Assessing symbiont extinction risk using cophylogenetic data

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Abstract: Symbionts 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 host-symbiont interactions. In contrast, the discipline of symbiont conservation is still in a foundational stage. Here, we aim to integrate methodologies on symbiont coevolutionary biology with the perspective of conservation. We focus on host-symbiont cophylogenies, because they have been widely used to study symbiont diversification history and contain information on symbiont extinction. However, cophylogenetic information has never been used nor adapted to the perspective of conservation. Here, we propose a new statistic, "cophylogenetic extinction rate" (*Ec*), based on coevolutionary knowledge, that uses data from event-based cophylogenetic analyses, and which could be informative to assess relative symbiont extinction risks. 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 of coevolutionary biology and cophylogenetics into future symbiont conservation studies and practices.

Keywords: coevolution, coextinction risk, conservation biology, cophylogenies, host-symbiont interactions, parasites.

Highlights:

- We apply coevolutionary knowledge to symbiont conservation biology.
- We propose a new statistic to assess symbiont extinction risk from cophylogenies.
- We suggest potential future opportunities for advancing the field.

1. Introduction

Symbionts, defined as parasites, mutualists, and commensals that interact intimately with their hosts (Leung and Poulin, 2008), are highly relevant 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 a high percentage of symbiont species are expected to go extinct due to climate change (e.g., 10 % of parasite species by 2070, Carlson et al., 2017a; Dunn et al., 2009; Koh et al., 2004). However, despite their relevance and 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).

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, these studies have not considered the implications or relevance of their findings for conservation biology. Host-symbiont cophylogenies are one example of this rationale. Host-symbiont cophylogenies have been used to uncover the diversification history of many symbiont groups. However, though never used for assessing symbiont extinction risk, they might also provide valuable information on symbiont extinctions across phylogeny.

Symbiont (i.e. affiliated, associated, or dependent species) extinction risk has been commonly assessed in a coextinction framework, using host information (e.g., host extinction probabilities) to calculate symbiont extinction probability (Colwell et al., 2012; Dunn et al., 2009; Koh et al., 2004; Moir et al., 2014, 2010). Overall, current available approaches to estimate coextinction rates can be summarized as follows (Colwell et al., 2012; Moir et al., 2010): 1) Probabilistic models based on host likelihood of becoming extinct (e.g., estimated from historical data) that may also include some symbiont-specific traits, such as host specificity (Campião et al., 2015; Carlson et al., 2017a; Dunn et al., 2009; Koh et al., 2004). 2) Host-breadth models, which can handle uncertainty in estimating host-breadth (Vesk et al., 2010), and may be used along with decision protocols not only to estimate coextinction rates but also identify actions that may increase the persistence of threatened species (Moir et al., 2012, 2011). 3) Models based on ecological networks, which are more focused on identifying overall consequences in network structure after species removal (Bascompte and Stouffer, 2009). These models can handle more than two trophic levels, and have been recently improved to model more realistic situations (e.g., to integrate the variation in the interaction dependence, compensation after species extinctions, and the formation of new interactions; Baumgartner et al., 2020; Dunne et al., 2002; Vieira and Almeida-Neto, 2015). While these approaches have significantly advanced our knowledge of coextinction of interacting species (Bascompte and Stouffer, 2009; Carlson et al., 2017a; Dunn et al., 2009; Koh et al., 2004; Taylor and Moir, 2014; Thacker et al., 2006; Vieira and Almeida-Neto, 2015), some improvements in assessing coextinction rates are still needed (see Carlson et al., 2019; Colwell et al., 2012; Moir et al., 2010; Strona, 2015).

Important gaps have been identified in the ability to estimate coextinction risk (Colwell et al., 2012; Moir et al., 2010). For instance, Moir et al., (2010) identified three categories of gaps:

accuracy in 1) host data (e.g., threat of the host status), 2) dependent data (host specificity), and the 3) interactions between these two components (e.g., differences in the interactions across geographic regions). In addition, Colwell et al. (2012) call for incorporating demographic and evolutionary dynamics, host switching, affiliate phylogeny, and risk factors for affiliate extinction. Overall, while some of the current gaps in assessing coextinction risk have already been overcome (e.g., better estimates of host specificity, Vesk et al., 2010; or allowing new interactions to emerge, Baumgartner et al., 2020), most of these aspects are yet to be implemented in current methodologies.

One example of a gap in assessing coextinction risk is that correlated extinctions of host and symbionts are not currently implemented in coextinction estimation (Colwell et al., 2012; Moir et al., 2010; Rezende et al., 2007). Particular groups of species might be more prone to extinction due to different factors, for example shared life-history traits due to phylogenetic relatedness. Indeed, current methodologies to assess coextinction risk generally do not consider symbiont evolutionary history (but see Hoyal Cuthill et al., 2016; Moir et al., 2016). This lack of consideration is especially important for traits that might be related to the likelihood of a symbiont group becoming extinct (Cizauskas et al., 2017; Colwell et al., 2012; Moir et al., 2014). These traits could include host-switching capability (Clayton et al., 2015), effective population sizes (Allendorf, 2017), potential for rapid evolution (Villa et al., 2019), or hybridization dynamics (Detwiler and Criscione, 2010; Doña et al., 2019c; Vallejo-Marín and Hiscock, 2016). Accordingly, new approaches able to obtain estimates of symbiont extinction rates, including more aspects of symbiont evolutionary history, might enhance our ability in assessing symbiont extinction risk (Colwell et al., 2012; Moir et al., 2010; Strona, 2015). However, to our knowledge, these approaches are still non-existent.

Current cophylogenetic methodologies might offer a possibility to include evolutionary history in symbiont extinction risk assessments (Section 2). Cophylogenetic methods have been useful to disentangle which ecological and evolutionary traits drive the evolutionary history of symbionts (Clayton et al., 2015, and references therein). For instance, from cophylogenetics, we know that at an evolutionary scale, lower dispersal capabilities are associated with higher cospeciation rates and lower host-switching rates (Clayton et al., 2015; Doña et al., 2017b; Sweet and Johnson, 2018). Similarly, cophylogenetic methods could be used to increase our knowledge of which symbiont traits are behind particular extinction rates (e.g., transmission, aggregation, or geographic patchiness, see Box 1). Also, among the most remarkable advantages of a cophylogenetic-based statistic would be that this statistic would not directly derive from host extinction probabilities, and thus might allow uncovering symbiont groups with high extinction probabilities inhabiting hosts with low extinction probabilities, in contrast to current approaches to estimate coextinction.

In this overview, we propose a new statistic derived from cophylogenetic analyses "cophylogenetic extinction rate" (*Ec*), to assess symbiont extinction risks (Section 2). As this statistic derives largely from coevolutionary theory, we list different ecological and evolutionary variables that are expected to influence this statistic and might be useful to consider when interpreting *Ec* values (Box 1, Figure 1). Moreover, given the novelty of the approach, we propose potential future research to further develop estimation of cophylogenetic symbiont extinction risks and the inclusion of these data into current modeling practices.

Box 1. Ecological and evolutionary variables influencing cophylogenetic extinction rate (*Ec*)

The variables listed below, along with their predictions regarding extinction risk, are derived from well-studied topics in coevolutionary, coextinction, and conservation biology. Note that we place the most emphasis on those variables that are the most unique and relevant to symbionts (e.g., we do not include a "habitat" variable, apart from the host, because it might be less relevant for symbionts than for other interacting systems, such as plant-pollinator or predator-prey systems). Some of these variables have already been reviewed in depth (Colwell et al., 2012; Moir et al., 2014, 2010; Strona, 2015). Cophylogenetic extinction risk (*Ec*) derives mostly from coevolutionary biology theory; therefore, the value of this parameter is expected to be congruent with predictions from this theory.

1. Host specificity: In the most basic sense, host specificity can be defined as the number of recorded hosts for a given symbiont species (Lymbery, 1989). Also, it can include the phylogenetic relationships among hosts (phylogenetic host specificity) and the variation across the geographic range (geographic host-specificity) (Poulin et al., 2011; Wells and Clark, 2019). This variable has been widely integrated in coextinction models (Colwell et al., 2012; Moir et al., 2010; Strona, 2015). In short, highly host-specific symbionts are expected to have a higher extinction risk. However, Strona et al., (2013) found that host-stability instead of host-specificity was the main determinant of the risk of becoming extinct.

2. Mode of transmission: The mode of transmission of a symbiont species (e.g., vertically: from parents to offspring vs. horizontally: between individual hosts that are not parents and offspring) is associated with major ecological and evolutionary aspects that may be relevant to consider in symbiont extinction risk assessments (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; Poulin, 2011; Antonovics et al., 2017; Fisher et al., 2017; Doña et al., 2019c). 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).

3. Virulence: Virulence can be defined as the reduction of host fitness caused by the symbiont (Cressler et al., 2016; Herre, 1993; Read, 1994). 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 coextinction of the host and parasite, because there may be no time for natural selection to adjust virulence.

4. Straggling and host-switching: Straggling (i.e., symbiont dispersal to a novel host) seems to be frequent at an ecological scale, whereas successful host-switches (i.e., not only reaching a new host but also reproducing on the new host) are comparatively rare (Whiteman et al., 2004; Rivera-Parra et al., 2017; Doña et al., 2019b, 2018). Higher straggling and host-switching capabilities might be associated with a higher likelihood of escaping from host extinctions (Agosta et al., 2010; Agosta and Klemens, 2008; Clayton et al., 2015; Engelstädter and Fortuna, 2019). However, 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 (Settele et al., 2014; Carlson et al., 2017a; Cizauskas et al., 2017).

5. Symbiont population genetic structure: Intermediate degrees of population subdivision generally yield the highest adaptive potential (Allendorf et al., 2007; Futuyma, 2013). 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 (Clayton et al., 2015; Doña et al., 2019a; Huyse et al., 2005; Mazé-Guilmo et al., 2016; McCoy et al., 2003; Poulin, 2011). However, 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.

6. Aggregation: Symbionts are generally aggregated among the available hosts so that most host individuals are inhabited by few to no symbionts, while many symbionts inhabit just a few host individuals (Poulin, 2011; Rózsa et al., 2000). Aggregation can be an important parameter for symbiont persistence (Clayton et al., 2015; Cornell et al., 2003; Criscione and Blouin, 2005; Dhamarajan, 2015; Montarry Josselin et al., 2019), affecting levels of genetic diversity and increasing the probability of stochastic extinction.

7. Host population size: Symbionts from hosts with small population sizes (and low-density) are expected to be more vulnerable because they typically have lower abundances (Arneberg Per et al., 1998; Ellis et al., 2017), higher coextinction risks (Strona, 2015), and even higher probabilities of extinction than that of their hosts because of the aggregated distributions of symbionts.

8. Symbiont effective population size: Symbionts often have life-history features that may reduce the effective population size (N_e) (Criscione and Blouin, 2005; Dabert et al., 2015; Dobson, 1986; Doña et al., 2015; Monsion et al., 2008). Obtaining precise estimates of symbionts N_e is a complicated task (Crellen et al., 2016; Thiele et al., 2018; Criscione, 2013; Strobel et al., 2019). Large and small N_e may be expected in symbionts depending on conditions (Seger et al., 2010; Criscione, 2013; Strobel et al., 2019; Hughes and Verra, 2001), and factors such as aggregation, bottlenecks, prevalence, and intensity influence N_e(Criscione and Blouin, 2005; Dabert et al., 2015; Dobson, 1986; Doña et al., 2015; Monsion et al., 2008). Knowledge of these parameters may provide useful insights regarding symbiont N_e.

9. Geographic patchiness: 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; Wells and Clark, 2019; Bush and Kennedy, 1994; Bush et al., 2013).

Symbionts restricted to reduced areas of host distribution may be expected to have a higher vulnerability of becoming extinct.

10. Host effects: Not all hosts are equally suitable for the symbionts. Apart from host extinction risk (which may lead to coextinction processes), several host features also have a substantial effect on symbiont traits when there is an intimate association (Clayton et al., 2015). This effect might derive from coadaptative (e.g., arm-races dynamics) or non-coadaptive processes (e.g., host-density influencing parasite abundance) (Clayton and al, 2010; Clayton et al., 2015; Bush and Clayton, 2018; Villa et al., 2016, 2018; Bush et al., 2019; Arneberg Per et al., 1998; Ellis et al., 2017; Clausen, 1939; Hall et al., 2014). Furthermore, hosts may possess traits that hamper symbiont colonization (Poulin et al., 2012). Taken together these host features may be related to the likelihood of a symbiont becoming extinct.

11. Symbiont body size and life-cycle: Large bodied symbionts tend to have smaller effective population sizes and to depend on larger hosts, which are also more vulnerable to extinction (Bush and Clayton, 2006; Clayton et al., 2015; Ripple et al., 2017). Also, symbionts with complex life-cycles and limited climatic tolerances (e.g., ectotherms, Cizauskas et al., 2017) might be at an increased risk of extinction (Colwell et al., 2012; Koh et al., 2004; Lafferty, 2012; Poulin and Morand, 2004).

12. Trait matching: Due to the coevolutionary process, symbionts tend to possess traits that match very tightly those of their hosts (Clayton et al., 2015). 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 (Agosta et al., 2010; Remold, 2012; Thompson, 1994). However, factors such as overestimates of the level of host specificity (Braga et al., 2018; Dallas et al., 2017; Doña et al., 2019b), ability for rapid evolution (Bush et al., 2019; Koch et al., 2014; Villa et al., 2019), and host stability (Strona et al., 2013) may counteract this prediction.

13. Inter- and intraspecific competition: Symbionts not only interact with their hosts, but they also interact with diverse communities (including other symbionts) with whom they share their host (Bush and Malenke, 2008; Clayton et al., 2015; Doña et al., 2017a; Harbison et al., 2008; Johnson et al., 2009; Perez and Atyeo, 1984; Proctor, 2003). Overall, competitively superior species are expected to be less vulnerable to extinction than competitively inferior species (Clayton et al., 2015). However, due to asymmetries in resource distribution and competition, competitively superior species, counterintuitively, may not necessarily be the winners in a rapidly changing climate scenario (Northfield and Ives, 2013; Van Den Elzen et al., 2017).

2. Obtaining symbiont extinction rates from cophylogenies

In cophylogenetic analyses, 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 symbiont trees and statistically evaluate whether the congruence is higher than expected by chance (Huelsenbeck et al., 2003; De Vienne et al., 2013; Martínez-Aquino, 2016). In these methods, significantly high levels of congruence are generally assumed to be the result of codivergence between host and symbionts (Huelsenbeck et al., 2003; De Vienne et al., 2013; Martínez-Aquino, 2016). Event-based methods (e.g., Jane; Conow et al., 2010) use costs for macroevolutionary events (i.e., events such as cospeciation, host-switches, and losses that occur at a macroevolutionary scale, see below) which must be previously specified by the user, to reconcile host and symbiont phylogenetic trees (De Vienne et al., 2013; Charleston and Libeskind-Hadas, 2014; Martínez-Aquino, 2016). The result of an event-based cophylogenetic analysis generally includes the optimal solution to reconcile both trees (i.e., given the costs specified) and the corresponding number of macroevolutionary evolutionary events of each category that were needed to reach that solution. These events typically include cospeciation, duplication, host-switching, loss, and failure to diverge (De Vienne et al., 2013; Charleston and Libeskind-Hadas, 2014; Martínez-Aquino, 2016).

Here, we propose a way to obtain a rough estimate of the relative extinction rate of a particular symbiont lineage using the proportional number of losses (i.e. "sorting events") from an event-based cophylogenetic reconstruction (Fig. 2). This approach is similar to the current practice of using the percentage of cospeciation events as a measure of the relative importance of cospeciation in a symbiont lineage (Johnson and Clayton, 2003; De Vienne et al., 2013; Doña et al., 2017b). In cophylogenetic reconstructions, the inferred losses can be interpreted as the consequence of two distinct processes (Fig. 2; Clayton et al., 2015): (1) as genuine events of parasite extinctions; or (2) as sorting events (e.g., 'missing the boat'), when a symbiont fails to disperse along with one host lineage. Note that even though sorting events are not directly indicative of symbiont species extinctions, they do contain information regarding 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: $Ec = \left(\frac{L}{E+2S}\right)$; where L represents the number of losses, E the total number of macroevolutionary events other than host-switches (i.e., cospeciation + duplication + losses), and S the number of host-switches. The number of host-switches (S) is included twice because, in contrast to the other macroevolutionary events, it should effectively lower the extinction risk (Carlson et al., 2017a; Cizauskas et al., 2017; Clayton et al., 2015; Colwell et al., 2012; Dunn et al., 2009; Koh et al., 2004; Moir et al., 2010, 2014). Consequently, Ec can discriminate between two symbiont groups with the same ratio of losses (L) vs. all the other events (E+S) but differing in the number of host-switches; so that the lowest Ec will be that of the group with a higher number of host-switches. The parameter Ec increases linearly with the number of losses, and decreases as host-switching increases (Fig 3). We encourage accompanying *Ec* with a confidence interval to show the level of precision in the estimate (e.g., the modified Wilson confidence interval for a binomial proportion; (Brown et al., 2001; Signorell et al., 2019). To aid in calculating *Ec* and 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* = 0.04; CI = 0-0.21) than for *Proctophyllodes* (*Ec* = 0.01; CI = 0-0.07) mites. This result agrees with existing comparative knowledge from the ecology and evolution of these mites. Specifically, *Trouessartia* mites are known to have: 1) a lower species diversity on Passeriformes (Doña et al., 2016, 2018), 2) lower prevalence (i.e., the proportion of individuals inhabited by a symbiont species within a host sample; Reiczigel et al., 2019) and intensity (i.e., the number of individual symbionts inhabiting a particular host; Reiczigel et al., 2019) (Fernández-González et al., 2018; Doña et al., 2019b), 3) lower genetic diversity (Fernández-González et al., 2018; Doña et al., 2019b), and 4) infrapopulations genetically more structured (i.e., with lower gene flow among infrapopulations —all the individual symbionts inhabiting an individual host—, than *Proctophyllodes* species (Doña et al., 2019a).

3. Future opportunities

Global symbiont diversity is at a high risk of extinction (Carlson et al., 2017a; Dunn et al., 2009; Koh et al., 2004). The situation is highly concerning because symbionts have not received appropriate scientific and public attention, especially when compared to free-living species (see this special issue; Carlson et al., 2020). Here, we have proposed the first cophylogenetic-based statistic (*Ec*) for assessing symbiont extinction risk. Previous studies on coextinctions have repeatedly called for including evolutionary information in symbiont extinction risk assessments, and *Ec* allows one to do so. Also, in contrast to most methods to estimate coextinction, *Ec* does not rely upon host extinction probabilities, and therefore, it allows uncovering symbionts with a high extinction risk associated with hosts with a low extinction risk. Overall, we believe that *Ec* represent a highly valuable addition to current methods in assessing symbiont extinction rates. Moreover, the calculation of this parameter can act as a first step, thus stimulating further advance in symbiont conservation biology and cophylogenetics. In this vein, we anticipate the following three areas as valuable for future research efforts to advance symbiont conservation theory towards better extinction risk assessments:

3. 1. Meta-analyses of current cophylogenetic data: To date, several cophylogenetic studies on symbionts have been carried out (De Vienne et al., 2013; Clayton et al., 2015). 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. These studies might allow obtaining new information on the drivers of symbiont extinction (Cizauskas et al., 2017; Moir et al., 2014), similarly as how it has been done to uncovers the drivers of cospeciation and host-switching (Clayton et al., 2015 and references therein). Moreover, 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.

3. 2. Integrating symbiont conservation biology into coevolutionary and 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. 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.

3. 3. Expanding modeling of symbiont extinction (and coextinction) rates: As stated above, cophylogenies might offer an opportunity to include data from evolutionary history in coextinction assessments. One way to do so would be, for example, to incorporate cophylogenetic extinction rate data as a proxy of the evolutionary propensity of extinction of a given group of symbionts into current coextinction models. Indeed, species distribution and evolutionary models that are often used to calculate species extinction risk of free-living species, already accommodate different variables (e.g., dispersal, demography, genetic data) to improve their predictions (Carlson et al., 2019). On the other hand, because cophylogenetic methods still do not allow using time-calibrated phylogenies (see section 3.2), another related avenue for improvement would be to also incorporate lineage-specific extinction rates 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 on extinction risk from phylogenies should be treated with caution (particularly when including non-sequenced species; Rabosky, 2016), the increasing availability of robust-comprehensive phylogenetic trees offers an opportunity to use these phylogenetically based methods in symbionts (Johnson, 2019).

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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).

References

Agosta, S.J., Janz, N., Brooks, D.R., 2010. How specialists can be generalists: resolving the "parasite paradox" and implications for emerging infectious disease. Zoologia (Curitiba) 27, 151–162. https://doi.org/10.1590/S1984-46702010000200001

Agosta, S.J., Klemens, J.A., 2008. Ecological fitting by phenotypically flexible genotypes: implications for species associations, community assembly and evolution. Ecology Letters 11, 1123–1134. https://doi.org/10.1111/j.1461-0248.2008.01237.x

Alcala, N., Jenkins, T., Christe, P., Vuilleumier, S., 2017. Host shift and cospeciation rate estimation from co-phylogenies. Ecology letters 20, 1014–1024.

Allendorf, F.W., 2017. Genetics and the conservation of natural populations: allozymes to genomes. Molecular Ecology 26, 420–430.

Allendorf, F.W., Luikart, G., Aitken, S.N., 2007. Conservation and the genetics of populations. Blackwell Publishing, Malden, Massachusetts.

Antonovics, J., Wilson, A.J., Forbes, M.R., Hauffe, H.C., Kallio, E.R., Leggett, H.C., Longdon, B., Okamura, B., Sait, S.M., Webster, J.P., 2017. The evolution of transmission mode. Philos Trans R Soc Lond B Biol Sci 372. https://doi.org/10.1098/rstb.2016.0083

Arneberg Per, Skorping Arne, Grenfell Bryan, Read Andrew F., 1998. Host densities as determinants of abundance in parasite communities. Proceedings of the Royal Society of London. Series B: Biological Sciences 265, 1283–1289. https://doi.org/10.1098/rspb.1998.0431

Barrett, L.G., Thrall, P.H., Burdon, J.J., Linde, C.C., 2008. Life history determines genetic structure and evolutionary potential of host–parasite interactions. Trends Ecol Evol 23, 678–685. https://doi.org/10.1016/j.tree.2008.06.017

Bascompte, J., Stouffer, D.B., 2009. The assembly and disassembly of ecological networks. Philosophical Transactions of the Royal Society B: Biological Sciences 364, 1781–1787. https://doi.org/10.1098/rstb.2008.0226

Baumgartner, M.T., Almeida-Neto, M., Gomes, L.C., 2020. A novel coextinction model considering compensation and new interactions in ecological networks. Ecological Modelling 416, 108876. https://doi.org/10.1016/j.ecolmodel.2019.108876

Beaulieu, J.M., O'Meara, B.C., 2015. Extinction can be estimated from moderately sized molecular phylogenies. Evolution 69, 1036–1043. https://doi.org/10.1111/evo.12614

Braga, M.P., Guimarães, P.R., Wheat, C.W., Nylin, S., Janz, N., 2018. Unifying host-associated diversification processes using butterfly–plant networks. Nat Commun 9, 1–10. https://doi.org/10.1038/s41467-018-07677-x

Brown, L.D., Cai, T.T., DasGupta, A., 2001. Interval estimation for a binomial proportion. Statistical science 101–117.

Bush, A.O., Kennedy, C.R., 1994. Host fragmentation and helminth parasites: Hedging your bets against extinction. International Journal for Parasitology 24, 1333–1343. https://doi.org/10.1016/0020-7519(94)90199-6

Bush, S.E., Clayton, D.H., 2018. Anti-parasite behaviour of birds. Philosophical Transactions of the Royal Society B: Biological Sciences 373, 20170196.

Bush, S.E., Clayton, D.H., 2006. The role of body size in host specificity: reciprocal transfer experiments with feather lice. Evolution 60, 2158–2167.

Bush, S.E., Harbison, C.W., Slager, D.L., Peterson, A.T., Price, R.D., Clayton, D.H., 2009. Geographic Variation in the Community Structure of Lice on Western Scrub-Jays. para 95, 10–13. https://doi.org/10.1645/GE-1591.1

Bush, S.E., Malenke, J.R., 2008. Host defence mediates interspecific competition in ectoparasites. Journal of Animal Ecology 77, 558–564.

Bush, S.E., Reed, M., Maher, S., 2013. Impact of forest size on parasite biodiversity: implications for conservation of hosts and parasites. Biodiversity and conservation 22, 1391–1404.

Bush, S.E., Villa, S.M., Altuna, J.C., Johnson, K.P., Shapiro, M.D., Clayton, D.H., 2019. Host defense triggers rapid adaptive radiation in experimentally evolving parasites. Evolution Letters 3, 120–128. https://doi.org/10.1002/evl3.104

Campião, K.M., de Aquino Ribas, A.C., Cornell, S.J., Begon, M., Tavares, L.E.R., 2015. Estimates of coextinction risk: how anuran parasites respond to the extinction of their hosts. International Journal for Parasitology 45, 885–889. https://doi.org/10.1016/j.ijpara.2015.08.010

Carlson, C., Hopkins, S., Bell, K., Doña, J., Godfrey, S., Kwak, M., Lafferty, K.D., Moir, M., Speer, K., Strona, G., Torchin, M., Wood, C., 2020. A global parasite conservation plan. Biological Conservation.

Carlson, C.J., Burgio, K.R., Dallas, T.A., Getz, W.M., 2019. The Mathematics of Extinction Across Scales: From Populations to the Biosphere, in: Kaper, H.G., Roberts, F.S. (Eds.), Mathematics of Planet Earth: Protecting Our Planet, Learning from the Past, Safeguarding for the Future, Mathematics of Planet Earth. Springer International Publishing, Cham, pp. 225–264. https://doi.org/10.1007/978-3-030-22044-0_9

Carlson, C.J., Burgio, K.R., Dougherty, E.R., Phillips, A.J., Bueno, V.M., Clements, C.F., Castaldo, G., Dallas, T.A., Cizauskas, C.A., Cumming, G.S., Doña, J., Harris, N.C., Jovani, R., Mironov, S., Muellerklein, O.C., Proctor, H.C., Getz, W.M., 2017a. Parasite biodiversity faces extinction and redistribution in a changing climate. Science Advances 3, e1602422. https://doi.org/10.1126/sciadv.1602422

Carlson, C.J., Muellerklein, O.C., Phillips, A.J., Burgio, K.R., Castaldo, G., Cizauskas, C.A., Cumming, G.S., Dallas, T.A., Doña, J., Harris, N., Jovani, R., Miao, Z., Proctor, H., Yoon, H.S., Getz, W.M., 2017b. The Parasite Extinction Assessment & Red List: an open-source, online biodiversity database for neglected symbionts. bioRxiv 192351. https://doi.org/10.1101/192351

Charleston, M., Libeskind-Hadas, R., 2014. Event-based cophylogenetic comparative analysis, in: Modern Phylogenetic Comparative Methods and Their Application in Evolutionary Biology. Springer, pp. 465–480.

Cizauskas, C.A., Carlson, C.J., Burgio, K.R., Clements, C.F., Dougherty, E.R., Harris, N.C., Phillips, A.J., 2017. Parasite vulnerability to climate change: an evidence-based functional trait approach. Royal Society Open Science 4, 160535. https://doi.org/10.1098/rsos.160535

Clausen, C.P., 1939. The Effect of Host Size upon the Sex Ratio of Hymenopterous Parasites and Its Relation to Methods of Rearing and Colonization. Journal of the New York Entomological Society 47, 1–9.

Clayton, D., al, et, 2010. How Birds Combat Ectoparasites. Open Ornothological Journal 3, 41–71.

Clayton, D.H., Bush, S.E., Johnson, K.P., 2015. Coevolution of life on hosts: integrating ecology and history. University of Chicago Press, Chicago, IL.

Colwell, R.K., Dunn, R.R., Harris, N.C., 2012. Coextinction and persistence of dependent species in a changing world. Annual Review of Ecology, Evolution, and Systematics 43, 183–203.

Conow, C., Fielder, D., Ovadia, Y., Libeskind-Hadas, R., 2010. Jane: a new tool for the cophylogeny reconstruction problem. Algorithms for Molecular Biology 5, 16. https://doi.org/10.1186/1748-7188-5-16

Cornell, S.J., Isham, V.S., Smith, G., Grenfell, B.T., 2003. Spatial parasite transmission, drug resistance, and the spread of rare genes. PNAS 100, 7401–7405. https://doi.org/10.1073/pnas.0832206100

Crellen, T., Allan, F., David, S., Durrant, C., Huckvale, T., Holroyd, N., Emery, A.M., Rollinson, D., Aanensen, D.M., Berriman, M., Webster, J.P., Cotton, J.A., 2016. Whole genome resequencing of the human parasite *Schistosoma mansoni* reveals population history and effects of selection. Scientific Reports 6, 20954. https://doi.org/10.1038/srep20954

Cressler, C.E., McLeod, D.V., Rozins, C., Hoogen, J.V.D., Day, T., 2016. The adaptive evolution of virulence: a review of theoretical predictions and empirical tests. Parasitology 143, 915–930. https://doi.org/10.1017/S003118201500092X

Criscione, C.D., 2013. Chapter 8 - Genetic Epidemiology of Ascaris: Cross-transmission between Humans and Pigs, Focal Transmission, and Effective Population Size, in: Holland, C. (Ed.), Ascaris: The Neglected Parasite. Elsevier, Amsterdam, pp. 203–230. https://doi.org/10.1016/B978-0-12-396978-1.00008-2

Criscione, C.D., Blouin, M.S., 2005. Effective sizes of macroparasite populations: a conceptual model. Trends in Parasitology 21, 212–217. https://doi.org/10.1016/j.pt.2005.03.002

Dabert, M., Coulson, S.J., Gwiazdowicz, D.J., Moe, B., Hanssen, S.A., Biersma, E.M., Pilskog, H.E., Dabert, J., 2015. Differences in speciation progress in feather mites (Analgoidea) inhabiting the same host: the case of Zachvatkinia and Alloptes living on arctic and long-tailed skuas. Experimental and Applied Acarology 65, 163–179.

Dallas, T., Huang, S., Nunn, C., Park, A.W., Drake, J.M., 2017. Estimating parasite host range. Proceedings of the Royal Society B: Biological Sciences 284, 20171250.

De Vienne, D.M., Refrégier, G., López-Villavicencio, M., Tellier, A., Hood, M.E., Giraud, T., 2013. Cospeciation vs host-shift speciation: methods for testing, evidence from natural associations and relation to coevolution. New Phytol 198, 347–385.

Detwiler, J.T., Criscione, C.D., 2010. An infectious topic in reticulate evolution: introgression and hybridization in animal parasites. Genes 1, 102–123.

Dhamarajan, G., 2015. Inbreeding in stochastic subdivided mating systems: the genetic consequences of host spatial structure, aggregated transmission dynamics and life history characteristics in parasite populations. J Genet 94, 43–53. https://doi.org/10.1007/s12041-015-0488-y

Dobson, A., Lafferty, K.D., Kuris, A.M., Hechinger, R.F., Jetz, W., 2008. Homage to Linnaeus: How many parasites? How many hosts? PNAS 105, 11482–11489. https://doi.org/10.1073/pnas.0803232105

Dobson, A.P., 1986. Inequalities in the individual reproductive success of parasites. Parasitology 92, 675–682.

Doña, J., Moreno-García, M., Criscione, C.D., Serrano, D., Jovani, R., 2015. Species mtDNA genetic diversity explained by infrapopulation size in a host-symbiont system. Ecology and Evolution 5, 5801–5809. https://doi.org/10.1002/ece3.1842

Doña, J., Osuna-Mascaró, C., Johnson, K.P., Serrano, D., Aymí, R., Jovani, R., 2019a. Persistence of single species of symbionts across multiple closely-related host species. Scientific Reports.

Doña, J., Potti, J., De La Hera, I., Blanco, G., Frias, O., Jovani, R., 2017a. Vertical transmission in feather mites: insights into its adaptive value. Ecological Entomology 42, 492–499.

Doña, J., Proctor, H., Mironov, S., Serrano, D., Jovani, R., 2018. Host specificity, infrequent major host switching and the diversification of highly host-specific symbionts: The case of vane-dwelling feather mites. Global Ecology and Biogeography 27, 188–198.

Doña, J., Proctor, H., Mironov, S., Serrano, D., Jovani, R., 2016. Global associations between birds and vane-dwelling feather mites. Ecology 97, 3242–3242.

Doña, J., Serrano, D., Mironov, S., Montesinos-Navarro, A., Jovani, R., 2019b. Unexpected bird–feather mite associations revealed by DNA metabarcoding uncovers a dynamic ecoevolutionary scenario. Mol Ecol 28, 379–390.

Doña, J., Sweet, A., Johnson, K., 2019c. Comparing rates of introgression in parasitic feather lice with differing dispersal capabilities. bioRxiv 527226.

Doña, J., Sweet, A.D., Johnson, K.P., Serrano, D., Mironov, S., Jovani, R., 2017b. Cophylogenetic analyses reveal extensive host-shift speciation in a highly specialized and host-specific symbiont system. Molecular Phylogenetics and Evolution 115, 190–196. https://doi.org/10.1016/j.ympev.2017.08.005

Dougherty, E.R., Carlson, C.J., Bueno, V.M., Burgio, K.R., Cizauskas, C.A., Clements, C.F., Seidel, D.P., Harris, N.C., 2016. Paradigms for parasite conservation. Conservation Biology 30, 724–733. https://doi.org/10.1111/cobi.12634

Dunn, R.R., Harris, N.C., Colwell, R.K., Koh, L.P., Sodhi, N.S., 2009. The sixth mass coextinction: are most endangered species parasites and mutualists? Proceedings of the Royal Society B: Biological Sciences 276, 3037–3045.

Dunne, J.A., Williams, R.J., Martinez, N.D., 2002. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecology letters 5, 558–567.

Ellis, V.A., Medeiros, M.C.I., Collins, M.D., Sari, E.H.R., Coffey, E.D., Dickerson, R.C., Lugarini, C., Stratford, J.A., Henry, D.R., Merrill, L., Matthews, A.E., Hanson, A.A., Roberts, J.R., Joyce, M., Kunkel, M.R., Ricklefs, R.E., 2017. Prevalence of avian haemosporidian parasites is positively related to the abundance of host species at multiple sites within a region. Parasitol Res 116, 73–80. https://doi.org/10.1007/s00436-016-5263-3

Engelstädter, J., Fortuna, N.Z., 2019. The dynamics of preferential host switching: Host phylogeny as a key predictor of parasite distribution. Evolution 73, 1330–1340. https://doi.org/10.1111/evo.13716

Fernández-González, S., Pérez-Rodríguez, A., Proctor, H.C., De la Hera, I., Pérez-Tris, J., 2018. High diversity and low genetic structure of feather mites associated with a phenotypically variable bird host. Parasitology 1–8.

Fisher, R.M., Henry, L.M., Cornwallis, C.K., Kiers, E.T., West, S.A., 2017. The evolution of host-symbiont dependence. Nature Communications 8, 1–8. https://doi.org/10.1038/ncomms15973

Futuyma, D.J., 2013. Evolution. Sunderland, MA. Sinauer Associates, Inc.

Groom, M.J., Meffe, G.K., Carroll, C.R., 2012. Principles of Conservation Biology. Sinauer.

Hall, R.J., Altizer, S., Bartel, R.A., 2014. Greater migratory propensity in hosts lowers pathogen transmission and impacts. Journal of Animal Ecology 83, 1068–1077. https://doi.org/10.1111/1365-2656.12204

Harbison, C.W., Bush, S.E., Malenke, J.R., Clayton, D.H., 2008. Comparative transmission dynamics of competing parasite species. Ecology 89, 3186–3194.

Herre, E.A., 1993. Population Structure and the Evolution of Virulence in Nematode Parasites of Fig Wasps. Science 259, 1442–1445. https://doi.org/10.1126/science.259.5100.1442

Hoyal Cuthill, J.F., Sewell, K.B., Cannon, L.R.G., Charleston, M.A., Lawler, S., Littlewood, D.T.J., Olson, P.D., Blair, D., 2016. Australian spiny mountain crayfish and their temnocephalan ectosymbionts: an ancient association on the edge of coextinction? Proceedings of the Royal Society B: Biological Sciences 283, 20160585. https://doi.org/10.1098/rspb.2016.0585

Huelsenbeck, J.P., Rannala, B., Larget, B., 2003. A statistical perspective for reconstructing the history of host-parasite associations, in: Tangled Trees: Phylogeny, Co-Speciation and Co-Evolution. University of Chicago Press, pp. 93–119.

Hughes, Verra, 2001. Very large long–term effective population size in the virulent human malaria parasite Plasmodium falciparum. Proceedings of the Royal Society of London. Series B: Biological Sciences 268, 1855–1860. https://doi.org/10.1098/rspb.2001.1759

Huyse, T., Poulin, R., Theron, A., 2005. Speciation in parasites: a population genetics approach. Trends in parasitology 21, 469–475.

Johnson, K.P., 2019. Putting the genome in insect phylogenomics. Current Opinion in Insect Science. https://doi.org/10.1016/j.cois.2019.08.002

Johnson, K.P., Clayton, D.H., 2003. Coevolutionary history of ecological replicates: comparing phylogenies of wing and body lice to Columbiform hosts. Tangled Trees. Edited by: Page RDM. Chicago, IL: University of Chicago Press.

Johnson, K.P., Malenke, J.R., Clayton, D.H., 2009. Competition promotes the evolution of host generalists in obligate parasites. Proceedings of the Royal Society B: Biological Sciences 276, 3921–3926. https://doi.org/10.1098/rspb.2009.1174

Koch, H., Frickel, J., Valiadi, M., Becks, L., 2014. Why rapid, adaptive evolution matters for community dynamics. Front. Ecol. Evol. 2. https://doi.org/10.3389/fevo.2014.00017

Koh, L.P., Dunn, R.R., Sodhi, N.S., Colwell, R.K., Proctor, H.C., Smith, V.S., 2004. Species coextinctions and the biodiversity crisis. Science 305, 1632–1634. https://doi.org/10.1126/science.1101101

Krasnov, B.R., Mouillot, D., Shenbrot, G.I., Khokhlova, I.S., Poulin, R., 2004. Geographical variation in host specificity of fleas (Siphonaptera) parasitic on small mammals: the influence of phylogeny and local environmental conditions. Ecography 27, 787–797. https://doi.org/10.1111/j.0906-7590.2004.04015.x

Lafferty, K.D., 2012. Biodiversity loss decreases parasite diversity: theory and patterns. Philosophical Transactions of the Royal Society B: Biological Sciences 367, 2814–2827.

Lafferty, K.D., Dobson, A.P., Kuris, A.M., 2006. Parasites dominate food web links. PNAS 103, 11211–11216. https://doi.org/10.1073/pnas.0604755103

Legendre, P., Desdevises, Y., Bazin, E., 2002. A statistical test for host-parasite coevolution. Syst. Biol. 51, 217–234. https://doi.org/10.1080/10635150252899734

Leung, T.L.F., Poulin, R., 2008. Parasitism, commensalism, and mutualism: exploring the many shades of symbioses. Vie et Milieu 58, 107.

Lipsitch, M., Nowak, M.A., Ebert, D., May, R.M., 1995. The population dynamics of vertically and horizontally transmitted parasites. Proceedings of the Royal Society of London. Series B: Biological Sciences 260, 321–327. https://doi.org/10.1098/rspb.1995.0099

MacLeod, C.J., Paterson, A.M., Tompkins, D.M., Duncan, R.P., 2010. Parasites lost – do invaders miss the boat or drown on arrival? Ecology Letters 13, 516–527. https://doi.org/10.1111/j.1461-0248.2010.01446.x

Martínez-Aquino, A., 2016. Phylogenetic framework for coevolutionary studies: a compass for exploring jungles of tangled trees. Curr Zool 62, 393–403. https://doi.org/10.1093/cz/zow018

Mazé-Guilmo, E., Blanchet, S., McCoy, K.D., Loot, G., 2016. Host dispersal as the driver of parasite genetic structure: a paradigm lost? Ecology Letters 19, 336–347. https://doi.org/10.1111/ele.12564

McCoy, K.D., Boulinier, T., Tirard, C., Michalakis, Y., 2003. Host-dependent genetic structure of parasite populations: differential dispersal of seabird tick host races. Evolution 57, 288–296.

Moir, M.L., Coates, D.J., Kensington, W.J., Barrett, S., Taylor, G.S., 2016. Concordance in evolutionary history of threatened plant and insect populations warrant unified conservation management approaches. Biological Conservation 198, 135–144. https://doi.org/10.1016/j.biocon.2016.04.012

Moir, M.L., Hughes, L., Vesk, P.A., Leng, M.C., 2014. Which host-dependent insects are most prone to coextinction under changed climates? Ecology and Evolution 4, 1295–1312. https://doi.org/10.1002/ece3.1021

Moir, M.L., Vesk, P.A., Brennan, K.E.C., Keith, D.A., Hughes, L., McCARTHY, M.A., 2010. Current Constraints and Future Directions in Estimating Coextinction. Conservation Biology 24, 682–690. https://doi.org/10.1111/j.1523-1739.2009.01398.x

Moir, M.L., Vesk, P.A., Brennan, K.E.C., Keith, D.A., McCARTHY, M.A., Hughes, L., 2011. Identifying and Managing Threatened Invertebrates through Assessment of Coextinction Risk. Conservation Biology 25, 787–796. https://doi.org/10.1111/j.1523-1739.2011.01663.x

Moir, M.L., Vesk, P.A., Brennan, K.E.C., Poulin, R., Hughes, L., Keith, D.A., McCARTHY, M.A., Coates, D.J., 2012. Considering Extinction of Dependent Species during Translocation, Ex Situ Conservation, and Assisted Migration of Threatened Hosts. Conservation Biology 26, 199–207. https://doi.org/10.1111/j.1523-1739.2012.01826.x

Monsion, B., Froissart, R., Michalakis, Y., Blanc, S., 2008. Large bottleneck size in Cauliflower mosaic virus populations during host plant colonization. PLoS pathogens 4, e1000174.

Montarry Josselin, Bardou-Valette Sylvie, Mabon Romain, Jan Pierre-Loup, Fournet Sylvain, Grenier Eric, Petit Eric J., 2019. Exploring the causes of small effective population sizes in cyst nematodes using artificial Globodera pallida populations. Proceedings of the Royal Society B: Biological Sciences 286, 20182359. https://doi.org/10.1098/rspb.2018.2359

Nee, S., Holmes, E.C., May, R.M., Harvey, P.H., 1994. Extinction Rates can be Estimated from Molecular Phylogenies. Philosophical Transactions: Biological Sciences 344, 77–82.

Northfield, T.D., Ives, A.R., 2013. Coevolution and the Effects of Climate Change on Interacting Species. PLOS Biology 11, e1001685. https://doi.org/10.1371/journal.pbio.1001685

Page, R.D.M., 2003. Tangled Trees: Phylogeny, Cospeciation, and Coevolution. University of Chicago Press.

Paterson, A.M., Palma, R.L., Gray, R.D., 1999. How Frequently do Avian Lice Miss the Boat? Implications for Coevolutionary Studies. Systematic Biology 48, 214–223.

Perez, T.M., Atyeo, W.T., 1984. Feather mites, feather lice, and thanatochresis. The Journal of Parasitology 807–812.

Pickles, R.S., Thornton, D., Feldman, R., Marques, A., Murray, D.L., 2013. Predicting shifts in parasite distribution with climate change: a multitrophic level approach. Global Change Biology 19, 2645–2654.

Poulin, R., 2011. Evolutionary ecology of parasites. Princeton university press, Princeton, NJ.

Poulin, R., Closs, G.P., Lill, A.W.T., Hicks, A.S., Herrmann, K.K., Kelly, D.W., 2012. Migration as an escape from parasitism in New Zealand galaxiid fishes. Oecologia 169, 955–963. https://doi.org/10.1007/s00442-012-2251-x

Poulin, R., Krasnov, B.R., Mouillot, D., 2011. Host specificity in phylogenetic and geographic space. Trends in Parasitology 27, 355–361. https://doi.org/10.1016/j.pt.2011.05.003

Poulin, R., Morand, S., 2004. Parasite biodiversity. Smithsonian Institution, Washington, DC.

Proctor, H.C., 2003. Feather mites (Acari: Astigmata): ecology, behavior, and evolution. Annual Review of Entomology 48, 185–209.

Rabosky, D.L., 2016. Challenges in the estimation of extinction from molecular phylogenies: A response to Beaulieu and O'Meara. Evolution 70, 218–228. https://doi.org/10.1111/evo.12820

Read, A.F., 1994. The evolution of virulence. Trends in Microbiology 2, 73–76. https://doi.org/10.1016/0966-842X(94)90537-1

Reiczigel, J., Marozzi, M., Fábián, I., Rózsa, L., 2019. Biostatistics for Parasitologists – A Primer to Quantitative Parasitology. Trends in Parasitology 35, 277–281. https://doi.org/10.1016/j.pt.2019.01.003

Remold, S., 2012. Understanding specialism when the jack of all trades can be the master of all. Proceedings of the Royal Society B: Biological Sciences 279, 4861–4869. https://doi.org/10.1098/rspb.2012.1990

Rezende, E.L., Lavabre, J.E., Guimarães, P.R., Jordano, P., Bascompte, J., 2007. Non-random coextinctions in phylogenetically structured mutualistic networks. Nature 448, 925–928. https://doi.org/10.1038/nature05956

Ripple, W.J., Wolf, C., Newsome, T.M., Hoffmann, M., Wirsing, A.J., McCauley, D.J., 2017. Extinction risk is most acute for the world's largest and smallest vertebrates. Proceedings of the National Academy of Sciences 114, 10678–10683.

Rivera-Parra, J.L., Levin, I.I., Johnson, K.P., Parker, P.G., 2017. Host sympatry and body size influence parasite straggling rate in a highly connected multihost, multiparasite system. Ecology and Evolution 7, 3724–3731. https://doi.org/10.1002/ece3.2971

Rocha, C.F.D., Bergallo, H.G., Bittencourt, E.B., Rocha, C.F.D., Bergallo, H.G., Bittencourt, E.B., 2016. More than just invisible inhabitants: parasites are important but neglected components of the biodiversity. Zoologia (Curitiba) 33. https://doi.org/10.1590/S1984-4689zool-20150198

Rózsa, L., Reiczigel, J., Majoros, G., 2000. Quantifying parasites in samples of hosts. para 86, 228–232. https://doi.org/10.1645/0022-3395(2000)086[0228:QPISOH]2.0.CO;2

Seger, J., Smith, W.A., Perry, J.J., Hunn, J., Kaliszewska, Z.A., Sala, L.L., Pozzi, L., Rowntree, V.J., Adler, F.R., 2010. Gene Genealogies Strongly Distorted by Weakly Interfering Mutations in Constant Environments. Genetics 184, 529–545. https://doi.org/10.1534/genetics.109.103556

Settele, J., Scholes, R., Betts, R.A., Bunn, S., Leadley, P., Nepstad, D., Winter, M., 2014. Terrestrial and Inland water systems: in, Climate Change 2014 Impacts, Adaptation and Vulnerability: Part A: Global and Sectoral Aspects (pp. 271–360). Cambridge University Press, DOI.

Signorell, A., Aho, K., Alfons, A., Anderegg, N., Aragon, T., 2019. DescTools: Tools for descriptive statistics. R package version 0.99. 28. R Found. Stat. Comput., Vienna, Austria.

Soulé, M.E., 1980. Conservation Biology: An Evolutionary-ecological Perspective. Sinauer Associates.

Strobel, H.M., Hays, S.J., Moody, K.N., Blum, M.J., Heins, D.C., 2019. Estimating effective population size for a cestode parasite infecting three-spined sticklebacks. Parasitology 1–14. https://doi.org/10.1017/S0031182018002226

Strona, G., 2015. Past, present and future of host–parasite co-extinctions. Int J Parasitol 3, 431–441.

Strona, G., Galli, P., Fattorini, S., 2013. Fish parasites resolve the paradox of missing coextinctions. Nature Communications 4, 1718. https://doi.org/10.1038/ncomms2723

Sweet, A.D., Johnson, K.P., 2018. The role of parasite dispersal in shaping a host–parasite system at multiple evolutionary scales. Mol Ecol 27, 5104–5119. https://doi.org/10.1111/mec.14937

Taylor, G.S., Moir, M.L., 2014. Further evidence of the coextinction threat for jumping plant-lice: three new Acizzia (Psyllidae) and Trioza (Triozidae) from Western Australia. Insect Systematics & Evolution 45, 283–302. https://doi.org/10.1163/1876312X-00002107

Thacker, J.I., Hopkins, G.W., Dixon, A.F.G., 2006. Aphids and scale insects on threatened trees: co-extinction is a minor threat. Oryx 40, 233–236. https://doi.org/10.1017/S0030605306000123

Thiele, E.A., Eberhard, M.L., Cotton, J.A., Durrant, C., Berg, J., Hamm, K., Ruiz-Tiben, E., 2018. Population genetic analysis of Chadian Guinea worms reveals that human and non-human hosts share common parasite populations. PLOS Neglected Tropical Diseases 12, e0006747. https://doi.org/10.1371/journal.pntd.0006747

Thompson, J.N., 1994. The coevolutionary process. University of Chicago Press, Chicago, IL.

Vallejo-Marín, M., Hiscock, S.J., 2016. Hybridization and hybrid speciation under global change. New Phytologist 211, 1170–1187. https://doi.org/10.1111/nph.14004

Van Den Elzen, C.L., Kleynhans, E.J., Otto, S.P., 2017. Asymmetric competition impacts evolutionary rescue in a changing environment. Proceedings of the Royal Society B: Biological Sciences 284, 20170374.

Vesk, P.A., McCarthy, M.A., Moir, M.L., 2010. How many hosts? Modelling host breadth from field samples. Methods in Ecology and Evolution 1, 292–299. https://doi.org/10.1111/j.2041-210X.2010.00026.x

Vieira, M.C., Almeida-Neto, M., 2015. A simple stochastic model for complex coextinctions in mutualistic networks: robustness decreases with connectance. Ecology Letters 18, 144–152.

Villa, S.M., Altuna, J.C., Ruff, J.S., Beach, A.B., Mulvey, L.I., Poole, E.J., Campbell, H.E., Johnson, K.P., Shapiro, M.D., Bush, S.E., Clayton, D.H., 2019. Rapid experimental evolution of reproductive isolation from a single natural population. PNAS 116, 13440–13445. https://doi.org/10.1073/pnas.1901247116

Villa, S.M., Goodman, G.B., Ruff, J.S., Clayton, D.H., 2016. Does allopreening control avian ectoparasites? Biology Letters 12, 20160362. https://doi.org/10.1098/rsbl.2016.0362

Villa, S.M., Koop, J.A., Le Bohec, C., Clayton, D.H., 2018. Beak of the pinch: anti-parasite traits are similar among Darwin’s finch species. Evolutionary ecology 32, 443–452.

Wells, K., Clark, N.J., 2019. Host Specificity in Variable Environments. Trends in Parasitology 0. https://doi.org/10.1016/j.pt.2019.04.001

Whiteman, N.K., Santiago-Alarcon, D., Johnson, K.P., Parker, P.G., 2004. Differences in straggling rates between two genera of dove lice (Insecta: Phthiraptera) reinforce population genetic and cophylogenetic patterns. Int J Parasitol 34, 1113–1119.

Windsor, D.A., 1995. Equal rights for parasites. Conservation Biology 9, 1–2.

Fig. 1. Diagram depicting predictions of variables influencing *Ec* (see Box 1). Note that this is a highly simplified summary, with greater detail provided in Box 1 and references therein. Also, to ease rapid access to these predictions, we have set line thickness to represent different extinction risk levels (thicker = higher; thinner = lower) according to our interpretation of current knowledge on these topics.

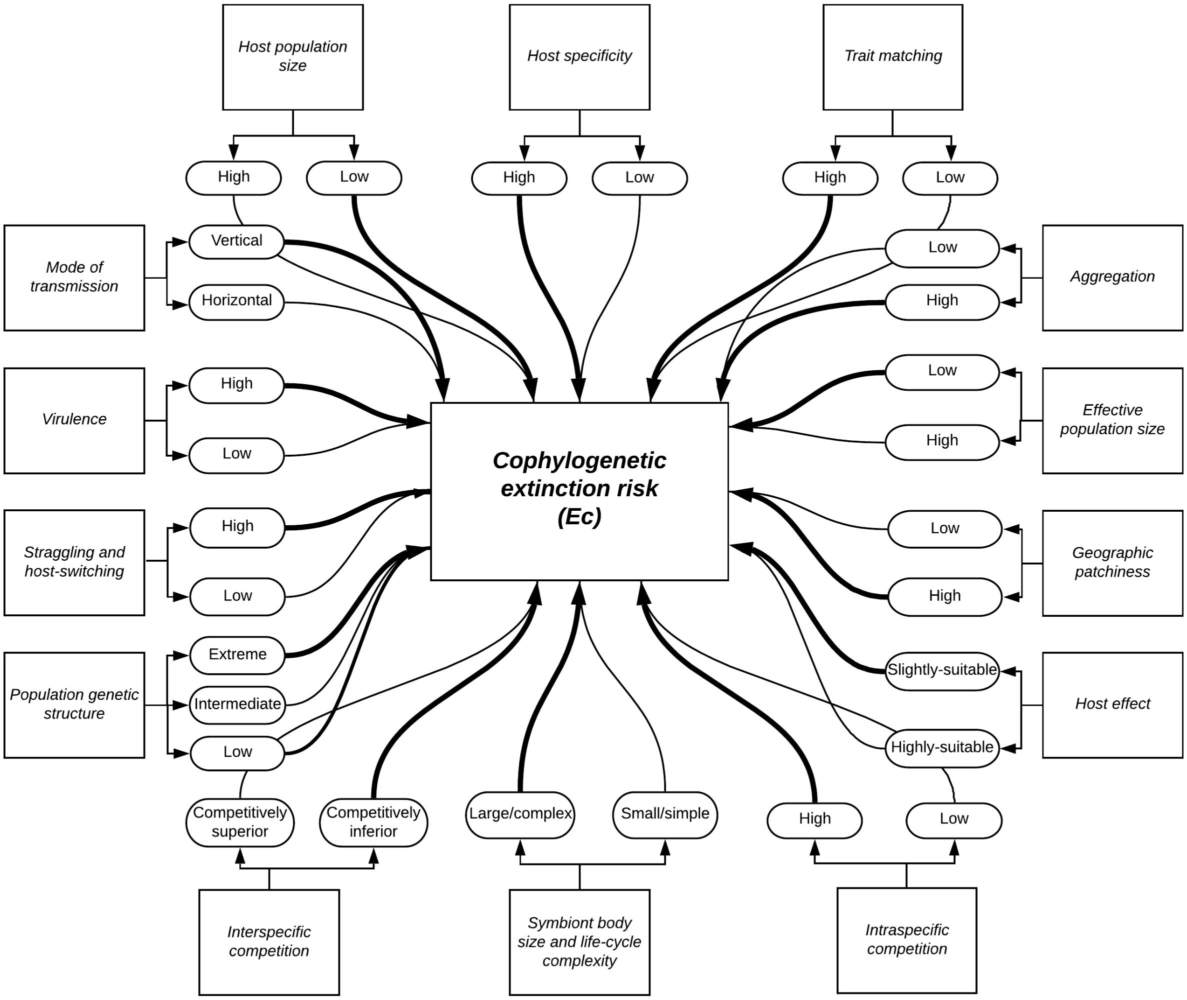

Fig. 2. Diagram depicting symbiont losses in an event-based cophylogenetic reconstruction. Inferred losses from a cophylogenetic reconstructions can be interpreted as the consequence of two distinct processes (Clayton et al., 2015): (1) as genuine events of parasite extinctions (top figure); or (2) as sorting events (e.g., ‘missing the boat’, bottom figure), when a symbiont fails to disperse with one host lineage. Note that even though sorting events are not directly indicative of symbiont species extinctions, they do provide information 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).

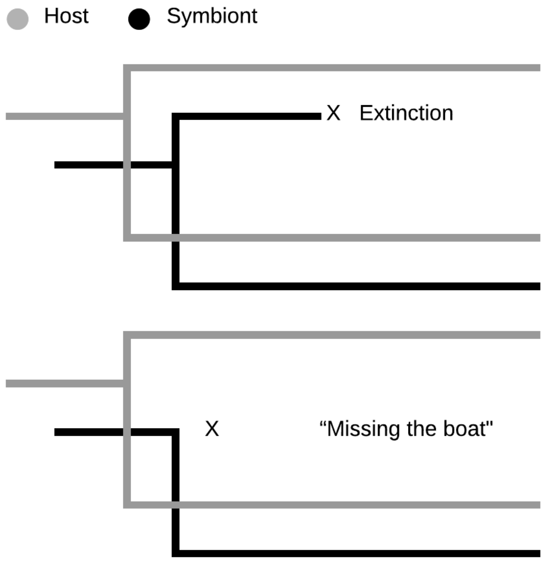

Fig. 3. Results of simulations showing the behavior of *Ec* under increasing numbers of losses and host-switches. The number of total events (*E*) is 200 in both plots. Note that in a) there were no switches in any iteration while in b), the same number of losses and switches is held across all the iterations (e.g., one loss and one switch or two losses and two switches)