Assessing symbiont extinction risk: insights from host-symbiont cophylogenetics and coevolutionary theory

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Highlights

- We apply coevolutionary knowledge to conservation biology.
- We propose a new statistic (*Ec*) that uses data from cophylogenetic analyses.
- We suggest potential future opportunities for advancing the field.

Abstract

Symbionts (i.e., parasites, mutualists, and commensals that interact intimately with their hosts) have a unique mode of life that has attracted the attention of ecologists and evolutionary biologists for centuries. As a result of this attention, these disciplines have produced a mature body of literature on these interactions. In contrast, the discipline of symbiont conservation is still in a foundational stage. Further, given the particularities of the life-history of symbiont species, some problems may arise when directly applying knowledge from Conservation Biology of free-living species to symbiont conservation. Here, we aim to adapt existing ecological and evolutionary knowledge of symbionts to the perspective of biological conservation. Specifically, we first propose a new statistic "cophylogenetic extinction rate" (*Ec*) that uses data from event-based cophylogenetic analyses and might be informative to assess relative symbiont extinction risks. Then, we outline aspects of ecology or evolution that may be relevant to consider for assessing symbiont vulnerability to extinction. Finally, we propose potential future research to further develop estimation of symbiont extinction risk from cophylogenetic analyses and continue the integration of this existing knowledge into future symbiont conservation studies and practices.

1. Introduction

Symbionts (i.e., parasites, mutualists, and commensals that interact intimately with their hosts) are vital components of ecosystems, comprising up to 75% of all ecological interactions (Lafferty et al., 2006; Dobson et al., 2008). A major concern is that conservative estimates predict that up to 10% of symbiont species are expected to go extinct by 2070 due to climate change (Carlson et al., 2017a). However, despite their ecological relevance and the conservation status, symbiont Conservation Biology is still in a foundational stage (e.g., Windsor, 1995; Dougherty et al., 2016; Rocha et al., 2016; Cizauskas et al., 2017; this special issue). Indeed, apart from these studies, research on symbiont conservation can be summarized as follows: 1) a few examples of studies on iconic endangered or extinct species (e.g., the California condor louse *Colpocephalum californici;* Dunn et al., 2009; Rózsa and Vas, 2015); and 2) theoretical work on the impact of coextinctions (Koh et al., 2004; Dunn et al., 2009; Strona, 2015). Contrarily to work on free-living species, studies on symbiont Conservation Biology relating ecological and evolutionary variables (e.g., dispersal or population dynamics) to conclusions relevant for conservation are lacking.

In contrast, many studies of symbionts have covered various aspects of their ecology and evolution (Poulin, 2011; Clayton et al., 2015), some of which may be useful for assessing symbiont extinction risks (Soulé, 1980; Groom et al., 2012). However, the unique life-history of symbiont species may pose some problems for directly importing knowledge from Conservation Biology theory of free-living species. For instance, in symbionts, the mode of dispersal might be a much better proxy of dispersal capabilities than the mean of dispersal distances. Overall, these specific features and the lack of studies integrating the existing ecological and evolutionary knowledge of symbionts into conservation practices may be inhibiting Conservation Biologists

lacking experience on symbionts from working on symbiont conservation. Thus, here we aim to adapt existing knowledge from ecological and evolutionary studies of symbionts into a biological conservation perspective. As an example of this rationale, there is a likely relationship between symbiont prevalence and extinction risk. From ecological and evolutionary studies, we expect symbionts exhibiting low prevalence and intensity to possess an increased probability of stochastic extinction (Clayton et al., 2015). Consequently, we could use species prevalence data to classify low-prevalence symbionts as more at risk of extinction.

In this overview 1) we first propose a new statistic derived from cophylogenetic analyses to assess symbiont extinction risks; 2) then, we focus on potential ecological and evolutionary predictors of symbiont vulnerability to extinction, which, although studied in great detail by ecological and evolutionary biologists, have not been linked directly to Conservation Biology. We most emphasize those predictors covering aspects that are most unique to symbionts and that have not been extensively reviewed by previous publications. In addition, we discuss high level of interrelation among these ecological and evolutionary factors. Although our examples focus largely on groups we have studied ourselves, the feather lice and mites of birds, we attempt to generalize our conclusions.

2. Obtaining symbiont extinction rates from cophylogenetics

Cophylogenetic analyses are widely used methods in which host and symbiont evolutionary trees are compared to uncover the processes driving symbiont diversification (Page, 2003; De Vienne et al., 2013; Clayton et al., 2015; Martínez-Aquino, 2016). Several cophylogenetic methods exist, and these can be classified into two main categories: distance-based and event-based methods (Page, 2003; De Vienne et al., 2013; Martínez-Aquino, 2016). In short, distance-based methods (e.g., ParaFit; Legendre et al., 2002) measure the topological distance between host and

84 symbiont trees and statistically evaluate whether the congruence is higher than expected by
85 chance (Huelsenbeck et al., 2003; De Vienne et al., 2013; Martínez-Aquino, 2016). In these
86 methods, significantly high levels of congruence are generally assumed to be the result of
87 codivergence between host and symbionts (Huelsenbeck et al., 2003; De Vienne et al., 2013;
88 Martínez-Aquino, 2016). Event-based methods (e.g., Jane; Conow et al., 2010) use costs for
89 macroevolutionary events (e.g., cospeciation, host-switches, losses) which must be previously
90 specified by the user, to reconcile host and symbiont phylogenetic trees (De Vienne et al., 2013;
91 Charleston and Libeskind-Hadas, 2014; Martínez-Aquino, 2016). The result of an event-based
92 cophylogenetic analysis generally includes the best solution to reconcile both trees (i.e., given
93 the costs specified) and the corresponding number of macroevolutionary evolutionary events of
94 each category which were needed to reach that solution. These events typically include
95 cospeciation, duplication, host switch, loss, and failure to diverge (De Vienne et al., 2013;
96 Charleston and Libeskind-Hadas, 2014; Martínez-Aquino, 2016).

97 Here, we propose using the proportional number of losses (i.e., "sorting events") from an
98 event-based cophylogenetic reconstruction to obtain a rough estimate of the relative extinction
99 rate of a particular symbiont lineage (Fig. 1). This approach is similar to the current practice of
100 using the percentage of cospeciation events as a measure of the relative importance of
101 cospeciation in a symbiont lineage (Johnson and Clayton, 2003; De Vienne et al., 2013; Doña et
102 al., 2017b). In cophylogenetic reconstructions, the inferred losses can be interpreted as the
103 consequence of two distinct processes (Fig. 1; Clayton et al., 2015): (1) as genuine events of
104 parasite extinctions; or (2) as sorting events (e.g., 'missing the boat'), when a symbiont fails to
105 disperse with one host lineage. Note that even though sorting events are not directly indicative
106 of symbiont species extinctions, they do inform about symbiont transmission efficiency and

reflect the probability of stochastic extinction, and therefore might be valuable for assessing symbiont extinction at a species scale (Paterson et al., 1999; MacLeod et al., 2010; Poulin, 2011; Clayton et al., 2015).

The estimation of *Ec* (i.e., cophylogenetic extinction rate) would be as follows: $Ec = \left(\frac{L}{E+S}\right)$; where *L* represents the number of losses, *E* the total number of macroevolutionary events (e.g., cospeciation + duplication + losses + host-switches), and *S* the number of host-switches which is included as an additional term to account for differences in colonization capabilities, which should effectively lower the extinction risk. The parameter *Ec* increases linearly with the number of losses, and decreases as host-switching increases (Fig 2). Consequently, two symbiont lineages with the same proportion of losses but a different number of switches will possess different *Ec* values; so that the lineage with the lowest number of switches will possess the highest *Ec* value. We encourage accompanying *Ec* with a confidence interval to show how good the estimate is (e.g., the modified Wilson confidence interval for a binomial proportion; Brown et al., 2001; Signorell et al., 2016; Appendix 1, Supplementary material). To help calculating *Ec* and the confidence intervals (modified Wilson), we provide a Shiny app (https://jdona.shinyapps.io/extinction/).

As a proof of concept of this approach, we calculated *Ec* for two symbiont lineages; the feather mite genera *Proctophyllodes* and *Trouessartia* (Acari: Astigmata: Analgoidea and Pterolichoidea). As input for the calculations, we used the results of event-based cophylogenetic reconstructions from Doña et al., (2017b). In this study, *Trouessartia* mites were found to have 1 loss and 9 host-switches out of 14 events, and *Proctophyllodes* mites 1 loss and 32 host-switches out of 42 events. From these values, the estimated *Ec* is slightly higher for *Trouessartia* (*Ec* =

129 0.04; CI = 0-0.21) than for *Proctophyllodes* (*Ec* = 0.01; CI = 0-0.07) mites. This result agrees
130 with existing comparative knowledge from the Ecology and Evolution of these mites.
131 Specifically, *Trouessartia* mites are known to have: 1) a lower species diversity on Passeriformes
132 (Doña et al., 2016, 2018), 2) lower prevalence and intensity (Fernández-González et al., 2018;
133 Doña et al., 2019b), 3) lower genetic diversity (Fernández-González et al., 2018; Doña et al.,
134 2019b), and 4) infrapopulations genetically more structured (Doña et al., 2019a).

135 **3. Potential ecological and evolutionary predictors of symbiont vulnerability to extinction**
136 *Mode of transmission*
137 Symbionts transmit (or disperse) from one host to another in different ways (Poulin, 2011;
138 Clayton et al., 2015; Antonovics et al., 2017). Among the many individual strategies, symbiont
139 transmission strategies can be classified into two main modes: vertical and horizontal (Poulin,
140 2011; Clayton et al., 2015; Antonovics et al., 2017).
141 Vertically-transmitted symbionts tend to be more specialized to their hosts than
142 symbionts that are horizontally-transmitted (Douglas, 1998; Poulin, 2011; Clayton et al., 2015).
143 This level of specialization is often manifested by, among other things, populations genetically
144 more structured. Vertically transmitted parasites also tend to have lower dispersal capabilities,
145 virulence, levels of genetic diversity, rates of straggling and host-switching, and levels of
146 introgression from other symbiont species (Lipsitch et al., 1995; Whiteman et al., 2004; Huyse et
147 al., 2005; Barrett et al., 2008; Clayton et al., 2015; Doña et al., 2017b; Sweet and Johnson, 2018;
148 Doña et al., 2019c).
149 Conversely, horizontally-transmitted symbionts are often less specialized to their hosts
150 (Douglas, 1998; Poulin, 2011; Clayton et al., 2015) and have less genetically structured
151 populations. In addition, horizontal transmission favors higher dispersal capabilities, virulence,
152 rates of straggling and host-switching, and levels of introgression from other symbiont species
153 (Lipsitch et al., 1995; Whiteman et al., 2004; Huyse et al., 2005; Barrett et al., 2008; Clayton et

al., 2015; Doña et al., 2017b; Sweet and Johnson, 2018; Doña et al., 2019c).

Overall, the mode of transmission of a symbiont species is associated with major ecological and evolutionary aspects which may be relevant to consider in symbiont extinction risk assessments. All else being equal, *vertically-transmitted symbionts would be predicted to have a higher probability of extinction given their level of specialization and other relevant features that increase extinction risk* (e.g., high virulence or low levels of genetic diversity).

Virulence

Virulence can be defined as the reduction of host fitness caused by the symbiont (i.e., parasites, Herre, 1993; Read, 1994). Different factors, such as the mode of transmission (i. e., horizontally-transmitted parasites are typically more virulent) or parasite-parasite competition (i. e., the higher the competition between distantly-related parasites, the higher the virulence), are known to drive the evolution of virulence in parasites (Cressler et al., 2016).

In a scenario of host vulnerability due to climate change, *more virulent parasites might increase the risk of extinction of the host, because of the morbidity of host individuals that harbor virulent parasites*. This process will lead to a greater chance of co-extinction of the host and parasite, as there may be no time for natural selection to adjust virulence intensity.

Straggling and host-switching

Symbionts, even though highly specialized to their particular hosts, can sometimes colonize new hosts (Agosta et al., 2010; Clayton et al., 2015). Ecological and evolutionary factors, such as dispersal ability, can determine the potential for straggling (i.e., dispersal to a novel host) and host-switching (i.e., not only reaching a new host but also reproducing on the new host) (Whiteman et al., 2004; Clayton et al., 2015). Vertically-transmitted symbionts tend to exhibit lower rates of straggling and host-switching. However, most symbiont lineages, even those with

177 relatively low dispersal capabilities, have at least modest capacities to colonize new hosts (Doña
178 et al., 2019b, 2017b).

179 In general, straggling seems to be frequent at an ecological scale, whereas successful
180 host-switches are comparatively rare (Whiteman et al., 2004; Rivera-Parra et al., 2017; Doña et
181 al., 2019b). This pattern can be explained by the fact that successful colonization requires many
182 conditions to be met for survival and reproduction on a novel host species (Clayton et al., 2015;
183 Doña et al., 2019b). Thus, most successful host-switches are clade limited (i.e., to closely related
184 hosts) in which symbiont traits fit ecologically to those of the host (Agosta and Klemens, 2008;
185 Agosta et al., 2010; Engelstädter and Fortuna, 2019, but see *Host effect*). In contrast, major host-
186 switches (i.e., switches to phylogenetically distant hosts) are infrequent at an ecological scale but
187 can be observed at evolutionary time scales (Doña et al., 2018). Interspecific interactions (e.g.,
188 competition against other symbiont species, or hybridization) and the availability of potential
189 hosts are also relevant factors that influence straggling and host-switching dynamics (Harbison et
190 al., 2008; Johnson et al., 2009; Harbison and Clayton, 2011; Doña et al., 2019c).

191 Host-switches have been considered as a way for symbionts to escape extinction. Indeed,
192 *symbionts with higher straggling and host-switching rates may be predicted to have a lower*
193 *probability of becoming extinct*. However, even though the frequency of host-switches at an
194 ecological scale is likely underestimated (Brooks and Hoberg, 2007; Doña et al., 2019b), the
195 unusual speed of current climate change may make host-switching ineffective for mitigating
196 short-term extinction risks, especially considering the limited success in overcoming climate
197 change effects that most free-living species are already projected to have (Settele et al., 2014;
198 Carlson et al., 2017a; Cizauskas et al., 2017). In other words, while host-switching could
199 potentially be helpful for symbionts to escape from host extinctions, the low rate of successful

host colonization suggests that it is probably unrealistic to think that host-switching may save symbiont species from becoming extinct.

Symbiont population genetic structure

Intermediate degrees of population subdivision generally yield the highest adaptive potential, with possibilities for local adaptation to local environments, yet with occasional gene flow and large enough local effective size to prevent rapid inbreeding and loss of variation (Allendorf et al., 2007). Populations of symbionts tend to be subdivided in nature (Huyse et al., 2005; Poulin, 2011; Clayton et al., 2015). Populations of symbionts can also be further subdivided because individual symbionts are grouped into infrapopulations (i.e., multiple symbionts on an individual host). At higher level, different infrapopulations which maintain gene flow form a metapopulation (Huyse et al., 2005; Poulin, 2011; Clayton et al., 2015). An important consequence of such a level of population subdivision is that it is expected to increase the effective population size, according to population genetics theory (Futuyma, 2013). Indeed, symbiont species usually show high levels of genetic diversity (e.g., Doña et al., 2015). On the other hand, if the level of subdivision is extreme, new beneficial mutations that arise will not readily spread across the species and populations may lose adaptive potential on an evolutionary time scale (Allendorf et al., 2007). Overall, different factors have been identified as major drivers of levels of symbiont population structure.

The dispersal mode of symbionts has a profound impact on the population structure of symbionts (Clayton et al., 2015; Sweet and Johnson, 2018). Vertically-transmitted symbionts typically accumulate genetic differences that lead to population genetic structure (Clayton et al., 2015; Sweet and Johnson, 2018). In contrast, in horizontally-transmitted symbionts, dispersal tends to erode the population genetic structure among infrapopulations (Clayton et al., 2015;

Sweet and Johnson, 2018). Nonetheless, host vagility also influences the degree of symbiont population genetic structure (McCoy et al., 2003). Thus, vertically-transmitted symbionts can sometimes show low levels of population genetic structure (Doña et al. 2019).

Metapopulation structure is also important in shaping the population genetic structure of symbiont populations (Gandon, 2002; Huyse et al., 2005). For instance, infrapopulations that are part of a metapopulation, have a higher probability of recolonization and thus are less likely to become extinct (Futuyma, 2013; Clayton et al., 2015).

Lastly, infrapopulation parameters can also affect the degree of genetic structure overall (Clayton et al., 2015). Specifically, symbiont species which possess larger infrapopulation sizes are expected to show less evidence of inbreeding, less population structure, and higher levels of genetic diversity (Nadler, 1995; Futuyma, 2013; Doña et al., 2015).

In summary, *most symbiont species have levels of gene flow between populations that are often higher than between host populations, and therefore extreme levels of population subdivision are not expected to be the norm* (Mazé-Guilmo et al., 2016). This pattern is true even for symbiont species with minimal dispersal capabilities (Doña et al 2019). *Nonetheless, symbiont populations are theoretically expected to become more fragmented due to anthropogenic causes* (Pickles et al., 2013; Carlson et al., 2017a); *leading to situations in which worrisome levels of subdivision can become more frequent.*

Aggregation

Just as free-living organisms are not evenly distributed across their geographic range (Dallas et al., 2017a); symbionts are not uniformly distributed among their hosts (Poulin, 2011; Clayton et al., 2015). Indeed, symbionts are generally aggregated among the available hosts, so that most host individuals are inhabited by no or few symbionts, while many symbionts inhabit just a few

host individuals (Rózsa et al., 2000; Poulin, 2011).

The level of aggregation may affect the levels of genetic diversity of symbiont populations (e.g., a high level of aggregation may lead to smaller effective population sizes or influence the spread of rare alleles through populations, Cornell et al., 2003; Criscione and Blouin, 2005; Dhamarajan, 2015; Montarry Josselin et al., 2019). Also, symbionts exhibiting a higher level of aggregation may be more sensitive to go extinct due to stochastic host mortality (Clayton et al., 2015). That is, if the host individuals harboring most of the symbionts die, the symbiont species will lose most of its population.

Thus, *aggregation can be an important parameter for symbiont persistence, affecting levels of genetic diversity and increasing the probability of stochastic extinction*.

Host population size

Organisms exhibit population sizes which can vary in orders of magnitude and that are experiencing drastic changes in the Anthropocene (McArdle et al., 1990; Dornelas et al., 2019).

Host densities are known to influence, to some extent, symbiont abundance (Arneberg Per et al., 1998; Ellis et al., 2017). In addition, abundant hosts tend to harbor both generalist and specialist symbionts, whereas less abundant hosts tend to more often harbor only generalist symbionts, a pattern that is known as asymmetry of interactions (Vázquez et al., 2005). It is still unclear whether generalists or specialist symbionts are more vulnerable to climate change, as specialists may be inhabiting hosts with a lower probability of becoming extinct (Strona et al., 2013). Nonetheless, hosts with small population sizes can increase the likelihood that the host and the symbiont become co-extinct (Strona, 2015). Similarly, low host population sizes can increase the likelihood of the symbiont becoming extinct even if the host does not go extinct (e.g., because of the aggregated distributions of the symbiont).

Overall, *symbionts from hosts with small population sizes (and low-density) are expected to be more vulnerable because they typically have lower abundances, higher coextinction risks, and higher probabilities of extinction than that of their hosts because of the aggregated distributions of symbionts.*

Symbiont effective population size

The effective population size (N_e) is a relevant factor determining rates of genetic drift, loss of genetic variability, and modulating the effectiveness of selection (Waples, 2016; Ryman et al., 2019). Symbionts often have life-history features that may reduce N_e (Criscione and Blouin, 2005). Examples of these features include (but are not restricted to): 1) frequent bottlenecks, which can erode genetic diversity (Monsion et al., 2008; Dabert et al., 2015; Doña et al., 2015) or 2) aggregated distributions in which, due to inequalities in reproduction, N_e may be closer to the number of infected hosts than to the total number of symbionts (Dobson, 1986; Criscione and Blouin, 2005). Most studies of the N_e of symbionts have focused on coalescence-based estimations of long-term N_e (Crellen et al., 2016; Thiele et al., 2018), and whilst promising, only a few studies have been carried out over short time spans (Criscione, 2013; Strobel et al., 2019). Overall, studies of symbiont N_e have found N_e to be small (Seger et al., 2010; Criscione, 2013; Strobel et al., 2019). However, there are some cases where the effective population size is large (Hughes Austin L. and Vierra Federica, 2001). In general, the factors shaping symbiont N_e are not yet well understood and warrant further study (Criscione et al., 2005; Criscione and Blouin, 2005; Criscione, 2016).

Among the factors shaping symbiont N_e, several studies have found strong relationships between variables related to symbiont census size (e.g., genetic diversity or host body size) and N_e (Criscione et al., 2005; Doña et al., 2015; Strobel et al., 2019). For instance, median species

infrapopulation size has been found to correlate with genetic diversity (which is expected to correlate with N_e; Kimura, 1968, 1983; Romiguier et al., 2014; Grundler et al., 2019) in some symbiont groups (Criscione et al., 2005; Doña et al., 2015). Even though the generality of this prediction in other symbiont groups is yet to be studied (Doña et al., 2015; Criscione, 2016), these results may suggest that parameters that are easy to calculate, such as mitochondrial genetic diversity may provide crude estimates of species N_e in symbionts.

Overall, the effective population size is still a central parameter in conservation biology, and different methods to estimate N_e from molecular data have been extensively used and tested (Gilbert and Whitlock, 2015; Wang, 2016). However, recent research support that estimations of contemporary N_e could be consistently underestimated in subdivided populations, and that different population structures may require different sample sizes to reach a similar level of accuracy (Barbosa et al., 2018). An alternative strategy may be to concentrate on levels of inbreeding and reduce the focus on N_e (Ryman et al., 2019). *In summary, obtaining precise estimates of symbionts N_e is a complicated task. Large and small N_e can be expected in symbionts, and factors such as aggregation, bottlenecks, prevalence, and intensity, influence N_e, and therefore, may provide useful insights of symbiont N_e.*

<u>*Geographic patchiness*</u>

While symbionts often possess adaptations to be highly successful on their host species (e.g., a high reproductive potential), the geographic ranges of symbionts and hosts do not always match perfectly, with some symbionts almost mirroring the whole distribution of their hosts and others restricted to some small areas of host distribution (Krasnov et al., 2004; Bush et al., 2009; Poulin, 2011; Clayton et al., 2015). The reasons for these patchy distributions are varied. For example, environmental conditions external to the host may make symbiont survival impossible.

315 Alternatively, interspecific interactions, such as competition, may play a role (Clayton et al.,
316 2015; Wells and Clark, 2019). However, given the adaptations of symbionts to population
317 fragmentation, the lack of a symbiont in a specific place should not compromise the species on a
318 global scale (Bush and Kennedy, 1994). Nonetheless, the accelerated anthropogenic
319 fragmentation of host populations may increase the number of local extinctions of parasite
320 populations (Bush et al., 2013), thus increasing the likelihood of the symbiont species to become
321 extinct on a global scale.
322 Overall, *symbionts restricted to reduced areas of host distribution may be expected to*
323 *present a higher vulnerability of becoming extinct*.

324 *Host effects*

325 Not all hosts are equally suitable for the symbionts. Indeed, several host features have a
326 substantial effect on symbiont traits (Clayton et al., 2015). This effect may be the outcome of a
327 co-adaptative process (e.g., arm-races dynamics). In host-parasite systems, for instance, hosts
328 usually have evolved strategies that impose a direct effect on parasites such as avoidance,
329 tolerance, and resistance strategies (Clayton and al, 2010; Clayton et al., 2015; Bush and
330 Clayton, 2018). Examples of these strategies include chemical compounds (e.g., batrachotoxins
331 in the skin and feathers of some species of New Guinea birds; Dumbacher et al., 1992),
332 behavioral responses (e.g., preening; Villa et al., 2016, 2018; Bush et al., 2019), or
333 immunological responses (e.g., inflammatory responses; Owen et al., 2009). Also, host traits
334 may impose effects on symbiont traits which may not be the result of coadaptation (Clayton et
335 al., 2015). Examples of these kind of effects of hosts on symbionts traits include, host-density
336 influencing parasite abundance (Arneberg Per et al., 1998; Ellis et al., 2017), host-body size
337 influencing the sex-ratio of the parasites (Clausen, 1939), or migratory hosts lowering parasite

338 survival (Hall et al., 2014).

339 As discussed above (see *Straggling and host-switching*), host-switches could potentially
340 serve as escape routes for symbionts to avoid co-extinction with their hosts. Though symbionts
341 exhibit phenotypic plasticity and can often survive across varied phylogenetically related hosts,
342 some hosts may possess key traits (which may not be present in closely related hosts) that
343 hamper symbiont colonization. These traits could be host adaptations that exert a direct or
344 indirect negative effect on particular symbiont taxa. For example, a new host with a migratory
345 behavior, that the "original" host did not possess, may make symbiont survival difficult (Poulin
346 et al., 2012). That is to say, hosts that are not inhabited by a particular symbiont lineage that is
347 present in closely related hosts may be free of the symbiont lineage because that particular host is
348 not suitable for that particular symbiont lineage, and not because of a lack of colonization
349 opportunities. Notably, this highlights the need for understanding the basic biology of symbionts
350 when using modeling approaches to assess potentially suitable hosts.

351 In sum, *host features exert pressure on symbiont traits when there is an intimate*
352 *association*. Also, *hosts may possess traits that hamper symbiont colonization*. Altogether,
353 *these host features may be related to the likelihood of a symbiont becoming extinct.*

354 *Trait matching*

355 Due to the coevolutionary process, symbionts tend to possess traits that match very tightly those
356 of their hosts (Clayton et al., 2015). Matching traits are not always the result of co-adaptation
357 (i.e., microevolution of two or more interacting species in response to reciprocal selection
358 between them; Janzen, 1980). Indeed, many traits fit ecologically (i.e., due to ecological fitting;
359 Janzen, 1985) even though they have evolved due to historical interactions with entirely different
360 species.

Independently of the process behind the evolution of the matching traits, highly host-specific symbionts (i.e., those inhabiting a single or just a few host species) are expected to be more specialized to their hosts, and therefore to possess traits exhibiting a higher degree of matching (Agosta et al., 2010; Thompson, 1994). This level of matching may constrain their capabilities to colonize new hosts (Remold, 2012). Nonetheless, several non-mutually exclusive factors may act against this prediction and need to be considered. First, many highly host-specific and specialized symbionts are revealed as less host-specific and specialized after careful study (Dallas et al., 2017b). This finding is supported by recent large-scale molecular field studies that have found that straggling is much more frequent than predicted in supposedly highly host-specific symbionts (Doña et al., 2019b). In addition, theoretical studies have found a generalized evolutionary signal of intimate herbivores continuously probing new hosts (Braga et al., 2018). Recent studies are also demonstrating that host-specific symbionts can become quickly adapted to new hosts (i.e., rapid evolution; Koch et al., 2014; Bush et al., 2019; Villa et al., 2019). Third, highly host-specific symbionts may inhabit hosts with low vulnerability to extinction, as a result of specialism been favored as an evolutionary strategy on hosts with less demographic stochasticity (Strona et al., 2013).

Therefore, all else being equal, *highly host-specific and specialized symbionts might be predicted to be more endangered because they depend more upon their hosts and their odds of successfully colonizing a new host species in ecological time are lower than that of multi-host and often more generalist species*. However, factors such as overestimates of host specificity levels, rapid evolution, and host stability may act to counter this prediction.

Inter- and intraspecific competition

Symbionts not only interact with their hosts, they also interact with diverse communities

(including other symbionts) with whom they share their host. On the one hand, symbionts can obtain benefits from interacting with other organisms. For instance, feather mites molt inside the empty eggshells of feather lice (with whom they coexist on wing feathers). By doing so, they get protection from predation, reduce the loss of moisture, and obtain a frictional surface against which to rub off their old exoskeleton (Perez and Atyeo, 1984; Proctor, 2003). In other cases, however, interactions with other organisms on the host have a negative effect due to (direct or indirect) competition for limiting resources (Clayton et al., 2015). Competition is known to produce numerical effects (e.g., exclusion, reduced growth, survival) or niche shifts (e.g., resource partitioning, character displacement) in symbionts (Clayton et al., 2015). Importantly, competition is linked to ecological and evolutionary traits relevant to assess symbiont extinction risks, such as host-specificity or the mode of dispersal (Harbison et al., 2008; Johnson et al., 2009; Doña et al., 2017a). For example, on pigeons, body lice compete for resources (food and space) with wing lice (Bush and Malenke, 2008). Body lice are competitively superior, and coexistence is mediated by a competition-colonization trade-off in which wing lice (i.e., the competitively inferior species) possess higher dispersal capabilities (Harbison et al., 2008). In other cases, intraspecific competition can be more important. For example, the magnitude of vertical transmission in feather mites has been found to respond to the degree of intraspecific competition. Specifically, by transmitting vertically, feather mites abandon a more stable host (i.e., the adult bird), but reduce intraspecific competition for resources and space by dispersing to young birds (Doña et al., 2017a).

Overall, a deep understanding of the interaction dynamics of symbiont species can be highly valuable to forecast symbiont extinction risk (Lau and terHorst, 2019). However, for most species, not only is this information not yet available but also seems unlikely to be

available any time soon given the difficulties in conducting experiments that collect this type of data. Nonetheless, some patterns of competition related to climate change, such as condition-dependent competition, can be extracted from existing data. In condition-dependent competition, inferior competitors that can withstand harsh environmental conditions can minimize or avoid competition by exploiting environments that are unsuitable for superior competitors (Clayton et al., 2015). In other words, condition-dependent competition is expected to produce a pattern of symbiont co-exclusion correlated to environmental conditions, and this kind of information can be extracted/analyzed from global host-symbiont datasets (e.g., Gibson et al., 2005; Doña et al., 2016). Condition-dependent competition is generally not included in current symbiont extinction predictions, thus suggesting that these predictions may, therefore, underestimate symbiont loss (Clayton et al., 2015; Carlson et al., 2017a). This increased rate of losses would be because symbionts experiencing condition-dependent competition may go extinct long before their hosts show any evidence of decline.

Overall, *competitively superior species are expected to be less vulnerable to extinction than competitively inferior species*. However, including competition into symbiont extinction assessments is a complicated task. Modeling studies are still starting to develop theoretical predictions on the impact of climate change on interacting species. For instance, depending on the form that coevolution takes between species (e.g., whether selection is acting to increase or avoid competition), coevolution may increase or decrease the effect of environmental change (Northfield and Ives, 2013). Besides, due to asymmetries in resource distribution and competition, competitively superior species, counterintuitively, may not necessarily be the winners in a rapidly changing climate scenario (Van Den Elzen et al., 2017).

4. Future opportunities

We anticipate the following four areas as valuable for future research efforts to advance symbiont conservation theory from cophylogenetics and coevolutionary theory:

4. 1. Meta-analyses of current cophylogenetic data: To date, several cophylogenetic studies on symbionts have been carried out (e.g., De Vienne et al., 2013; Clayton et al., 2015, and references therein). These studies usually report the number of reconstructed macroevolutionary events of each type. Accordingly, *Ec*, may be calculated from already published studies and compared between studies in a meta-analytic framework. By doing so, lineage-specific *Ec* will be generated and available for symbiont initiatives that list their conservation status (e.g., PEARL; Carlson et al., 2017b), and future conservation-focused studies.

4. 2. Integrating Conservation Biology into cophylogenetic research agenda: Future studies are encouraged to improve how extinction rates are estimated from cophylogenetic comparisons. For example, some types of host-switches often imply that an extinction event has happened on the old host (i.e., host-switching with extinction or host-switching with speciation and extinction). On the other hand, host-switching can save a symbiont from extinction (i.e., if the host goes extinct after the switch). To our knowledge, current event-based cophylogenetic methods do not allow computing these types of host-switches. Future research is needed here. Also, levels of host-specificity can influence extinction probabilities (Cizauskas et al., 2017; see *Trait matching*). Accordingly, further research is needed so that future statistics of symbiont extinction rate from cophylogenetic comparisons could include current host-specificity levels into extinction rate predictions. Lastly, given that the extinction rate is likely not constant throughout the evolution of a lineage, providing information on the variation of the extinction rate through time would be useful. However, to our knowledge, no event-based cophylogenetic method allows for use as an input fully-dated phylogenies nor produces as a result dated

macroevolutionary events. Future improvements in cophylogenetic methods may allow providing extinction rate estimations through time.

4. 3. Expanding symbiont extinction rate modeling practices: Species distribution and evolutionary models are often used to calculate species extinction risk (Carlson et al., 2018). These models usually accommodate different variables to improve their predictions. Examples of these variables include dispersal, rescue processes, demography, genetic data, and coextinction probabilities (Carlson et al., 2018). Indeed, in symbionts, studies using species distribution models, including coextinction probabilities and the possibility of dispersal have been conducted (Carlson et al., 2017a). On the other hand, lineage-specific extinction rates can be calculated from time-calibrated phylogenies (Beaulieu and O'Meara, 2015; Rabosky, 2016). These methods are based on the notion that speciation and extinction processes leave distinct signatures on the branching structure of a phylogeny (Nee et al., 1994). While these approaches have been extensively used in free-living species, to our knowledge, extinction rates from phylogenies have almost not been yet used in symbiont studies (but see Alcala et al., 2017). Thus, even though these estimates should be treated with caution (Rabosky, 2016), the increasing availability of robust-comprehensive phylogenetic trees offers an opportunity to use these methods to estimate extinction rates of symbionts (Johnson, 2019). Future studies on symbiont extinctions should ideally combine information on extinction rates obtained from phylogenies and cophylogenetic comparisons. In the same vein, species distribution and evolutionary models would benefit from including these estimates in their predictions.

4. 4. Advancing the knowledge on drivers of symbiont extinction: The ecological and evolutionary drivers highlighted in this perspective (see section 3) are connected to symbiont extinction risks based on existing knowledge of symbiont species and Conservation Biology

theory of free-living species. However, dedicated studies investigating the relationship of these factors with symbiont extinction risks are nonexistent though highly encouraged. In-depth investigations of these drivers across symbiont species will help to obtain a more detailed picture that will allow, for example, measuring the relative contribution of each of the different drivers to symbiont extinction risk. In addition, drivers that have not been covered in this perspective but have been identified as predictors of symbiont vulnerability by previous studies (e.g., symbiont metabolic strategies or host body size; Cizauskas et al., 2017) should be considered for studies on symbiont conservation. Last but not least, additional drivers that may play a role in symbiont extinction but no covered by us nor by previous studies should require further attention. Among the most obvious candidates are processes and factors which are becoming to be acknowledged as important for the ecology and evolution of symbionts and known to be associated with the extinction of free-living species, such as hybridization and introgression (Vallejo-Marín and Hiscock, 2016), microbiomes (Trevelline et al., 2019) or epigenetic processes (Bossdorf et al., 2008).

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Appendix A. Supplementary data

A shiny application to directly calculate *Ec* and confidence intervals from the number of macroevolutionary events estimated from an event-based cophylogenetic reconstruction can be

found here (https://jdona.shinyapps.io/extinction/). The R function is also available at GitHub (https://github.com/Jorge-Dona/cophylogenetic_extinction_rate).

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843 **Fig. 1.** Diagram depicting symbiont losses in an event-based cophylogenetic reconstruction.

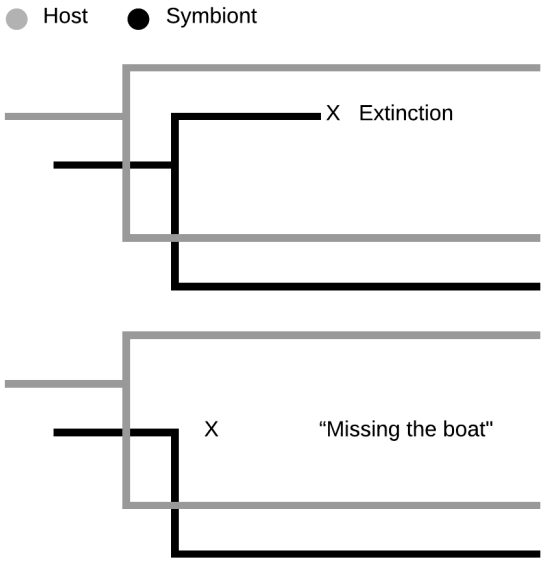

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Fig. 2. Results of simulations showing the behavior of *Ec* under different numbers of losses and host-switches. The number of total events (*E*) is 200 in both plots.

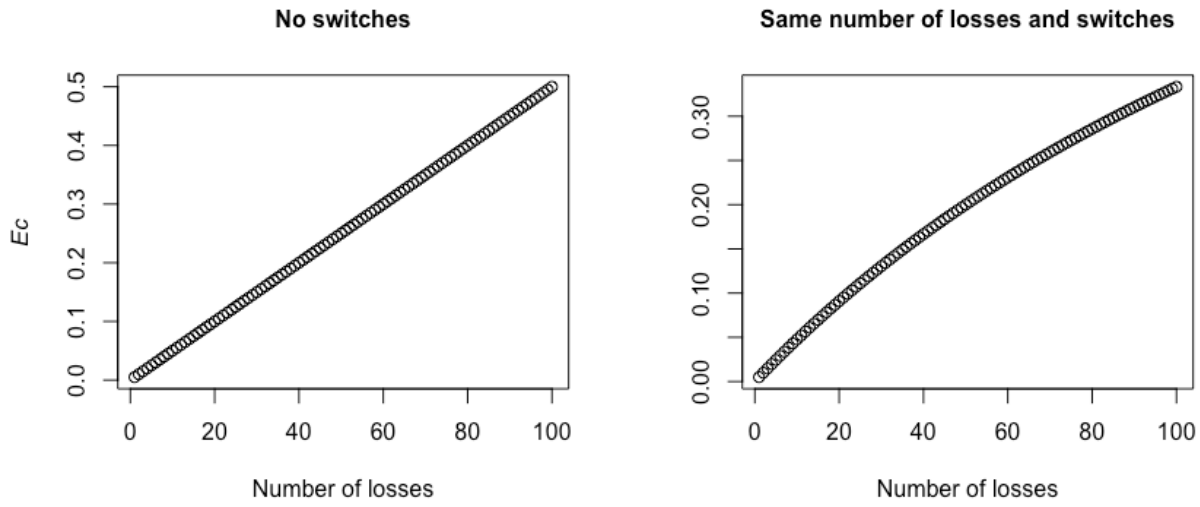

Fig. 3. Diagram depicting predictions of symbiont extinction derived from ecological and evolutionary drivers. Note that this is a highly simplified summary, with greater detail provided in the text. Thicker lines represent a higher extinction risk.