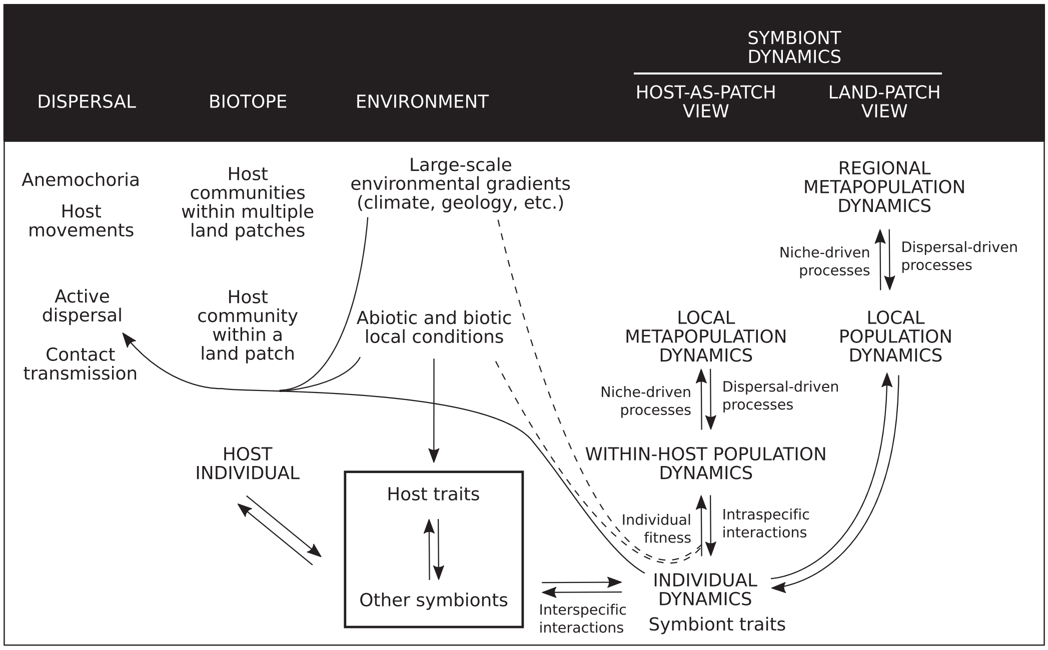


Fig. 2. Scale dependence of the relationships among the biotope of symbionts, the environment experienced by symbionts, the dispersal processes and symbiont organisation levels that, together, govern range expansion of symbionts. Dashed arrows only apply to symbionts with in-host population dynamics directly influenced by the external environment (e.g. ectosymbionts hosted by arthropods and small mammals).

fragmented populations connected by dispersal), which can adopt different spatial structures depending on the relative rates of host and symbiont dispersal (see Fig. 1 in Thrall & Burdon, 1997). This 'land-patch' view has been used to investigate spatial patterns in evolutionary dynamics and local adaptation in host–pathogen interactions inhabiting structured landscapes (e.g. resistance/virulence structure; Thrall & Burdon, 1997, 2003; Barrett *et al.*, 2008). We combine these two metapopulation views – focused on different scales – to build a framework of symbiont biological organisation herein. The conceptual framework presented here serves to understand potential impacts of the drastic habitat narrowing driven by a symbiotic life on organism's spatial and niche dynamics, and how niche-driven and dispersal-driven processes interact across scales to govern range dynamics of symbionts. Based on both host-as-patch and land-patch metapopulation views of symbiont dynamics, we define the levels of biological organisation of symbionts as follows (Fig. 2).

(1) Individual dynamics

Individual variation is the basis of eco-evolutionary processes, the interaction of species with the environment, and large-scale range dynamics (Bolnick *et al.*, 2011). Adaptive evolution operates on heritable variability in traits that determine how an individual performs in a given environment (Charlesworth, Barton & Charlesworth, 2017). The performance of an individual is expressed by its fitness, which can be defined, in a broad sense, as the relative success of an individual at passing its genes to the next generation (Orr, 2009). Individual dynamics of symbionts often alternate within-patch survival and reproduction with dispersal among patches (either hosts or land fragments). Thus, the individual fitness of a symbiont has two components: (*i*) intra-patch fitness; and (*ii*) fitness during dispersal among patches. From the host-as-patch view, this fitness dichotomy creates trade-offs between levels of selection arising from coupled within- and between-host dynamics (Mideo, Alizon & Day, 2008; Mideo *et al.*, 2011; Park *et al.*, 2013; Borer, Laine & Seabloom, 2016). Overall, symbiont individuals provide the source of trait variation required for the interaction of natural selection, genetic drift, gene flow and ecological processes that modulate the symbiont's capacity to survive and reproduce in a given environment, or migrate to more favourable environments (Hendry, 2016). In particular, dispersal traits are also potentially involved in eco-evolutionary dynamics of symbionts operating from individual to higher levels (Kubisch *et al.*, 2014).

(2) Within-host dynamics

Applying the host-as-patch metapopulation view of symbiont dynamics, the set of conspecific symbiont individuals inhabiting a host can be interpreted as a within-host population subjected to extinction rates driven by host death or other factors like host defences (Borer, Laine & Seabloom, 2016). Thus, within-host populations are often characterised by an extraordinarily high dynamism and instability as a consequence of the ephemeral nature of hosts. Moreover, they are usually regulated by other disruptive processes like immune responses and moult or grooming behaviours of hosts (Stanko, Krasnov & Morand, 2006; Fernandez-Leborans, 2010). The main drivers of within-host population dynamics are host characteristics, such as lifespan, abundance, body size or immunological defences (Poulin, 2007*a*, 2007*b*), and off-host environmental conditions, such as water chemistry or climate (DeWitt *et al.*, 2013; Mestre, Monrós & Mesquita-Joanes, 2014). Other coexisting symbiont taxa can also shape within-host dynamics of symbionts (Mihaljevic, 2012; Borer, Laine & Seabloom, 2016). Intraspecific interactions potentially affect within-host population dynamics in two ways, depending on the population density context. At low population densities, positive density dependence occurs when an increase in the density of symbionts within a host favours mate encounters, cooperation behaviours, etc., thereby increasing mean in-host fitness (Allee effects; Stephens & Sutherland, 1999; Courchamp, Berec & Gascoigne, 2008). At high population densities, intraspecific competition for host resources generates negative density dependence. High symbiont densities may produce resource depletion and host death induced by the symbiont (Anderson & Gordon, 1982; Shaw & Dobson, 1995; Stanko, Krasnov & Morand, 2006).

(3) Local dynamics

Local dynamics of symbionts can be interpreted in two ways depending on the type of processes of interest at local scale (either spatial or niche based). Following the host-as-patch view, a local metapopulation is defined here as the set of symbiont populations inhabiting a community of available hosts interconnected by symbiont dispersal through the external environment, or direct contacts among hosts (Fig. 1). Metapopulations can be subject to source–sink dynamics (Pulliam, 1988), wherein the patches differ in suitability, and unsuitable patches – acting as sinks – can remain occupied by high rates of immigration from suitable patches – acting as sources (i.e. a classical rescue effect; Brown & Kodric-Brown, 1977; Hanski, 1998; Eriksson *et al.*, 2014). From a host-as-patch view, symbiont local metapopulations differ from the classical metapopulation concept in that the patch is the host. For a given symbiont species the patches are host individuals of the same or different host species. Because hosts are often mobile and experience changes during their lifespan, they represent spatially dynamic patches with temporal variation in quality and availability of resources over time. Further, patches disappear by host death. Host death can lead to symbiont population loss, equivalent to local extinction in classical metapopulation models (Hanski & Gaggiotti, 2004), or symbiont release to the dispersal environment (Barfield, Orive & Holt, 2015). The perspective of interpreting the set of symbionts inhabiting a community of hosts as a local metapopulation emphasises the interactions between local transmission dynamics among hosts and within-host dynamics. It highlights the role of colonisation and extinction processes at the scale of host individuals in driving local dynamics of symbionts. Thus, the host-as-patch view assumes that local spatial structure in symbiont populations matters. By contrast, the land-patch view at the local scale interprets symbionts inhabiting a host community as a local population without spatial structure, thus emphasising purely niche-based processes as drivers of symbiont dynamics at this scale. Therefore, the land-patch view does not consider local spatial structure, focusing instead on the interaction between local population dynamics and large-scale dispersal processes.

(4) Regional dynamics

At the regional scale, we adapt the concept of interaction metapopulation proposed by Thrall & Burdon (1997), wherein the habitat patch is a land fragment containing a local population of symbionts inhabiting a community of hosts. Based on Thrall & Burdon's (1997) view, we define a regional metapopulation of symbionts as the set of local populations of symbionts interconnected by dispersal (Fig. 1). The spatial dimension of a regional metapopulation depends on the relative rates of host and symbiont dispersal (see Fig. 1 in Thrall & Burdon, 1997). For symbionts dispersed by host movements and, therefore, having similar dispersal ranges to their hosts (e.g. sexually transmitted symbionts or those transmitted by close contact among animal hosts), the regional metapopulation parallels host metacommunity structure and functioning, wherein connections among patches are governed by host dispersal among host communities *sensu lato* (see Leibold & Chase, 2018). The spatial extent of the regional metapopulation would be more restricted for symbionts with a lower dispersal range than their hosts. For instance, soil-borne pathogens only transmitted by direct contact among individual host plants may experience strong isolation among host populations that are mainly connected by the dispersal of seeds and/or pollen. By contrast, symbionts with higher dispersal than their hosts (e.g. wind-dispersers) may develop regional metapopulations that cover larger spatial extents than those delimited by host metacommunity dynamics. Geographical range expansion would occur either when a symbiont colonises a land fragment inhabited by a host community from a novel geographical area, or when a host community harbouring a symbiont expands its geographical range.

(5) Cross-scale dependence

Individual dynamics influence the upper levels of symbiont organisation by constituting a fundamental basis that provides intraspecific trait variation for the action of eco-evolutionary processes like adaptation (Bolnick *et al.*, 2011). From individual to population dynamics, population growth rates are dependent on the fitness of individuals related to intra-patch survival and reproduction. In addition, emigration propensity of individuals (i.e. their tendency to leave the patch) also influences growth rates and mean abundances of symbiont populations inhabiting patches (Jansen & Vitalis, 2007; Barfield, Orive & Holt, 2015). Conversely, both intra-patch fitness and emigration propensity are in turn affected by population densities due to intraspecific competition (Roughgarden, 1972; Poethke & Hovestadt, 2002; Araújo, Bolnick & Layman, 2011). From population to metapopulation dynamics, immigration rates of populations depend on dispersal dynamics at higher levels. Inversely, metapopulation dynamics depend on the average performance of individual populations at lower levels. It follows that cross-scale interactions are a key functional aspect of symbiont eco-evolutionary dynamics.

III. THE BIOTOPE AS A CONCEPTUAL LINK BETWEEN SPACE AND ENVIRONMENT

A robust and detailed conceptualisation of the linkage between physical space and the environment is mandatory when approaching range dynamics, which encompass niche-based and dispersal processes in a complex interactive fashion. The biotope is a bio-physical entity with abiotic and biotic conditions providing a living arena for a given species assemblage (Hutchinson, 1978). In our case, the species assemblage is a symbiont community. The biotope links therefore the physical space used by a species with its niche (Colwell & Rangel, 2009). As living conditions and the mode of interaction with the physical space differ among organisms, the biotope is a plastic entity that also differs among organisms.

(1) Metapopulation patch as biotope unit

Here we define a biotope for symbionts at two scales based on the metapopulation views of symbiont dynamics. For that, we interpret the metapopulation patch as a biotope unit, which can be a host individual or a land fragment. From the host-as-patch view, host individuals are biophysical entities that maintain symbiont populations within or on their bodies, and where within-host population dynamics take place. Hosts represent an unusual type of biotope because they can be highly dynamic in space and time when they are motile, and they are essentialy ephemeral, as they emerge at birth and disappear at death (i.e. a minor habitat *sensu* Elton, 1949). Scaling the biotope following the land-patch view, a land fragment inhabited by a community of hosts provides a living place for a local population of symbionts. The biotope is therefore a useful conceptual tool to link metapopulation and niche theories because it defines the intra-patch living conditions that determine how a population performs within a patch, which are directly related to the symbiont's niche.

(2) Symbiont–biotope interactions mediated by a dual environment

The interactions between an organism and its biotope determine, to a great extent, how the organism experiences and alters the environment. Symbionts experience a dual environment with a biotic component composed of traits of the host bodies where symbionts live, and the abiotic conditions external to the hosts (Krasnov *et al.*, 2015; Campbell & Crist, 2016; Fig. 2). At the scale of hosts, symbiont traits and the in-host living conditions regulate individual fitness and population performance of symbionts within or on their hosts. On the other hand, symbionts impact the in-host environment through direct and indirect effects on hosts. The direct effects range from negative to neutral or positive depending on the interaction type (parasitic, commensal or mutualistic), and can be context dependent (Leung & Poulin, 2008; Skelton *et al.*, 2013, 2016; Zug & Hammerstein, 2015). Direct symbiont–host interactions exhibit spatiotemporal variation across scales (Penczykowski, Laine & Koskella, 2015) and can be subject to strong feedback with mutual regulatory mechanisms (Anderson & May, 1978; Stanko, Krasnov & Morand, 2006). For instance, birds and mammals have a broad repertoire of strategies to reduce ectoparasite loads (Clayton, Bush & Johnson, 2015). Moreover, symbionts affect hosts indirectly through density-mediated and trait-mediated indirect effects (Dunn *et al.*, 2012). In turn, alternative hosts indirectly affect symbiont dynamics *via* amplification and dilution effects (Telfer & Bown, 2012). Furthermore, symbionts within a host interact with heterospecifics through competition for host resources (Smith & Holt, 1999; Mideo, 2009), apparent competition mediated by host immune responses (Holt & Bonsall, 2017) and enemy–victim interactions like intraguild predation (e.g. Thomas *et al.*, 2016).

The off-host environment exerts two main types of direct influence on symbionts. First, it can affect in-host fitness, especially that of symbionts living directly exposed to external conditions such as ectosymbionts (e.g. epiphytic organisms). In particular, populations of ectosymbionts inhabiting crustaceans or small mammals should be particularly sensitive to the off-host environment compared to endosymbionts inhabiting large mammals (e.g. Mestre, Monrós & Mesquita-Joanes, 2014; Krasnov *et al.*, 2015). Second, the off-host environment also regulates dispersal among hosts and the off-host living conditions of symbionts, especially those with active off-host transmission (e.g. Studer & Poulin, 2013; Goedknegt *et al.*, 2015) and/or free-living developmental or adult stages (e.g. ticks or butterflies). Finally, the off-host environment can influence the symbiont indirectly through its effects on hosts. The phenotypic plasticity in the proficiency with which a host transmits a symbiont to other hosts has been suggested as a strong contributor to symbiont dynamics (Gervasi *et al.*, 2015). In fact, many of the host traits associated with symbiont fitness depend on the response of the host to the off-host environment, such as body size (Angilletta, Steury & Sears, 2004; Ashton, 2004) or pathogen resistance (e.g. Schade, Shama & Wegner, 2014; Rollins-Smith, 2017).

IV. COLONISATION OF A BIOTOPE BY SYMBIONTS

Colonisation and extinction processes are the basis of range dynamics. Based on a simple conceptual model grounded in metapopulation theory (Hanski & Gilpin, 1997; Hanski, 1999), we define colonisation as the process of occupation of an empty biotope, either a host individual or a land fragment inhabited by a host community. A colonised biotope is inhabited by a population of symbionts. In our framework we define symbiont populations at two scales: (*i*) a within-host population inhabiting a host individual, and (*ii*) a local population inhabiting a land fragment. Colonisation comprises symbiont arrival, and survival or establishment. Establishment – the development of a thriving symbiont population – may occur when the biotope is suitable. An unsuitable biotope is a biotope with environmental conditions that do not allow for positive intrinsic population growth rate within the biotope, so that it can only sustain a surviving population by permanent immigration from suitable biotopes (i.e. rescue effect; Hanski, 1998). In our conceptual model, establishment involves long-term persistence of a symbiont population within its biotope without the need for immigration. Considering hosts as biotopes, because hosts are subject to permanent change during their development until they die, persistence for symbiont populations within their hosts extends at most to the host lifespan. Nevertheless, long-lived hosts such as trees or large mammals may function as relatively stable biotopes at the relevant temporal scales of some of their symbionts. Likewise, from the land-patch view, the off-host biotopes may also be ephemeral, such as temporary ponds that disappear during the dry season.

(1) Types of biotope colonisation

We define four potential types of biotope colonisation by symbionts based on the key underlying process, which can be applied to either host-as-patch or land-patch views (see Fig. 3 for a host-as-patch view of the concepts). First, *dispersal facilitation* involves colonisation by removal of a dispersal barrier, wherein an inaccessible but suitable biotope becomes accessible. Second, *demographic facilitation* is the colonisation of an accessible but unsuitable biotope mediated by rescue effect (akin to 'demographic rescue'; Brown & Kodric-Brown, 1977; Hanski, 1998; Kanarek *et al.*, 2015). Here, long-term persistence is highly dependent on the maintenance of high immigration rates. Third, *environmental facilitation* is colonisation driven by any environmental change (either abiotic or biotic), whereby an unsuitable biotope becomes suitable by environmental improvement in intra-patch living conditions. Fourth, *evolutionary facilitation* refers to colonisation with the intervention of adaptive evolution, in which an unsuitable biotope becomes suitable by evolutionary change in symbiont traits (akin to 'evolutionary rescue'; Gomulkiewicz & Holt, 1995; Kanarek & Webb, 2010; Carlson, Cunningham & Westley, 2014). Thus, evolutionary facilitation involves symbiont adaptation to intra-patch living conditions. These four types of biotope colonisation can be classified into two groups: (*i*) dispersal-driven colonisations that improve intra-patch migration inputs, comprising dispersal and demographic facilitations; and (*ii*) niche-driven colonisations that improve biotope suitability for symbiont population growth within the patch, which include environmental and evolutionary facilitations.

For the sake of clarity, we add here a conceptual precision. Because dispersal facilitation implicitly involves environmental or evolutionary changes increasing either connectivity among biotopes or symbiont dispersal capacity (Delgado, Ratikainen & Kokko, 2011; Boeye *et al.*, 2013), it could be interpreted as a specific case of environmental or evolutionary facilitation. Following a metapopulation perspective, we interpret as dispersal facilitation those colonisations driven by environmental or evolutionary changes directly affecting symbiont dispersal among patches. We explicitly restrict the terms environmental and evolutionary facilitation to colonisations involving changes directly affecting intra-patch population dynamics. Likewise, in the land-patch view, colonisations mediated by environmental or evolutionary changes altering local dispersal within a land fragment will be interpreted as either environmental or evolutionary facilitations (because the driver affects directly intra-patch population dynamics).

V. SYMBIONT RANGE EXPANSION MECHANISMS

Symbiont range expansion is a highly complex and dynamic process that is likely to involve massive events of colonisation and extinction of symbiont populations within both hosts and land fragments, interacting together with multiple dispersal, environmental and evolutionary factors across landscapes and timescales (Fig. 4; see also Hatcher, Dick & Dunn, 2012*a*; Lymbery *et al.*, 2014). In order to clarify such complexity, here we present a classification of range expansion mechanisms based on the most relevant types of biotope colonisation involved in the process. This simplified classification provides a global picture of the essential types of barriers experienced by symbionts, and the variety of ways symbionts may overcome them to expand their repertoire of suitable hosts and/or geographical range. The conceptual framework will serve to describe in Sections VI and VII how the niche relates to range expansion mechanisms of symbionts.

(1) Dispersal facilitation

The key mechanism behind dispersal facilitation is a change in connectivity among suitable biotopes within reachable distance of the metapopulation. At a local scale, an increase in host abundance may favour colonisations by boosting local symbiont dispersal (e.g. Stanko, Krasnov & Morand, 2006; Almberg *et al.*, 2012). Demographic and genetic data strongly suggest that the postglacial range expansion of the parasitic plant *Epifagus virginiana* was primarily driven by high population densities of its host *Fagus grandifolia* (Tsai & Manos, 2010). Evolution of symbiont life-history traits associated with dispersal is another potential driver of dispersal facilitation. For instance, the nematode *Rhabdias pseudosphaerocephala*

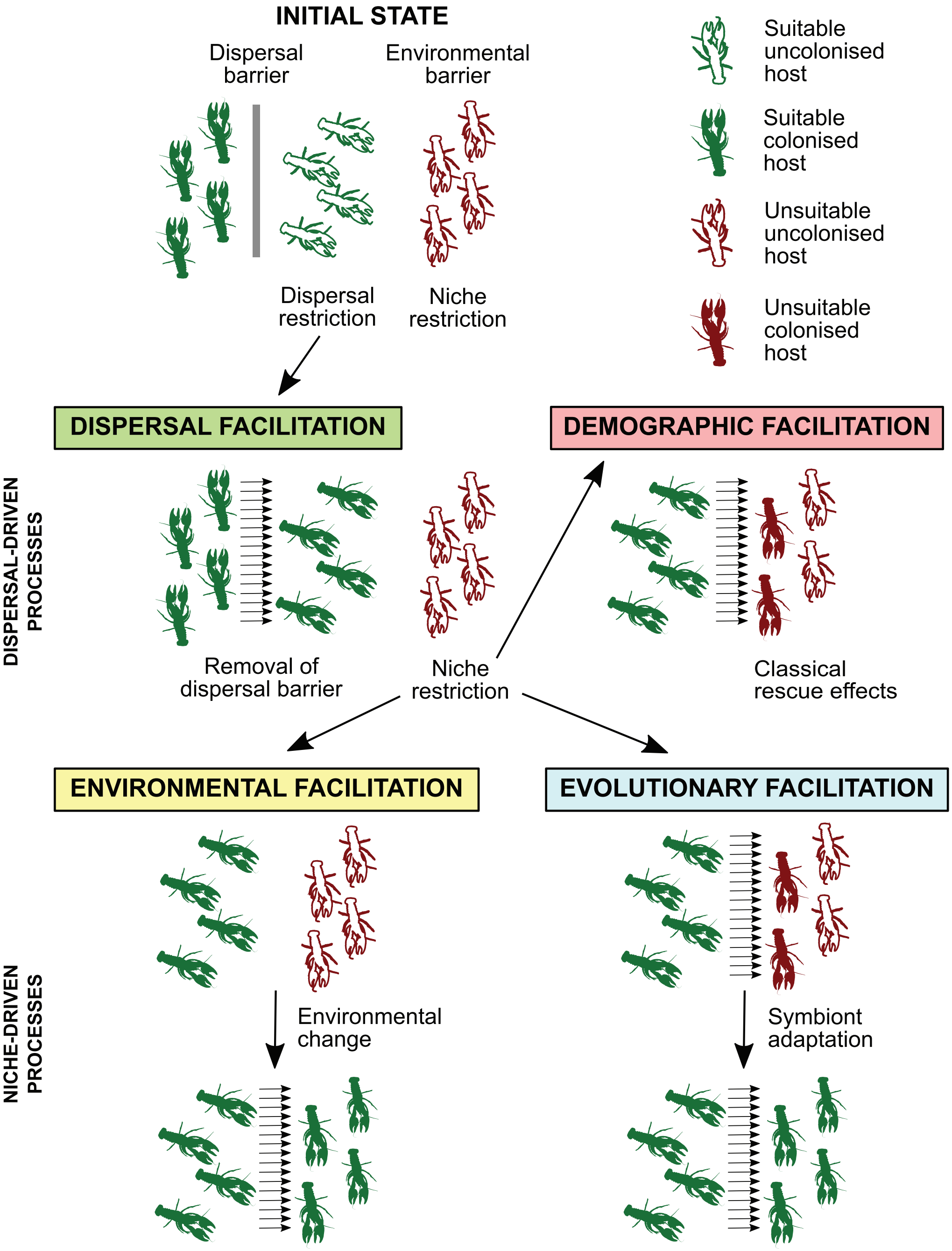


Fig. 3. Types of biotope colonisation potentially involved in range expansion of symbionts, based on the interpretation of hosts as biotopes (i.e. host-as-patch view). First, dispersal facilitation involves colonisation by removal of a dispersal barrier, wherein inaccessible but suitable hosts become accessible. Second, demographic facilitation is the colonisation of accessible but unsuitable hosts mediated by rescue effects. Third, environmental facilitation is colonisation by environmental change (abiotic or biotic), whereby unsuitable hosts become suitable by environmental improvement in in-host living conditions. Fourth, evolutionary facilitation is colonisation driven by adaptation to in-host living conditions. Note that the same concepts apply to the land-patch view if we replace hosts by land fragments inhabited by host communities as biotope units.

inhabits invasive populations of the cane toad *Rhinella marina* in tropical Australia. A common-garden experiment demonstrated that populations of *R. pseudosphaerocephala* from the expanding range edge exhibited reduced age at maturity and larger sizes of eggs, infective larvae and free-living adults, when compared to populations from the distribution core. Low host density at the expanding front selected for symbiont traits that enhanced transmission opportunities, thereby favouring symbiont range expansion (Kelehear, Brown & Shine, 2012). In addition, changes in host behaviour such

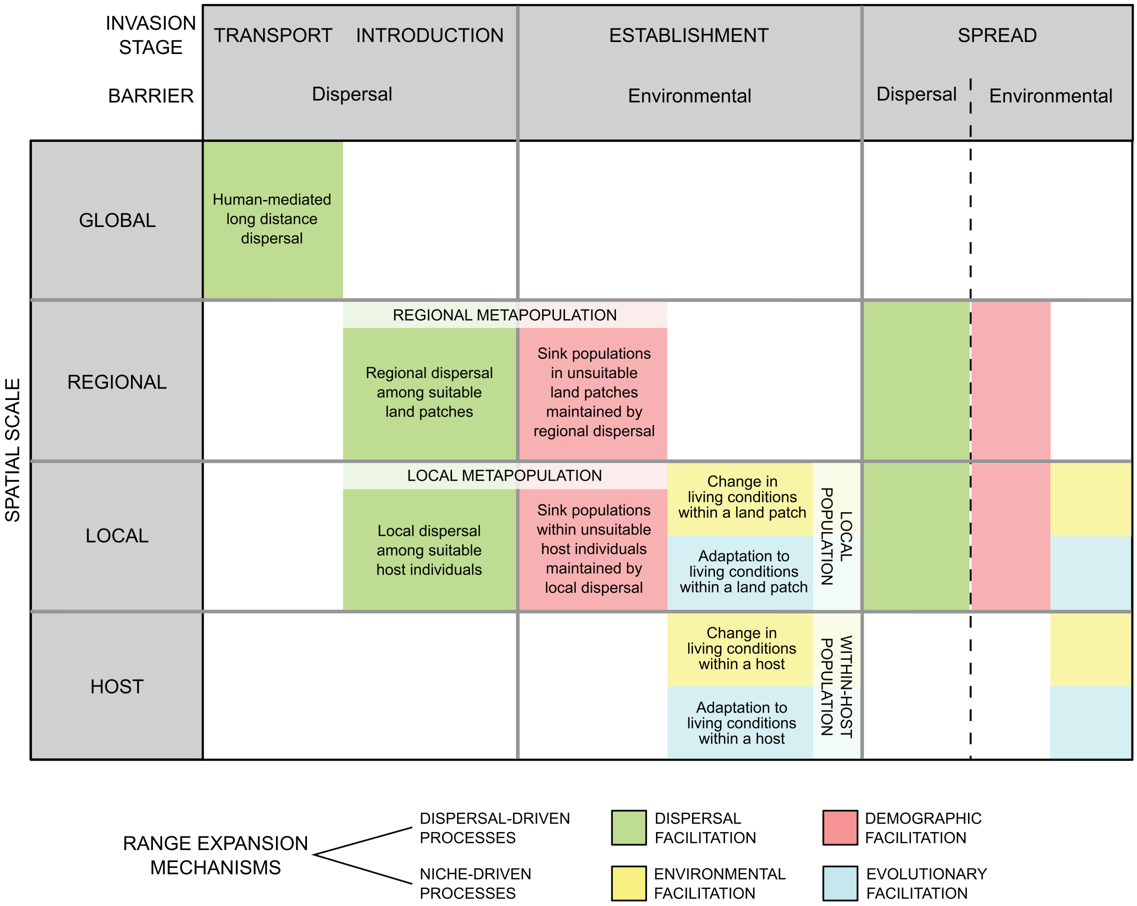


Fig. 4. Hypothetical spatiotemporal relationships among types of biotope colonisation involved in symbiont invasion processes, considering both hosts and land patches inhabited by host communities as biotopes. The conceptual framework for the invasion process (grey boxes) is derived from Blackburn *et al.* (2011). Dispersal-driven processes operate directly on metapopulation dynamics (from local to global scales), whilst niche-driven processes operate directly on population dynamics (from individual hosts to local scales). Dispersal facilitation is most relevant during transport, introduction and spread stages. The establishment stage involves scenarios wherein invasion requires colonisation of novel unsuitable biotopes by environmental or evolutionary facilitations. Unsuitable biotopes can be novel host species (host-as-patch view) or novel land fragments (land-patch view). New environmental barriers represented by unsuitable biotopes are likely to appear during the spread stage, so that establishment and subsequent spread could be replicated further.

as habitat choice or activity levels, can favour symbiont acquisition by hosts (Koprivnikar, Gibson & Redfern, 2012). Recent urban habituation and sedentarisation of *Pteropus* bats has allowed Hendra virus to colonise the major east coast cities of Australia, increasing the risk of outbreaks to human and domestic animal populations (Plowright *et al.*, 2011). At a regional scale, connectivity among host communities can be enhanced by alterations of exposure or transmission routes by human activities, changes in land use (Gottdenker *et al.*, 2014) or climate change (Utaaker & Robertson, 2015; Chapman *et al.*, 2016). For instance, the American crayfish *Procambarus clarkii* was introduced in Southern Spain for aquaculture purposes in 1973. The symbiotic ostracod *Ankylocythere sinuosa* was co-introduced with the crayfish. Subsequent intentional crayfish translocations by humans facilitated the geographical expansion of *A. sinuosa* into the entire Peninsula and the Balearic Islands (Mestre *et al.*, 2016).

(2) Demographic facilitation

Demographic facilitation is a metapopulation process and, therefore, operates at the symbiont metapopulation levels. At the local metapopulation level, unsuitable hosts can be colonised by symbiont dispersal from suitable hosts (i.e. hosts acting as sinks; Holt & Hochberg, 2002; Dennehy *et al.*, 2010; Gandon *et al.*, 2013). Likewise, regional metapopulation dynamics allow for colonisation of unsuitable land fragments from suitable host communities by large-scale dispersal (e.g. host movements or anemochory). The existence of high variation in host suitability (e.g. measured as host competence in transmitting symbionts after infection) is well recognised within and among species (Gervasi *et al.*, 2015), as well as among host communities (Johnson *et al.*, 2013). The eventual presence of symbionts in non-competent hosts (i.e. hosts unable to disseminate the symbionts after infection) is evidence of demographic facilitation at host scale (Randhawa, Saunders & Burt, 2007; Telfer & Bown, 2012). For instance, *Ixodes ricinus* is a generalist tick that feeds on mammals, birds and lizards. The tick is used as vector by diverse spirochete bacteria of the genus *Borrelia*, responsible for vertebrate diseases. Among them, *Borrelia afzelii* specialises on rodents whilst *B. garinii* is adapted to birds. *B. afzelii* is killed by the complement system of birds, whereas *B. garinii* is killed by the complement system of rodents (Berret & Voordouw, 2015). Because their vector is a generalist tick, they are likely to be exposed often to their respective incompetent host reservoirs. The tick-borne *Borrelia burgdorferi* and its vector *Ixodes pacificus* illustrate another intriguing case. Rodents serve as competent reservoirs for *B. burgdorferi*, and lizard blood kills the bacterium. However, lizards are more heavily utilised by *I. pacificus* than are rodents (Lane & Quistad, 1998; Casher *et al.*, 2002; Salkeld & Lane, 2010). Demographic facilitation can impair symbiont dynamics due to symbiont losses driven by attempted transmissions to unsuitable hosts or land fragments (dilution effect; Johnson & Thieltges, 2010; Civitello *et al.*, 2015). However, demographic facilitation also exerts a propagule pressure for the action of evolutionary facilitation on unsuitable biotopes (Simberloff, 2009), although excessive gene flow can disrupt or slow local adaptation (Dennehy *et al.*, 2010; Hatcher, Dick & Dunn, 2012*a*).

(3) Environmental facilitation

Environmental facilitation results from an environmental change that makes biotopes suitable because it improves intra-patch living conditions for the symbiont, and it is linked directly to either within-host or local population dynamics of symbionts. Influential host traits for symbionts like body size or immunological defences can undergo alterations favouring the symbiont, by host evolution (Penczykowski, Forde & Duffy, 2011) or off-host environmental change (e.g. Angilletta, Steury & Sears, 2004; Schade, Shama & Wegner, 2014). Alternatively, specific variation in symbiont community composition may favour host suitability (Mihaljevic, 2012; Borer, Laine & Seabloom, 2016). For instance, a non-indigenous symbiont can experience a competitive release because other symbionts were filtered out during the invasion process of the originally shared host (Torchin *et al.*, 2003). Improvements in host suitability mediated by environmental facilitation can extend to a locality or a region. For example, symbiotic dinoflagellates of the genus *Symbiodinium* are responsible for the photosynthetic productivity of corals. Ocean warming destabilises the symbiont–coral mutualism resulting in symbiont expulsion by corals ('coral bleaching'; Herre *et al.*, 1999). The coral reef ecosystems of the Greater Caribbean have been severely impacted in recent decades from warming climate and environmental degradation. *Symbiodinium trenchii* is a stress-tolerant symbiont from the Indo-Pacific Ocean that has colonised the Greater Caribbean. Under mild conditions, hosts are unsuitable for *S. trenchii* because host-typical symbionts outcompete *S. trenchii*. Recent stressful conditions in the Greater Caribbean have allowed the opportunistic symbiont to expand its geographical range by displacing native symbiont populations (Pettay *et al.*, 2015). The larvae of the pine processionary moth *Thaumetopoea pityocampa* live on pines where they build silk nests and feed on pine foliage during the winter. Feeding activity and survival of larvae are linked to winter temperature. The northward expansion of European populations of *T. pityocampa* during recent decades has been attributed to increased winter survival of larvae due to global warming (Battisti *et al.*, 2005). Historically, populations of the butterfly *Aricia agestis* in southern Britain were largely restricted to the plant species *Helianthemum nummularium*. Because this host plant is perennial and selects for warm microclimates, the butterfly was able to persist during past cooler periods. Recent global warming enabled *A. agestis* to exploit the widespread annual plant species *Geranium molle*, a change in host use that allowed its rapid range expansion (Pateman *et al.*, 2012). The European tick *Ixodes ricinus* has been experiencing a geographical expansion at its northern range margins (Jore *et al.*, 2014). During its life cycle, *I. ricinus* alternates feeding periods on three different hosts with long transitional free-living periods of diapause and host-seeking (Gray *et al.*, 2016). Warmer winters favour the activity, development and survival of free-living ticks. Range expansion of *I. ricinus* was most likely driven by the combination of climate change and increased local abundances of its main host, the roe deer *Capreolus capreolus* (Lindgren, Tälleklint & Polfeldt, 2000; Jaenson *et al.*, 2012). This tick is another example of environmental facilitation through improvements in suitability of the off-host biotopes at the regional metapopulation level.

(4) Evolutionary facilitation

Evolutionary facilitation is colonisation driven by symbiont evolution leading to improvements in biotope suitability and is linked directly to either within-host or local population dynamics of symbionts. Thus, unlike environmental facilitation, the improvements in biotope suitability underlying evolutionary facilitation originate from an evolutionary change in the symbiont by adaptation to intra-patch living conditions. Range expansion driven by adaptation to a novel host is a scenario of evolutionary facilitation. The conifer-feeding aphid genus *Cinara* is widely distributed in the Holarctic. Phylogenetic data suggest that host switching from *Pinus* to the novel host genus *Picea* during the Miocene facilitated the Holarctic colonisation of *Cinara* species (Meseguer *et al.*, 2015). Evolution in mechanisms of host detection and choice during host seeking can also be involved in evolutionary facilitation. Revisiting the example of the butterfly *Aricia agestis*, the use of *Geranium molle* driven by climate change that initiated the range expansion of the butterfly was followed by evolution of host preference (Buckley, Butlin & Bridle, 2012; Bridle *et al.*, 2014). Compared to long-established areas, butterflies from the recently colonised sites consistently preferred to lay eggs on *G. molle*, even if the plant was locally rare. The specialisation of *A. agestis* on the host plant species that was geographically widespread throughout the region of expansion facilitated the geographical spread of the butterfly. Furthermore, butterflies from the expanding region showed higher dispersal abilities. This example illustrates a complex case wherein range expansion was driven by the combination of environmental, evolutionary and dispersal facilitations. Adaptation to harsh off-host environmental conditions is another scenario of evolutionary facilitation. The Asiatic fungus *Cryphonectria parasitica*, the causal of chesnut blight, is spreading throughout Europe using the European chestnut *Castanea sativa* as main host. The range of *C. parasitica* is currently expanding in northern Europe. An experimental study provided evidence of thermal adaptation associated with northern expansion. Fungal isolates from northern populations exhibited better growth at low temperatures (below 16°C) than southern isolates. The study strongly suggests that range expansion of *C. parasitica* in Europe is facilitated by rapid thermal adaptation (Robin *et al.*, 2017).

VI. PARTICULARITIES OF THE SYMBIONTS' NICHE

Niche concepts have a very long history in ecology and have served as fruitful tools for developing, organising and synthesising knowledge about eco-evolutionary phenomena across levels of biological organisation (Chase & Leibold, 2003). Two main conceptual approaches were initially introduced that focused on two different niche aspects: (*i*) the responses of an organism to environmental conditions (Grinnell, 1917; Hutchinson, 1957); and (*ii*) the impacts of an organism on the resources available in the environment (Elton, 1927; MacArthur & Levins, 1967). Leibold (1995) merged both views by proposing a niche concept that integrates requirements and impacts (see also Hutchinson, 1978). Living on hosts not only has implications for the spatial dynamics of organisms as described in previous sections, but also involves profound changes in the ways organisms respond to and impact their environment. The application of niche theory to range expansion of symbionts requires paying specific attention to the alterations of symbiont–environment relationships mediated by the symbiotic lifestyle and, in particular, the relevance of hosts in the configuration of the symbionts' niche.

(1) Host as a fundamental part of the niche of symbionts

The most successful conceptual variant that persisted through time and contributed to modern ecology is the Hutchinsonian niche (Colwell & Rangel, 2009; Holt, 2009). Hutchinson (1957, 1978) defined the niche as a hyperspace constituted of multiple axes representing the relevant environmental conditions for a species to live. Hutchinson proposed two conceptual niche variants: fundamental and realised niches. He defined the fundamental niche as a hypervolume of permissive abiotic environmental conditions for living. The realised niche was introduced by Hutchinson as a concept to capture the effects of species interactions on the niche, emphasising competition as the most relevant interaction type (Colwell & Rangel, 2009). Modern biogeographers incorporate the effects of spatial processes by defining a realised niche as the fundamental niche modulated by biotic restrictions and dispersal limitations faced by the species (Soberón, 2007; Soberón & Nakamura, 2009; Guisan *et al.*, 2014). Thus, the traditional definitions of the Hutchinsonian niche exclude biotic interactions from the fundamental niche (but see Hutchinson, 1978). However, positive biotic interactions challenge this conception, especially those involving strong dependences (Peay, 2016). In general, survival and reproduction of heterotrophs depends on other organisms to supply organic carbon. Without interactions with these organisms, heterotrophs cannot subsist. Symbionts are an extreme case because biotic interactions are directly involved in the configuration of a symbiont's habitat. That is, symbiont survival, reproduction and population growth all may occur within a biotic environment (Rohde, 1994). In order to address this problem, our conception of the niche for symbionts integrates both positive and negative biotic interactions as part of the fundamental niche. This makes sense from an evolutionary perspective, because biotic environments are typical driving forces of adaptive evolution in symbionts, thereby leading to fundamental niche evolution. Thus, in our view of the fundamental niche applied to symbionts, unsuitability produced by any kind of biotic restrictions falls outside of the fundamental niche, whereas facilitative biotic interactions, such as adaptation to a novel host, expand the fundamental niche.

(2) Individual and population niches

The relevant niche processes in symbionts act at the scale of hosts and/or land fragments. From the host-as-patch view, host bodies often provide the developmental and reproductive environment for symbionts to establish within-host populations, although individual symbionts can also experience external environments during dispersal among hosts (e.g. symbiotic ostracods inhabiting crayfish; Mestre, Monrós & Mesquita-Joanes, 2014). From the land-patch view, land fragments also provide off-host places with environmental conditions external to the hosts for development and/or reproduction of local populations of symbionts with free-living developmental or adult stages (e.g. ticks or butterflies, see Section V.3). In that case, individual symbionts also experience environments outside their biotopes during dispersal among land fragments. For this reason, we scale the niche of symbionts at two levels of organisation: individual and population (either within-host or local).

The *individual niche* is associated with the fitness response of individual symbionts to the environment. The fundamental niche at the individual level is the set of environments that allow for positive individual fitness, which includes both intra-patch fitness and fitness during dispersal among patches. The individual niche differs among phenotypes (Dall *et al.*, 2012). Thus, symbiont populations contain a source of individual niche variants that differ in their fitness responses, as well as in their impacts on the environment. Such intraspecific niche variation can be moulded by natural selection and niche construction (see Section VIII). This allows for adaptation to intra-patch living conditions involved in evolutionary facilitation, or evolution of dispersal among patches involved in dispersal facilitation. Hence, the individual niche is an essential concept for understanding niche evolution associated with evolutionarily mediated colonisation processes.

The *population niche* characterises the central role of biotopes (either hosts or land fragments) in determining the environment experienced by populations of symbionts. The fundamental niche at the population level can be expressed in terms of positive intrinsic population growth rate (Hutchinson, 1978; Schurr *et al.*, 2012; Godsoe *et al.*, 2017). Intrinsic population growth rate is related to average individual fitness in a symbiont population when the symbiont is rare, and it measures biotope performance for developing thriving symbiont populations. From the host-as-patch view, the within-host population niche relates to the ability of symbionts to encounter the host, and the adequacy of in-host living conditions for development of symbiont populations (Rohde, 1994; Combes, 2001; Poulin, 2007*b*). For instance, condition-dependent chemical cues excreted to the environment by the snail host *Lymnaea stagnalis* determine its attractiveness to cercariae of the trematode *Echinoparyphium aconiatum*. Experimental studies show that snails in poor physiological condition due to starvation were unsuitable for the parasite because they were not located by the chemo-orientation mechanism of larvae (Seppälä & Leicht, 2015). The relevant dimensions of the within-host population niche are characterised by: (*i*) host traits associated with encounter and compatibility filters (Rohde, 1994; Poulin, 2007*b*; Telfer & Bown, 2012); (*ii*) the in-host symbiont community (Telfer & Bown, 2012); and (*iii*) the off-host conditions influencing the in-host microhabitat (e.g. Mestre, Monrós & Mesquita-Joanes, 2014; Krasnov *et al.*, 2015). From the land-patch view, the local population niche also includes the off-host environmental conditions that influence development, reproduction and/or local dispersal of symbionts outside their hosts within the land fragment (i.e. all the local factors influencing intra-patch dynamics). In addition, the realised niche is a complementary and useful concept at the population level that accounts for the set of intra-patch environments that are actually used by a symbiont in a locality or region during a given time.

(3) The dual niche of symbionts

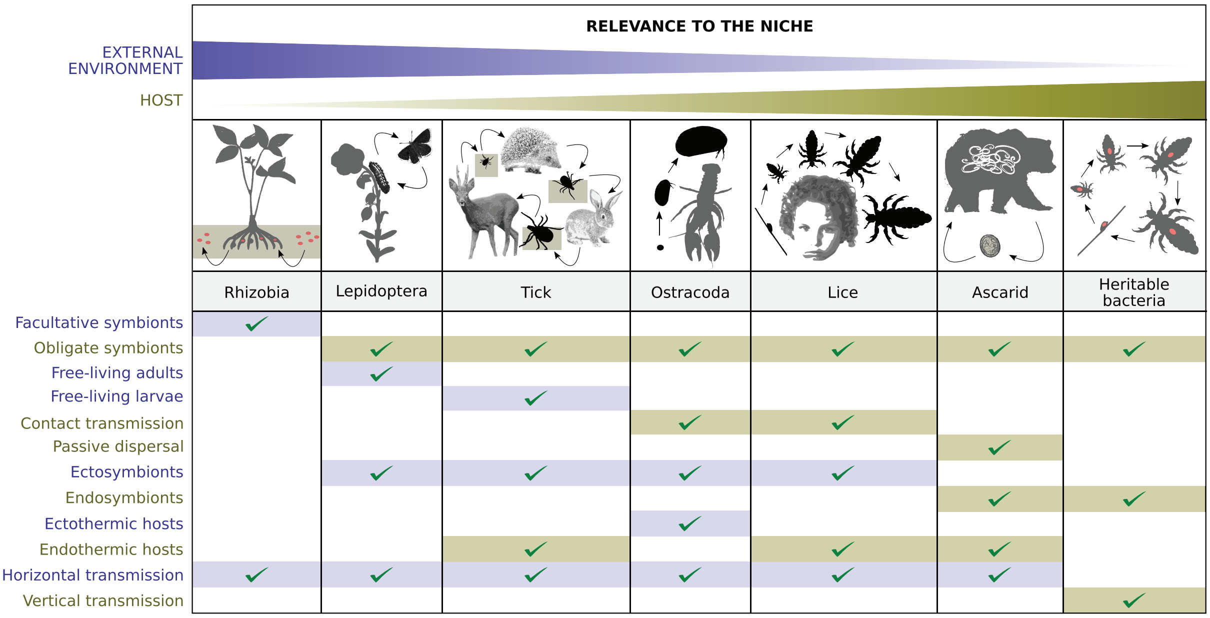
Symbionts have a dual niche composed of traits of their hosts and the abiotic environment external to the hosts (Krasnov *et al.*, 2015; Campbell & Crist, 2016). Here we propose that the relative relevance of the external environment and host traits to the symbiont's niche should depend on the life history of the symbiont and the homeostatic properties of hosts (Fig. 5). Facultative symbionts such as some rhizobial bacteria can adopt free-living lifestyles completely independent of hosts, wherein the external environment may govern the niche fully throughout the whole life cycle (Bright & Bulgheresi, 2010). Other symbionts such as ticks and lepidoptera have free-living developmental or adult stages, thus having a niche governed fully by the external environment during part of their life cycle (e.g. Pateman *et al.*, 2012; Gray *et al.*, 2016). By contrast, symbionts living permanently within or on their hosts should be more dependent on the in-host environmental conditions. Among them, symbionts transmitted by host-to-host contact (e.g. lice; Mehlhorn, 2012), or those with passive transmission through resistant eggs (e.g. ascarids; Sapp *et al.*, 2017) should be less dependent on the external conditions during dispersal among hosts than symbionts with active transmission through the off-host environment. Moreover, symbionts inhabiting homeothermic hosts such as large mammals (e.g. ascarids and lice) should be less influenced by the external environment during their in-host existence than those that use ectothermic hosts such as crustaceans (e.g. symbiotic ostracods; Mestre, Monrós & Mesquita-Joanes, 2014). Among symbionts inhabiting homeothermic hosts, endosymbionts (e.g. ascarids) should be more isolated from the external environment than ectosymbionts (e.g. lice). Finally, vertically transmitted endosymbionts illustrate an extreme case wherein the symbiont's niche may be almost fully governed by the host (e.g. heritable bacteria; Bright & Bulgheresi, 2010). In such cases, the symbiont's niche would approach that of its host.

VII. INTEGRATION OF RANGE AND NICHE DYNAMICS

In Section VI, we scaled the niche of symbionts at two organisational levels: individual and population. The individual niche provides the intraspecific niche variation required for the action of niche evolution underlying dispersal and evolutionary facilitations. In this section, we describe how the population niche serves to define biotope properties that characterise the different types of biotope colonisation processes involved in range expansion of symbionts.

(1) Correspondence between geographical and niche spaces

Biotopes are bio-physical entities that occur in geographical space, but they are characterised by biotic and abiotic environmental conditions that link biotopes to the niche. As defined by Leibold (1995), the niche determines how an organism performs in a given biotope, and also how the organism impacts the biotope. Thus, the biotope connects both geographical and niche spaces, a linkage conceptualised by the Hutchinsonian duality (Colwell & Rangel, 2009). Such duality refers to the idea that a biotope can be projected into the niche space and, conversely, a set of conditions (i.e. a niche point) can be projected into the geographic space where the biotope is located. This niche–biotope duality is



	Rhizobia	Lepidoptera	Tick	Ostracoda	Lice	Ascarid	Heritable bacteria
Facultative symbionts	✓						
Obligate symbionts		✓	✓	✓	✓	✓	✓
Free-living adults		✓					
Free-living larvae			✓				
Contact transmission				✓	✓		
Passive dispersal						✓	
Ectosymbionts		✓	✓	✓	✓		
Endosymbionts						✓	✓
Ectothermic hosts				✓			
Endothermic hosts			✓		✓	✓	
Horizontal transmission	✓	✓	✓	✓	✓	✓	
Vertical transmission							✓

Fig. 5. Variations in the relative relevance of the external environment and host traits to the symbiont's niche across systems, as illustrated by a variety of symbionts with different life cycles. Described from left to right, first, the soybean *Glycine max* takes up free-living bacteria *Bradyrhizobium* spp. from the soil (where they can live without the host) to establish an intracellular symbiosis in root nodules (Bright & Bulgheresi, 2010). Second, the lepidopteran *Aricia agestis* combines a larval symbiotic stage as caterpillar on the perennial plant *Helianthemum nummularium*, with an adult free-living stage as butterfly (Pateman *et al.*, 2012). Third, the three-host cycle of the tick *Ixodides ricinus* alternates feeding periods attached to hosts with long transitional free-living periods of larval development and host-seeking (Gray *et al.*, 2016). Fourth, the ostracod *Ankylocythere sinuosa* lives on the exoskeleton of the crayfish *Procambarus clarkii*, and is transmitted by host-to-host contact or active dispersal through the water (Mestre, Monrós & Mesquita-Joanes, 2014). Fifth, the louse *Pediculus humanus capitis* lives permanently on human hair and requires direct contact among hosts for transmission (Mehlhorn, 2012). Sixth, the parasitic nematode worm *Baylisascaris transfuga* is an endosymbiont of bears with no intermediate hosts and passive transmission through resistant eggs in host faeces (Sapp *et al.*, 2017). Seventh, the bacterium *Candidatus Riesia pediculicola* is an intracellular endosymbiotic mutualist of *Pediculus humanus capitis* (Bright & Bulgheresi, 2010); the endosymbiont colonises internally the eggs of the female louse, thus its whole cycle (including transmission) occurs within the host.

characterised by a partial reciprocity: (*i*) a biotope is always represented by a unique point in niche space; and (*ii*) a point in niche space can be represented by one biotope, multiple biotopes, or not be present at all in the geographical space.

The niche serves to assess two fundamental biotope properties of our framework through the Hutchinsonian duality (Fig. 6): the fundamental niche is related to biotope suitability, whilst the realised niche is linked to biotope occupancy. For instance, applying the host-as-patch view, a host with a suite of conditions that belong to the fundamental niche of a given symbiont is a suitable host for the symbiont. That means the host can be encountered by and is compatible with the symbiont (Rohde, 1994; Poulin, 2007*b*; Telfer & Bown, 2012). Thus, the symbiont is capable of establishing thriving populations within that host provided that the host is available. By contrast, hosts eventually occupied by a symbiont population have environmental conditions that belong to the realised niche, independently of whether they are suitable or not for the symbiont. The same concepts apply to the land-patch view as well.

Two kinds of mechanism produce a mismatch between fundamental and realised niches, affecting biotope properties as follows (Pulliam, 2000). First, demographic facilitation maintains occupied biotopes that are unsuitable. So, the biotopes are within the realised niche but outside the fundamental niche. Second, dispersal restrictions prevent occupation of suitable biotopes. Furthermore, not all suitable conditions for a given species are necessarily represented in the suite of biotopes of a given region and time interval. This additional aspect of the Hutchinsonian duality is conceptualised by the potential niche, i.e. portions of the fundamental niche that are outside the potential niche are unexpressed in the set of biotopes present in the geographical space.

(2) Colonisation of biotopes and population niche of symbionts

In this section we interpret colonisations of biotopes by symbionts from a niche perspective. Note that all the concepts apply to colonisations of either hosts or land fragments, depending on the scale of interest. As described above, the population niche reveals biotope properties: (*i*) biotope suitability through the fundamental niche; (*ii*) biotope occupancy through the realised niche; and (*iii*) biotope availability through the potential niche. It follows

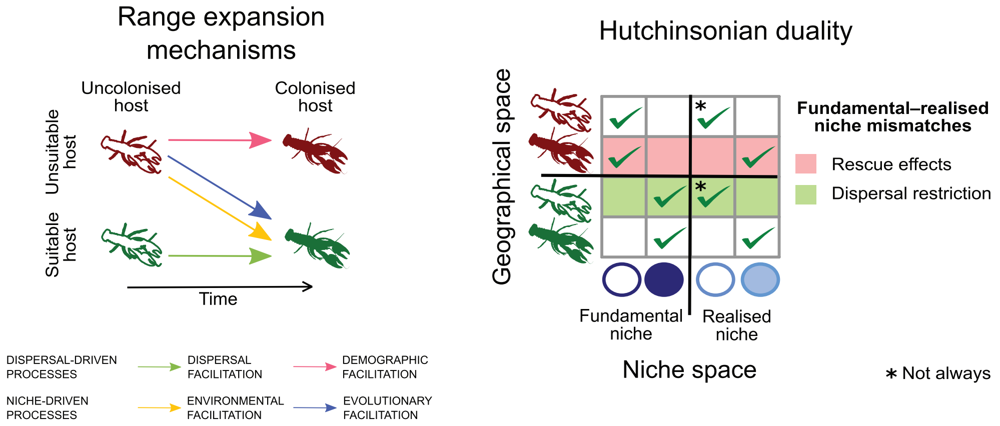


Fig. 6. Relationships between symbiont range expansion mechanisms (left) and the Hutchinsonian niche–biotope duality (right), from a host-as-patch view (i.e. interpreting host individuals as biotopes for symbionts). The left figure summarises the symbiont range expansion mechanisms based on the key process that enhances host colonisations by symbionts. On the right, the Hutchinsonian duality illustrates the association between host properties (suitability and occupancy) and location of the projected in-host living environment into the symbiont's niche space, either outside (empty blue circles) or inside (filled blue circles) the niche (fundamental and realised). The asterisk indicates that an unoccupied biotope is outside the realised niche provided that it has unique in-host living environmental conditions not represented in the community of occupied hosts [see Colwell & Rangel, 2009 for more details]. Note that the same concepts apply to the land-patch view if we replace hosts by land fragments inhabited by host communities as biotope units.

that colonisation of biotopes impacts niche dynamics at the population level in different ways depending on the colonisation type involved. In general, the occupation of empty biotopes tends to fill the realised niche space. Thus, all types of colonisation process potentially result in realised niche expansion. But they differ in their relationships with the fundamental niche, as follows.

Dispersal facilitation is the only colonisation type that operates inside the fundamental niche through colonisation of originally suitable biotopes. Thus, dispersal facilitation is the only colonisation type without environmental or evolutionary constraints and, in this sense, it is the most likely to be successful. Moreover, because biotopes colonised by dispersal facilitation already belong to the fundamental niche, they will harbour new source populations that will tend to produce high emigration outputs, thereby promoting further colonisations, which can involve unsuitable biotopes *via* demographic facilitation. By contrast, demographic facilitation produces an expansion of the realised niche beyond the fundamental niche. Because biotopes colonised by demographic facilitation are unsuitable, their symbiont populations will be highly dependent on immigration rates, with low capacity to produce dispersal outputs and replicate the process in other biotopes. However, unsuitable biotopes colonised by demographic facilitation set the stage for evolutionary facilitation that would expand the fundamental niche to track the new realised niche.

On the other hand, environmental facilitation involves colonisation of unsuitable biotopes driven by an environmental change that makes them suitable. Thus, environmental facilitation does not modify the fundamental niche of the symbiont. It actually shifts the intra-patch environmental conditions from outside to inside the fundamental niche. The mechanism behind the process is extrinsic to the symbiont and independent of the symbiont–biotope interaction. That is, the environmental change underlying the process can operate on empty biotopes prior to their contact with the symbiont. Finally, evolutionary facilitation results from the symbiont adapting to harsh intra-patch living conditions through eco-evolutionary processes that may involve multiple genetic, demographic and extrinsic factors (Lenormand, 2002; Carlson, Cunningham & Westley, 2014; Hendry, 2016). Evolutionary facilitation is the only colonisation process that expands the fundamental niche. Because it involves niche evolution, evolutionary facilitation requires a prior symbiont–biotope interaction for the action of natural selection.

VIII. NICHE CONSTRUCTION AND SYMBIONT RANGE EXPANSION

Standard evolutionary theory depicts natural selection as the main evolutionary process that promotes an adjustment of species traits to environmental factors (Bock, 1980). As a counterpoint to the unilateral direction of evolution driven by natural selection, Lewontin (1978, 1982, 1983) introduced the term 'niche construction' to emphasise the active role of organisms in their evolutionary trajectories through their impact on the environment they experience. Niche construction occurs when organisms modify their environment–traits relationships, thereby partly defining and creating their own niches (Laland, Odling-Smee & Feldman, 1996). From an evolutionary perspective, niche axes are dimensions of natural-selection pressures providing a selective environment that, as a whole, configures the organism's adaptive landscape (i.e. fitness–trait relationships; Wright, 1984). Combinations of traits that confer high fitness in a given environment represent peaks in the adaptive landscape that eventually attract evolutionary trajectories. It follows that organisms modify their selective environments through niche construction, thereby creating organism–environment eco-evolutionary feedbacks (Sultan, 2015).

Niche construction by organisms occurs in two ways: relocation and perturbation (Odling-Smee, Laland & Feldman, 2003). Relocation is a behavioural change that modifies the habitat choice of an organism, thereby altering the environment it experiences. Thus, relocation is linked to the Grinnellian niche that emphasises the responses to the environment (Grinnell, 1917). By contrast, perturbation occurs when organisms actively change a physical or biotic component of their environment at a specific location and time. Thus, perturbation is linked to the Eltonian view of the niche that focuses on the impacts to the environment (Elton, 1927). Niche construction by an organism can affect others, which is clear in tight associations such as symbiont–host interactions. Host bodies provide environmental conditions and/or resource supplies to symbionts. From the symbiont's point of view, hosts are micro-engineers that control and modulate the symbiont's environment by changing themselves (autogenic engineers; Odling-Smee *et al.*, 2013). Therefore, hosts construct the niche of symbionts. Likewise, symbionts also construct their own niches and modify host niches (Buser *et al.*, 2014; Lymbery, 2015;Moczek, 2015 ; Borges, 2017). From the perspective of hosts as biotopes for symbionts, niche construction by symbionts involves both selection of host microenvironments by relocation, and alteration of host eco-evolutionary dynamics by perturbation. For instance, manipulation of host phenotype by parasites is a well-studied phenomenon that leads to changes in host morphology, physiology and behaviour, which includes parasites inducing their hosts to relocate to different microhabitats (Poulin, 2010). Compelling data exist about the influences of symbiotic bacterial communities on animal physiology and development (McFall-Ngai *et al.*, 2013). Thus, hosts and symbionts co-construct their niches and co-participate in the creation and evolution of the selective environments of their associates (Moczek, 2015; Borges, 2017). Because the niche plays a fundamental role in range dynamics, it follows that influences of interactive, co-niche construction dynamics of symbionts and their hosts should extend to range expansion processes (Fig. 7).

(1) Host as environmental stabiliser

Organisms often select the habitat where they live (Rosenzweig, 1991). Here, the term habitat is akin to our biotope concept. Habitat selection has implications in eco-evolutionary dynamics (Morris, 2011). Behavioural changes affecting habitat and food selection are major drivers of shifts into new adaptive zones involved in drastic evolutionary events (Mayr, 1963), like transitions from free-living to symbiotic lifestyles or host switches. Changes in habitat selection are forms of relocational niche construction (Odling-Smee *et al.*, 2013). Microhabitat choice has the potential to alter environmental sources of selective pressures. Laland & Sterelny (2006) illustrate this with an example of nest selection in seabirds. An evolutionary transition from ground to burrow nesting would prevent eggs from direct visual exposure to predators, thereby making camouflaged egg shells irrelevant. Moreover, the burrow would provide a more uniform developmental environment that would alleviate selective pressures that maintain regulatory mechanisms of environmental variation, such as thermoregulation. Indeed, many activities of organisms, such as building a nest or choosing an environmentally homogeneous habitat, are adaptive precisely because they buffer environmental variation (Lewontin, 1982, 1983).

Convergent evolution at functional, ecological and genomic levels in parasites (Poulin, 2011; Poulin & Randhawa, 2015) provides strong evidence of long-term, evolutionary consequences of relocational niche construction. Genomic reduction and functional loss in many parasites (Poulin & Randhawa, 2015) indicate dramatic shifts in selective pressures resulting from transitions to symbiotic lives. Because host bodies provide habitats that are rich in resources and, often, environmentally stable and predictable, choosing a host as living place often triggers the loss of traits due to lack of functionality. For example, much evidence exists about loss or reduction of metabolic pathways in parasites because the host provides the metabolic products (e.g. Revill, Stanley & Hibberd, 2005; Müller *et al.*, 2012; Olson *et al.*, 2012). Parasitic nematodes associated with endothermic hosts exhibit more compact mitogenomes than those of ectothermic hosts (Lagisz, Poulin & Nakagawa, 2013), suggesting that host homeostatic properties also shape symbiont evolution. Internal homeostasis of host bodies resulting from a variety of evolved physiological, behavioural and life-history mechanisms offers a stable and predictable micro-habitat to the nearly always smaller symbionts, including availability of food resources (Sukhdeo, 1990; Sukhdeo & Sukhdeo, 1994). Hence, a potential benefit of symbiotic lifestyles is an increase in environmental stability.

The 'environmental stability' hypothesis was originally proposed by Hairston & Bohonak (1998) to explain the frequent independent transitions from free-living to parasitic lifestyles in inland water copepods. It focuses on the potential function of the host's body as an environmental stabiliser that could buffer the symbiont from the harsh and variable external environment. In this way, host properties could become fundamental in determining niche axes for the symbiont, such as those related to thermal or physico-chemical conditions. In turn, external conditions may have a diminished role in governing the symbiont's population niche as a consequence of host-driven environmental stability. An extreme case would be represented by vertically transmitted intracellular symbionts adapted to the cytoplasm of host cells, a homeostatic environment under total host control (Kooijman *et al.*, 2003). For instance, the bacterium *Candidatus Riesia pediculicola* is an intracellular endosymbiotic

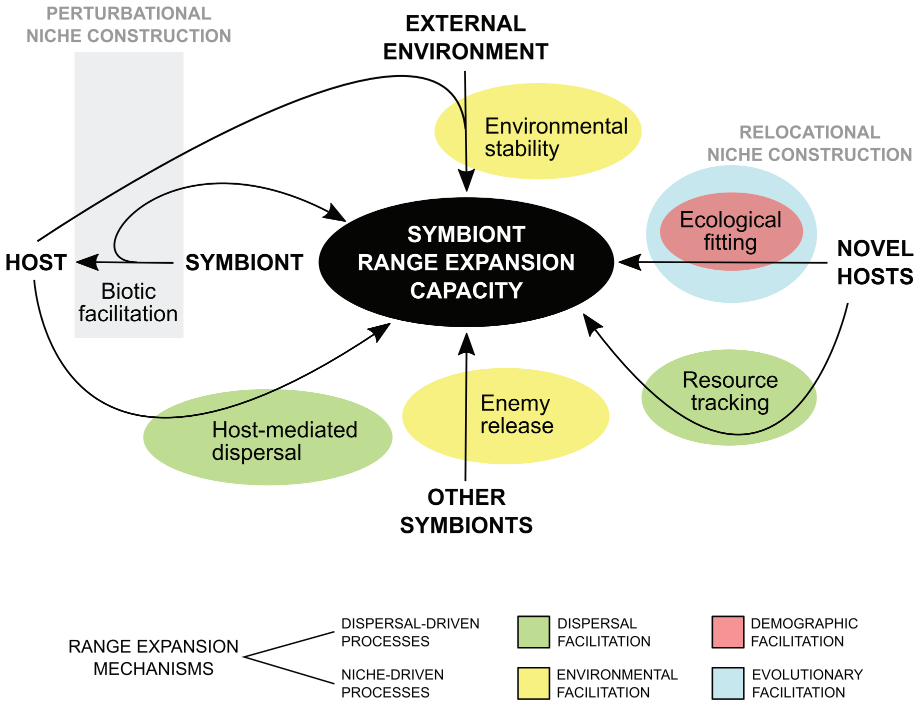


Fig. 7. Summary of processes potentially associated with range expansion capacity of symbionts based on the function of hosts as biotopes for symbionts. First, hosts can either protect symbiont populations from off-host environmental gradients (environmental stability hypothesis) or expand symbiont dispersal range by host-mediated dispersal. Environmental stability would release symbionts from dependence on environmental facilitation to expand their ranges. Improvements in host-mediated dispersal (e.g. host translocations by humans) represent a type of dispersal facilitation. Second, symbionts can improve their range expansion capacity through their impacts on hosts (perturbational niche construction) *via* protecting their affiliated hosts from environmental harshness (biotic facilitation). Third, symbionts can be favoured by competitive release during host range expansion because other symbiont competitors were lost during the process (environmental facilitation by enemy release). Fourth, colonisation of a novel host is a type of relocational niche construction that opens new ecological opportunities for symbionts eventually to expand their geographical ranges. If the novel host is suitable, the colonisation only requires accessibility by dispersal facilitation (resource tracking). Colonisation of novel, unsuitable hosts requires both accessibility by demographic facilitation and adaptation to novel in-host conditions by evolutionary facilitation (ecological fitting).

mutualist of the human louse *Pediculus humanus capitis* (Bright & Bulgheresi, 2010). The bacterium supplies vitamin B5 to the louse, which is deficient in its haematophagous diet. The endosymbiont colonises internally the eggs of the female louse, thus its whole cycle takes place within the host, including transmission. The mammalian immune system has evolved to maintain homeostasis with selected gut microbiota for their metabolic benefits (Hooper, Littman & Macpherson, 2012). Internal tissues of vertebrates have been proposed as highly predictable environments for endosymbionts like helminths (Sukhdeo, 1990; Sukhdeo & Sukhdeo, 1994). Even ectoparasites living on the skin of large vertebrates could obtain some benefit from homeostatic properties of host bodies like thermoregulation (e.g. body heat, hairs and feathers). We argue here that variation in the relative roles of host *versus* external environment in governing the symbiont's niche (see Fig. 5) may have implications for the range dynamics of symbionts. We use the metaphor of 'space travel' to illustrate our hypothesis. Humans are able to travel through outer space by using sophisticated spacecraft that recreate a habitable environment isolated from the external inhospitable conditions. Likewise, symbionts may 'travel' through external landscapes bringing their own suitable conditions within the spacecraft represented by the host. Thus, the environmental stability hypothesis suggests an important potential mechanism for symbionts to expand their ranges. The potential buffering effects of host bodies could, to a certain degree, make some symbionts insensitive to off-host environmental gradients, thereby protecting them from unsuitable external conditions when they expand their ranges. Hence, environmental stability would reduce the role of environmental facilitation as a range expansion mechanism for such symbionts. Resource sufficiency and environmental protection offered by the host would allow those symbionts to benefit from host phenotypic plasticity and adaptation when reaching novel environments (Agosta & Klemens, 2008).

(2) Host as a hitchhiker's ride

In addition to providing environmental stability, hosts may expand the dispersal range of an organism by niche construction (Buser *et al.*, 2014). Some organisms with limited dispersal abilities, such as mites and nematodes, use hosts exclusively to migrate among discrete, impermanent biotopes, in a phenomenon called phoresy (White, Morran & de Roode, 2017). The proximate ecological benefits of phoresy (Houck & OConnor, 1991) are equivalent to those provided by increased dispersal in metapopulations with ephemeral patches, i.e. avoidance of either local extinction or overcrowding (Ronce, 2007). Phoresy involves transport without in-host nutrition, development or reproduction, so that the ecological and evolutionary advantage from phoresy is purely linked to dispersal. Thus, phoresy is a primitive interaction whereby the host does not act as biotope, but as transport vector among biotopes. However, phoresy has been proposed as an intermediate step in the transition from free-living in temporary environments, such as mites living in bird nests, to a more stable symbiotic existence, such as mites living on birds (Houck & OConnor, 1991; Proctor, 2003; White, Morran & de Roode, 2017). In this sense, niche construction initiates an organism–host interaction *via* phoresy as a transitional evolutionary stage from living in ephemeral off-host biotopes towards living in a host biotope that provides all the resources and conditions required for development and reproduction. Thus, phoresy not only transforms the dispersal dynamics of an organism, but may also set the conditions for relocational niche construction that could completely reconfigure its niche around a new biotic environment governed by the host body, wherein environmental stability would start to operate. In our example, the bird skin and/or feathers would start providing protection, thermal stability and food to symbiotic mites (Proctor, 2003).

Host movements still play their role in non-phoretic symbionts because motile hosts transport symbiont populations through geographical space, thereby influencing contact and transmission rates of symbionts among hosts. Although the essential function of a biotope is to provide a living place for development and reproduction, motile hosts represent a singular type of biotope in the sense that they also allow for biotope-mediated range expansion. From this perspective, the possibility of moving across landscapes with their own suitable environmental conditions for development and reproduction, like humans travelling in a spacecraft through outer space, suggests a potential advantage for some symbionts compared to free-living species. However, the degree of ‘isolation’ should differ markedly among symbiont–host systems depending on the host homeostatic properties, the in-host microhabitat used by the symbiont (e.g. internal tissues or external surface of host bodies) and, in general, the symbiont’s life history (Fig. 5). Furthermore, a total dependence on hosts as a living place also involves strong dependence of geographical distribution and persistence on host availability (Stewart *et al.*, 2015). That is, dispersal and environmental barriers, and extinction risks suffered by available hosts also apply to their symbionts, unless host switch events release symbionts from constraints imposed by the original hosts (Dunn *et al.*, 2009; Colwell, Dunn & Harris, 2012).

During the range expansion of symbiont–host associations, symbionts also experience their own barriers. Theoretical models predict that uncoupled dispersal dynamics between both associates lead to symbiont loss in the range expansion fronts (Phillips *et al.*, 2010). Here, transmission mode is a relevant symbiont trait to consider. Range expansion of symbionts with density-dependent transmission, such as symbionts with free-living stages, should be especially compromised by low host abundances. By contrast, vertically transmitted symbionts are not dependent on host abundance and often exhibit low virulence, traits that may increase their likelihood of persisting during a range expansion event (Prenter *et al.*, 2004; Roy & Handley, 2012; Telfer & Bown, 2012). In addition, dispersal of symbionts with free-living transmission stages can be impeded by off-host environmental conditions. For instance, ultraviolet radiation and predatory pressure increase mortality in trematode cercariae (Studer & Poulin, 2013; Goedknegt *et al.*, 2015). The enemy release hypothesis provides additional indirect support for the existence of strong filters acting on symbionts during host invasion processes [Keane & Crawley, 2002; Torchin *et al.*, 2003; Prenter *et al.*, 2004; Tompkins *et al.*, 2011; Roy & Handley, 2012; Stewart *et al.*, 2015; see Colautti *et al.*, 2005 for criticisms]. This hypothesis states that non-indigenous hosts benefit from leaving behind parasitic symbionts, a release from enemies that enhances their competitive abilities against native hosts. Data from introduced birds in New Zealand suggest that symbiont losses occur mainly during host establishment in the new environment due to constraints in symbiont transmission efficiency (MacLeod *et al.*, 2010). From a symbiont’s point of view, enemy release is a potential mechanism for some symbionts to become released from in-host competition against other symbionts that were lost during the range expansion process (Telfer & Bown, 2012).

Applying a host-as-biotope perspective, a less-explored symbiont filtering mechanism is the existence of external environmental gradients during host range expansion that lead to unfavourable shifts in in-host living conditions. As discussed earlier, symbionts with within-host population dynamics directly influenced by external conditions, such as ectosymbionts hosted by ectothermic hosts, are potentially vulnerable to symbiont loss driven by environmental filters acting at the scale of hosts. The existence of environmental filters is well known in some mutualistic symbioses. Autotrophic symbionts of lichens often show distinct environmental preferences (Rolshausen *et al.*, 2018). High temperatures break down the mutualistic association between dinoflagellates and corals (Herre *et al.*, 1999). Severe environmental conditions such as salt stress, drought or acidity supress growth and nitrogen fixation by symbiotic Rhizobia (Zahran, 1999). In these mutualistic interactions, the symbiont’s niche is expected to limit the geographical distribution of hosts (e.g. Simonsen *et al.*, 2017). In other cases, environmental filters can potentially release hosts from their symbionts during host range expansion (Mestre *et al.*, 2013). In-host abundances of the freshwater ectosymbiotic ostracod *Ankylocythere sinuosa* are sensitive to salinity (Mestre, Monrós & Mesquita-Joanes, 2014). Likewise, air temperature and relative humidity strongly influence egg production, development and survival of fleas inhabiting small mammals, and their local community assembly is mainly affected by abiotic conditions (Krasnov *et al.*, 2015). Even though scarce evidence exists that links environmental filters directly affecting in-host living conditions with range expansion of symbionts (e.g. Battisti *et al.*, 2005), symbionts like those in the previous examples are strong candidates to face these circumstances. Future research on this would help to assess the potential relevance of environmental and evolutionary facilitations as range expansion mechanisms acting on this type of filter.

(3) Symbionts as harshness mitigators

Environmental perturbation is a pervasive niche construction mechanism in symbionts. From a host-as-biotope perspective, because biotopes of symbionts are living organisms from which symbionts directly obtain resources, symbionts are unusual in that resource consumption directly impacts their living place. That is, both niche conditions and resources are tightly linked to a single host organism. Symbionts impact their biotope directly through positive or negative effects on host fitness, and indirectly, in more subtle and varied ways that include trait-mediated and density-mediated indirect effects (Dunn *et al.*, 2012). It follows that symbionts can influence their own range expansion capacity through their impacts on hosts. The literature about host invasion mediated by symbionts is extensive (e.g. Dunn, 2009; Roy & Handley, 2012; Strauss, White & Boots, 2012; Hatcher, Dick & Dunn, 2012*a*; Lymbery *et al.*, 2014; Traveset & Richardson, 2014). Here, we provide a novel perspective from the lens of niche construction. For that, we describe some mechanisms whereby symbionts may enhance their range expansion capacity *via* alteration of the eco-evolutionary dynamics of their hosts. The examples serve to illustrate the role of perturbational niche construction as a mechanism for an organism to influence its own range expansion potential.

Parasitic symbionts often facilitate range expansion of non-indigenous hosts by acting as weapons against native host competitors, an indirect mutualism whereby the non-indigenous host benefits from an enemy alliance (Strauss, White & Boots, 2012). Virulence of non-indigenous parasites is usually greater in native hosts than in the non-indigenous host that introduced the parasite (Lymbery *et al.*, 2014). The naïve host syndrome hypothesis posits that both co-invaders may benefit from a long-term evolved, stable interaction through niche construction processes that regulate symbiont impacts on the host through evolution of host tolerance and symbiont virulence (Mastitsky *et al.*, 2010). As an alternative explanation, the invasion process most likely filters symbiont–host interactions wherein host damage is high (Lymbery *et al.*, 2014). When both associates establish novel contacts with native biota, a possible outcome is the local extinction of native hosts mediated by the symbiont, a phenomenon that has been called niche destruction (Holt, 2009), although we suggest a more accurate term is 'biotope destruction'. By 'destroying biotopes' due to an extremely high virulence, the symbiont indirectly assists the host co-invader to outcompete native hosts faster, thereby favouring its own range expansion. The colonisation of the UK by the American grey squirrel (*Sciurus carolinensis*) mediated by the squirrelpox virus, and the range expansion of American crayfish species (*Procambarus clarkii* and *Pacifastacus leniusculus*) mediated by the fungus *Aphanomyces astaci* are classical examples (reviewed in Strauss, White & Boots, 2012).

Mutualistic symbionts may also enhance their own range expansion capacity through biotic facilitation on hosts (Traveset & Richardson, 2014). Mutualistic symbionts expand the abiotic niche of their hosts (Poisot *et al.*, 2011; Peay, 2016), thus enabling colonisation of otherwise harsh abiotic environments for the host (Afkhami, McIntyre & Strauss, 2014; Rolshausen *et al.*, 2018). For instance, mutualistic fungal endophytes associated with the grass *Bromus laevipes* ameliorate drought stress and expand the geographical range of this host species into drier habitats (Afkhami, McIntyre & Strauss, 2014). On the other hand, some mutualistic symbionts facilitate range expansion of their host's associates because they disrupt mutualistic interactions of host competitors. For instance, co-invasion of the non-indigenous legume *Acacia longifolia* and its associate rhizobial symbionts can be enhanced by disruption of native plant–rhizobia interactions mediated by spillover of the non-indigenous rhizobia. The novel interaction reduces the fitness of native legumes because it is less effective, thus competitively favouring *A. longifolia* (Rodríguez-Echeverría, 2010; Rodríguez-Echeverría *et al.*, 2012). Defensive symbionts, i.e. symbionts that protect their hosts from natural enemies, represent a diverse and common type of mutualistic interaction (Hopkins, Wojdak & Belden, 2017). Jaenike *et al.* (2010) provided evidence of geographical spread of the bacterium *Spiroplasma*, a defensive symbiont that protects *Drosophila neotestacea* against the sterilising effects of a parasitic nematode. Populations of *D. neotestacea* became favoured by the spread of the symbiont-based mode of defence. The authors suggest that the rapid spread of *Spiroplasma* was likely driven by imposed selection on *D. neotestacea* to evolve symbiont-mediated protection. In summary, perturbational niche construction allows symbionts to act as harshness mitigators for their hosts through biotic facilitation, protecting them from either abiotic harshness or negative biotic interactions like competition or natural enemies. Biotic facilitation mediated by symbionts expands environmental ranges and influences resource use for both host and symbiont (Peay, 2016), potentially enhancing range expansion capacity of both co-associates.

(4) Colonisation of a novel host

Eventual encounters with novel hosts driven by environmental change or ecological perturbation provide new opportunities for symbionts to expand their repertoire of suitable hosts and/or geographical range (Hoberg & Brooks, 2008; Colwell, Dunn & Harris, 2012; Hoberg & Brooks, 2015). Now, we apply a host-as-biotope perspective to the colonisation of novel hosts by symbionts. When, opportunistically, a symbiont encounters a novel suitable host species, colonisation of the novel host is possible simply by dispersal facilitation. The colonisation occurs *via* resource tracking without the need for adaptive evolution (Agosta & Klemens, 2008). By contrast, unsuitable novel hosts pose evolutionary barriers to symbionts for optimal host use whereby evolutionary facilitation is required. The colonisation of a novel host by evolutionary facilitation can expand the repertoire of suitable hosts or lead to a host shift by speciation (Forbes *et al.*, 2017). Overall, the process can be interpreted as a case of relocational niche construction because it is an impact of changes in habitat selection on the experienced environment, with evolutionary consequences. When evolutionary facilitation is required, preliminary symbiont–host interactions by demographic facilitation may provide an opportunity through the establishment of a propagule pressure (Agosta & Klemens, 2008; Hatcher, Dick & Dunn, 2012*a*; Araujo *et al.*, 2015). Within such a context, theoretical models show that the success of both demographic and evolutionary facilitations can be highly dependent on Allee effects (e.g. Kanarek *et al.*, 2013, 2015). The success of evolutionary facilitation may depend on a variety of factors such as the rate and intensity of contacts with the novel host (Parrish *et al.*, 2008), the phylogenetic relatedness or similarity between the original host and the novel host (Nyman, 2010; Paterson *et al.*, 2012; de Vienne *et al.*, 2013), the fitness valley between both hosts (Geoghegan, Senior & Holmes, 2016), and host traits such as phenotypic plasticity or body size (Paterson *et al.*, 2012; Mason, 2016). Nevertheless, evolution on novel hosts can be rapid (e.g. Arbiv *et al.*, 2012; Forbes *et al.*, 2017).

The level of specialisation of symbionts is expected to influence the probabilities of host switching (Poisot *et al.*, 2011). However, data from phylogenetics (de Vienne *et al.*, 2013; Calatayud *et al.*, 2016; Nylin *et al.*, 2018) and biological invasions (e.g. Strauss, White & Boots, 2012; Lymbery *et al.*, 2014) strongly support that host switching is a common phenomenon across symbiont taxa on evolutionary as well as ecological timescales, suggesting that evolutionary constraints are generally not strong enough to act as overwhelming barriers against symbiont population niche expansion. Indeed, host switching is relevant even in vertically transmitted, highly specialist symbionts (Millanes *et al.*, 2014; Doña *et al.*, 2017). The classic version of the concept of ecological fitting (Janzen, 1985) has developed as a mechanism to explain the apparent evolutionary lability of symbionts, and their ability to colonise novel unsuitable or suboptimal hosts (Agosta & Klemens, 2008; Araujo *et al.*, 2015). First, phenotypic plasticity (West-Eberhard, 2003) allows symbionts positively to adjust their responses to novel environments in terms of fitness, without the need for mutations or changes in genetic frequencies. Second, correlated evolution of traits (Lande & Arnold, 1983) may speed up future adaptation to novel environments. Third, phylogenetic conservatism in symbiont traits associated with resource use, such as host detection cues, allows symbionts to track resources so that they only need to adapt to novel living environmental conditions which, in turn, can exhibit certain similarities if hosts belong broadly to the same taxa. The mountain pine beetle, *Dendroctonus ponderosae*, is indigenous to Western North America where it primarily feeds on lodgepole (*Pinus contorta*). The beetle is currently expanding its range eastward and has recently colonised the jack pine, *P. banksiana*. This host switch is expected to facilitate the geographical colonisation of the boreal forest by the beetle (Cullingham *et al.*, 2011). The jack pine has a similar chemistry to that of the historical hosts of *D. ponderosae*, and is thus compatible with beetle pheromone production, aggregation on host trees and larval development. In addition, the novel host has lower concentrations of defensive chemicals than historical hosts and large concentrations of chemicals that promote host colonisation. Further, the existence of a hybrid zone between lodgepole and jack pine forest likely facilitated host switch (Erbilgin, 2018). The parasitic mite *Varroa destructor* expanded its geographical range worldwide after a host switch from its Asian original host, *Apis cerana*, to the cosmopolitan *A. mellifera* (Navajas, 2010). *A. cerana* has adaptive reproductive, grooming and hygienic behaviours to control the mite. The host switch was likely favoured because such behaviours are limited in *A. mellifera* (Nazzi & Le Conte, 2016). Moreover, *V. destructor* is able to change its cuticular hydrocarbons to mimic the novel host. This plasticity in the ability to mimic host hydrocarbons to reduce host detection likely facilitated the host switch (Le Conte *et al.*, 2015). Overall, demographic facilitation provides the opportunity through propagule pressure, but ecological fitting may help to overcome encounter filters associated with host detection or in-host microhabitat selection, thereby directing the migration to the novel target host. Ecological fitting also allows positive plastic responses that moderate the reduction in fitness experienced in the novel host, thus favouring evolutionary facilitation.

Range expansion driven by host shift is a potential mechanism for symbionts to escape from co-extinctions (Colwell, Dunn & Harris, 2012; Galetti *et al.*, 2018). Symbiont extinction risk depends on both host specificity and the geographical range of host associates (Colwell, Dunn & Harris, 2012). Generalist symbionts with a wide repertoire of potential suitable hosts and good dispersal abilities should achieve wider geographical ranges as well as successfully colonise novel hosts easily simply by dispersal facilitation or minor adaptations (Poisot *et al.*, 2011; Roy & Handley, 2012; Stewart *et al.*, 2015). Moreover, a specialist symbiont associated with a common host should not be at risk. However, when associated with rare hosts, extinction risk of specialist symbionts should be particularly high (e.g. Cuthill *et al.*, 2016). In that case, an eventual host shift from rare to common and widespread hosts would allow the symbiont to expand its geographical range, thereby reducing extinction risk (Colwell, Dunn & Harris, 2012; Stewart *et al.*, 2015). Nonetheless, for a host shift to materialise, the symbiont must have opportunities for novel contacts. Indeed, phylogenetic studies of some symbionts indicate that host use is mostly determined by symbiont–host geographical co-occurrence regardless of the evolutionary relationships between the hosts (Calatayud *et al.*, 2016).

We are currently experiencing a massive breakdown of geographical and regional dispersal barriers for symbionts driven by anthropogenic factors (Hatcher, Dick & Dunn, 2012*a*; Hoberg & Brooks, 2015; Rogalski *et al.*, 2017). Given that dispersal barriers are major constraints for symbionts, we expect an increase in frequency of symbiont range expansion processes mainly driven by dispersal facilitation. Furthermore, given the documented ability of symbionts to colonise novel hosts by resource tracking or rapid evolution, the current massive biotic mixing resulting from globalisation and climate change is the perfect breeding ground for the establishment of novel symbiont–host interactions by evolutionary facilitation (e.g. Jones *et al.*, 2008), with potential implications for biological invasions, emergent diseases and dynamics of communities and ecosystems.

IX. RANGE EXPANSION, NICHE DYNAMICS AND DIVERSIFICATION

On evolutionary timescales, host switching is considered a major driver of symbiont diversification (Janz, 2011; Fecchio *et al.*, 2018). Co-evolutions of novel symbiont–host interactions originated by host switching have been proposed as biodiversity engines (Janz, 2011; Joy, 2013; Clayton, Bush & Johnson, 2015; Sudakaran, Kost & Kaltenpoth, 2017). Ecological opportunity, i.e. getting access to novel resources free of competitors, is a classic mechanism of adaptive radiation (Stroud & Losos, 2016). Access to novel resources is possible by geographical colonisation or by a key innovation that allows exploiting resources in novel ways. From the symbiont's point of view, encounters with novel hosts are ecological opportunities to exploit resources in novel ways (i.e. similar resources packaged in novel environmental envelopes; Nylin *et al.*, 2018). From the host's perspective, acquiring a novel mutualistic symbiont offers innovative ways to exploit novel environments (Joy, 2013; Sudakaran, Kost & Kaltenpoth, 2017). Further, selective pressures from parasitic symbionts push evolutionary dynamics of hosts towards an enemy-free space, i.e. ways to avoid parasite impacts, eventually leading to a co-evolutionary arms race (Janz, 2011).

The opportunity to access novel hosts is key to the action of co-evolutionary processes. Along the Earth's history, recurrent periods of massive biotic mixing and expansion driven by major environmental change and ecological perturbation have probably generated favourable contexts of frequent opportunities for host switching (Hoberg & Brooks, 2008). For instance, Galetti *et al.* (2018) suggest that a proportion of symbionts that inhabited megafauna in the Pleistocene likely escaped from co-extinction by switching to humans, domestic animals and cultivated plants, prior to the massive megafauna extinction driven by human geographical expansion. Along these lines, a mechanism has been proposed that explains historical events of symbiont and host diversification (Hoberg & Brooks, 2008, 2015), which we interpret here adopting a host-as-biotope perspective. Essentially, episodic events of major environmental change such as climate shifts break down regional and biogeographical barriers to dispersal of hosts and their affiliated symbionts. A consequent symbiont range expansion driven by dispersal facilitation provides novel opportunities for host switching and the eventual expansion of the repertoire of suitable hosts by evolutionary facilitation (i.e. niche expansion). This 'expansion phase' parallels the contemporary patterns of symbiont invasions on ecological timescales depicted in Fig. 4, suggesting that essential mechanisms behind symbiont range expansion processes, i.e. removal of large-scale barriers to dispersal promoting host switching, are recurrent across timescales (Hoberg & Brooks, 2015). The disruptive period is followed by a more climatically stable period of geographical isolation by the re-establishment of dispersal barriers, setting the stage for co-evolution and co-speciation processes (Clayton, Bush & Johnson, 2015) that promote symbiont specialisation on narrow host repertoires (i.e. niche diversification; Janz, 2011). Hence, cyclical periods of stability punctuated by major disruptive events generate temporal patterns of successive expansion and contraction of symbiont niches favoured by an evolutionary lability of host specificity, whereby geographical range expansion of both symbionts and their hosts as well as host switching, together play a fundamental role. Overall, the diversification mechanism suggests that complex interactions between symbiont range and niche dynamics governed by climatic cycles probably have been involved in the generation of current biodiversity.

X. CONCLUSIONS

(1) Symbionts are unique in that hosts provide them with both resources and living conditions. As Kennedy (1953, p. 110) said, 'the host ... is not just something fed on, it is something lived on'. Hosts, by acting as biotopes for symbionts, are not mere 'resource packages' as suggested for example by Agosta & Klemens (2008). Rather, they can play a central role in governing the Hutchinsonian niche of symbionts, thereby strongly determining the types of biotic, environmental or dispersal barriers that a symbiont may encounter during range expansion processes.

(2) Further, the host is also 'something travelled on'. From a host-as-biotope view, symbionts are organised spatially in discrete populations concentrated on hosts that often move across geographical space. Biotope-mediated dispersal is another singular phenomenon that allows symbiont populations within host bodies to travel across landscapes 'bringing their own homes' when joining the range expansion of their hosts associates, although symbionts are often subjected to strong filters during the process.

(3) In some symbiont–host systems, such as endosymbionts of large vertebrates, homeostatic properties of host bodies could minimise the influence of the external environment

in determining the population niche of symbionts. From a host-as-biotope view, regulation of the symbiont's population niche by host bodies has potential implications for range dynamics of symbionts because it may allow symbiont populations within host bodies to acquire insensitivity to off-host environmental gradients during host-mediated dispersal.

(4) Symbionts are not passive passengers during symbiont–host range expansions, but actively participate through alteration of the eco-evolutionary dynamics of their hosts. Symbionts often act as harshness mitigators for their hosts through biotic facilitation, protecting hosts from harsh abiotic or biotic conditions. Biotic facilitation mediated by symbionts expands the niche of both affiliates, potentially enhancing range expansion capacity of the symbiont–host association.

(5) Range expansion of symbionts driven by major environmental changes that remove large-scale barriers to dispersal followed by host-switching during arising opportunistic encounters with novel hosts is a pervasive process that has been likely involved in historical events of diversification on evolutionary timescales. This two-step process is currently influencing the outcomes of massive biotic mixing driven by anthropogenic factors on ecological timescales, with implications for biological invasions, emergent diseases and dynamics of communities and ecosystems.

XI. ACKNOWLEDGMENTS

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