Species splitting increases estimates of evolutionary history at risk

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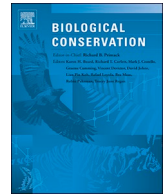
Perspective

Species splitting increases estimates of evolutionary history at risk

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A B S T R A C T

Changes in species concepts and the rapid advances in DNA-based taxonomy and phylogeny of the past decades have led to increasing splits of single species into several new species. The consequences of such splits include the delineation of post-split species that may have restricted ranges and potentially increased extinction risks. Species splitting also leads to a re-evaluation of phylogenetic trees, with post-split trees having more species, but species that are less evolutionarily distinctive compared to pre-split trees. Such changes in extinction risks and distinctiveness may influence strategies for the conservation of phylogenetic diversity (PD). In this study, we evaluated the effect of splitting a species into two sister species on two widely used measures to evaluate PD at risk: (i) the expected loss of phylogenetic diversity associated with a set of species and, (ii) for each species, the gain in the expected phylogenetic diversity if the species is saved from extinction. We developed theoretical predictions and then explored these in a real-world case study of species splitting in the Rhinocerotidae family. Species splitting increases both of our measures related to PD at risk, implying underestimation of PD at risk when valid species splitting is not recognised. This bias may lead to suboptimal conservation decisions: the subset of species or sites given priority for conservation may be different from the subset that actually deserves priority conservation attention. We discuss how our findings can be applied to more complex studies and the perspectives this highlights for accommodating new taxonomic knowledge in conservation strategies.

1. Introduction

The number of described species has increased rapidly over the last 30 years. For instance, the number of mammal species rose from 4629 in the second edition of *Mammal Species of the World* (MSW2; Wilson and Reeder, 1993) to 6495 in the recent work of Burgin et al. (2018), corresponding to an increase of ca. 40% in 25 years. While the discovery of undescribed forms in the field or in collections has contributed to augment the number of described species, most of this increase has resulted from species splits (Collen et al., 2011; Burgin et al., 2018). Species splits linked to the evolutionary nature of species result from speciation events, which may be directly observed by scientists such as the rapid hybrid speciation recently documented in Darwin's finches (Lamichhaney et al., 2018). However, the drastic increase in

species number observed in the last 30 years has two main non-mutually exclusive origins. The first one is the 'taxonomic inflation' (Isaac et al., 2004) due to the shift from the historical biological species concept (BSC; Mayr, 1963) to the more recent phylogenetic species concept (PSC; Cracraft, 1989). Under the BSC, species are defined as reproductively isolated taxa. Under the PSC, a species is the smallest set of organisms that share an ancestor and that can be distinguished from other such sets by at least one character; such phylogenetic species are not necessarily reproductively isolated and it can be difficult to know where to draw the line between species, notably if different datasets suggest different species delimitations. The number of species diagnosed under the PSC tends to be greater than under the BSC (Agapow et al., 2004). The second reason for the increase in species splits is taxonomic progress (Sangster, 2009). Indeed intensified naturalist

exploration coupled with rapid advances in DNA-based taxonomy and phylogeny reconstruction incorporating fossil information allowed in the past decades the discovery of a large number of cryptic species (Bickford et al., 2006) and a rapid increase in the resolution and availability of time-calibrated phylogenies (Diniz-Filho et al., 2013). Together with species lumping and the discovery of truly undescribed forms, species splits are thus the results of taxonomic revisions which formulate hypotheses about what species are and to which entities they correspond in nature. Depending on the species concept and/or the methods used in such taxonomic revisions, the hypothetical species produced may differ, therefore creating taxonomic uncertainty.

Many conservation policies depend on species extinction risk and endemism and/or on species numbers. Consequently, they rely on our ability to identify and name species (e.g. Agapow et al., 2004). Initially, the International Union for the Conservation of Nature (IUCN, 1980) also considered taxonomic distinctiveness as a factor relevant to conservation priorities because "the size of potential genetic loss is related to the taxonomic hierarchy". Extending these ideas to the broader preservation of evolutionary history, Faith (1992) developed a critical biodiversity measure called "phylogenetic diversity" (*PD*), and associated calculations of *PD* gains and losses. Integrative *PD*-based scores for species priority-setting have been developed (e.g. Isaac et al., 2007) which take into account both a species' contribution to *PD* - its "evolutionarily distinctiveness" (*ED*) - and also its extinction risk. While overall *PD* scores may be less sensitive to species definition than species richness, these species-centred scores nevertheless strongly rely on the definition of species.

The actual establishment of species conservation priorities based on the preservation of threatened phylogenetic diversity has been pioneered by the *EDGE* ("Evolutionarily Distinct and Globally Endangered") programme (Isaac et al., 2007). This approach attributes a priority score to a species by combining its *ED* score with its IUCN Red List status as an estimate of its extinction risk. The *EDGE* approach has been criticized because it does not consider that the extinction risk of internal branches in a phylogenetic tree depends on the extinction risk of all its descendants (Faith, 2008). Faith (2008) argued that effective prioritization should use variants of the existing probabilistic *PD* framework developed by Witting and Loeschcke (1995). Here, priorities can reflect the opportunity for averted loss of *PD*, assuming that conservation action on a species produces some nominated reduction in its probability of extinction. Using this framework, Steel et al. (2007) developed an improved *EDGE*-like score: for each species, the *HEDGE* ("Heightened Evolutionarily Distinct and Globally Endangered") score is the gain in expected phylogenetic diversity (*expPD*) if the species was secured (probability of extinction goes to 0), symmetrically corresponding to the decrease in expected loss of *PD* (*expPDloss*). Therefore, a species' *HEDGE* score integrates both its own probability of extinction and those probabilities of its close relatives. Following the calculation of *EDGE* or *HEDGE* scores, concrete conservation actions can be implemented to enhance the conservation of the species with the highest scores. For instance, the EDGE of Existence programme (https://www.edgeofexistence.org) provides funding, training and outreach for the species with the top 100 *EDGE* scores.

Species splitting has at least one major consequence for conservation policy (Agapow et al., 2004): the post-split species are likely more prone to extinction than pre-split species. Indeed, as post-split species arise through the splitting of pre-split species, they are likely to have narrower geographic ranges and smaller population sizes than the pre-split species. Reduced population size and geographic range are both associated with elevated risks of extinction (e.g. Robert, 2009) and are also widely used as criteria in formal classifications of endangered species like the IUCN Red List (IUCN, 2012). Therefore, species splits may amplify the number and proportion of endangered species thus reshuffling conservation priority and policy for each new split. Given that taxonomic revision leading to species splits is a continuous process, it creates instability hindering conservation policy. Moreover, there is

often an important time lag between the description of newly-delimited species resulting from the splitting of a species and the widespread uptake of these newly-delimited species. Consequently, the conservation status of split taxa may remain under-estimated for years (e.g. Groves et al., 2017). We thus need robust mechanisms to reconcile conservation policies with the rapidly evolving taxonomic knowledge (Raposo et al., 2017; Thomson et al., 2018).

Species splitting has another key consequence for the conservation of threatened evolutionary history: it is expected to decrease the *ED* component of the species' scores. Arguing that any increase in extinction risk due to species splitting is balanced by a decrease in *ED*, Isaac et al. (2007) found that *EDGE* scores for existing mammal species were robust to species splits. However, Isaac et al. (2007) used species names to calculate *EDGE* scores, whereas the correspondence between a species name and the set of individuals it represents in nature is altered in case of species splitting: a same species name may not represent the same set of individuals before and after split. In addition, the effect of species splitting may differ between *EDGE* and *HEDGE* scores because only the *HEDGE* approach acknowledges the fact that the magnitude of the evolutionary history at risk from any one species naturally depends on the fate of its close relatives (Faith, 2008).

Whether it is justified or not (Samadi and Barberousse, 2006), species splitting is a reality that conservation biologists have to face. However, adjusting conservation practices following species splitting may be long and/or difficult, e.g. in situations where there is debate among taxonomists, where there is not enough information to justify the splitting, or where there is a time lag between the taxonomic work justifying the splitting and its wide acceptance among taxonomists and ecologists. Therefore, our aim in this study is to quantify how species splits can influence conservation prioritization strategies aiming at preserving threatened phylogenetic diversity. To reach that aim, we used hypothetical case studies and a real-world case study of species splitting in the Rhinocerotidae family to evaluate the impact of species splitting on the *expPD* and *expPDloss* scores of a phylogenetic tree and the related species *HEDGE* scores.

2. Materials and methods

2.1. Context and notations

We consider a rooted tree *T* representing the known evolutionary relationships between *N* species at time *t* (see for example the hypothetical tree in Fig. 1a). $S(b)$ is the set of species descending from branch *b*, L_b the length of branch *b*, and $B(i)$ the set of branches on the path from species *i* to the root of the tree. $p(i)$ designates the risk that species *i* goes extinct in nature, i.e. that all individuals belonging to species *i* die. $p(i)$ is usually unknown and has to be estimated.

At time *t′* such that $t′ > t$, suppose that new taxonomic evidence suggests that one of the *N* species (*A* in Fig. 1) in fact consists of two sister species (A_1 and A_2 in Fig. 1). The tree *T′* represents the known evolutionary relationships between the $N + 1$ species at time *t′* (Fig. 1b).

We consider below a simple model where the extinction of each species in the tree is independent of the extinction of the other species. *expPD*, *expPDloss* and *HEDGE* scores which have been calculated with empirical data have relied on this assumption of independence (e.g. Kuntner et al., 2011). However, we show in Appendix A that our developments can be generalized to cases where the extinction probabilities of different species are dependent (as discussed for *PD* by Witting et al., 2000). Our results are valid for any ultrametric (e.g. time-calibrated) phylogenetic tree.

Consider any species *A*. A species is a set of individuals. Each individual that was assigned to *A* at *t* can be either assigned to A_1 or to A_2 at *t′*; therefore, A_1 and A_2 form a partition of *A*: $A = \{A_1, A_2\}$. Assuming the extinctions of A_1 and A_2 are independent events, $p(A)$ corresponds to the product of $p(A_1)$ and $p(A_2)$. By convention, let us assume that A_1
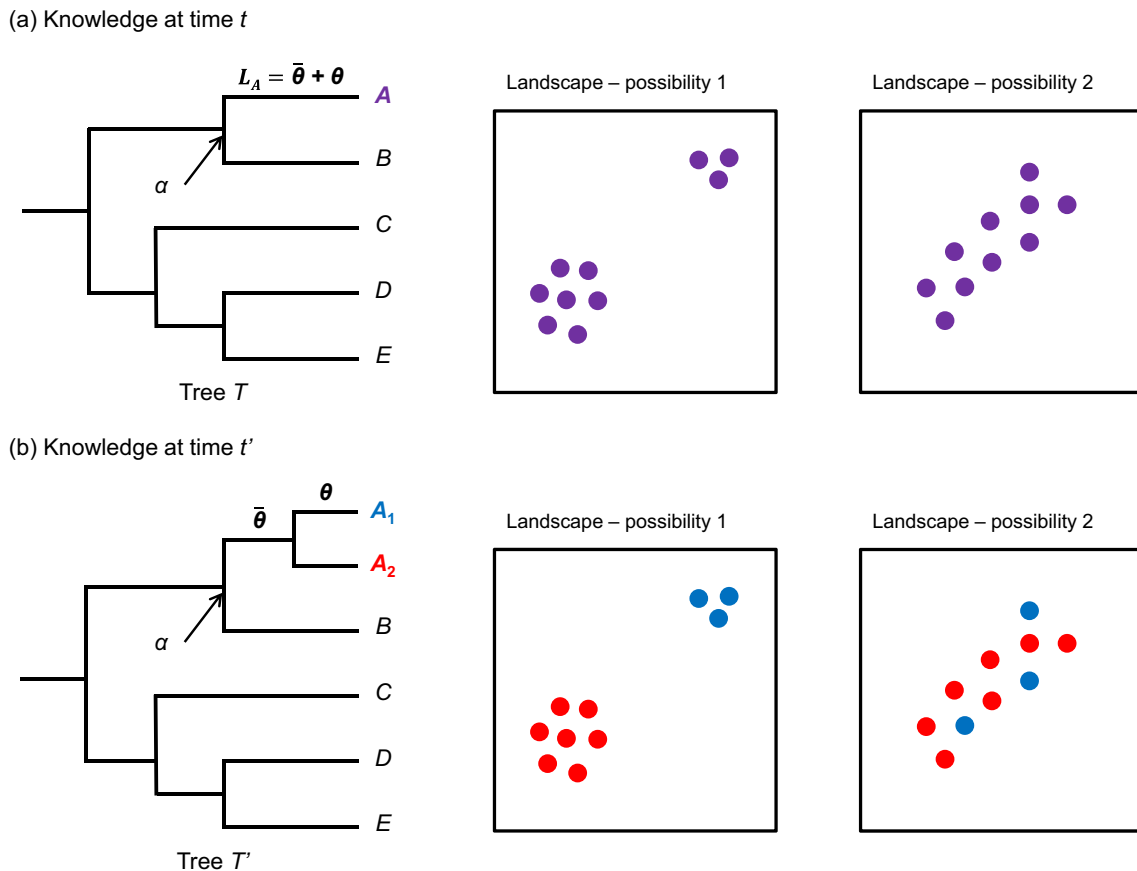
Fig. 1. (a) Hypothetical tree representing the known evolutionary relationships between the five hypothetical species *A*, *B*, *C*, *D* and *E* (left) and two possible spatial distributions of species *A* in the landscape (right) at time *t* and (b) hypothetical tree representing the known evolutionary relationships between the six hypothetical species A_1, A_2, *B*, *C*, *D* and *E* (left) and two possible spatial distributions of species A_1 and A_2 in the landscape (right) at time *t′*. Branch lengths used in the calculations are indicated above the branch. *α* designates the most recent common ancestor to *A* and *B*.

is more prone to extinction than A_2.

Let L_A be the length of the terminal branch leading to *A*, let *θ* be the time since the speciation event of A_1 and A_2 and let $\bar{\theta}$ be the length of the branch between the most recent common ancestor of A_1 and A_2 and the most recent common ancestor of A_1, A_2 and their closest relative (named *α*; see e.g. Fig. 1). The sum of *θ* and $\bar{\theta}$ corresponds to L_A.

Note that, while we focused on the implications of splitting *A* into A_1 and A_2, our framework below can also be used to analyse the implications of lumping A_1 and A_2 into *A*: the effect of lumping on our phylogenetic metrics is exactly opposite to the effect of splitting.

2.2. expPD, expPDloss and HEDGE

The *PD* of a subset of taxa corresponds to the sum of the lengths of all those branches that connect the members from the subset of taxa on a phylogenetic tree (Faith, 1992; see Eq. (B.1) in Appendix B). Conventionally, *PD* includes the length back to some common ancestor. Faith (2008), following Witting and Loeschcke (1995), also defined the expected amount of *PD* that may remain after a given period of time (*expPD*) as the sum of branch lengths weighted by their probability of survival (Eq. (B.2) in Appendix B). Conversely, the expected amount of *PD* that may be lost after a given period of time (*expPDloss*) can be expressed as the sum of branch lengths weighted by their probability of loss (Eq. (B.3) in Appendix B) so that *PD* corresponds to the sum of *expPD* and *expPDloss* (Eq. (B.4) in Appendix B).

The *HEDGE* score of any species *i* corresponds to the increase in *expPD* for the special case where the probability of extinction for species *i* changes from its current value to 0, or equivalently to the decrease in *expPDloss* (Steel et al., 2007; see Eq. (B.5) in Appendix B). For any

species *i*, this *HEDGE* score can be expressed as the sum of branch lengths weighted by their probability of extinction on the shortest path connecting species *i* to the root of the tree (Eq. (B.6) in Appendix B).

For our special case in which branch lengths reflect time, the indices *PD* and *expPD* are expressed in time of evolution, while *expPDloss* and *HEDGE* are expressed in loss of evolutionary time.

2.3. Effect of species splitting on expPD, expPDloss and HEDGE

To evaluate how the species splitting described in Section 2.1 affects the *expPD* and *expPDloss* scores of the tree, we computed the difference in the *expPD* (resp. *expPDloss*) of the tree between *t′* and *t*. We named this difference Δ*expPD* (resp. Δ*expPDloss*). Next we aimed to evaluate how such a species splitting affects (i) the *HEDGE* score of the split species (*A* in Fig. 1) and (ii) the *HEDGE* scores of relatives to the split species (for instance, *B* in Fig. 1). However, there are two ways of evaluating the impact of species splitting on species *A*.

The first method (hereafter method 1) consists in using the species' name as the comparison unit. We thus calculated $\Delta HEDGE(A)_{\text{method 1}}$ corresponding to the difference between *HEDGE* score of A_1 at *t′* and *A* at *t* considering that A_1 keeps the name of *A* and A_2, as a newly described species, takes a different name. The reasoning is similar if A_2 keeps the name of *A* and A_1 takes a different name. By using method 1, we are not comparing the same set of individuals in nature. However, this comparison based on species names is the method used in previous empirical studies to discuss the robustness of *EDGE* scores to species splits (Isaac et al., 2007) or, more broadly, to evaluate the robustness of *EDGE* scores to taxonomic and phylogenetic uncertainty (Collen et al., 2011; Curnick et al., 2015).

The second method (hereafter method 2) consists of using the set of individuals in nature as the comparison unit by calculating the difference in *HEDGE* scores between $A = \{A_1, A_2\}$ at t' and A at t (named $\Delta HEDGE(A)_{\text{method 2}}$). We calculated the *HEDGE* score of $\{A_1, A_2\}$ as the increase in *expPD* if we condition on the event that both species A_1 and species A_2 survive.

2.4. Numerical applications to hypothetical case studies

To illustrate the effect of species splitting on *expPD*, *expPDloss* and *HEDGE,* we represented all the possible values $\Delta expPD$, $\Delta expPDloss$ and $\Delta HEDGE(A)$ can take as functions of $p(A_1)$ and $p(A_2)$. Because $\Delta expPD$, $\Delta expPDloss$ and $\Delta HEDGE$ vary linearly with θ, we used an arbitrary value of $\theta = 1$ Ma. We also detailed the values of $\Delta expPD$, $\Delta expPDloss$ and $\Delta HEDGE$ in six case studies covering three increasing levels of $p(A)$. For these case studies, we assumed A is split into two species which both have higher or equal extinction probabilities than A: $p(A_1) \geq p(A)$ and $p(A_2) \geq p(A)$, with $p(A)$ corresponding to the product of $p(A_1)$ and $p(A_2)$.

2.5. Application to a real-world case study

To illustrate how our framework can be applied in the real-world, we studied the effect of species splitting on *expPD*, *expPDloss* and *HEDGE* scores of the Rhinocerotidae family. Currently, five extant species are recognised in the Rhinocerotidae family (MammalDiversity, 2019): the White Rhinoceros (*Ceratotherium simum*), the Black Rhinoceros (*Diceros bicornis*), the Indian Rhinoceros (*Rhinoceros unicornis*), the Javan Rhinoceros (*Rhinoceros sondaicus*) and the Sumatran Rhinoceros (*Dicerorhinus sumatrensis*). These species and their infra-specific taxa are under continuous evaluation and discussion by a dedicated IUCN Species Survival Commission specialist group (the African Rhino Specialist Group). According to the IUCN Red List (IUCN, 2018), the White Rhinoceros is currently "Near Threatened" and comprises two subspecies: the Southern White Rhino (*C. s. simum*), which is also "Near Threatened", and the Northern White Rhino (*C. s. cottoni*), which is "Critically Endangered". Note that, since this last IUCN evaluation, the last remaining male of the Northern White Rhino has died (Smith, 2018). In addition, Groves et al. (2010) argued that these two subspecies should be considered as distinct species: *C. simum* (Southern White Rhino) and *C. cottoni* (Northern White Rhino). They estimated that these two species diverged between 0.75 and 1.4 Ma ago while Harley et al. (2016) estimated they diverged around 0.2 Ma ago. Nonetheless, the recommendation of Groves et al. (2010) has not been universally accepted and the IUCN still considers that the White Rhinoceros consists of one species.

For our *PD* calculations, we extracted the Rhinocerotidae tree from the first mammal phylogenetic tree of the posterior distribution of 1000 trees available in Phylacine (Faurby et al., 2018). This was an arbitrary choice and the results would likely be very similar for any other tree in this set. We then calculated extinction probabilities by transforming the current IUCN Red List categories using the IUCN designations projected at 50 years (Mooers et al., 2008). We first calculated the *expPD*, *expPDloss*, and *HEDGE* scores in the Rhinocerotidae family under the assumption that *C. simum* consists of one species (acting as the hypothetical species A). We then calculated the change in *expPD*, *expPDloss* and *HEDGE* scores if the splitting of *C. simum* into two sister species *C. cottoni* (acting as the hypothetical species A_1) and *C. simum* (acting as the hypothetical species A_2) was recognised. We determined the extinction probability of *C. cottoni* from its current IUCN Red List category as for the other species. We consequently determined the extinction probability of the new entity corresponding to *C. simum* (acting as the hypothetical species A_2) as the ratio between the extinction probability of the old entity corresponding to *C. simum* (acting as the hypothetical species A) and the extinction probability of *C. cottoni* (acting as the hypothetical species A_1). We used three estimates of

divergence time between *C. simum* and *C. cottoni* ($\theta = 0.2$ Ma, $\theta = 0.8$ Ma and $\theta = 1.4$ Ma).

3. Results

We provide the equations for $\Delta expPD$, $\Delta expPDloss$ and $\Delta HEDGE$ in Appendix B. We use below our theoretical and empirical case studies to illustrate key properties of these metrics.

3.1. Effect of species splitting on expPD, expPDloss and HEDGE: theoretical developments

The values for $\Delta expPD$ and $\Delta expPDloss$ are always positive (for proof see Appendix C and Fig. 2): species splitting increases both the *expPD* and *expPDloss* scores of the tree such as $\Delta expPD + \Delta expPDloss = \theta$. This paradox is explained by the fact that species splitting adds θ units of independent evolutionary history to the phylogenetic tree: *PD* at time t' is higher than *PD* at time t.

The effect of species splitting on *expPD* and *expPDloss* only depends on θ, $p(A_1)$ and $p(A_2)$ (Table 1, Appendix B). The amount of gain in *expPD* due to species splitting increases with θ and decreases with the difference between $p(A_1) + p(A_2)$ and $p(A_1)p(A_2)$. This gain is low when A_1 and A_2 are very threatened and reaches its highest values when A_1 and A_2 are less threatened (Table 1, Fig. 2). The increase in *expPDloss* due to species splitting rises with θ and with the difference between $p(A_1) + p(A_2)$ and $p(A_1)p(A_2)$. This increase is low when A_1 and A_2 are less threatened whereas it is high when A_1 and A_2 are very threatened (Table 1, Fig. 2).

The *HEDGE* scores of species not directly involved in the split (i.e. all species except A, A_1 and A_2) are unaffected by species splitting (Eq. (B.11) in Appendix B). While *HEDGE* properly takes probability of loss of other lineages into account for shared ancestral branches, the splitting does not change the overall probability of loss of these lineages.

Whatever the method used, the variations in $\Delta HEDGE(A)$ are always positive (Fig. 2, Table 1, Appendix B): A represents more threatened evolutionary history when it is split. However, the degree to which $HEDGE(A)$ increases with species splitting varies according to the method used to compute $\Delta HEDGE(A)$.

In all cases, the increase in $HEDGE(A)$ due to species splitting rises with θ (Table 1, Eqs. (12)–(14) in Appendix B). However, the increase in $HEDGE(A)$ due to species splitting reaches higher values and presents a higher range of values when comparing A to A_1 (i.e. the most threatened post-split species; Fig. 2c) than when comparing A to A_2 (i.e. the less threatened post-split species; Fig. 2d). The increase in *HEDGE* (A) due to species splitting reaches its maximum values and range of values when comparing A to $\{A_1, A_2\}$ (i.e. the same group of individuals before and after split; Fig. 2b). For instance, given $\theta = 1$ Ma, $p(A_1) = 0.90$ and $p(A_2) = 0.50$, the *HEDGE* score of species A increases by 0.05 Ma when comparing A to A_2, meaning that 0.05 Ma of evolution are more threatened if A is split. Using the same values, this increase raises to 0.45 Ma when comparing A to A_1 and 0.95 Ma when comparing A to $\{A_1, A_2\}$ (Table 1).

When comparing A to $\{A_1, A_2\}$, the increase in $HEDGE(A)$ due to species splitting rises with the difference between $p(A_1) + p(A_2)$ and $p(A_1)p(A_2)$ just as the gain in *expPDloss* (Table 1, Fig. 2b, Eq. (B.14) in Appendix B). When comparing A to A_1 (the most threatened post-split species), the increase in $HEDGE(A)$ due to species splitting rises with the difference between $p(A_1)$ and $p(A_1)p(A_2)$ (Table 1, Eq. (B.12) in Appendix B). Therefore, the increase in $HEDGE(A)$ is low when A_1 and A_2 both have low threat status or both have high threat status. Importantly, the increase in $HEDGE(A)$ is high when A_1 is highly threatened and A_2 considerably less threatened. For example, if A_1 and A_2 originated 1 Ma ago, the gain in $HEDGE(A)$ is 0.20 Ma when $p(A_1) = 0.25$ and $p(A_2) = 0.20$ while it reaches 0.79 Ma when $p(A_1) = 0.94$ and $p(A_2) = 0.16$ (Table 1, Fig. 2c). When comparing A to A_2 (the less threatened post-split species), the increase in $HEDGE(A)$
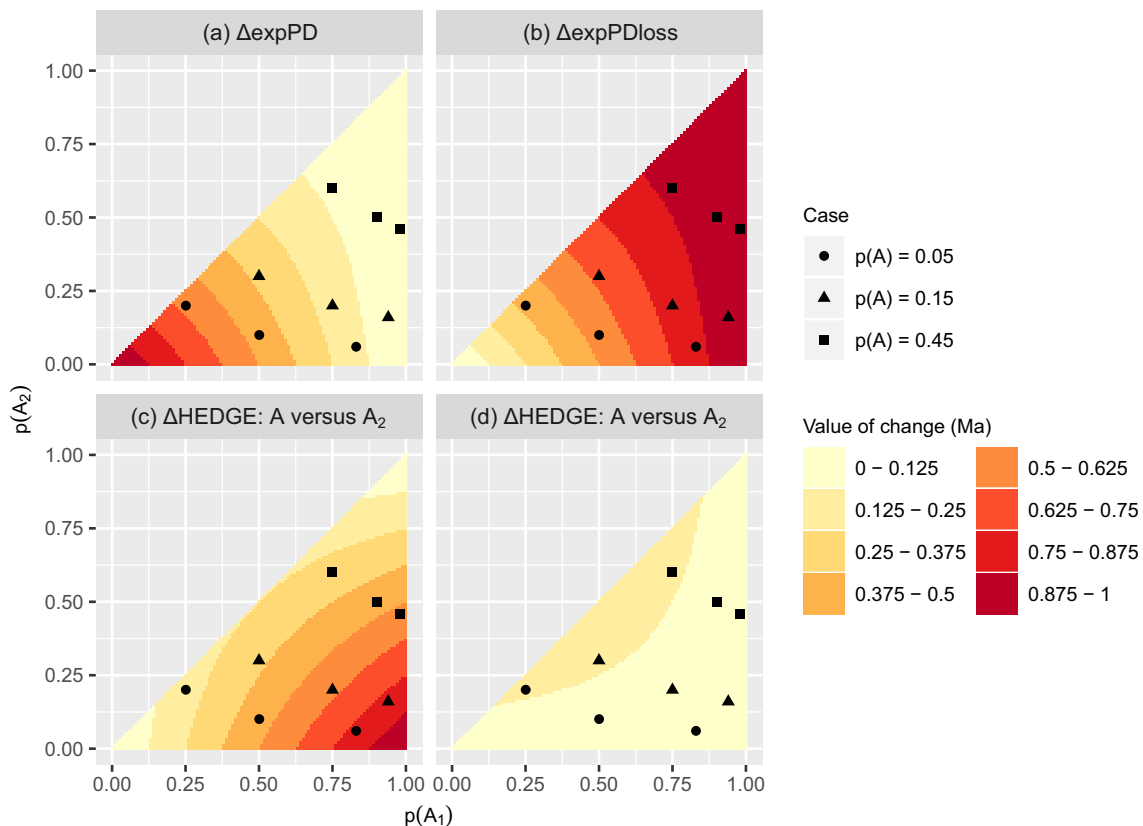
Fig. 2. Values of change due to the split of species A into two sister species A_1 and A_2 with respect to the extinction probability of A_1 ($p(A_1)$), and the extinction probability of A_2 ($p(A_2)$) in (a) the expected phylogenetic diversity ($expPD$), (b) the expected loss of phylogenetic diversity ($expPDloss$) of the tree, (c) in the $HEDGE$ score of species A by comparing $HEDGE$ score of A at t to $HEDGE$ score of A_1 (the more threatened post-split species) at t' and (d) in the $HEDGE$ score of species A by comparing $HEDGE$ score of A at t to $HEDGE$ score of A_2 (the less threatened post-split species) at t'. These values are represented for an arbitrary age of post-split species $\theta = 1$ Ma. Dots represent numerical applications for the six case studies described in Table 1. Note that the values of change in $expPDloss$ ($\Delta expPDloss$) are equal to the values of change in the $HEDGE$ score of species A when comparing $HEDGE$ score of A at t to $HEDGE$ score of $\{A_1, A_2\}$ at t'.

due to species splitting rises with the difference between $p(A_2)$ and $p(A_1)p(A_2)$ (Table 1, Eq. (B.13) in Appendix B). Therefore, the increase in $HEDGE(A)$ can reach moderate values when A_1 and A_2 are both moderately threatened and is small otherwise.

3.2. Effect of species splitting in the Rhinocerotidae family

Under the assumption that *C. simum* consists of one species, the $expPD$ of the Rhinocerotidae family is equal to 30.1 Ma, and its $expPDloss$ to 29.0 Ma. The $HEDGE$ scores range from 0.1 Ma for the lowest-ranked species *C. simum* to 13.8 Ma for the highest-ranked species *D. sumatrensis* (Fig. 3a). For any nominated value of θ, the splitting of *C. simum* in *C. simum* and *C. cottoni* produces only small increases in the $expPD$ of the Rhinocerotidae family (less than 0.1 Ma). However,

this splitting increases the $expPDloss$ of the Rhinocerotidae family to 29.2 Ma for $\theta = 0.2$ Ma, to 29.8 Ma for $\theta = 0.8$ Ma and to 30.4 Ma for $\theta = 1.4$ Ma.

The splitting of *C. simum* into *C. simum* and *C. cottoni* affects only slightly (by less than 0.1 Ma) the $HEDGE$ score associated to the name *C. simum* (which does not represent the same set of individuals in tree T and tree T': see Fig. 3). However, the splitting of *C. simum* leads to the appearance of a sixth Rhino species, *C. cottoni*, whose $HEDGE$ score increases with θ, from 0.3 Ma for $\theta = 0.2$ Ma to 1.4 Ma for $\theta = 1.4$ Ma. *C. simum* represents the lowest priority and *D. sumatrensis* the highest priority in the four scenarios (no split, split with $\theta = 0.2$ Ma, split with $\theta = 0.8$ Ma and split with $\theta = 1.4$ Ma). However, if the splitting is recognised, *C. cottoni* occupies the 5th rank ahead of *C. simum* for $\theta = 0.2$ Ma, and rises to the 4th rank ahead of *R. unicornis* for $\theta = 0.8$ or

Table 1
Numerical applications to investigate the effect of splitting species A into two sister species A_1 and A_2 on the expected phylogenetic diversity of the tree ($expPD$), its expected loss of phylogenetic diversity ($expPDloss$) and the $HEDGE$ score of species A ($HEDGE(A)$) in three case studies representing increasing extinction probability for A ($p(A)$). These numerical applications use an arbitrary value of $\theta = 1$ Ma.

| Extinction probabilities and PD at risk	Numeric case studies								
$p(A)$		0.05			0.15			0.45	
$p(A_1)$	0.83	0.50	0.25	0.94	0.75	0.5	0.98	0.90	0.75
$p(A_2)$	0.06	0.10	0.20	0.16	0.20	0.30	0.46	0.50	0.60
$\Delta expPD = \theta + \theta[p(A_1)p(A_2) - p(A_1) - p(A_2)]$	0.16	0.45	0.60	0.05	0.20	0.35	0.01	0.05	0.10
$\Delta expPDloss = \Delta HEDGE(A)_{\text{method 2}}$ $= \theta[p(A_1) + p(A_2) - p(A_1)p(A_2)]$	0.84	0.55	0.40	0.95	0.80	0.65	0.99	0.95	0.90
$\Delta HEDGE(A)_{\text{method 1 }(A \text{ versus } A_1)} = \theta p(A_1)[1 - p(A_2)]$	0.78	0.45	0.20	0.79	0.60	0.35	0.53	0.45	0.30
$\Delta HEDGE(A)_{\text{method 1 }(A \text{ versus } A_2)} = \theta p(A_2)[1 - p(A_1)]$	0.01	0.05	0.15	0.01	0.05	0.15	0.01	0.05	0.15
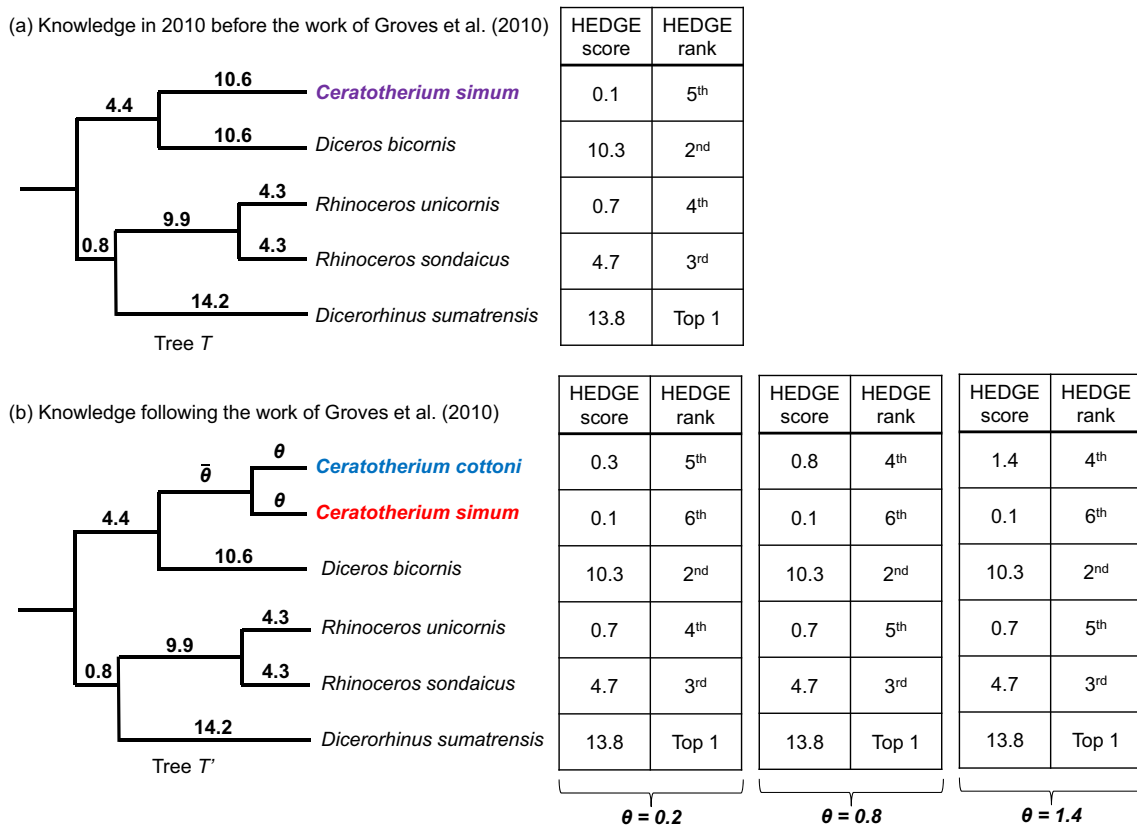
Fig. 3. (a) Phylogenetic tree *T* representing the known evolutionary relationships between the five extant species of the Rhinocerotidae family in 2010 before the work of Groves et al. (2010) and their corresponding *HEDGE* scores and ranks and (b) phylogenetic tree *T′* representing the known evolutionary relationships between the six extant species of the Rhinocerotidae family following the work of Groves et al. (2010) who suggested that *Cerathotherium simum* consists of two distinct species (previously recognised as subspecies: *Ceratotherium cottoni* and *C. simum*) their corresponding *HEDGE* scores and ranks calculated with three estimates of divergence time between *C. cottoni* and *C. simum* (θ = 0.2 Ma, θ = 0.8 Ma and θ = 1.4 Ma). Branch lengths (indicated above the branches) and topology of the tree *T′* have been extracted from the first tree of the posterior distribution of 1000 trees available in Phylacine (Faurby et al., 2018). The extinction probabilities, which have been calculated by transforming the current IUCN Red List categories using the IUCN designations projected at 50 years (Mooers et al., 2008), are the following: $p(C.\ simum)_t = 0.004$, $p(Rhinoceros\ unicornis) = 0.050$, $p(Diceros\ bicornis) = p(Rhinoceros\ sondaicus) = p(Dicerorhinus\ sumatrensis) = 0.970$, $p(C.\ cottoni)_{t′} = 0.970$ and $p(C.\ simum)_{t′} = p(C.\ simum)_t/p(C.\ cottoni)_{t′} = 0.004/0.970$.

1.4 Ma (Fig. 3b). Such changes in ranking would have consequences in conservation planning and management.

4. Discussion

Loss of *PD* is now regarded as "a resonant symbol of the current biodiversity crisis" (Davies and Buckley, 2011). *PD* loss can be interpreted as the loss of feature diversity (the variety of distinct character states among species). Feature diversity maintains a potential flow of (typically unanticipated) benefits (e.g. medicines, foods) for future generations. Thus, *PD* captures a fundamental value of biodiversity, called "option value" (Faith, 1992, 2018a, 2018b; Forest et al., 2007; Owen et al., 2019). Following the arguments in Faith (1992), *PD* is expected to reflect broad feature diversity, and not specific functional traits that are often prone to convergent evolution (for review, see Faith, 2018a). The well-corroborated *PD*-features relationship (Faith, 2018a) has supported the recent use by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), of estimated amounts of *PD* at risk as one global indicator for "maintenance of options" provided by nature (Faith, 2018b; Owen et al., 2019). This link between *PD* loss and the loss of a fundamental value of biodiversity highlights the importance of accurate estimates of *PD* at risk for conservation decision-making such as species or site prioritization.

Two main sources of uncertainties for such *PD* assessments have been identified: those related to phylogenies (incomplete sampling,

unresolved or poorly resolved nodes, lack of good calibration points) and those related to extinction probabilities (data deficiency and more broadly accuracy of estimates). Species splits change both the phylogenies (number of species, topology and branch lengths of the phylogenetic tree) and species' extinction probabilities. Consequently, they may have profound implications for conservation biology (Agapow et al., 2004; Isaac et al., 2004; Mace, 2004). As they increase the number of described species, the number and the proportion of endangered species, species splits question the accuracy of conservation policies which would need stable species lists. Yet, until now, the influence of species splits on *PD* at risk has rarely been studied. In this study, assuming that species extinctions constitute independent events, we highlighted that species splitting always increases estimates of *PD* at risk (Section 4.1). Although our theoretical developments need to be further validated with empirical data for which species extinctions do not necessarily constitute independent events (Section 4.2) and to consider taxonomic revisions that lead to more complex phylogenetic rearrangements than the splitting of one species into two sister species (Section 4.3), our work brings new thought-provoking inputs for dealing with new taxonomic knowledge in conservation strategies (Section 4.4).

4.1. Predicting the effect of species splitting on PD at risk if species extinctions constitute independent events

Assuming that species extinctions are independent, we found that

the effects of splitting a species into two sister species on *expPD*, *expPDloss* and *HEDGE* depend only on the age of divergence and on the probability of extinction of each post-split species. We first showed that species splitting increases the *expPD* and *expPDloss* scores of the phylogenetic tree, because it adds an amount of independent evolutionary history to the *PD* of the tree corresponding to the age of the post-split species. This highlights a major property of *PD* that Faith (1992) early emphasized: the *PD* of a tree (and consequently all measures based on *PD*) is not a fixed score and can change with novel or alternative taxonomic knowledge. Consequently, when we ignore a split, we always underestimate *expPD* and *expPDloss*, and the older the post-split species, the larger the underestimation.

Second, our results indicate that species splitting does not impact scores of species that were not split. Further, we highlighted that, regardless of comparison methods (A versus A_1, A versus A_2 and A versus $\{A_1, A_2\}$), species splitting always increases the absolute *HEDGE* score of the split species (i.e. it increases the gain in *expPD* if A_1, A_2 or both species were secured). This is because having two species instead of one increase the quantity of independent evolutionary history carried out by a lineage. Consequently, when we ignore that a lineage comprises two instead of one species, we underestimate its *HEDGE* score. This underestimation can be huge if the split concerns threatened species that diverged long ago, and if one of the two species has a very high probability of extinction. For instance, following the application of the PSC, the endangered species of ruffed lemur *Varecia variegata* has been split into two species which are now both critically endangered (Isaac et al., 2007; IUCN, 2018) and which diverged at least 2.5 Ma ago (Herrera and Dávalos, 2016): *V. variegata* and *V. rubra*.

ExpPDloss and *HEDGE* are among the recommended indices to guide species or sites prioritization strategies aiming at minimizing the expected loss of phylogenetic diversity after a certain time. Any delay in acknowledging valid species splitting can thus lead to suboptimal conservation decisions based on such measures: the species or sites that actually require conservation actions may be entirely overlooked. This is particularly obvious in our real-world case study. Ignoring the splitting of *C. simum* (the White Rhinoceros) into two sister species *C. simum* (the Southern White Rhino) and *C. cottoni* (the Northern White Rhino) leads to different species conservation priorities than if the Southern White Rhino and the Northern one are recognised as distinct species. Here, we showed that disregarding this splitting masked the conservation attention the Northern White Rhino deserved based on its *HEDGE* score. Had this splitting been recognised earlier, the Northern White Rhino would maybe have benefited from dedicated conservation actions such as those provided for the top 100 *EDGE* species. These actions may have prevented or delayed the recent extinction of the Northern White Rhino (Smith, 2018).

4.2. What if species extinctions are not independent?

Even if most empirical studies calculating *expPD*, *expPDloss* and *HEDGE* scores rely on the assumption of independence of species extinction (e.g. Kuntner et al., 2011), the reality is often more complex (e.g. Veron et al., 2018). If species extinctions are not independent, our framework still allows prediction of the effects of species splitting on these three scores. However, these effects will depend not only on the probabilities of extinction of the post-split species but also on the probability of extinction of the pre-split species (see Appendix A).

This point is important because non-independent extinctions in closely related taxa are not rare. For instance, many ecological traits tend to remain similar over evolutionary time (i.e. niche conservatism, Wiens et al., 2010). Niche conservatism implies that sister species tend to have similar environmental niche requirements (Warren et al., 2008), which means that post-split species will be vulnerable to similar communities of pathogens (Gilbert and Webb, 2007) and/or to similar regimes of disturbances (Helmus et al., 2010). Conservation research has provided evidence that the extinction risk of unconnected but closely related populations can be driven by similar causes (McKinney, 1997), either because these populations are located in the same area, have similar ecology, are vulnerable to the same threats, or because these threats are global. Examples include the response of closely related plants to climate change (Willis et al., 2008) or the vulnerability of parrot species to deforestation (Goerck, 1997). This pattern of clustered extinction might be particularly strong in exploited species, because they are often exploited for similar use. This may be important even to taxa with completely disjointed distributions, because the globalization of human markets and practices may drive similar demands (Ehrenfeld, 2003). For example, the international demand for horn and the weakness of global policies to control poaching are common threats of all rhinoceros species in two continents (IUCN, 2018). Finally, the extinction of an exploited species might directly influence the exploitation regime of its sister species if it can also provide the same product/benefit. Such collapse-replacement mode is well documented in the context of fisheries (Essington et al., 2006). Overall, there are multiple ways by which extinctions of two closely related species can covary and covariation is likely to be positive in most cases. Nonetheless, some human threats are so intense and widespread that they tend to affect a wide range of species independently of their intrinsic traits, and therefore extinction risk becomes unpredictable in relation to species' evolutionary relationships.

4.3. Predicting the effect of taxonomic uncertainty beyond a split of one species into two sister species

In this study, we focused on the splitting of one species into two sister species. However, taxonomic revisions can lead to the splitting of one species into more than two species or, on the contrary, the lumping of several species into one. Examples of a split of one species into several tend to be more frequent for invertebrates, either in terrestrial (e.g. Hebert et al., 2004) and/or marine environments (Nygren and Pleijel, 2011), but it was also observed for vertebrates (Hotaling et al., 2016). Such a split of one into several species is a simple extension of the model studied here. So, the way it will impact *expPDloss* and *HEDGE* scores depends on the number of species raised, the population size, the distribution range and the threats faced by each of the new species. A simple illustration is the polychaete *Eumida sanguinea* (Phyllodocidae, Annelida) in the Northeast Atlantic (Nygren and Pleijel, 2011), in which each of the 7 post-split species are limited to a similar fraction of the range of the pre-split species. If we assume that population sizes are similar, the influence of the split on *expPDloss* and *HEDGE* will depend on the amount of unique evolutionary history added, and on the threats faced by each new species.

The effect of lumping several species into one on the probability of extinction of post-lump species is the opposite of the effect of splitting. As the lumped species is older than the pre-lumped ones, lumps reduce the amount of unique evolutionary history of the lumped species and of the tree. So, the deeper the divergence of the lumped group to its sister group, the higher the impact on *expPDloss* and *HEDGE* scores. In addition, because the range and population size of lumped species is the union of the original ones, they tend to be less threatened. So, all contribute to reduce *expPDloss* and *HEDGE* scores.

Splits and lumps can also lead to a new rearrangement of the phylogenetic tree. For instance, a split of one species into several ones can lead to a new tree with a different topology where the post-split species are no longer close relatives. This possibility is illustrated by the egg-brooding tree frog genus *Fritziana* (Walker et al., 2018). There is the potential for future theoretical studies to investigate the effects of these more complex cases of species splitting, lumping and more broadly new tree arrangements on scores that estimate *PD* at risk. In addition, such new tree arrangements could be investigated empirically by calculating scores before and after the taxonomic revision.

4.4. Implications for dealing with new taxonomic knowledge in conservation strategies

New taxonomic knowledge results in continuous changes in the number and the delineation of species. Such taxonomic uncertainty is both inevitable and desirable as it represents taxonomic progress (Hey et al., 2003; Raposo et al., 2017) which is the only solution to mitigate the loss of species awaiting description before their conservation is even considered in the first place (Costello et al., 2013). Nonetheless, as it can impact all conservation strategies based on species counts or individual species properties (Agapow et al., 2004; Isaac et al., 2004; Mace, 2004), we have to find solutions to deal with new taxonomic knowledge in conservation strategies.

A first solution is to build conservation strategies that are robust to taxonomic uncertainty (e.g. Collen et al., 2011). This robustness is usually evaluated by comparing how species prioritization changes across distinct taxonomic references using the species name as the unit of comparison (e.g. for phylogenetic conservation prioritization: Collen et al., 2011; Curnick et al., 2015). Our work suggests that this approach can be improved to better examine robustness to species splitting. Indeed, we highlighted that the sensitivity of *HEDGE* score associated to a species name depends on which post-split species will keep the name of the pre-split species: the increase in *HEDGE* score due to species splitting is bigger when the more threatened post-split species keeps the name of the pre-split species than when the less threatened one keeps the original name. Furthermore, species names are not conservation targets, they are labels to represent the sets of individuals in nature targeted by conservation strategies. Therefore, we also evaluated how the *HEDGE* score of the set of individuals submitted to split increase with species splitting and showed that the sensitivity of such *HEDGE* score to species splitting was even larger than the sensitivity of *HEDGE* score associated to a species name. These results demonstrate that the unit of comparison chosen to characterise the effect of taxonomic uncertainty influences the conclusions we can make about the robustness of conservation approaches to such uncertainty. More generally, there is still opportunity for future work to further search for units for protection (e.g. Evolutionary Significant Units or Management Units, Moritz, 1994, or supra-specific groups, Ennos et al., 2005) which would be robust to taxonomic uncertainty.

Finally, another way in which conservation strategies can deal with new taxonomic knowledge is to regularly re-evaluate priorities by integrating the most up-to-date taxonomic knowledge. Our theoretical framework provides useful guidelines to evaluate how priority settings based on *expPD*, *expPDloss* and *HEDGE* scores are affected by the splitting of one species into two sister species. As illustrated for the Rhinocerotidae family, our theoretical framework can be applied to real-world studies, using estimates for the age of the post-split species to evaluate the impact of species splitting on species priority-setting. This would be helpful in situations where initial taxonomic work suggests that a species should be split, and this this preliminary finding is not yet taken into account in conservation practice. In such situations, application of our framework could help to decide if, under a precautionary principle, the conservation effort needs to be re-allocated among the potential post-split species. Such applications highlight the range of scenarios that may be considered. Although our framework currently treats the splitting of one species into two sister species, it could be easily extended in future studies to investigate more broadly the consequences of new taxonomic knowledge (e.g. species splitting, lumping, and discovery of truly undescribed forms) on priority-setting for conserving *PD* at risk.

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