Opinion

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Darwinian shortfalls in biodiversity conservation

José Alexandre F. Diniz-Filho[1], Rafael D. Loyola[1], Pasquale Raia[2], Arne O. Mooers[3], and Luis M. Bini[1]

[1] Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, GO, Brazil
[2] Dipartimento di Scienze della Terra, dell'Ambiente e delle Risorse, Università di Napoli Federico II, Italy
[3] Biological Sciences, Simon Fraser University, Burnaby, BC, Canada

If we were to describe all the species on Earth and determine their distributions, we would solve the popularly termed 'Linnean' and 'Wallacean' shortfalls in biodiversity conservation. Even so, we would still be hindered by a 'Darwinian shortfall', that is, the lack of relevant phylogenetic information for most organisms. Overall, there are too few comprehensive phylogenies, large uncertainties in the estimation of divergence times, and, most critically, unknown evolutionary models linking phylogenies to relevant ecological traits and life history variation. Here, we discuss these issues and offer suggestions for further research to support evolutionary-based conservation planning.

Species, phylogenies, and biodiversity conservation

Species are considered indisputable units in conservation and biodiversity analyses. For example, Costello *et al.* [1] opened their recent evaluation of undiscovered biodiversity by stating that 'Species provide the most practical metric for distinguishing habitats and tracking progress in exploring Earth's biodiversity. They are as fundamental to biology as elements are to chemistry and particles to physics and are the first step in exploring biology'. The analogy between species and physical particles has been widely used in macroecology [2], and the importance of species as fundamental units in conservation planning and biodiversity analyses has been continuously discussed [3,4]. However, species, as opposed to physical particles diffusing in space and time, are not independent because they are lineages that evolve and diversify from shared ancestors. Therefore, related lineages are expected to share traits that both maintain present biodiversity [5] and impact future changes in biodiversity [6,7].

Methodological and conceptual advances to delimitate species (e.g., [8]) are useful for better defining and identifying fundamental units for biodiversity analyses. Yet, ecologists and evolutionary biologists have recognized the conceptual advantages of incorporating phylogenetic structure linking these fundamental units into their thinking ever since Darwin [9–14]. Thus, these units should be viewed mainly as operational units for further analyses, and the explicit consideration of biodiversity as comprising evolving and related lineages would add power and robustness to measures of biodiversity for conservation (Box 1). Indeed, phylogenetic conservation, pioneered during the early 1990s [15–17], has recently received increasing attention from researchers [18–21].

That said, and despite many syntheses and discussions on the need to better incorporate evolution into conservation [11,12,22–25], practical application lags far behind [26]. Indeed, we do not even have a comprehensive and integrative approach to using phylogenies in biodiversity conservation [27–29]. We suggest that, beyond operational problems [23], other deeper conceptual reasons hinder the use of phylogenetic information. Mirroring previously named Linnean and Wallacean shortfalls in the field [30,31], we propose that the difficulties regarding the incorporation of phylogenies into biodiversity conservation practice be called the 'Darwinian shortfall'. Here, we outline components of this shortfall, offer suggestions for further research, and clarify some of the important issues relating to the integration of phylogenies into biodiversity conservation planning.

The Darwinian shortfall

We recognize three closely coupled components of the Darwinian shortfall (Table 1): (i) the lack of fully resolved phylogenies for most groups of organisms; (ii) the limited knowledge of edge lengths and difficulties in absolute time calibrations; and, most critically (iii) unknown evolutionary models linking those phylogenies to ecological traits and life-history variation. We are aware that these components can be solved simultaneously by increasing biological knowledge and bioinformatics capacity, but we believe that they also reveal a sequence of increasingly complex issues.

Lack of comprehensive phylogenies

The first component is the lack of useable phylogenies for most groups of organism. First, few comprehensive (in the sense of including all species in a taxon) phylogenies exist [32–35]. Second, and linking the Darwinian, Wallacean,

Box 1. The effect of taxonomic inflation on phylogenetic diversity and conservation planning

Suppose that there are five species in a region, linked by a known phylogenetic structure with overlapping geographic ranges, but only three of these species (A, B, and C; Figure I) were recognized before 2013. In the context of spatial conservation prioritization, a single protected area established in 1985 would suffice to represent the known species under a complementarity approach, given the overlap among the geographic ranges of the species'. However, under taxonomic inflation, two new species were described in 2013, so that former species A becomes A1 and A2, whereas species B becomes B1 and B2. Under this scenario, the single protected area established in 1985 is no longer effective at ~~represented~~ all five species (under a simple target of representing a species in at least one selected site). A different network of protected areas would be needed for representing all species, with at least three areas being required to represent all of them. If these new protected areas are not implemented, 2/5 of the biodiversity would be unrepresented.

However, moving from counting species to phylogenetic diversity reveals that only 2/13 of the evolutionary history, estimated using Faith's phylogenetic diversity [16], would be lost if only the initial protected area remains. Another application based on this same hypothetical dataset follows from [9]. Suppose that, before 1985, species A was considered as threatened, hence 1/3 of the species in the group could go extinct. In this case, extinction of species A would lead to the lost of 4/11 of the evolutionary history of the group. Under taxonomic inflation and assuming the revised classification of the group with five species, the two new species derived from A (A1 and A2) are now also endangered (because former species A was endangered all through its range), increasing the proportion of threatened species to 2/5. However, a phylogenetic-based estimation of the proportion of threatened species would result in a figure similar to the one before 1985 (5/13) and is almost independent of the revised classification.
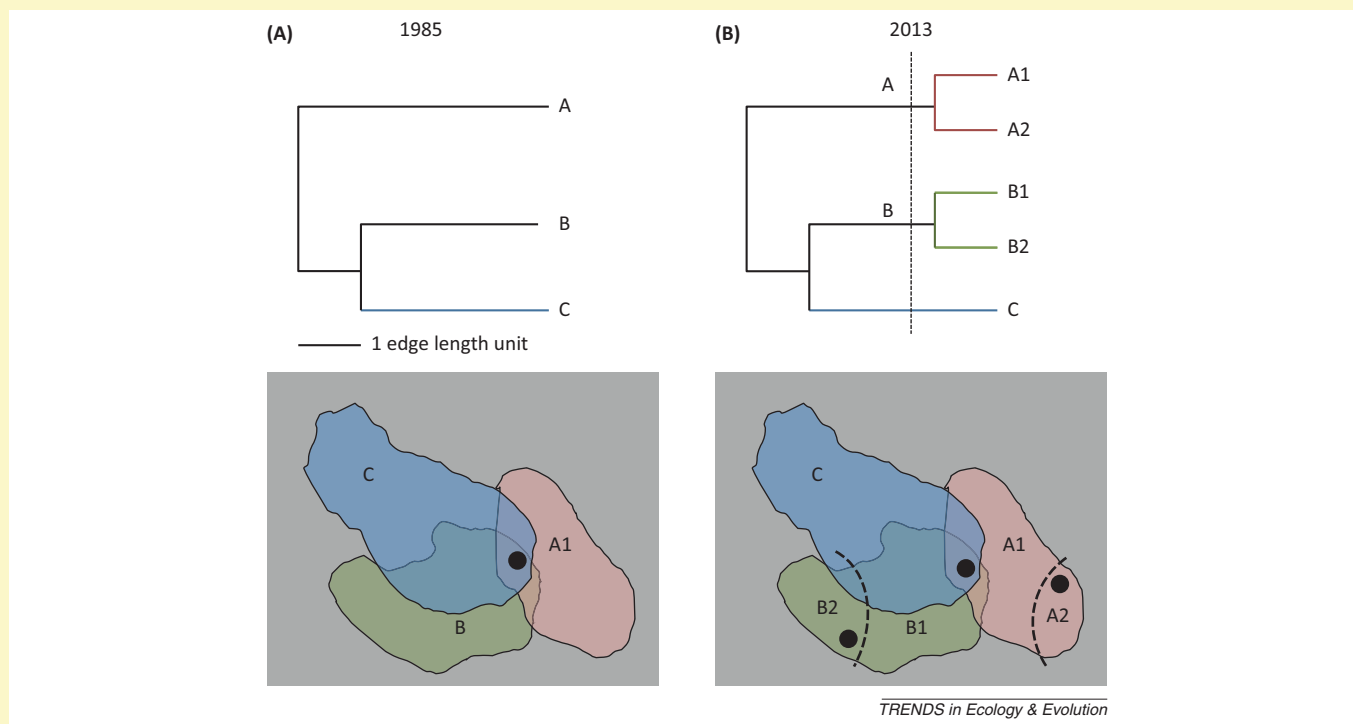

Figure I. Phylogeny and geographic ranges of a clade with three species, in 1985 **(A)**. After 2013 **(B)**, two new species are described by splitting species A and B. In 2013, that single protected area proposed to preserve the three original species (black dot on the map) is no longer enough to represent diversity in the group. As discussed in Box 1, estimating diversity using Faith's phylogenetic diversity rather than species counts would ~~allow for a more robust conservation action over time~~.

and Linnean shortfalls, there is often a poor match between the lists of species that have been studied phylogenetically and those that are important for particular local or regional analyses, especially in biologically rich and understudied regions of the world.

Rapid advances in molecular genetics, DNA sequence technology, bioinformatics, and phylogeny reconstruction have resulted in an exponential increase in both the quantity and quality of phylogenies over the past decades. Furthermore, the availability of large databases [such as GENBANK (http://www.ncbi.nlm.nih.gov/genbank) and TREEBASE (http://www.treebase.org)] enables researchers to ~~build their own phylogenies [36,37] or to download directly available ones~~. In addition, supertree approaches from the 1990s and supermatrix approaches from the past decade offered avenues for combining information from

disparate sources in increasingly sophisticated ways [38,39]. So, what is the problem?

First, building trees is difficult, requiring much technical expertise and specific data. There are still many methodological issues to be solved, particularly when managing new complex and large molecular data sets [36]. In addition, the focus for much tree inference remains systematics and diversification, and not biodiversity conservation. Thus, relevant taxa have not been targeted and so new approaches may be needed. The gradual adoption of cladistics for the classification of organisms, such as proposed in the Tree of Life web facility (http://www.tolweb.org/tree) is an important first step, enabling the construction and use of trees based on a 'backbone' phylogenetic structure at higher ranks (i.e., families) [32] (http://www.mobot.org and http://phylodiversity.net/phylomatic). Judicious selection

Table 1. Components of the Darwinian shortfall, including a description and short-term solutions that can be adopted given current knowledge

Darwinian shortfall	Description	Short-term solutions (and related references)
Lack of comprehensive phylogenies	For most groups of organism, phylogenetic relations among species are poorly known and have only been established mainly for a few species representing higher taxa	Couple phylogenies (higher levels) and cladistic classifications (lower levels) to produce initial approximations of phylogenies, particularly for megadiverse groups (e.g., PHYLOMATIC in http://phylodiversity.net/phylomatic) [32]
		Use phylogenetic targeting approaches [40] to select more important taxa to study for a given ecological or conservation question
		Use supertrees and supermatrix approaches [38,39] with available data to produce phylogenies for broad-scale analyses, as well as developing collaborative research networks to increase quality and quantity of molecular data across taxa [36]
		At local or regional scales, improve collaboration with research groups in molecular phylogenetics to build phylogenies for species of interest (giving positive feedback to GENBANK or TREEBASE) [36,41]
Uncertainties in the estimation of edge lengths and divergence times	Even when the relations among all species in a clade have been estimated, there are many calibration uncertainties in topologies, edge lengths, and time calibration	Improve procedures to obtain accurate estimates of edge lengths from molecular data (e.g., by combing rates for multiple genes) [36,42,43]
		Use computer simulations and modeling to obtain edge lengths in megaphylogenies [41], evaluating amount of uncertainty in analyses [34,44,45]
		Develop and apply better methods to integrate fossil record and molecular phylogenies to produce accurate calibrations [42,43,48]
Unknown evolutionary models underlying ecological traits and life-history variation	Even when phylogenies are known with low uncertainty in all aspects, there is a lack of knowledge about how traits evolved and how evolutionary processes create more complex patterns that cannot be described by phylogenetic relations alone	Establish the most important ecological traits for particular conservation targets and fit evolutionary models to these traits [57,63], then adjust edge lengths to account for these patterns and calculate diversity based on these phylogenies [14,64]
		Evaluate robustness of diversity estimates to multiple theoretical models of trait divergence and develop strategies to combine such models [14,64]
		Use empirical measures that combine phylogenetic information and trait data directly in generalized distance matrices [51]

of the species to be incorporated into phylogenetic analyses is possible, [40], as are multilevel approaches for constructing 'megatrees' [36–38]. Importantly, new approaches can combine genetic data, taxonomies, and reasonable diversification models to aid the placement of data-poor species [34,41].

Finally, the issue of sheer diversity remains: major groups of conservation concern (e.g., vertebrates, angiosperms, and butterflies) contain too many rare and hard-to-collect species, making even the taxonomic placement of potentially important components of biodiversity suspect. However, on local or regional geographic scales, where the number of species is smaller, it would be useful to develop collaborations among research groups in systematics, ecology, molecular biology, and bioinformatics to generate original molecular data and build complete 'local' phylogenies [36]. This would have the additional advantage of contributing to more comprehensive global phylogenies.

In the short term, mixed-method approaches and local and/or regional phylogenies may be more cost effective than projects aiming to produce fully resolved, comprehensive phylogenies for large groups. If we take this less-ambitious route, we will need to determine to what extent diversity patterns are robust to imperfect phylogenetic topologies [14]. We will also need new ways to estimate edge lengths on imperfect and mixed-method phylogenies [34].

Uncertainties in estimation of edge lengths and divergence times on phylogenies

Even when all species of a given group have suitable genetic data for producing reliable topologies, the difficulty in estimating edge lengths remains. Similar topologies produce different measures of phylogenetic diversity by modifying edge lengths (Box 2). Although topology, edge lengths, and absolute diversification times can be estimated simultaneously (e.g., using BEAST), common approaches for larger trees (e.g., using RaxML or GarLI) infer trees with edge lengths proportional to genetic change. Time is the most common measure of edge length in biodiversity conservation [9,18], and so genetic data must be scaled to time in some way.

However, transforming genetic differences into time remains challenging [42,43]. Indeed, there are debates regarding the type of data most suitable to reconstruct phylogenetic relations at different timescales (i.e., molecular markers or different regions of a genome) [36]. Given that regions evolve at distinct rates and are driven by

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Box 2. The three components of Darwinian shortfall

For most taxa, only a few species have been studied in a phylogenetic context, but knowing the topology of evolutionary relationships among species (Figure IA) may be a first step to calculate phylogenetic diversity and solve the first component of Darwinian shortfall. However, depending on edge length estimation and calibration (Figure IB), different phylogenies would appear and this would completely change estimates of phylogenetic diversity. Moreover, even after calibrating phylogenies, if ecological or life-history traits related to ecosystem function and community persistence evolved under more complex models than BM, it would be necessary

to model these traits and then warp edge lengths according to these models (Figure IC) [7,64]. Calculating phylogenetic diversity based on these warped trees is more informative with respect to functional diversity and evolutionary distinctiveness, although it may be still challenging to combine different phylogenies (for different traits) to get a single diversity estimate that maximize persistence and ecosystem functions related to these traits. The two possibilities are the use of multivariate analyses to reduce dimensionality and/or to combine *a posteriori* the phylogenetic diversity patterns for different traits.
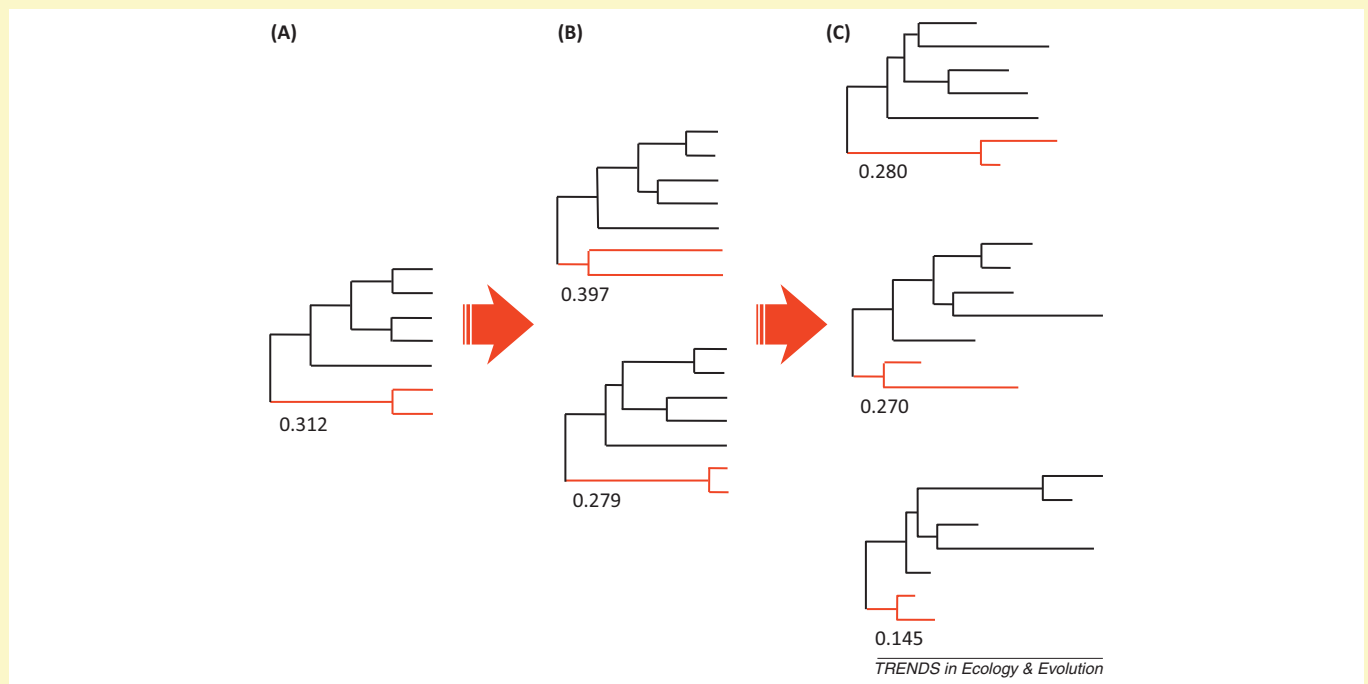

Figure I. Different phylogenies reflecting improved knowledge in respect to Darwinian shortfall. Numbers reflect the amount of phylogenetic diversity lost [17,18] if the two species whose lineages are highlighted in red become extinct. A full topology can solve the first component of Darwinian shortfall **(A)**, but the amount of phylogenetic diversity lost may vary depending on estimation of edge lengths and calibrations, as shown by two alternative phylogenies in **(B)**. Finally, regardless of estimated edge lengths or time calibration shown in (II), it may be possible to fit evolutionary models to different ecological and life history traits and warp edge lengths in the phylogenies to better represent diversity and distinctiveness for these traits **(C)**. All these possibilities provide different amounts of phylogenetic diversity for the same set of species, but notice that, for component (C), if nonultrametric phylogenies reflecting evolutionary patterns for distinct traits are considered, it may also be important to consider other metrics for establishing phylogenetic patterns, including distinctiveness (originality) [67] for each of the species.

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different evolutionary mechanisms, combining data for an entire genome, or combining morphological and molecular data, is also problematical. Such heterogeneous input data and processes mean that the task of quantifying the amount of uncertainty in time-calibrated edge lengths should not be neglected [44,45].

Fossil information is now routinely incorporated into phylogeny estimation, although primarily acting as anchors to calibrate molecular trees [42,43,46]. However, including these fossil calibrations is still challenging [47]. That said, for mammals, large phylogenies of fossil species are available and these can provide more precise information on divergence times if sampling artifacts can be incorporated into analyses [48]. Fossil data for other groups of conservation concern are more rare.

Besides calibration issues, fossil information is important to better understand how events in the past shaped the phylogenetic structure of extant assemblages (see [46]). For example, it is clear that past recent extinctions (such as

the Late Pleistocene megafauna extinction, and the countless extinctions of species from insular environments after human colonization) leave a strong signature on phylogenetic structure; therefore, relying on only living species to understand patterns of diversity and trait evolution could be misleading [49]. In conjunction, it is becoming clear that incorporating fossil information into phylogenetic analyses may help understand biodiversity patterning [46,50] and, in particular, may help with the most vexing aspect of the Darwinian shortfall, the fitting of evolutionary models of ecological traits and life-history variation to phylogenies.

Unknown evolutionary models underlying ecological traits and life-history variation
Even if a fully resolved and time-calibrated phylogeny is available, we still lack knowledge of how traits evolved to create the complex present-day patterns of ecological and life-history variation. This lack of knowledge undermines the argument that phylogenetic diversity can be a

surrogate for functional diversity [14,51]. There is growing evidence that increased phylogenetic diversity predicts some measures of increased ecosystem functioning [52–55]. If general, this would offer a powerful argument for including phylogenetic measures of biodiversity in conservation: even if building trees is hard, collecting the necessary genetic data is easier than collecting ecological functional data on every species [14]. However, any emerging argument linking phylogenetic diversity to ecosystem functioning [56] would seem to require knowledge on the relation among genetic divergence, time, and ecological divergence, knowledge that is still lacking [23].

Given that evolution is divergent, total genomic change will be correlated with elapsed time since divergence and, thus, time-calibrated phylogenetic diversity may be a straightforward metric for biodiversity conservation [27]. It is also often assumed that phenotypic variation increases linearly with time, a process usually described by a Brownian Motion (BM) model of trait evolution [57]. Indeed, a large set of independent traits evolving over long timescales may be well modeled by BM and, if this set of traits governed ecological function, then a time-calibrated phylogenetic diversity would be a suitable measure of overall functional diversity [14,58]. This argument has the advantage that it is not necessary to know what traits are linked with a particular ecosystem function.

However, the particular traits associated with specific ecological functions (e.g., nutrient cycling) could evolve under more complex evolutionary models driven by physiological, evolutionary, and ecological constraints [57,59,60]. This would lead to different divergence rates and trajectories in different taxa; thus, a time-calibrated phylogeny would be a poor descriptor of the interspecific variation of those traits [14]. Although popular methods for evaluating departures from BM exist (e.g., [59,60]), there are few studies testing the relation between relevant traits and phylogenies. Freckleton *et al.* [59] found evidence for phylogenetic signal in 62 of 103 heterogeneous traits across 26 phylogenies, with 48 of these being consistent with the BM model (thus, less than 50% of traits evolved under BM). A second survey focusing on adaptive radiations [61] found that BM was the best model for 25 (out of 38) taxa for body-size evolution and for 14 (out of 29) taxa for size-corrected morphological variation.

If phylogenetic diversity is a good predictor of ecosystem function [52], but BM is not the best model describing interspecific variation in functional traits, then we need methods for integrating these two apparently paradoxical results. We are just starting to couple models of phenotypic evolution with concepts of phylogenetic diversity measures [14], and further development is needed to link mechanistic and heuristic models [62], and to represent multitrait divergence in the form of useful single-diversity patterns (e.g., maps of diversity) in such a way as to guide practical conservation. Even so, at least two integrative approaches have been recently proposed to incorporate functional and phylogeny patterns simultaneously into diversity analysis.

Assuming that components one and two of Darwinian shortfall are solved, it is possible to fit evolutionary models to traits and then warp original edge lengths to describe their evolution (Box 2). If ecological traits linked

to ecosystem function show no phylogenetic structure, diversity estimates will converge to a metric based on traits alone. Besides gaining knowledge on how function evolves, conservation planning could be explicitly based on such warped phylogenies ([63,64], see [7] for an interesting recent application within the context of climate change). Using this technique, we still need methods to combine functional traits evolving under different models to achieve a common diversity estimate

A second approach is to combine phylogenetic and functional information into a single among-species metric [51]. The practical advantage is that such an empirical metric is independent of any evolutionary model underlying functional variation. By using ordinated trait distances, it also solves the problem of how to address multiple traits potentially evolving under distinct models. Even so, the relative contribution of phylogenetic distance to the overall patterns must be defined empirically; thus, we still need phylogenies with meaningful edge lengths, as well as trait data specifically linked with the functional aspects that we want to evaluate.

Further studies using the approaches described above may help solve the apparent paradox of phylogenies being good surrogates for ecosystem function and the poor performance of a BM model in describing trait evolution. For at least a few examples, coupling functional and phylogenetic diversity improves the description of biodiversity patterns and provides a better predictor of ecosystem functioning [51–55]. Perhaps this is because different functional traits are described by different evolutionary models, so that the final net result is that phylogeny describes better the loss of functional diversity than of particular traits *per se* [14]. If this is true, it may be possible to bypass the third Darwinian shortfall in the short term, although knowledge of evolutionary models would still be important to understand both functional and phylogenetic components of diversity and to deal with particular ecosystem functions related to more specific traits.

Integrating research on Linnean, Wallacean, and Darwinian shortfalls

Minimizing the impacts of the three components of the Darwinian shortfall begins with the knowledge of the tips of the phylogenies and performing analyses to establish the relations among those tips. However, species have an unclear and confusing meaning in biology [3,9,10,65,66]. Basic taxonomic work to better define these basic biodiversity units [8,65] is still pivotal to reduce the lack of knowledge of species identities (the Linnean shortfall). Moreover, defining operational taxonomic units (OTUs) for biodiversity analyses and conservation planning is not straightforward [65], and genetically distinct local populations or phylogeographic units and/or lineages within species may be important for conservation programs (e.g., for widely distributed species or for species that may be potentially useful as natural resources) (but see [10,66] and Box 1).

The overall criticism regarding the use of species counts as estimates of diversity [10,11] must be understood in the context of community-based and process-based conservation actions. Species-based conservation approaches are

still important, particularly in regard to its social aspect, because flagship or endangered species are usually well known to the general public. Given the old tradition of defining species and the still-incipient evolutionary thinking in our society, this aspect should not be underestimated. However, even in a species-centered approach it seems important to add evolutionary information to evaluate the evolutionary distinctiveness of these species and to better evaluate the relative impact of their loss to biodiversity overall (e.g., [67]).

At the same time, geographically structured processes at the population level, such as habitat selection, dispersal ability, and interspecific interactions, are important drivers of biodiversity patterns. Therefore, it is also important to delineate the geographic distribution of basic units, producing maps of phylogenetic and functional diversity, and this requires solving the Wallacean shortfall [68,69]. This in turn requires the simultaneous solution of the Linnean shortfall, the definition of the best possible OTUs, as well as an increased ability to cope with large data sets [69,70].

Thus, there are clear links among the Linnean, Wallacean, and Darwinian shortfalls, and solving them will require more effort in integration, potentially creating new challenges for improving knowledge of the different facets of biodiversity [11,69]. One main challenge is the need for funding ecological and biodiversity research at broad geographical and taxonomic scales (i.e., funding to do ecological research at ~~scales~~ similar to those of other areas of science).

Concluding remarks

Challenging the Darwinian shortfall requires a deep intellectual shift for scientists and conservation practitioners who are accustomed to thinking of species as independent units in conservation. Evolutionary-based approaches reveal that species embody different amounts of unique versus shared evolutionary information and this is important to understand diversity and to help develop better strategies to preserve it. Unfortunately, using metrics based on species counts may not be helpful for addressing the diversity of most groups of organisms, precisely because of the Darwinian shortfall.

Ecologists and conservation biologists increasingly wish to use phylogenies in their work, but may be deterred by the many technical challenges of producing a reliable phylogeny. We think that it is critical that researchers are aware of the problems involved in phylogeny reconstruction to better interpret phylogenetic-based biodiversity analyses and the outcome of conservation planning based on such metrics. Awareness of and responsiveness to uncertainties arising from the components of Darwinian shortfall raised here are also paramount. Although all the issues raised above will be well known to researchers working on phylogenetic reconstruction or comparative methods, many ecologists may still need a better understanding of how and why to integrate phylogenies in their day-to-day research. Highlighting the importance of the Darwinian shortfall, in addition to the conceptual and methodological advantages of overcoming them, may be a first step towards improving the collaboration that we feel is necessary among ecology, systematics, and conservation research programs to aid the sound management of the diversity of life on Earth.

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