In Defense of Living Fossils

[Forthcoming in *Biology and Philosophy*, accepted 27 January, 2019.]

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10,951 words (including abstract and references)

**Abstract**

Lately there has been a wave of criticism of the concept of living fossils. First, recent research has challenged the status of paradigmatic living fossil taxa, such as coelacanths, cycads, and tuataras. Critics have also complained that the living fossil concept is vague and/or ambiguous, and that it is responsible for misconceptions about evolution. This paper defends a particular phylogenetic conception of living fossils, or taxa that (a) exhibit deep prehistoric morphological stability (b) contain few extant species; and (c) make a high contribution to phylogenetic diversity. The paper shows how this conception of living fossils can make sense of recent research on contested cases. The phylogenetic living fossil concept has both theoretical and practical importance: theoretical, because it picks out an important explanatory target for evolutionary theory; and practical, because it picks out taxa that we might wish to prioritize for conservation. The best way to defend the *concept* of living fossils is to get clearer about the reasons for defending living fossil *taxa*.

**Keywords:** coelacanth, cycad, horseshoe crab, living fossil, phylogenetic diversity, stasis, tuatara

1. **Introduction**

It may be easier to list examples of living fossil taxa than to say what it is, if anything, that makes those examples comprise a unified group. Familiar examples include coelacanths, cycads, tuataras, horseshoe crabs, chambered nautiluses, and the Wollemi pine (a.k.a., the “dinosaur tree”). Recently, however, the living fossil concept has fallen on hard times. Biologists have challenged the status of some paradigmatic cases of living fossil taxa, such as cycads (Nagalingum et al. 2011), coelacanths (Casane and Laurenti 2013), tadpole shrimp (Mathers et al. 2013), and tuataras (Hay et al. 2008). If not even coelacanths or cycads count as living fossils, then perhaps there is something wrong with the concept. In a recent popular essay, Mark Carnall, of the Oxford University Museum of Natural History, writes that the concept of a living fossil is “meaningless, incorrect, and gets in the way of understanding” (Carnall 2016). Other science writers have complained that the notion of a living fossil is a “useless concept” (Brouwers 2012); that “there is no such thing as a living fossil” (Nuwer 2013); and that the term is “inaccurate and misleading” (Yong 2013).[[1]](#footnote-1) In this paper, I argue that these calls to jettison the idea of a living fossil are too hasty.

Lidgard and Love (2018) also offer a defense of the living fossil concept, but the approach taken here contrasts with theirs. They point out that there are a variety of different features that have been associated with living fossils in the recent literature (2018, p. 761). These include:

1. Prolonged geological duration or persistence of lineage;
2. Morphological similarity to fossils from the distant past;
3. Slow rate of evolutionary change, or in the limiting case, stasis;
4. Low taxonomic richness today compared to the past;
5. Small geographic range today compared to the past;
6. Genealogical divergence in the very distant past;
7. Presence of characters that seem plesiomorphic (or ancestral);
8. Known from fossils before the extant population was discovered.

Different researchers emphasize different features, and different taxa exhibit these features in varying degrees. This has led to some confusion about what does or does not count as a living fossil. Take, for example, cycads. They seem to exhibit remarkable morphological stability (feature 2). Wang et al. (2009) describe a cycad megafossil from the Triassic period, over 200 million years old, that looks just like a sago palm—a type of modern-day cycad that many people keep as houseplants. But Nagalingum et al. (2011) argue on the basis of molecular clock evidence that most living cycad species share a fairly recent common ancestor, and that the group underwent a radiation around 12 million years ago. The 300-odd cycad species that exist today are, in some sense, in the middle of an evolutionary comeback. Cycads therefore seem to lack some of the other features associated with a living fossils, such as feature (6). What then should we say about them? Are they living fossils, or not? There is currently a lot of uncertainty about what does or does not count as a living fossil, and this is attributable to uncertainty about which of the above criteria are the ones that really matter. Small wonder, then, that some might conclude that the concept itself is so unclear and ambiguous that we are better off doing without it.

 Lidgard and Love argue that “instead of viewing the living fossil concept in terms of categorization—what criteria should define living fossils—it is better to understand its role as setting a unified agenda for research” (Lidgard and Love, 2018, p. 768). Lidgard and Love are making a pragmatic move here: many of the features traditionally associated with living fossil-ness, features that occur in different combinations in different taxa, point to different sorts of research questions about evolution and development. And it’s those investigative questions that really matter, as opposed to the definitional issue of whether this or that taxon really is a living fossil. Lidgard and Love argue that the living fossil concept—messy and confusing as it may be—has some value insofar as it helps to highlight phenomena that stand in need of explanation.

 A more direct way to answer the living fossil skeptics would be to show that a cluster of the traditional criteria listed above really do sometimes co-occur in ways that are theoretically and practically interesting. This is the approach that I will take in this paper. In what follows, I tackle the definitional issue head-on and defend a *phylogenetic living fossil* concept. I’ll argue that this phylogenetic living fossil concept has both practical and theoretical advantages. The core idea is that phylogenetic living fossils are taxa having the following three features. These features do not always co-occur, but sometimes they do:

1. Prehistorically deep morphological stability;
2. Few extant species;
3. High contribution to phylogenetic diversity.

These correspond with features (1 and 2), (4), and (6) from Lidgard and Love’s original list. In the remainder of the paper, I’ll make the case for retaining this phylogenetic living fossil concept, while motivating the decision to zero in on these three features in particular. I’ll begin developing the argument with a historical overview, which I think is important for understanding the current state of play (section 2). Then I will offer some justification for the decision to highlight these three features (section 3). Finally, in section 4, I reply to a series of common worries about the living fossil concept—that it is too unclear, that it conflicts with tree-thinking, and that it reflects misunderstandings about evolution.

 One limitation of Lidgard and Love’s discussion is that it makes no contact with conservation biology. In what follows, I argue that the main philosophical motivations for picking out criteria (a), (b), and (c) are normative. That is, there are reasons why existing taxa that have these features should be prioritized for conservation efforts. One might think that the loss of a coelacanth or horseshoe crab species would be especially tragic, that it would be worse than other extinctions. My claim is that the phylogenetic living fossil concept helps explain why. If I am right, then the best way to clarify and defend the living fossil *concept* is to get clear about why living fossil *taxa* should be defended. This line of argument has broader implications, for it suggests that normative (broadly environmental, ethical, or aesthetic) considerations have a legitimate role to play in the formation and clarification of biological concepts. Although I am sympathetic to Lidgard and Love’s pragmatic turn, I argue that the living fossil concept should do more than just guide empirical research; it also has a role to play in setting conservation priorities.

**2. Historical Background**

 It is often said that Darwin coined the term ‘living fossil,” but that is not entirely accurate. It’s true that Darwin was the first to use the term in the context of evolutionary theory, but the concept also has a fascinating prehistory.

 In Europe in the 1700s and early 1800s, miners circulated many stories about living animals—usually toads or frogs—that emerged from cavities in solid rock. This was known as the “toad-in-the-hole” phenomenon, but some writers referred to the animals as “living fossils.” This non-metaphorical usage invokes the traditional meaning of the term “fossil,” as any interesting item dug up from the ground (Rudwick 1972). Many people thought that the toads were antediluvian creatures that had gotten trapped in rock during Noah’s flood. These stories caught the attention of naturalists, and in 1826, William Buckland conducted a series of experiments with the aim of testing their plausibility (Gordon 2010, p. 89). He had cavities carved in two blocks of stone—one sandstone and one limestone. Then he stuck living toads in the cavities, sealed them up, and buried the blocks of stone. A year later, he dug them up to see if the toads had survived. Nearly all had died, except for a couple in the limestone block whose niches had not been perfectly sealed. So Buckland tried again. He fixed the seals, and after another year, he found that all the toads had died.

 Darwin quite likely knew about these implausible stories of (literal) living fossils. In 1856 there was even a report—widely recognized by people at the time as a hoax—of a living pterodactyl that emerged from a rock when French railway workers blasted it open (Creisler 2015). The story received extensive coverage in French and British newspapers, where the pterodactyl was sometimes described as a “living fossil.” So rather than coining a new term, Darwin was probably co-opting a term that had a different meaning.

 In the chapter of the *Origin of Species* devoted to natural selection, Darwin reasons that in environments with reduced competition, one might also see lower rates of evolutionary change. He then gives his two famous examples:

. . . and in fresh water we find some of the most anomalous forms now known in the world, such as the Ornithorhynchus [the platypus] and Lepidosiren [the South American lungfish], which, like fossils, connect to a certain extent orders now widely separated in the natural scale. These anomalous forms may almost be called living fossils; they have endured to the present day, from having inhabited a confined area, and from having thus been exposed to less severe competition (1859, p.107).

Darwin here throws in a couple of different ideas. On the one hand, he thinks living fossils have low rates of evolutionary change. But Darwin also adds something else. What makes the platypus anomalous is that it seems intermediate between mammals and reptiles, with some mammal-like features (fur) and some reptile-like features (laying eggs). The platypus almost looks a bit like one of the elusive “intermediate forms” that Darwin might have liked to find more of in the fossil record.

 The aspect of Darwin’s discussion that may be most important, from the perspective of evolutionary theory, is the idea that living fossils exhibit a low rate of morphological change, and in the limiting case, morphological stasis. He revisits the issue of evolutionary rates elsewhere in the *Origin*, though without using the term “living fossil” (1859, pp. 313-14). He clearly sees that his theory needs to account for variability in evolutionary rates, an issue that Hugh Falconer would raise again a few years later when corresponding with Darwin about morphological stasis in fossil elephants (Turner 2017).

 Darwin’s co-opting of the term “living fossil” has to be understood in the context of his adducing evidence for evolution. He knew that his theory implied that there must have been intermediate forms in the past. But as of 1859, no clear instances of transitional forms had shown up in the fossil record. *Archaeopteryx* was still waiting in the wings. So it makes sense that Darwin would take a special interest in living animals that look a bit like the sort of intermediate forms that must (according to his theory) have existed in the deep past. In that context, something like the platypus, with its mix of reptile-like and mammal-like traits, becomes especially interesting. One thing that today’s critics of the living fossil concept get right is that the theoretical context has shifted considerably since Darwin’s time. Rather than making the case for evolution, researchers today have other theoretical and practical interests. As Lidgard and Love (2018) argue, we might want to pick out certain evolutionary phenomena that pose distinctive explanatory challenges, such as the challenge of explaining stasis, or of explaining why some groups have low speciation rates. From a more practical point of view, there is a need to prioritize taxa and habitats for conservation (Sarkar 2010). Scientific concepts such as “living fossil” have histories; they get put to work in different ways, and for different purposes, at different times. Much as Darwin borrowed a concept that was already out there in use, and put it to work in ways that reflected his own theoretical interests, I argue that we should likewise re-appropriate the living fossil concept, putting it to work in a way that reflects going concerns about biodiversity loss. Because our interests and goals have changed, it is reasonable that we should conceive of living fossils in a way that differs somewhat from Darwin’s earlier usage.

**3. Phylogenetic Living Fossils**

 According to the phylogenetic conception, a living fossil taxon is a taxon above the species level that has:

 (a) Prehistorically deep morphological stability;

 (b) Few extant species;

 (c) High contribution to phylogenetic diversity.

There is a continuity here with Darwin’s understanding of living fossils, for as we saw in section 2, he also thought of living fossils as having a low rate of morphological change. His examples are also examples of taxa—lungfish and platypuses—with few extant species. However, the phylogenetic conception of living fossils replaces Darwin’s interest in intermediate or transitional forms with current ethical and aesthetic interests in biodiversity.

**[Figure 1 here]**

 Horseshoe crabs afford an especially clear example of a phylogenetic living fossil taxon. Horseshoe crabs comprise not only their own family (*Limulidae*) but their own order (*Xiphosura*). First, they exhibit prehistorically deep morphological stability. The horseshoe crabs that you can find today in places along the east coast of the US look a lot like fossils dating as far back as the Ordovician period, some 450 million years ago (Rudkin, Young, and Nowlan 2008). For perspective, horseshoe crabs survived all five of the major mass extinction events that paleontologists have documented, including the devastating Permian-Triassic extinction pulse 250 million years ago, the event that undid their close relatives the trilobites. Second, there are only four species of horseshoe crabs around today: one in eastern North and Central America, and three other species in east Asia. Third, horseshoe crabs make a high contribution to phylogenetic diversity. This third, historical feature needs a bit more spelling out.

 Philosophers have noted that phylogenetic diversity might be one thing we care about when we set out to protect biodiversity (MacLaurin and Sterelny 2010, section 7.3). Lean and McLaurin even make the case that some form of phylogenetic diversity will be the “best justified general measure of biodiversity” (2016, p. 19). There are a number of different approaches to characterizing phylogenetic diversity in a quantitative and precise way. (For an early attempt, see Faith 1992; Vellend et al. 2011 offer a helpful overview; and see Isaac et al. 2007 for a quantitative measure of evolutionary distinctiveness). For present purposes, a simple example will help to illustrate this notion of phylogenetic diversity. Imagine two islands, A and B, that have the same five bird species but no other vertebrates. Suppose we introduce a new species of bird to island A—say, a new type of gull or cormorant. Suppose that there are already some gulls and cormorants on both islands. We’ve increased the species richness just a bit, but we haven’t done much to improve how well the overall vertebrate tree of life is represented in this ecosystem. Next, suppose that we add a lizard species to island B. This would make for exactly the same species richness in both cases. Both islands now have six vertebrate species. But there is nevertheless an interesting sense in which island B has greater biological diversity. The newly introduced lizard on B is only distantly related to the other island residents, whereas the new bird species on island A is a close relative of the species already living there. Intuitively, we get more phylogenetic diversity when we introduce a species that is relatively distantly relate to the species already present.[[2]](#footnote-2)

 It’s clear that horseshoe crabs exhibit high evolutionary distinctiveness, or that they add a good deal of phylogenetic diversity. Horseshoe crabs are arthropods, like all insects, spiders, and scorpions, as well as crabs and lobsters. But they are not technically crabs at all. They are probably more closely related to spiders and scorpions than to ordinary crabs. The precise evolutionary relationships are difficult to make out, but we would probably have to go back in time around 450 million years before finding a common ancestor that horseshoe crabs share with any other extant arthropod groups. They branched off from other arthropods way back in the deep past, and they’ve persisted with little modification to the basic horseshoe crab *Bauplan*. Not only that, but the group is species-poor. These features make *Limulidae* a clear example of a phylogenetic living fossil taxon.

 With this clear illustration in mind, it’s worth pausing to consider some of the things that are *not* implied by the phylogenetic living fossil concept: (1) There is no suggestion that any of the four species of *Limulidae* have been around that long. Calling something a phylogenetic living fossil says nothing about species duration. (2) There is no suggestion that horseshoe crabs have not evolved in 450 million years. Here it’s easy for confusion to arise when we’re not careful to distinguish character stasis from species stasis (Levinton 1983). Species stasis is the stronger of these two notions, and occurs when a species persists for some time without noticeable morphological change. The phylogenetic living fossil concept does not imply species stasis, but only character stasis. All that’s needed is that certain morphological traits exhibit long-term stability. (3) Nor is there any suggestion that horseshoe crabs are primitive or less evolved (whatever that means), or holdovers from some earlier era. There is no reason why these normative notions need to come into play. (4) There is no requirement that horseshoe crabs be a relict group. I take it that the widely used notion of a relict group is distinct from that of a phylogenetic living fossil. A relict is the last remnant of a group that was much more abundant and/or species rich in the (possibly deep) past. Many living fossils are in fact relict groups, but the two concepts are distinct. For example, horseshoe crabs would be living fossils on this conception even if the taxon had always been species-poor. (5) There is no suggestion here at all concerning the discovery of taxa. Lazarus taxa are taxa thought to have gone extinct, but which later turn out to have persisted well past the supposed extinction date. For example, ceolacanths—perhaps the paradigmatic case of a living fossil (about which more below)—were thought to be extinct, until a live one was caught in 1938 (Weinberg 2001). Other cases of Lazarus taxa involve the discovery of fossils that are much younger than a supposed extinction date. The concept of a Lazarus taxon is clearly distinct from the notion of a phylogenetic living fossil, a notion that has nothing to do with the contingencies of human discovery. Horseshoe crabs, for example are not a Lazarus taxon.

 One interesting feature of phylogenetic living fossils, as defined here, is that they come in degrees. So “living fossil,” on this view, will be a category with vague boundaries. One reason for this is that morphological stability is a matter of degree. Degree of stability depends in part on the grain at which traits are described. For example, if one describes the traits at a coarse enough grain—focusing, perhaps, on the tetrapod body plan—then the lineage leading to humans exhibits just as much morphological stability as horseshoe crabs. Stability is also affected by the number of characters surveyed, and the degree of change in each morphological character. Then there is also variation with respect to the duration of the morphological stability. Contribution to phylogenetic diversity is a matter of degree, too. This is context-dependent, as it depends partly on how much phylogenetic diversity is already represented in the biological community. Finally, the number of extant species in the taxon is also a matter of degree. There are two extant species of coelacanths, and four species of horseshoe crabs. There are several hundred species of cycads. Horseshoe crabs are an illustrative case of a taxon that lies at one extreme with respect to each of these three measures: there are few extant species, lots of evolutionary distinctiveness, and morphological stability in many characters stretching back hundreds of millions of years. The fact that the phylogenetic concept exhibits some vagueness may help explain why some are so skeptical. But vagueness, in general, is not a very good reason for dismissing a scientific concept, especially when there are interesting, clear-cut cases to which the concept applies.

 In order to further clarify this conception of living fossils—especially condition (a) of morphological stability—it’s worth pausing to consider a counterfactual scenario in which we happen not to have any horseshoe crab fossils. Our main evidence for (a) deep prehistoric morphological stability involves comparing living organisms to fossils. One might worry that this would make somethings status as a phylogenetic living fossil dependent upon contingencies of fossilization and discovery.[[3]](#footnote-3) If there were no horseshoe crab fossils to which we could compare living horseshoe crabs, it might seem really odd to call them living fossils at all. My own view here—odd though it may sound—is that horseshoe crabs would still be phylogenetic living fossils even if we had never found a single horseshoe crab fossil. In that case, we just wouldn’t have any evidence that condition (a) is satisfied. In other words, the phylogenetic living fossil concept is a biological or an evolutionary concept, not an epistemic one.

 One might grant that the phylogenetic living fossil concept is reasonably clear, and yet still wonder about its usefulness. What, in particular, are the reasons for zeroing in on criteria (a), (b), and (c), and taking those to be central? Perhaps surprisingly, the most important reasons are practical and normative. However, I’ll begin with a theoretical consideration that should also carry some weight. Note that in developing this argument, I am not using traditional conceptual analysis, or testing different definitions of ‘living fossil’ against anyone’s intuitions. The claim, rather, is that there are compelling theoretical and (especially) practical, normative motivations for defining “living fossil” in a particular way.

 To start with, the phylogenetic living fossil concept picks out a potentially interesting evolutionary *pattern*: Sometimes you do see species-poor groups with high evolutionary distinctiveness and considerable morphological stability. That this is a pattern is closely related to the above observation that phylogenetic living fossil-ness comes in degrees (for more discussion of patterns and degrees of signal strength, see Turner 2011, Ch. 6). This sort of pattern, moreover, stands in need of explanation. For example, why is it that we sometimes see extreme morphological stability in species poor groups? Why do the three features of phylogenetic living fossils sometimes co-occur? Is this just coincidence, or is there something about the underlying evolutionary *processes* that generates all three phenomena? This is a causal question, and a classic instance of reasoning from pattern to process. If these sorts of questions are worth exploring at all, then it would seem that the phylogenetic living fossil concept picks out an interesting explanatory target for evolutionary theory.

 This theoretical importance of the phylogenetic living fossil concept is underscored by some recent research that explores the connection between evolutionary distinctiveness (a measure of contribution to phylogenetic diversity) and speciation and extinction rates. Bennett, Sutton, and Turvey (2017) used modeling techniques to explore the idea that low speciation and extinction rates could help explain what’s going on in groups that are species-poor and evolutionarily distinct. They constructed 10,000 hypothetical phylogenetic trees, systematically varying the biases in extinction and speciation rates. Then they compared the generated hypothetical trees to empirical trees for real taxa. They found that the trees that best matched the empirical trees were ones that incorporated the idea that greater evolutionary distinctiveness correlates with lower extinction rates and lower speciation rates. They conclude that

ED [evolutionarily distinct] species are generally the product of the same macroevolutionary phenomenon and can therefore be grouped as a “real category” of biodiversity and are able to persist without speciating or going extinct for long periods of time (Bennett, Sutton, and Turvey 2017, p. 44).

The important thing here is that speciation and extinction are macro-level evolutionary processes. It’s an interesting question why some groups would have especially low speciation and extinction rates. Bennett, Sutton, and Turvey entertain the possibility, originally due to Schopf (1984), that living fossil taxa are just a kind of statistical phenomenon: It’s not surprising that some taxa would lie in the tails of the distribution with respect to extinction and speciation rates. But seeing the connection between depressed extinction and speciation rates and evolutionary distinctness points the way to generating new explanations. For example, consider the old idea, from Eldredge and Gould’s (1972) work on punctuated equilibria, that most morphological change happens during speciation events. If that were correct, it might help explain why a group with especially low speciation rates might also exhibit morphological stability. The low extinction rates help explain why the group might persist for so long, while the low speciation rates help explain why it stays species-poor. Bennett, Sutton, and Turvey’s modeling work shows we might begin to bring some important tools of macroevolutionary theory to bear on the explanatory problem. This suggests that the phylogenetic living fossil concept is picking out an interesting cluster of features that pose an explanatory challenge for evolutionary theory. Of course, as Lidgard and Love point out, there might be other clusters of features whose co-occurrence also raises interesting evolutionary questions.

 Second, and more importantly, the phylogenetic living fossil concept also does a good job of picking out taxa that we might wish to prioritize for conservation. Here again, the horseshoe crab is a good example. Human activities do pose a significant threat to horseshoe crabs. (For a nice discussion, see Frazier 2014). One major problem in the eastern US is habitat destruction due to shoreline development. Another problem has to do with the desirability of their blue blood, which contains hemocyanin rather than hemoglobin. Because horseshoe crab blood has medical applications—it’s used to test for the presence of bacterial toxins—it also has economic value. It’s a common but surely deleterious practice to collect horseshoe crabs, harvest some of their blood, and then release them. The ethical and aesthetic issues deserve more attention than I can give them here, but it is worth considering the possibility that the loss of even one of the four species of horseshoe crabs would be especially bad, from the point of view of conservation. Indeed, I think there are interesting normative reasons for focusing on criteria (a), (b), and (c).

 To start with, consider (a) the morphological stability of the horseshoe crab body plan across deep time, indeed, across all five mass extinction events in Earth’s history. This morphological stability might give us compelling aesthetic reasons for prioritizing horseshoe crabs for conservation. Carolyn Korsmeyer (2016) offers an account of aesthetic engagement with artifacts—with “real old things”—that can help shed some light on why we might care about horseshoe crabs. According to Korsmeyer, our aesthetic engagement with artifacts is not limited to appreciating their current sensory qualities. We also have reason to care about their genuineness or authenticity—which is to say, their history—because those objects have the ability to place us into contact with the past. Family heirlooms afford a good illustration of what Korsmeyer means. Consider, for example, a quilt that was made by a family member long ago, and that has been passed down through the family. You might appreciate it for its current qualities, but your knowledge of its history mediates your aesthetic experience. An exact replica would not be the same, because it would not place you into contact with the earlier quilter, or the earlier time or place. Korsmeyer’s insightful account is transferrable. Perhaps part of the appeal of living fossils is aesthetic: living horseshoe crabs place us into contact with the deep past, in somewhat the same way that actual fossils do. When you see one, you know that creatures *rather like this* lived on similar beaches hundreds of millions of years ago. Of course, every living organism has ancestors that lived during the Ordovician. But it’s the (relative) morphological stability of the horseshoe crab body plan that creates the sense of being placed into contact with the deep past. If Korsmeyer’s account gives us reason to preserve old artifacts, it surely also gives us reason to preserve things that put us in touch with a vastly deeper past.

 Although Korsmeyer is primarily interested in the aesthetic value of “real old things,” horseshoe crabs and other taxa that exhibit morphological stability over time might also have epistemic value to scientists interested in reconstructing the deep past. For example, observations of living horseshoe crabs can surely tell us something about the prehistoric ones, even if we have tread very cautiously. For example, the fossil record does not tell us that ancient horseshoe crabs had hemocyanin in their blood. But that seems like a fairly safe inference, given our background knowledge of phylogeny plus the observation that living ones do have hemocyanin in their blood. This epistemic or evidential value might be another reason to think that their morphological stability makes horseshoe crabs worth protecting.

 Next, consider condition (c). Most conservation biologists agree that biodiversity involves more than just species richness. And phylogenetic diversity is one kind of biodiversity that we might decide is important (Lean and McLaurin 2016). Indeed, some conservationists already use evolutionary distinctiveness as a way of prioritizing species for conservation (Cavin and Kemp 2011; see Winter, Devictor, and Schweiger 2013 for a review). Note that phylogenetic diversity is really a matter of evolutionary history. If we decide to prioritize species for conservation on the grounds that they are evolutionarily distinctive, we are basically saying that our understanding of evolutionary history should inform conservation policy. I will not attempt here to make an argument for the value of phylogenetic diversity, though I suspect that such value, like the value of Korsmeyer’s “real old things” will turn out to be aesthetic. The important point, for present purposes, is just that there could be environmental/aesthetic grounds for saying that extinction of all four species of horseshoe crabs would be worse than the extinction of, say, four other arthropod species that have lots of other close evolutionary relatives, because it would mean the loss of a whole branch of the tree of life.

 Finally, what about (b), the requirement that phylogenetic living fossil taxa be relatively species-poor? The motivation for including this criterion is also normative and policy-oriented. Suppose that our conservation goal is to protect horseshoe crabs. The fact that there are only four extant species of horseshoe crabs suggests that the loss of even one of those species would place the whole group at higher risk of extinction. To bring this into focus, imagine a counterfactual scenario in which there are dozens of horseshoe crab species. In such a case, there would be less reason to prioritize the protection of each particular species, because the clade could more readily absorb an extinction or two. In short, criterion (b) has mainly to do with vulnerability. Interestingly, this might sit uneasily with the idea that phylogenetic living fossil taxa, some of which have persisted across multiple mass extinction events, are especially tough to drive to extinction. Horseshoe crabs might seem to have lower extinction risk than other species. However, it’s also likely that some of the threats posed by human activities are novel ones. At any rate, we might say that holding other things equal, a taxon with fewer species is generally more vulnerable to extinction. Criterion (b) also links up with (c) in the following way. If there were dozens of species of horseshoe crabs, and if an ecosystem contained many of those species, then a particular horseshoe crab species would not add as much phylogenetic diversity to the system.

 To sum up: the phylogenetic living fossil concept is reasonably well defined. It’s distinct from related notions like Lazarus taxa and relict groups. It’s theoretically interesting because it picks out an important explanatory target for evolutionary theory. And most importantly of all, it has policy relevance because it picks out taxa that we might want to prioritize for conservation. Taken together, these considerations strongly suggest that the concept of a phylogenetic living fossil is both scientifically legitimate and useful. In making the case for this view, I have placed environmental and aesthetic values in the driver’s seat. One advantage of the phylogenetic living fossil concept is that it picks out things that we have some reasons to care about protecting.

**4. Contested Cases**

 The wave of criticism of the living fossil concept, especially on the part of science writers and educators, has been driven by a series of recent studies challenging the status of some paradigmatic living fossil taxa. Here I look at three such studies, involving coelacanths, cycads, and tuataras. But none of the research in these cases casts any doubt on the usefulness of the phylogenetic living fossil concept. Indeed, tuataras and coelacanths, if not cycads, are still good examples of phylogenetic living fossils. But let’s start with cycads, which may not be.

 Another goal of this section is to further develop the response to Lidgard and Love (2018). They are skeptical about the possibility that any living fossil concept can do a good job sorting taxa into those that count as living fossils and those that don’t. They would be right, *if* there were no principled reasons for zeroing in on particular criteria. In section 3, however, I argued that there are indeed some normative considerations that weigh in favor of the phylogenetic living fossil concept. In this section, I will show how that concept can bring some clarity to the current discussion.

*4.1 Cycads*

 Nagalingum et al. define living fossils as “modern survivors of previously more diverse lineages” (2011, p. 796). Notice how this differs from the phylogenetic living fossil concept. Nagalingum and colleagues are thinking of living fossils as more like relict groups—the last living representatives of groups that were much more diverse and abundant in the deep past. For a long time, people took cycads to be living fossils in this sense. The cycads that remain today seemed like the last vestiges of a group whose heyday was back in the Mesozoic, when they were wildly diverse and abundant. Nagalingum et al. challenge this traditional view.

 There are around 300 existing cycad species. Nagalingum et al. (2011) undertook a molecular clock study to see how far back in the past the existing cycad species diverged from one another. They looked at the structure of just one gene (Phytochrome P) as it occurs in about two thirds of living cycad species. Knowing the substitution rate—or the rate at which DNA sequences in the genome get replaced by other sequences—enables scientists to reconstruct evolutionary divergence times. They can count up small differences in the structure of a gene that occurs in multiple lineages and estimate how long it must have taken for those differences to arise. Using this approach, the scientists found something quite surprising: virtually all of the cycad species they looked at showed recent evolutionary divergence times, not much more than 12 million years ago. The molecular evidence suggests that long after the end-Cretaceous mass extinction likely decimated the cycads, the group experienced a completely new evolutionary radiation. This means the existing cycad species are probably not terribly old: they arose maybe 10 or 12 million years ago during a relatively brief spurt of speciation. Cycads, according to Nagalingum et al., are not really living fossils.

 The Nagalingum group’s work does show that cycads are not a very good example of a relict group. Could they be phylogenetic living fossils? Here the answer is mixed. They do exhibit remarkable, prehistorically deep morphological stability. For example, Wang et al. (2009) describe a cycad megafossil from China—an unusual case where a whole plant was preserved—that looks just like a sago palm, a kind of modern cycad that many people keep as houseplants. The fossil from China is around 200 million years old. Where cycads differ from other phylogenetic living fossils is that thanks to that recent radiation, there are relatively many living species. This affects how we think about phylogenetic diversity as well. In an ecosystem with several cycad species, adding one more cycad won’t increase phylogenetic diversity much, because the newly added species will (again, thanks to that recent radiation) probably be a close relative of the ones already there. Thus, even though Nagalingum et al. work with a different definition of ‘living fossil,’ the recent radiation of the cycads does suggest that they may not be such a good example of a phylogenetic living fossil taxon. Note that the Nagalingum group’s work also shows that the cycads do not have an especially low speciation rate.

 Interestingly, the cycads could *become* phylogenetic living fossils. This could happen if the group were to suffer a lot of extinctions. Imagine that all but a handful of the cycad species go extinct. That would leave the group species poor and evolutionarily distinct.

*4.2 Tuataras*

 Tuataras are small reptiles, native to New Zealand. To the casual observer, they look a lot like lizards, and their closest living relatives are the squamates (lizards and snakes), but tuataras are not really lizards. They are the last remaining members of a group called the sphenodontids, which were relatively diverse and abundant during the late Triassic and Jurassic. The sphenodontids flourished around 200 – 150 million years ago, but had disappeared from the fossil record by the end of the Cretaceous. All that’s left of them is a single species in New Zealand, *Sphenodon punctatus*. Their skeletal morphology is barely distinguishable from that of their Mesozoic predecessors. In recent times, they narrowly avoided extinction by rats and other invasive predators by hanging out in refugia on small, difficult-to-access islands.

 Tuataras have some other interesting features that point toward a slow rate of molecular evolution. For example, it’s known that the rate of molecular change depends upon generation time. In species with longer generation times (say, elephants) the rate of molecular change is generally lower. In species with shorter generation times, the rate of molecular change is higher. Now, tuataras have a remarkably long generation time as compared with lizards of the same size. It takes them 10 or 15 years to reach sexual maturity, and after that, they only reproduce every 2 to 5 years. Not only that, but they have slow metabolisms and slow growth rates, traits which correlate in other species with slower molecular substitution rates. All of this suggests that in tuataras, the molecular clock should tick relatively slowly.

 A few years ago, however, a research group based in Auckland came up with a bizarre result when they actually tried to measure the tick rate of the tuatara’s molecular clock (Hay et al. 2008). They took the most direct possible approach: rather than trying to compare regions in the tuatara genome with those of close phylogenetic relatives—a difficult task, since there are none—they used ancient DNA. They sequenced part of the mitochondrial genome from tuatara bones ranging in age from 650 to 8,750 years old, and compared those sequences with the same region in living tuataras. What they found was that tuataras, contrary to all expectations, have a much *higher* rate of molecular evolution than most other animals do. This has been touted by some (e.g. Carnall 2016) as evidence that tuataras are not “living fossils.” The reasoning seems to be that living fossils must have especially slow rates of evolutionary change, whereas the molecular evidence points toward especially rapid evolution in tuataras.

 The evidence of rapid molecular evolution in no way disqualifies tuataras from counting as phylogenetic living fossils. In fact, tuataras, like horseshoe crabs, could serve as a paradigm case: the group is species poor, and exhibits prehistorically deep morphological stability. The group is also evolutionarily distinct: we would have to go back a couple of hundred million years to find the common ancestor that tuataras share with, say, squamates. The evidence for a high rate of molecular evolutionary change just raises additional puzzling questions about the relationship between molecular evolution and morphological stasis and change. It’s not clear exactly what is going on in this case, but we should keep in mind that the Hay et al. (2008) study only looked at mitochondrial DNA sequences; the study was not even looking at nuclear DNA that might make a difference to morphology. And even if it had, developmental processes might insulate morphology from rapid molecular change. Rapid molecular change in the nuclear genome could also reflect selection pressures on aspects of the organism, like the immune system, that never show up in the fossil record.

 Another source of doubt about the tuatara’s status as a living fossil comes from recent research suggesting that tuataras have adapted in significant ways to their local environments. For example, Jones (2008) identifies some morphological changes in skull morphology and dentition that seem related to changes in food preference. This raises some questions about whether the tuataras really exhibit prehistorically deep morphological stability. Indeed, some theorists may be tempted to treat evidence of any morphological evolution at all as indicating that the taxon is not really a living fossil. We should bear in mind here, however, that morphological stability is not an all-or-nothing issue: it depends in complex ways on which traits we focus on, on the grain at which those traits are described, and on temporal scale. So some adaptive change in skull morphology is compatible with a fairly high degree of morphological stability. Herrera-Flores, Stubbs, and Benton (2017) investigate this issue by constructing a morphospace for lower jaw morphology in sphenodonts. They define a living fossil as having “a slow rate of morphological evolution and a morphology close to the centroid of clade morphospace” (2017, p. 319). And they argue that tuataras count as living fossils in this sense of having conservative morphology. For my purposes, Herrera-Flores, Stubbs, and Benton (2017) are focusing on just one of the three components of the phylogenetic living fossil concept—the deep prehistoric morphological stability. But this makes sense, because that’s the component that’s most contested in this case. It’s rather obvious that tuataras are evolutionarily distinct and species-poor. This recent research shows that in spite of the high rate of molecular change, tuataras are a clear instance of a phylogenetic living fossil taxon.

*4.3 Coelacanths*

 Coelacanths are represented by Devonian fossils from as far back as 390 million years, before any vertebrates lived on land. There is little fossil record of them persisting past the end of the Cretaceous period, 66 million years ago. However, scientists have described two coelacanth species, one in the Indian Ocean off the eastern coast of Africa, and the other in Indonesia (Erdmann, Caldwell, and Moosa 1998). Scientists have assigned both to the genus *Latimeria*. Coelacanths are sarcopterygian, or lobe-finned fishes, a group that’s actually more closely related to lungfish and tetrapods than to ray-finned fish, though the precise phylogenetic relationships are still under investigation (see e.g. Brinkmann 2004). In a paper that challenges conventional wisdom, Casane and Laurenti (2013) argue that coelacanths should not be considered living fossils at all.

**[Figure 2 here.]**

 Casane and Laurenti (2013) argue that the actinistian fishes (the family to which coelacanths belong, and of which *Latimeria* is the sole remainder) exhibit quite a bit of morphological variation in the fossil record. For example, scientists think that *Latimeria* forms a sister group with *Macropoma*, which shows up in the Cretaceous fossil record. However, there are a number of significant morphological differences between the two. To start with, *Latimeria* is about three times longer than *Macropoma*—a potentially interesting case of evolutionary size increase. The two genera also have different skull morphologies that are evident even to an amateur observer. For example, *Latimeria* has a shorter mouth that opens upward, while *Macropoma* has a longer mouth (relative to skull size) that opens forward. More generally speaking, members of the actinistian family that lived between the Devonian (ca. 390 million years ago) and the Cretaceous (ca. 80 mya) exhibited a lot of variation in size and shape. Casane and Laurenti also observe that the Devonian fish had asymmetrical fins, while *Latimeria*’s four lobed fins are all symmetrical—another significant morphological change.

 Coelacanths do clearly exhibit two of the three features of phylogenetic living fossils: they are a species-poor group, with just two extant species, and they are highly evolutionarily distinct. Casane and Laurenti do not challenge these points at all. But they do challenge the idea that coelacanths have not undergone much morphological evolution. For much of the coelacanths’ time on Earth, the group saw a lot of morphological evolution, and a lot of morphological variety. There are, however, three potential problems with Casane and Laurenti’s argument.

 First, their story about evidence of morphological disparity and change in the Paleozoic and Mesozoic coelacanth fossil record is actually compatible with morphological stability over the last 60-80 million years. We just don’t have any fossil record for Coelacanths during that recent interval, due in part to where they live, and partly to their low abundance.

 Second, whether you “see” morphological stability in coealacanths depends a lot on which traits you choose to measure, as well as the grain at which you individuate traits. It’s true that their body size has shown a good deal of variability. But other aspects of the lobe-finned *Bauplan*, described at a coarser grain, have remained very stable. Both of these first two issues make it somewhat difficult to get clear about how stable the coelacanth morphology has really been.

 Third, other research does point to slow rates of morphological change in coelacanths. For example, Cavin and Guinot (2014) use a comparative study to argue that coelacanths are “almost” living fossils. They compare rates of morphological change in the evolutionary histories of three extant taxa: hummingbirds, perch, and coelacanths. They start with the same phylogenetic tree that Casane and Laurenti (2011) used for actinistian fish. Then for each taxon on that tree, they identify corresponding taxa in the evolutionary histories of hummingbirds and perch that lived at the same time as the ancient coelacanths. In order to measure degree of morphological change, they counted the number of unique derived traits that occurred in each of the three evolutionary histories. By this measure, the evolutionary history leading to hummingbirds exhibits a much higher rate of morphological change: twice the rate of the ray-finned fish, and six times the rate of the lobe-finned fish. Of course, one limitation of this work is the choice of comparison groups. It’s not too surprising that small birds would exhibit a higher rate of morphological change. But still, this is some evidence that coelacanth morphology is relatively conservative.

 The overall picture is messy, but Casane and Laurenti’s claim that coelacanths are not really living fossils seems premature. With respect to deep prehistoric morphological stability, the verdict is somewhat ambiguous. But coelacanths certainly possess the other features of phylogenetic living fossils.

**5. Further worries**

 In section 4, I considered three contested cases of living fossils. One of those cases, the tuatara, is pretty obviously a phylogenetic living fossil. Another, the coelacanth, remains a pretty good candidate. Cycads, perhaps not so much. So far, then, I’ve shown (in section 3) how certain normative environmental concerns might motivate the phylogenetic living fossil concept, as well as (in section 4) how that concept might apply to contested cases. In this section, I turn to some further worries about the very idea of living fossils. These are not objections against the phylogenetic living fossil concept, *per se*, but rather more general worries that the notion of a living fossil is confusing or misleading. I’ll show how the phylogenetic living fossil concept addresses these worries.

 First, one worry is that the concept of a living fossil is hopelessly ambiguous, because different researchers use the term indifferent ways. This, as we saw in the introduction, is what motivates Lidgard and Love’s (2018) effort to rethink living fossils in a more forward-looking, pragmatic spirit. My discussion of the contested cases suggests that different scientists do use the term in different ways. For example, Nagalingum et al. (2010) come close to equating “living fossil” with relict group. On the other hand, Herrera, Stubbs, and Benton (2017), work with a strictly morphological conception of living fossil. This suggests that scientists who disagree about the contested cases may sometimes be talking past one another. One reply to this is to point out that ambiguity can sometimes be productive (see, e.g. Currie 2016). Indeed, there is even a bit of a research tradition of looking at putative cases of living fossils to assess their living fossil-ness. And this tradition has led to some surprising empirical results, like the discovery of the recent cycad radiation, as well as the tuatara’s rapidly changing mitochondrial genome. Lidgard and Love (2018) could well point to the fruitfulness of this research tradition as support for their view that the living fossil concept has a role to play in guiding investigation. I’ve shown here, however, how to resolve much of the ambiguity in a relatively straightforward way. The phylogenetic living fossil concept captures much of what scientists care about—both from theoretical and more policy-oriented perspectives—while clearly distinguishing living fossils from Lazarus taxa and relict groups. The phylogenetic living fossil concept can actually help to provide a scaffolding for understanding the recent research on contested cases.

 Second, another lingering worry is that the term “living fossil” has contributed to misunderstandings about evolution. It might seem to suggest that some lineages do not evolve. Perhaps some scientists worry here about the possibility that creationists might misappropriate the notion of a living fossil (Carnall 2016 is explicit about this). However, the phylogenetic living fossil concept clearly does not have the connotation that living fossils are taxa that have not evolved. Morphological stability in certain characters is entirely compatible with evolutionary change happening under the geological radar. And morphological stability is itself just a pattern that is sustained by underlying evolutionary processes. More generally, it’s hard to see why the fact that nonscientists might misunderstand or misappropriate a concept would ever be a good reason for jettisoning the concept. For comparison, the fact that creationists sometimes misappropriated punctuated equilibria is not evidence against that idea.

 Third, Casane and Laurenti (2013) argue that the very idea of a living fossil is incompatible with tree thinking in biology. They are worried in particular about the connotation that a certain taxon, such as *Latimeria*, is primitive or early branching. It’s easy to draw a tree that makes *Latimeria* look like the result of an early evolutionary branching event that occurred way back in the Paleozoic. However, one can just as easily draw a tree that makes our own genus, *Homo*, look like the result of an early branching event. Both trees are perfectly accurate, but you can alter the appearance of primitiveness by deciding which taxa to include in the tree, as well as which taxon to put at the top vs. the bottom. So whether something looks like a living fossil may just be an artifact of our decisions about how to construct phylogenetic trees. “No species” they argue, “should be flagged as ‘basal’ or ‘early branching’ per se” (Casane and Laurenti 2013, p. 337).

 Casane and Laurenti are right that whether a lineage is early branching depends on how we construct our phylogenetic trees. In a tree with six species of actinistian fishes plus humans, humans will look like the “early branching” lineage. Indeed, one could make a parallel point about phylogenetic diversity. No taxon makes a “high contribution” to phylogenetic diversity per se. A taxon’s contribution to phylogenetic diversity depends on what’s already there, in the ecosystem. Consider again a case of two islands. Suppose that neither island A nor island B has any vertebrates. Both islands have a rich mix of arthropod species, including lots of spiders and scorpions. Now suppose we introduce horseshoe crabs to island A, and humans to island B. As in the earlier thought experiment, both islands receive the same boost to species richness. But the addition of humans would seem to give island B more phylogenetic diversity than island A, which still has no vertebrates. Island A got one more arthropod species, but it already had lots of arthropods. This shows something important about phylogenetic diversity, namely that it’s always relative to context, or to what else is already present in the system. But this does not mean that the notion of phylogenetic diversity is somehow bogus or arbitrary. When we think about phylogenetic diversity, we should focus on the ecological communities to which the taxa in question actually belong. Horseshoe crabs, for example, add more phylogenetic diversity to their actual coastal ecosystems than humans do.

 Fourth, some people worry a lot about vagueness. As noted above (section 3), the phylogenetic living fossil concept does have vague boundaries, because the crucial notions of morphological stability, species poverty, and evolutionary distinctiveness are all matters of degree. Some critics of the living fossil concept make a big deal of this. For example, vagueness gets played up in the recent PBS *Eons* documentary on living fossils (see fn. 1 above). There are some clear-cut cases of phylogenetic living fossils, to be sure: tuataras, horseshoe crabs, the wollemi pine (Gilmore and Hill 1997). But the term “living fossil” is sometimes used much more widely. Are crocodiles living fossils? In the *Eons* documentary, it is suggested that humans might even count as living fossils, since humans living today are morphologically indistinguishable from fossils that are well over 100,000 years old. The critics are right about the vagueness, but wrong to see it as a reason for rejecting the living fossil concept. The ordinary concept of a fossil is quite vague, and in much the same way. For example, we naturally say that teeth and bones that have been lying in the bottom of a cave for 50,000 years are fossils—even though those teeth and bones are unaltered remains. They have not been mineralized (like dinosaur bones). But the bones of the dog that someone buried in the backyard a few years ago are not fossils, even though they, too, are unaltered remains. The only real difference is how long the bones have been lying around, and from a geological perspective, the age difference of 50,000 years is trivial (for more discussion of this problem, see Turner 2011, Ch. 10). Crucially, nobody thinks that the vagueness of the ordinary fossil concept is a reason for rejecting it. So why should anyone think that the vagueness of the living fossil concept is a reason for rejecting it?

 To sum up, then: Four worries about the very idea of living fossils turn out to be fairly easy to address, once we adopt the phylogenetic living fossil concept. (1) The phylogenetic living fossil concept helps resolve some of the ambiguity that has plagued recent discussions; (2) far from promoting misunderstanding about evolution, it incorporates evolutionary thinking; (3) there is no suggestion that phylogenetic living fossils are somehow “primitive” or “basal” or “less evolved” than other taxa; and (4) although the phylogenetic living fossil concept does exhibit some vagueness around the edges, this is exactly what one should expect, since morphological stability and evolutionary distinctiveness come in degrees.

**6. Conclusion**

 Both living fossils and the concept of a living fossil are, hopefully, here to stay. In this paper, I’ve argued that there is a legitimate *phylogenetic living fossil* concept that has three components: (a) deep prehistoric morphological stability; (b) few extant species; and (c) high contribution to phylogenetic diversity. This resolves some of the confusion about which taxa do or don’t count as living fossils, and does so in a way that is both principled and surprising—namely, by bringing normative considerations to bear. Whereas Darwin first appropriated and refined the notion of a living fossil in accord with his own scientific interests, current concerns about biodiversity loss might reasonably motivate us to conceive of living fossils in a particular way. Some classic examples of living fossil taxa, such as tuatara and horseshoe crabs, clearly count as phylogenetic living fossils. The phylogenetic living fossil concept picks out taxa that we might want to prioritize for conservation, and it also picks out evolutionary patterns that pose a distinctive explanatory challenge for macroevolutionary theory. Finally, some of the other worries that theorists have raised about the very idea of living fossils are easily addressed from the perspective of the phylogenetic living fossil concept.

 Some might agree that the phylogenetic living fossil concept is philosophically and biologically well-motivated, and yet still think that we should stop using the term “living fossil.” Perhaps we could call horseshoe crabs *evolutionarily* *MAD* taxa, for “Morphologically stable-and-distinct.” But I do not really share these terminological scruples. Of course, the term “living fossil” is a metaphor, but so are many other scientific terms that nobody thinks we should abandon—including “natural selection” and “genetic drift.” In section 2, we saw how Darwin also took a term that was out there in the culture and co-opted it, putting it to work in the context of his own evolutionary theory. In our current moment of alarm about biodiversity loss, it seems reasonable to try to reclaim the term “living fossil” again, putting it to work in a way that reflects the going concerns of conservation biology.

**Acknowledgments**

Early work on this project was supported by a visiting fellowship at the KLI in Klosterneuburg, Austria, in the fall of 2015. I am also grateful to Fulbright Canada for support during the spring of 2017, which enabled me to spend a semester at the University of Calgary. I shared an early version of this paper with an audience in Calgary in January 2017, and am grateful to the philosophers there for invaluable feedback: Soohyun Ahn, Megan Delahanty, David Dick, Marc Ereshefsky, Alison McConwell, Mark Migotti, Celso Neto, Ken Waters, and others. I am also deeply grateful to the Calgary philosophy department for being such a wonderful and welcoming place to work on this project. The paper has benefitted immensely from comments from two anonymous referees for this journal, and from Adrian Currie’s philosophical and editorial help and advice.

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Figure 1. Horseshoe crab. Sketch by the author.



Figure 2. The coelacanth at the bottom is the extant genus, *Latimeria*, while the one on the top is the Cretaceous coelacanth *Macropoma*. Sketches by the author. These are not precisely to scale. *Latimeria* is also bigger than *Macropoma*.

1. See also this educational video from the PBS *Eons* series, which declares that living fossils aren’t really “a thing”: https://www.pbs.org/video/living-fossils-arent-really-a-thing-tlkrnz/ [↑](#footnote-ref-1)
2. For present purposes, this simple intuitive example suffices. However, if we wanted to make this more precise, we should begin by constructing phylogenetic trees for the species on islands A and B. We’d then need a quantitative measure of evolutionary distinctiveness, so that we can assign each species an index. Most scientists start out by counting the nodes (branching points) between each species and the root of the tree (where the root is the nearest ancestor that all of them have in common.) From there, things get more complicated, and there is much debate about what other information, such as branch length, should be included in a measure of evolutionary distinctiveness (Vellend et al. 2011). [↑](#footnote-ref-2)
3. I thank Adrian Currie for raising this issue. [↑](#footnote-ref-3)