The hierarchy-of-hypotheses approach: A synthesis method for enhancing theory development in ecology and evolution

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Abstract

In the current era of Big Data, existing synthesis tools (e.g. formal meta-analysis) are useful for handling the deluge of data and information. However, there is a need for complementary tools that help to (i) structure data and information, (ii) closely connect evidence to theory and (iii) further develop theory. We present the hierarchy-of-hypotheses (HoH) approach to address these issues. In an HoH, hypotheses are conceptually and visually structured in a hierarchically nested way, where the lower branches can be directly connected to empirical results. Used as an evidence-driven, bottom-up approach, it can (i) show connections between empirical results, even when derived through diverse approaches; and (ii) indicate under which circumstances hypotheses are applicable. Used as a theory-driven, top-down method, it helps uncover mechanistic components of hypotheses. We offer guidance on how to build an HoH, provide examples from population and evolutionary biology and propose terminological clarifications.

Keywords: bottom-up approach, hierarchy-of-hypotheses approach, knowledge synthesis, theory development, top-down approach

Introduction

Big data and a diversity of ideas have been major contributors to critical advances in science. In ecology and evolution, big data are becoming increasingly available for synthesis, making it possible to describe and analyze complex systems in much greater detail than ever before (Soranno and Schimel 2014). However, this increase in information availability does not necessarily correspond to an increase in knowledge and understanding (Jeschke et al. 2019), as publishing results in scientific journals and depositing data in public archives does not guarantee their utilization for the advancement of theory. We suggest that this situation can be improved by the development and establishment of methods that have the explicit aim to link data, research questions and hypotheses towards more efficient theory development.

Links between data and theory can be created along two pathways, following either a theory-driven, top-down approach, or an evidence-driven, bottom-up approach (Fig. 1). While the theory-driven narrowing of conclusions from a general idea into hypotheses or predictions about specific cases can provide an efficient linkage from theory to empirical research (see e.g. Scheiner and Willig 2011), tools and guidelines for taking this path are surprisingly scarce. For the evidence-driven pathway, on the other hand, there is a wealth of methods available for analyzing empirical data and statistically combining the results of multiple studies (Pullin et al. 2016, Dicks et al. 2017). These methods enable a synthesis of research results stemming from different studies that address a joint specific question (Koricheva et al. 2013). In environmental sciences, evidence synthesis has increased both in frequency and importance (Lortie 2014), aiming to make empirical evidence readily available and more suitable as a basis for decision-making (evidence-based decision making, Cook et al. 2017, Dicks et al. 2017, Diefenderfer et al. 2016, Pullin et al.

2016, Sutherland 2006). Moreover, methodological guidelines have been developed, and web portals implemented to collect and synthesize the results of primary studies. Prime examples are the platforms www.conservationevidence.com and www.environmentalevidence.org, alongside the EU-funded projects EKLIPSE (www.eklipse-mechanism.eu) and BiodiversityKnowledge (Nesshöver et al. 2016). These initiatives have promoted significant advances in the organization and assessment of evidence and the implementation of synthesis, thus allowing for an unbiased representation of applied knowledge in environmental sciences.

Despite these major achievements, the described approaches have limitations that we address here. First, while the initiatives fostering evidence-based decision-making are crucial to solving specific applied research questions, their findings are usually not re-connected to a broader body of theory. Thus, they do not consistently contribute to a structured or targeted advancing of theory, e.g. by assessing the usefulness of conceptual ideas. The re-evaluation and advancement of theory by feeding results from empirical studies back into the theoretical framework within which these studies were developed has long been viewed as a vital aspect of theory development (e.g. Jeltsch et al. 2013), but this process has been found to lag behind (Scheiner 2013). Second, all synthesis methods described above focus on the evidence-driven approach. A comprehensive theory development, however, requires the theory-driven approach as well.

To address these limitations, we outline a synthesis tool that has been specifically developed to guide theory development: the hierarchy-of-hypotheses (HoH) approach (Heger et al. 2013, Jeschke et al. 2012). It augments the existing evidence-based methods, while providing a significant improvement in the theory-driven approach, thus contributing to a rectification of the imbalance between these two pathways for theory development. The representation of broad ideas as nested hierarchies of hypotheses can be a powerful tool. For example, an HoH can link one or more studies to a body of theory which would not have been explicitly linked to theory otherwise, thus providing these studies with a more solid theoretical underpinning and strengthening their case. Combining disparate studies under a common theoretical hypothesis presents them in a more comprehensive way and simultaneously provides evidence for testing the hypothesis. Additionally, an HoH can be used to conceptually structure a body of literature that is too heterogeneous for statistical meta-analysis. Alternatively, it can be used to refine a broad idea on theoretical grounds, and to identify different possibilities of how an idea, concept or hypothesis can become more specific, less ambiguous and better structured. Taken together, the approach can help to strengthen the theoretical foundations of a research field.

The HoH approach has already been introduced as a tool for synthesis in invasion ecology (Heger and Jeschke 2014, Heger et al. 2013, Jeschke et al. 2012, Jeschke and Heger 2018a), though explicit guidance on how to build a hierarchy of hypotheses had been missing until now. Such guidance is provided here. In the following, we (i) outline the main ideas behind the HoH approach and the history of its development, (ii) present a primer for creating HoHs, (iii) provide examples for applications within and outside of invasion ecology, and (iv) discuss its strengths and limitations.

The hierarchy-of-hypotheses approach

The basic tenet behind the hierarchy-of-hypotheses (HoH) approach is that complexity can often be mastered by hierarchically structuring the topic under study (Heger and Jeschke 2018). The approach has been developed to clarify the link between big ideas and experiments or surveys designed to test them. Usually, such studies actually test smaller, more specific ideas that represent an aspect or one manifestation of the big idea. Different studies all addressing a joint major hypothesis consequently may each address different versions of it, which makes it hard to reconcile their results. The HoH approach addresses this challenge by dividing the major hypothesis into more specific formulations or sub-hypotheses. These can be further divided until the level of refinement allows for direct empirical testing. The result is a tree that visually depicts different ways in which a major hypothesis can be formulated. The empirical studies can then be explicitly linked to the branch of the tree they intend to address, thus making a conceptual and visual connection to the major hypothesis. The hierarchical nestedness therefore allows to structure and display relationships between different versions of an idea, and to conceptually collate empirical tests addressing the same overall question with divergent approaches. A hierarchical arrangement of hypotheses has also been suggested by Pickett et al. (2007, see Fig. 1.5) in the context of the method of pairwise alternative hypothesis testing (or strong inference, Platt 1964). However, we are not aware of studies that picked up on or further developed this idea.

The HoH approach in its first version (Heger and Jeschke 2014, Heger et al. 2013, Jeschke et al. 2012) was not a formalized method with a clear set of rules on how to proceed. It emerged and evolved during a literature synthesis project through dealing with the problem of how to merge results of a set of highly diverse studies without losing significant information on what precisely these studies were addressing. In that first iteration of the HoH method, the branches of the hierarchy were selected by the respective author team, based on expert knowledge and assessment of published data. Thus, pragmatic questions guided the creation of the

HoH (e.g.: which kind of branching helps group studies in a way that enhances interpretation?). Through further work on the approach, helpful discussions with colleagues, and constructive critical comments (Farji-Brener and Amador-Vargas 2018, Griesemer 2018, Scheiner and Fox 2018), suggestions for its refinement were formulated (Heger and Jeschke 2018b, c). This article amounts to a further step in the methodological development and refinement of the HoH approach.

A primer for building a hierarchy of hypotheses

With the methodological guidance provided in the following, we would like to take steps towards formalizing the application of the HoH approach. However, we advocate that its usage should not be confined by too strict rules. While we can see the advantages of strict methodological guidelines, as e.g. provided by The Collaboration for Environmental Evidence (2018) for synthesizing the evidence in systematic reviews, we believe that theory development needs room for creativity and methodological flexibility.

Figure 2 gives an overview of suggested steps for building a hierarchy of hypotheses. We distinguish two basic approaches for creating an HoH: the theory-driven approach (‘top-down’) and the evidence-driven approach (‘bottom-up’; Fig. 1). Usually in the theory-driven approach, theoretical considerations will be inspired by empirical work; and conversely in the evidence-driven approach, theoretical knowledge will be influencing the construction of the HoH. It is worth noting that distinctions between the two approaches can sometimes be ambiguous, and in practice it can be useful to use both methods in a single study (see example 1 below). There is, however, an important difference between these two approaches that we want to highlight here: In the first case, i.e. the theory-driven approach, the process of creating the hierarchy starts with the conceptual question of which different aspects an overarching hypothesis contains, and it has the aim to make the meaning and implications of this overarching hypothesis explicit. In the second case (the evidence-driven approach), the process starts with a diverse set of empirical tests and the question of how these can be grouped to enhance their joint interpretation or further analysis. Distinguishing these two approaches enhances methodological clarity in outlining basic steps of creating an HoH and in showing different options for the choice of branching criteria.

Step 1. The starting point for an HoH-based analysis in both the theory- and evidence-driven approach is the identification of a focal hypothesis (or research question; Heger and Jeschke 2018c). This starting point is followed by the compilation of information (Step 1 in Fig. 2). Which information needs to be compiled depends on whether the research interest is more in the theoretical structure and sub-division of the overarching hypothesis (see examples 2 and 3 below) or whether the aim is structuring and synthesizing empirical evidence provided by a set of studies (e.g. Jeschke and Heger 2018a and example 1 below).

Step 2. The next step is the creation of the hierarchy (Step 2 in Fig. 2). In the case of the evidence-driven approach, Step 1 will have led to the compilation of a set of studies empirically addressing the overarching hypothesis. In Step 2, these studies will need to be grouped. Depending on the aim of the study, it can be helpful to group the empirical tests of the overarching hypothesis according to study system (e.g. habitat, taxonomic group) or research approach (e.g. measured response variable). For example, in tests of the biotic resistance hypothesis in invasion ecology, which posits that an ecosystem with high biodiversity is more resistant against non-native species than an ecosystem with lower biodiversity, Jeschke et al. (2018a) grouped empirical tests according to how the tests measured biodiversity and resistance against non-native species. Some tests measured biodiversity as species richness, others as evenness or functional richness. The groups resulting from such considerations can be interpreted as representing operational hypotheses because they explicate diverse options for measuring the hypothesized effect (see also Griesemer 2018, Heger and Jeschke 2018c). Thus, branching based on an evidence-driven approach is done based on the methods the respective studies used to test the hypothesis. Another example can be found in Heger and Jeschke (2014) (see Fig. 3a and Example 1 below).

In the theory-driven approach, the overarching hypothesis is split into independent components based on conceptual considerations (Fig. 3b and c). This splitting of the overarching hypothesis can be done by creating branches according to which exact mechanisms could be responsible for the process or pattern postulated as a higher-level hypothesis. For example, the density-dependence hypothesis postulates that population size is regulated by processes depending on the density of the organisms in the population (e.g. Silvertown and Charlesworth 2001). Two mechanisms that narrow and specify the general proposition of density dependent regulation are resource limitation and predation; these can be used to formulate two mechanistic sub-hypotheses (Fig. 3b; see also example 2 below and Fig. 4).

Broad, overarching ideas often consist of several complementary parts that are necessary elements. If any of such necessary elements is missing, the overarching idea is not useful anymore. As an example, the hypothesis that enduring interaction with enemies drives evolutionary changes presupposes that (i) there are enemies that act as the primary selective agents and drive populations toward greater performance, but also that (ii) evolutionary change is possible, i.e. there are environmental factors enabling the expression of traits that increase performance (Fig. 3c and example 3 below, Fig. 5). Decomposition of overarching hypotheses into their mechanistic parts by means of formulating separate mechanistic hypotheses can enhance conceptual clarity.

For any type of branching, it is critical to identify components or groups (i.e. branches) that are mutually exclusive and not overlapping, so that an unambiguous assignment of single cases or observations into a 'box' (i.e. sub-hypothesis) can be possible. If this does not prove feasible, it may be necessary to use conceptual maps, networks or Venn diagrams rather than hierarchical structures (Fig. 2 Step 2; see also Table S1).

For many applications, the process can stop here. The resulting HoH can be used, for example, to show the connection of a planned study to a body of theory, to explicate and visualize the complexity of ideas implicitly included in a major hypothesis, or to develop a research program around an overarching idea.

Step 3. If the aim is to identify research gaps, or to assess the generality or range of applicability of a major hypothesis, however, a further step must be taken (Fig. 2 Step 3): The HoH needs to be directly linked to empirical data. In previous studies (e.g. Jeschke and Heger 2018a), this was done by assigning empirical studies to the sub-hypotheses they addressed and assessing the level of supporting evidence for each (sub-)hypothesis. This assignment of studies to sub-hypotheses can be done either using expert judgment, or by applying machine learning algorithms (for further details, see Heger and Jeschke 2014, Jeschke and Heger 2018a, Ryo et al. 2019). For guidance on how to interpret the level of evidence for overarching hypotheses, mechanistic hypotheses and operational hypotheses, see the Supplementary Material (Table S2).

Step 4. Once the HoH is complete, besides using it for the purpose it was created for, it could be published in order to enter the public domain and facilitate the advancement of the methodology and theory development. For the future, we envision a platform for the publication of HoHs, to make the structured representations of research topics available not only via the common path of journal publications. The webpage www.hi-knowledge.org (Jeschke et al. 2018b) is a first step in this direction and is planned to allow for the upload of results in the future.

Application of the HoH approach: three examples

We will now exemplify each of the two major approaches for creating an HoH, i.e. the theory- and the evidence-driven approach. The first example starts with a diverse set of empirical tests addressing one overarching hypothesis (evidence-driven approach), whereas the second and third examples start with conceptual considerations on how different aspects are linked to one overarching hypothesis (theory-driven approach).

Example 1: The enemy release hypothesis as a hierarchy

The first published study showing a detailed version of an HoH focused on the 'enemy release hypothesis' (Heger and Jeschke 2014). This is a prominent hypothesis in invasion biology which posits: "The absence of enemies is a cause of invasion success" (e.g. Keane and Crawley 2002). With a systematic literature review, Heger and Jeschke (2014) identified studies addressing this hypothesis. This review revealed that the hypothesis has been tested in many, different ways. After screening the empirical tests with a specific focus on which research approach had been used, the authors decided to use three branching criteria: (i) indicator for enemy release (actual damage, infestation with enemies or performance of the invader); (ii) type of comparison (alien vs. natives, aliens in native vs. invaded range or invasive vs. non-invasive aliens); and (iii) type of enemies (specialists or generalists). Based on these criteria, Heger and Jeschke created a hierarchically organized representation of the hypothesis' multiple aspects. The order in which the three criteria were applied to create the hierarchy in this case was based on practical considerations. Empirical studies providing evidence were then assigned to the respective branch of the corresponding hierarchy to reveal specific sub-hypotheses that were more, and others that were less supported (Heger and Jeschke 2014).

In later publications, Heger and Jeschke suggested some optional refinements of the original approach (Heger and Jeschke 2018b, c). One of the suggestions was to distinguish between mechanistic hypotheses (originally termed working hypotheses) and operational hypotheses as different forms of sub-hypotheses when building the hierarchy. Mechanistic hypotheses serve the purpose of refining the broad, overarching idea in a conceptual sense (Fig. 3b and c), whereas operational hypotheses refine the hypotheses by explicating the diversity of study approaches (Fig. 3a).

The enemy release hypothesis example indicates that it can be useful to apply different types of branching criteria within one study. Here, the authors started out with an evidence-based approach and looked for helpful ways of grouping diverse empirical tests. Some of the branches they decided to create were based on differences in the research methods, such as the distinction between comparisons of aliens vs. natives and comparisons of aliens in their native vs. the invaded range (Fig. 3a). Other branches explicate complementary mechanistic parts of the major hypothesis: studies asking whether aliens are confronted with less enemies were separated from tests asking whether aliens that are released show enhanced performance.

In this example, the HoH approach was used (i) to expose the variety of manifestations of the enemy release hypothesis, and (ii) to display the level of evidence for each branch of the HoH (see Heger and Jeschke 2018b and Table S2 for an interpretation of the results).

Example 2: Illustrating the potential drivers of the snowshoe hare–Canadian lynx population cycles

Understanding and predicting the spatio-temporal dynamics of populations is one of ecology's central goals (Sutherland et al. 2013), and population ecology has a long tradition of searching for mechanistic explanations of observed patterns in population dynamics. However, research efforts do not always produce clear conclusions, and often lead to competing explanatory hypotheses. A good example, which has been popularized through textbooks, is the 8-11-year synchronized population cycles of the snowshoe hare (*Lepus americanus*) and the Canadian lynx (*Lynx canadensis*) (Fig. 4a). From 18th- to 19th-century fur trapping records across the North American boreal and northern temperate forests, it has been known that predator (lynx) and prey (hare) exhibit broadly synchronous population cycles, which have been the focus of research since the late 1930s (Elton and Nicholson 1942, MacLulich 1937). A linear food chain of producer (vegetation) – primary consumer/prey (snowshoe hares) – secondary consumer/predator (Canadian lynx) proved too simplistic an explanation (Stenseth et al. 1997). Instead, multiple drivers could have been responsible, resulting in the development of multiple competing explanations.

Here, we created an HoH using the theory-driven approach (i.e. we started with theoretical ideas, not a set of empirical studies) to organize the current suggestions on what drives the snowshoe hare–lynx cycle (Fig. 4b). The aim of this exercise is to visualize conceptual connections rooted in current population ecological theory, and thus to enhance understanding of the complexity of involved processes.

A major hypothesis in population ecology is that populations are regulated by the interaction between biotic and abiotic factors. This regulation can either happen through processes coupled with the density of the focal organisms (density-dependent processes) or through density-independent processes, such as variability in environmental conditions or disturbances. This conceptual distinction can be used to branch out multiple mechanistic hypotheses that specify particular hypothetical mechanisms inducing the observed cycles. For example, potential drivers of the hare-lynx cycles include density-dependent mechanisms linked to bottom-up resource limitation and top-down predation, and density-independent mechanisms related to 10-year sun-spot cycles. Figure 4b also summarizes the kind of experiments that have been performed, and how they relate to the corresponding mechanistic hypotheses. For example, food supplementation and fertilization experiments were used to test the resource limitation hypothesis, and predator exclusion experiments to test the hypothesis that hare cycles are induced by predator abundance. Figure 4b thus highlights why it can be useful to apply very different types of experiments to test one broad overarching hypothesis.

The experiments that have been performed suggest that the predator-prey cycles result from an interaction between predation and food supplies combined with other modifying factors including social stress, disease and parasitism (Krebs et al. 2018, Krebs et al. 2001). Other experiments can be envisioned to test additional hypotheses, such as snow-removal experiments to test whether an increase in winter snow, induced by changed sun-spot activity, causes food shortages and high hare mortality (Krebs et al. 2018).

In this example, alternate hypotheses are visually contrasted, and the different experiments that have been done are linked to the nested structure of possible drivers. This allows one to intuitively grasp the conceptual contribution of evidence stemming from each experiment to the overall explanation of the pattern. In a next step, quantitative results from these experiments could be summarized and displayed as well, e.g. applying formal meta-analyses to summarize and display evidence stemming from each type of experiment. This is an example for how hierarchically structuring hypotheses can (i) help to visually organize research done in a complex system, and (ii) enhance conceptual understanding of a complex system of drivers potentially causing a pattern (for comparison see Fig. 11 in Krebs et al. 2018).

Example 3: The escalation hypothesis of evolution

The escalation hypothesis is a prominent hypothesis in evolutionary biology. It states that enemies are the predominant agents of natural selection, and that enemy-related adaptation has brought about long-term evolutionary trends in the morphology, behavior and distribution of organisms. Escalation, however, is an intrinsically costly process that can proceed only as long as resources are both available and accessible. Since the publication of Vermeij’s book *Evolution and Escalation* in 1987, which is usually considered the start of the respective modern research program, escalation has represented anything but a fixed theory in its structure or content. The growth of escalation studies has led to the development of an increasing number of specific (sub)hypotheses derived from Vermeij's original formulation and thus to an expansion of the theoretical domain of the escalation hypothesis. Escalation has been supported by some tests but questioned by others.

Similar as in example 2, an HoH can contribute to conceptual clarity by structuring the diversity of escalation ideas that have been proposed (Fig. 5). To create the HoH for the escalation hypothesis, we did not start by assembling empirical studies that have tested it, but instead went through the conceptual exercise of arranging existing ideas on what drives escalation based on expert knowledge (theory-driven approach).

In its most generalized formulation—that is “enemies direct evolution”— the escalation hypothesis can be situated at the top of a branch (Fig. 5) along with other hypotheses positing the importance of interaction-related adaptation, such as Van Valen’s (1973) Red Queen Hypothesis and hypotheses derived from Thompson’s (2005) Geographic Mosaic Theory of Coevolution. Hypotheses in escalation theory can be further partitioned along two main branches, explicating the two main preconditions of escalation to happen: There have to be selective agents driving escalation (e.g. predation), and enabling factors providing the possibility for species to respond (e.g. external circumstances—temperature, primary productivity—that affect the supply of, and access to, essential resources). For this example, we will focus on the side of the escalation HoH that is concerned with selective agents.

Vermeij’s original (1987) formulation of the hypothesis of escalation is actually composed of two separate testable propositions: (1) “biological hazards due to competitors and predators have become more severe over the course of time in physically comparable habitats” (Vermeij 1987 p. 49); and (2) “traits that enhance the competitive and anti-predatory capacities of individual organisms have increased in incidence and in degree of expression over the course of time within physically similar habitats” (Vermeij 1987 p. 49). As is the case with other composite hypotheses, these ideas must be singled out before the overarching idea can be unambiguously tested. This requirement creates another natural branching point in the escalation HoH, the “risk” and “response” sub-hypotheses (Fig. 5). Other lower-level hypotheses and aspects of the “risk” and “response” sub-hypotheses are possible. The “risk” side of the HoH can be further branched into sub-hypotheses suggesting either that the enemies evolved enhanced traits through time (e.g. allowing for greater effectiveness in prey capture), or that interaction intensity has increased through time (e.g. due to greater abundance or power of predators, Fig. 5). The “response” side of the HoH also can be further branched into several sub-hypotheses (all addressed by Vermeij 1987). In particular, species’ responses could take the form of (1) a trend toward more rapid “exploitation” of resources through time; (2) an increased emphasis on traits that enable individuals to “combat” or interfere with competitors; (3) a trend toward reduced “detectability” of prey through time; (4) a trend of increased “mobility” (that is, active escape defense) through time; or (5) an increase in the development of “armor” (or passive defense) through time.

The HoH shown in Fig. 5 can be used as a conceptual backbone for further work in this field. Also, it can be related to existing evidence. This will allow to identify data gaps, and to understand which branches of the tree receive support by empirical work, and thus should be kept as important components of escalation theory.

Strengths and limits of the HoH approach

We suggest that theory development in ecology and evolution requires two ingredients: first, a greater emphasis on connecting data and theory, and second, an explicit acknowledgement and consequent application of the top-down path for theory development. The HoH approach can accommodate both needs.

Regarding the first need of more strongly connecting data and theory, an HoH can be used to visually and conceptually connect single empirical studies, or groups of studies, to operational, mechanistic and overarching hypotheses in a hierarchical tree (see example 1 and Jeschke et al. 2018b, Jeschke and Heger 2018a). Such an HoH can make the rationale underlying a specific study explicit and can elucidate the conceptual connection of the study to a concrete theoretical background. Critically, it can be used to improve this theoretical background through a process of feedback between top-down and bottom-up approaches. For example, the HoH-based literature analyses presented in Jeschke and Heger (2018a) showed that several major hypotheses in invasion biology are not generally backed by evidence. The authors consequently suggested to reformulate them (Jeschke and Heger 2018b), and to explicitly assess their range of applicability (Heger and Jeschke 2018a). Because an HoH visually connects data and theory, the approach motivates one to use empirical data for assessing conceptual ideas and for improving theory. Steps to improve theory can include highlighting strongly supported sub-hypotheses, pointing out hypotheses with low unification power and breadth of applicability, shedding light on previously unnoticed connections, and revealing gaps in research.

The examples on the hare-lynx cycles and the escalation hypothesis showed that the HoH approach can also guide theory-driven reasoning in both the ecological and evolutionary domains, respectively. That is, the HoH approach can allow the reconsideration and reorganization of conceptual ideas without directly referring to data. Major hypotheses or research questions are usually composed of several elements, and above we suggest how these elements can be exposed and visualized (Fig. 3b and c). In this way, applying the HoH approach can help to enhance conceptual clarity by displaying different meanings and components of broad concepts. Conceptual clarity is not only useful to avoid miscommunication or misinterpretation of empirical results, but it will also facilitate theory development by enhancing accurate thinking and argumentation. In addition, the nested, hierarchical structure also invites one to look for connections ‘upwards’: Fig. 5 shows the escalation hypothesis as one variant of an even broader hypothesis, positing that “Species interactions direct evolution”. This in turn can enhance the search for patterns and mechanisms across unconnected study fields. We hope that by explicitly suggesting theory-driven reasoning as a methodological step, we can stimulate its increased application alongside the well-established path of evidence-driven synthesis.

In addition to these two strengths of the HoH approach – i.e. enhancing the connection between empirical results and theory and facilitating theory-driven reasoning – applying the HoH approach can help reveal knowledge gaps and biases (Braga et al. 2018). It can furthermore be used to reveal which research approaches have been used to assess an overarching idea (for examples see Jeschke and Heger 2018a; other methods can be used to reach these aims, too, e.g. systematic maps, Pullin et al. 2016, The Collaboration for Environmental Evidence 2018).

Importantly, the HoH approach can be easily combined with existing synthesis tools. For example, as outlined above and in Fig. 2, a systematic literature review can be used to identify and structure primary studies to be used for building an HoH. Statistical approaches, such as machine learning, can be used to optimize branching with respect to levels of evidence (Ryo et al. 2019), and empirical data structured in an HoH can be analyzed with formal meta-analysis, e.g. separately for each sub-hypothesis (Jeschke and Pyšek 2018). An HoH could also be one way to visualize the results of a research-weaving process, in which systematic mapping is combined with bibliometric approaches (Nakagawa et al. 2019). Further, HoHs can be linked to a larger network. An example is the website hi-knowledge.org (Jeschke et al. 2018b) where the conceptual connections of 12 major hypotheses of invasion ecology are displayed as a hierarchical network. We believe that the combination of HoH with other knowledge synthesis tools, such as Venn diagrams, ontologies, controlled vocabularies, and systematic maps, can be useful as well and should be explored in the future.

Despite the multiple possible areas of application for the HoH approach, this method is no panacea for the simplification of complexity. Not all topics interesting for scientific inquiry can be organized hierarchically, and in certain cases imposing a hierarchy may lead to wrong conclusions, thus actually hindering theory development. For example, to focus a conceptual synthesis on one major overarching hypothesis may conceal that other factors not addressed by this single hypothesis have a major effect on underlying processes as well. Evidence assessed with respect to this one hypothesis can in such cases only provide partial explanations, whereas for a more complete understanding of the underlying processes, interactions with other factors need to be considered. Further, displaying interacting aspects of a system as discrete entities within a hierarchy can obfuscate the true dynamics of a system.

In our three examples - the enemy release hypothesis, the hare-lynx cycles and the escalation hypothesis (Figs 4, 5) - connections between the different levels of the hierarchies do not necessarily depict causal relationships. However, it has been argued that approaches directly focusing on explicating causal relationships could be more helpful for advancing theory (Scheiner and Fox 2018).The HoH approach is currently primarily a tool to provide conceptual structure. We suggest that revealing causalities represents an additional objective and regard it as an important aim also for further developing the HoH approach. Combining existing approaches for revealing causal relationships (e.g. Eco Evidence, Norris et al. 2012, or CADDIS, www.epa.gov/caddis) with the HoH approach seems to be a promising path forward.

The guidelines on how to build an HoH presented above and in Figure 4 will help to increase the reproducibility of the process. Full reproducibility is unlikely to be reached for most applications because researchers need to make individual choices. For example, Step 1 involves creative reasoning and may thus potentially lead to differing results if repeated by different researchers. Certain steps of the process can be automated using artificial intelligence, such as with the use of decision tree algorithms to enhance reproducibility (Ryo et al. 2019). We believe, however, that the benefits of applying methods that involve creative steps for theory development by far outweigh the potential lack of reproducibility. Moreover, other approaches for knowledge synthesis are not fully reproducible either, interestingly not even formal meta-analysis (de Vrieze 2018).

Conclusions

With this detailed methodological outline of the HoH approach, we hope to stimulate a stronger focus on theory development in ecology and evolution. The current emphasis on statistical approaches for synthesizing evidence, with the purpose of facilitating decision making in environmental management and nature conservation, is without a doubt important and necessary. We suggest, however, that results from empirical studies should in addition, and on a regular basis, be used to improve theoretical knowledge and understanding. By enhancing and visually stimulating conceptual thinking, the HoH approach can be used as a tool to reach this aim.

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Glossary

Evidence: Available body of data and information indicating whether a belief or proposition is true or valid (Howick 2011, Mupepele et al. 2016). These data and information can e.g. stem from an empirical observation, model output or simulation.

Evidence-driven approach: Process of extrapolating from evidence about specific cases to more general rules (bottom-up approach; Fig. 1).

Hypothesis: Assumption or proposed explanation that is in principle testable.

Overarching hypothesis: General idea or concept, major principle (i.e. theoretical model).

Mechanistic hypothesis: Narrowed version of an overarching hypothesis, resulting from specialization or decomposition of the general idea with respect to the underlying mechanisms.

Operational hypothesis: Narrowed version of an overarching hypothesis, accounting for a specific study design. Operational hypotheses explicate by which method (e.g. which study system or research approach) the general idea is being tested.

Synthesis: Process of identifying, compiling and combining relevant knowledge from multiple sources

Theory: A high-level, i.e. general, system of conceptual constructs or devices to explain and understand ecological, evolutionary or other phenomena and systems (adapted from Pickett et al. 2007). Theory can consist of a worked-out, integrated body of mechanistic rules or even natural laws, but it may also consist of a loose collection of conceptual frameworks, ideas and hypotheses.

Theory-driven approach: Creation or refinement of ideas, concepts or hypotheses based on theoretical knowledge; the resulting theory can in a following step be confronted with evidence (top-down approach; Fig. 1).

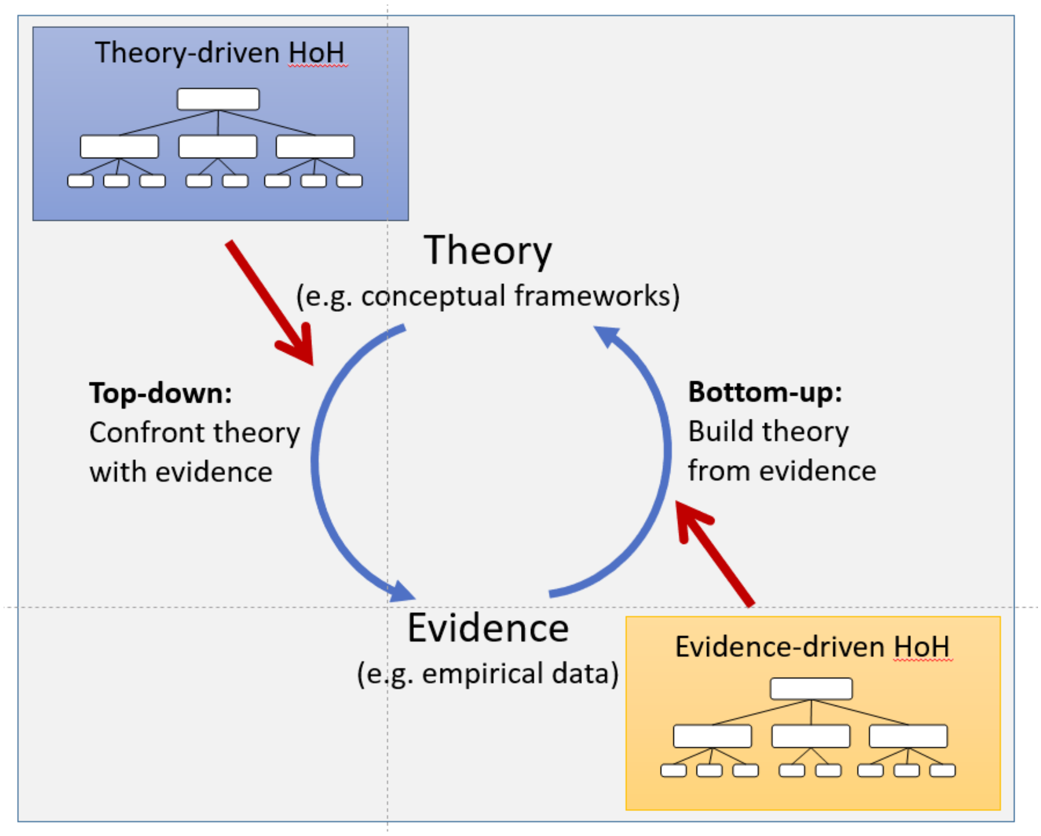

Fig. 1: Both traditional approaches for theory development, top-down and bottom-up, can be assisted by the hierarchy-of-hypotheses (HoH) approach.

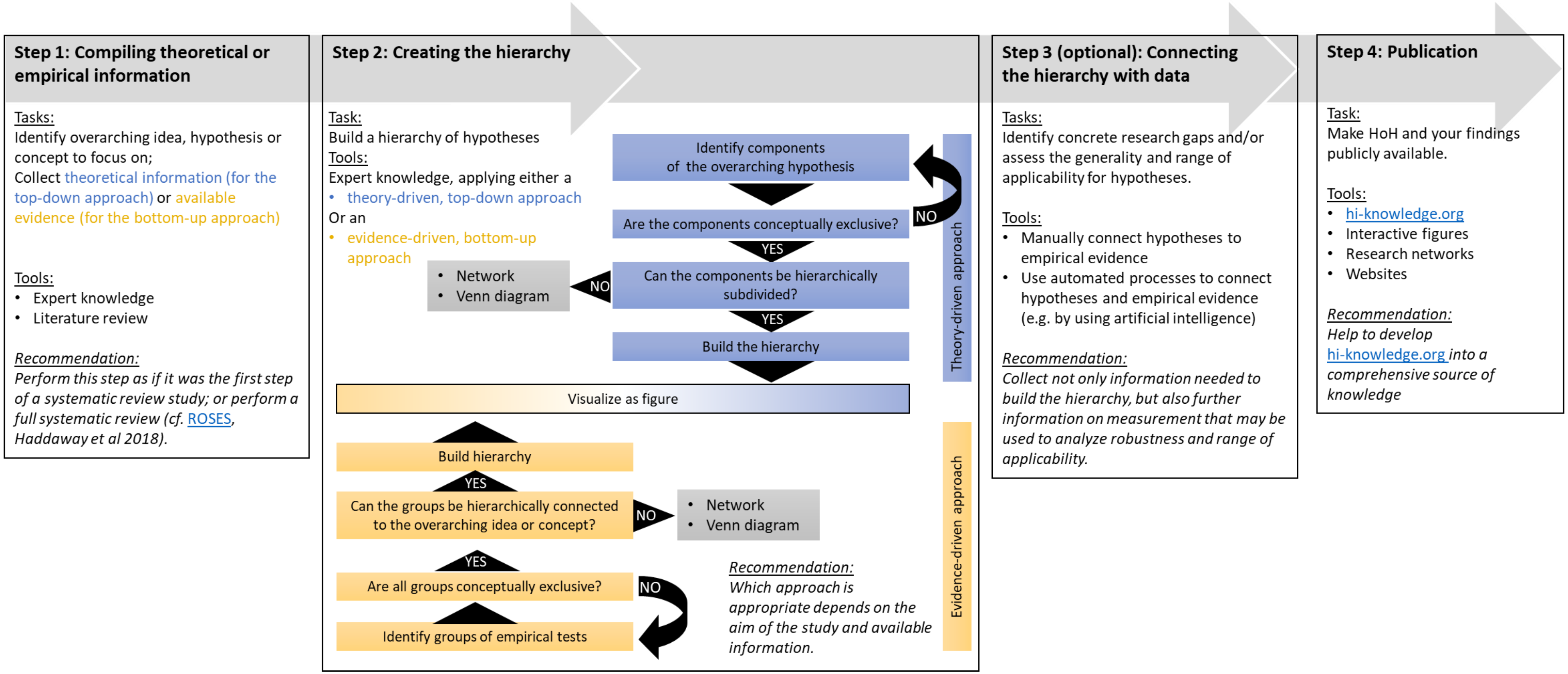

Fig. 2: Workflow for the creation of a hierarchy of hypotheses. For detailed explanation, see main text.

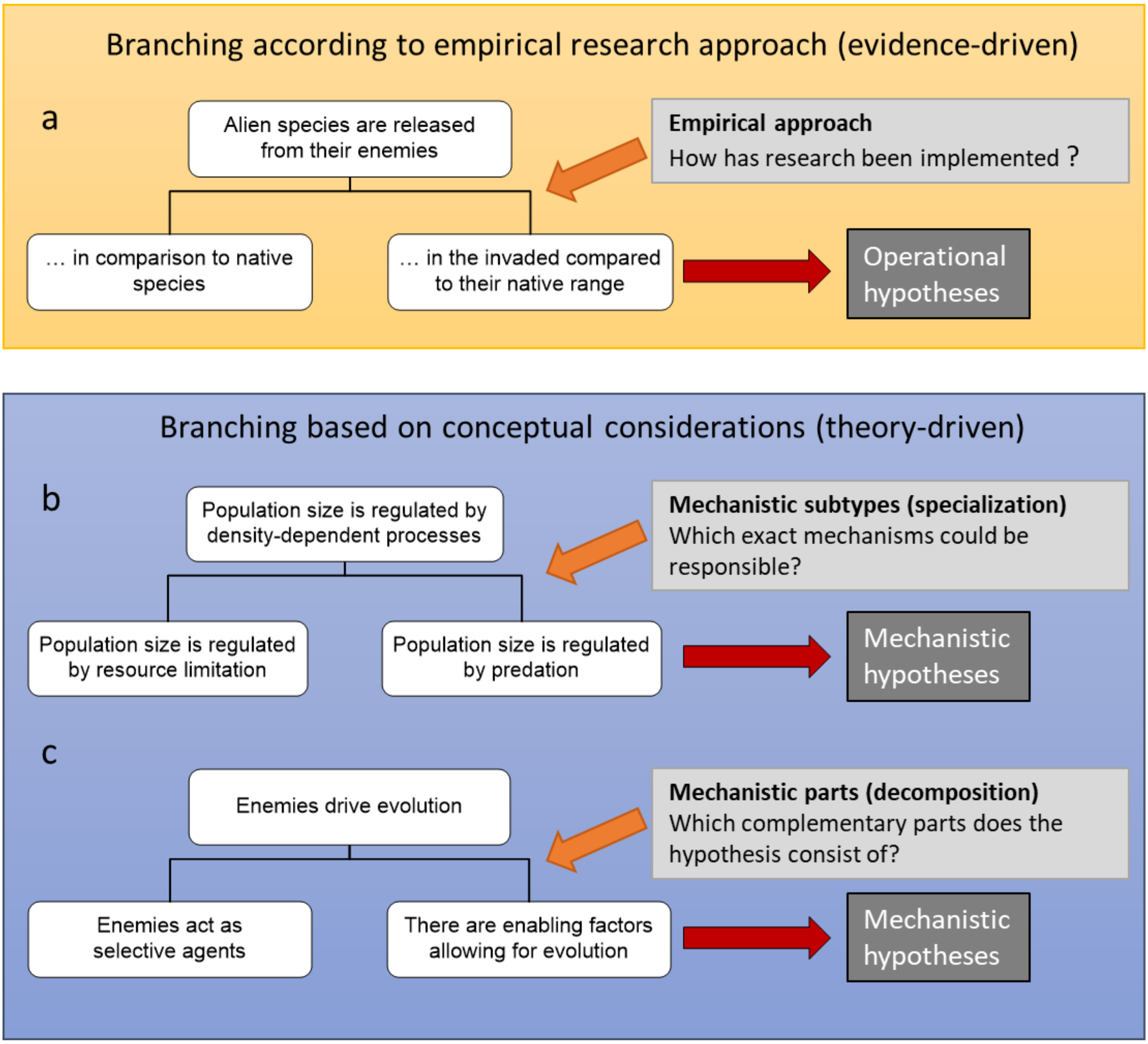

Fig. 3: Three different types of branching in an HoH. The branching example shown in (a) is inspired by example 1 in the main text, (b) by example 2 (see also Fig. 4b), and (c) by example 3 (see also Fig. 5).

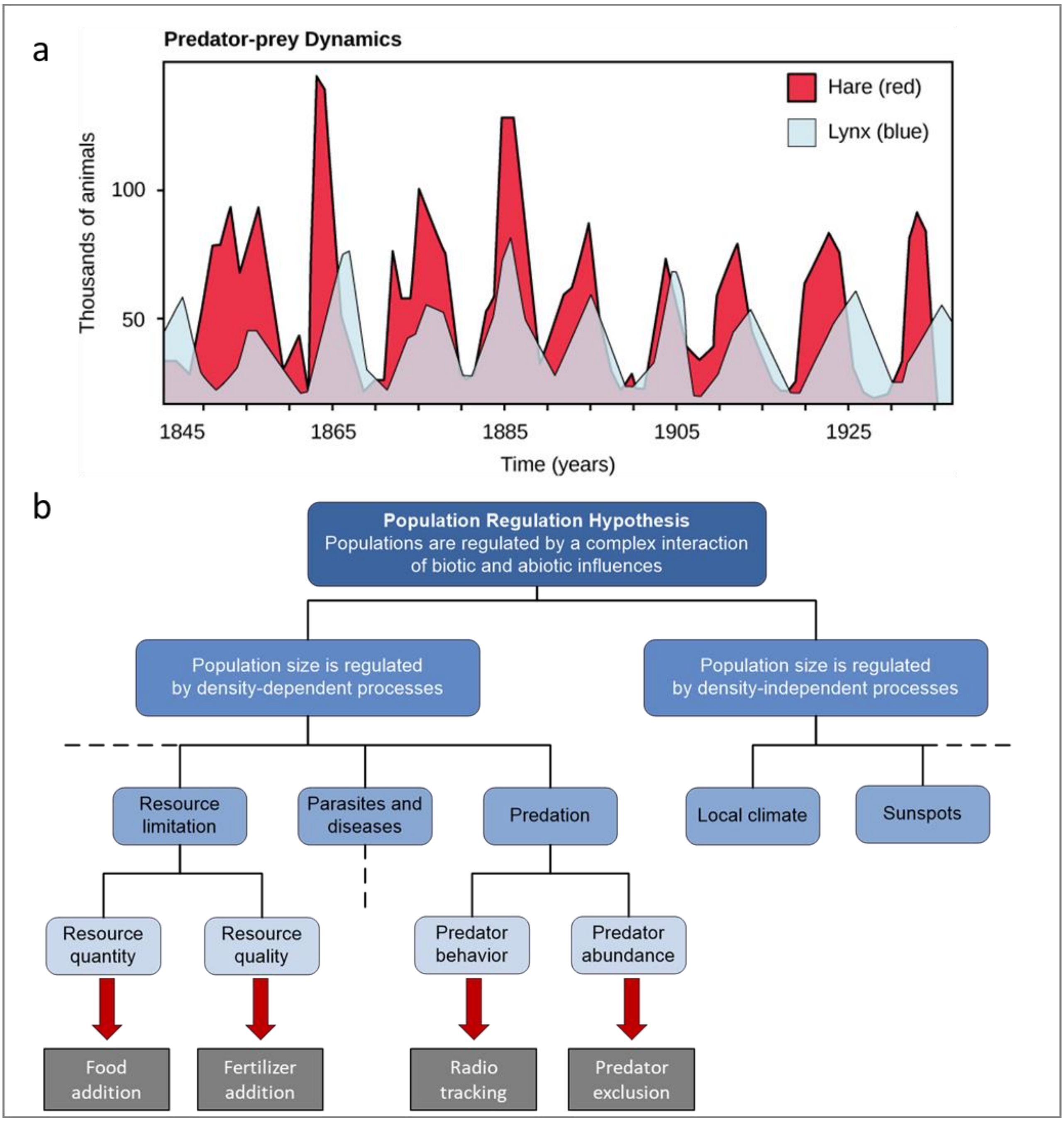

Fig. 4: (a) The population cycle of snowshoe hare and Canadian lynx (figure taken from: OpenStax Biology, Chapter 45.6 Community Ecology, Rice University Publishers, Creative Commons Attribution License (by 4.0)), and (b) a hierarchy of hypotheses illustrating its potential drivers. Hypotheses (blue boxes) branch from the overarching hypothesis into more and more precise mechanistic hypotheses and are confronted with empirical tests (arrows leading to grey boxes) at lower levels of the hierarchy. Broken lines indicate where the hierarchy may be extended. Based upon the summary of snowshoe hare–Canadian lynx research (Krebs et al. 2018, Krebs et al. 2001 and references therein).

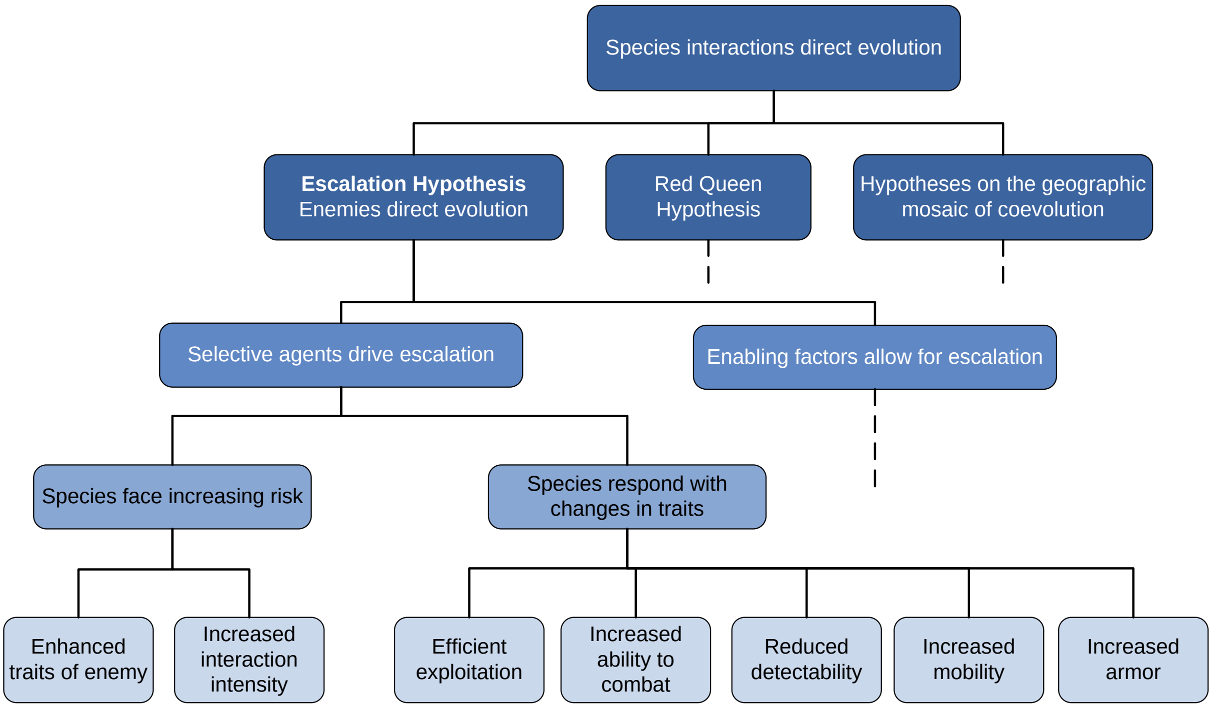

Fig. 5: An HoH for the escalation hypothesis in evolutionary biology. Broken lines indicate where the hierarchy may be extended