Phylogenetic Diversity and Conservation Priorities under Distinct Models of Phenotypic Evolution

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Abstract: *Phylogenetics sometimes plays a major role in conservation planning, although there are still discussions about what to conserve, the evolutionary novelty revealed by adaptive process or the evolutionary potential expressed by neutral genetic divergence. I discuss the relationship between general models of phenotypic evolution and branch-length transformations used in phylogenetic diversity (PD) indices. Phylogenetic diversity based on molecular phylogenies will be satisfactory under a neutral model of evolution with constant divergence rates. If evolution of phenotypes occurs under stabilizing or directional selection, however, PD will overestimate and underestimate evolutionary diversity, respectively. I took into account phenotypic patterns in quantitative traits by finding ancestral states and, for each ancestral-descendent pathway, transforming branch length into amounts of phenotypic evolution before calculating PD. As an example, I applied the method in an evaluation of PD in the eight New World biodiversity hotspots. I based the evaluation on the phylogeny of terrestrial Carnivora and transformed and untransformed (time) branch lengths. In all hotspots, time-only PD values were larger than their respective phenotypic PD estimates, as expected if stabilizing selection drives most of body size evolution. Both PD estimates were highly correlated with species richness across the hotspots, but the priority ranks changed when loss of species restricted to one hotspot was considered. If phenotypic evolution usually occurs under stabilizing selection processes, conservation efforts and resources would be reduced and/or restricted to a few distinct species with high evolutionary rates, reflecting new adaptive peaks. This may be a liberal conservation strategy, however, compared with PD values calculated from time-calibrate supertrees or molecular phylogenies, and it is still necessary to understand how adaptive processes drive the evolution of complex phenotypes.*

Key Words: body size, carnivore, conservation priorities, hotspots, phenotypic evolution, phylogenetic diversity, supertree

Diversidad Filogenética y Prioridades de Conservación Bajo Diferentes Modelos de Evolución Fenotípica

Resumen: *La filogenética a veces juega un papel importante en la planificación de conservación, aunque aun hay discusión sobre que conservar, sobre la novedad evolutiva revelada por el proceso adaptativo y sobre el potencial evolutivo expresado por la divergencia genética neutral. Discuto la relación entre modelos generales de evolución fenotípica y transformaciones de longitud de rama utilizadas en índices de diversidad filogenética (DF). La diversidad filogenética basada en filogenias moleculares será satisfactoria bajo un modelo neutral de evolución con tasas de divergencia constantes. Sin embargo, si la evolución de fenotipos ocurre bajo selección estabilizadora o direccional, DF sobreestimará y subestimará la diversidad filogenética respectivamente. Antes de calcular la DF consideré los patrones fenotípicos en caracteres cuantitativos al encontrar estados ancestrales y, para cada ruta ancestral descendiente, transformar la longitud de rama en cantidades de evolución fenotípica. Como ejemplo, apliqué el método en una evaluación de DF en ocho sitios prioritarios para la biodiversidad en el Nuevo Mundo. Basé la evaluación en la filogenia de carnívoros terrestres y longitudes de rama transformadas y no transformadas (tiempo). En todos los sitios prioritarios para la conservación, los valores de DF de tiempo únicamente, fueron mayores que sus respectivas estimaciones DF fenotípicas, como se esperaba si la selección estabilizadora dirige la mayoría de la evolución del tamaño*

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corporal. Ambas estimaciones de DF estuvieron sumamente correlacionadas con la riqueza de especies en los sitios prioritarios para la conservación, pero las escalas de prioridad cambiaron cuando se consideró a la pérdida de especies restringidas a un sitio, Si la evolución fenotípica generalmente ocurre bajo procesos de selección estabilizadora, los esfuerzos y recursos de conservación se reducirían y/o se restringirían a unas pocas especies con altas tasas evolutivas, reflejando nuevos picos adaptativos. Sin embargo, esto puede ser una estrategia de conservación liberal comparada con los valores DF calculados de superárboles calibrados en tiempo o filogenias moleculares, y aun es necesario comprender como los procesos adaptativos dirigen la evolución de fenotipos complejos.

Palabras Clave: carnívoro, diversidad filogenética, evolución fenotípica, prioridades de conservación, sitios prioritarios para la conservación, superárbol, tamaño corporal

Introduction

Recently, phylogenetic and evolutionary patterns of variation among species and populations have begun to influence conservation priorities (Moritz 1994; Crozier 1997; Crandall et al. 2000). In this context, many algorithms and diversity indices have been proposed (Vane-Wright et al. 1991; Faith 1992, 1994; Crozier 1992) under the general reasoning that distinctiveness of a taxon (species) is inversely proportional to the relative number and closeness of its phylogenetic relatives. It is now clear that the advances in molecular systematics that have occurred in the last 20 years (Swofford et al. 1996; Pagel 1999; Sunnucks 2000) have contributed to the methodological and theoretical developments that allowed incorporation of evolutionary patterns and processes in conservation planning. However, there have been many recent discussions about using only neutral molecular markers to establish evolutionarily significant units (both within and among species), stressing that new tools must be developed to take into account more complex patterns of phenotypic evolution (Paetkau 1999; Crandall et al. 2000; Owens & Bennett 2000; Fraser & Bernatchez 2001; Diniz-Filho & Telles 2002; Pérez-Losada et al. 2002). The center of the debate is what should be conserved: evolutionary novelty (as measured by the amount of phenotypic divergence among species) or evolutionary potential (as measured through estimates of genetic diversity)?

In this context, Owens and Bennett (2000) recently proposed a new method to establish conservation priorities that "can be used to explore the evolutionary history of phenotypic variation" at a broad evolutionary scale. They also stated that previous methods, including phylogenetic diversity (PD) indices (Crozier 1992, 1997; Faith 1992, 1994; Crozier & Kusmierski 1994), implicitly assume that all interspecific divergences are equivalent and thus are inadequate for evaluating phenotypic diversity in an explicit phylogenetic framework. Faith (2002) responded to this criticism and pointed out that it must be applied only to old methods based only on counting nodes on a cladogram (i.e., Vane-Wright et al. 1991; for a recent application, see Posadas et al. 2001). Faith's (1992, 1994) PD index is calculated, for a given locality or region, through the sum of branch lengths involving the species that occur there (that can be compared with the PD for the entire clade or compared with localities within the entire region; see Sechrest et al. 2002). The index then reflects overall evolutionary diversity exactly because the branch lengths account for phenotypic changes.

Indeed, the original formulation of PD by Faith (1992) was based on cladograms, and the branch lengths were calculated specifically to incorporate distinct levels of anagenetic changes among the lineages (Faith 2002). Owens and Bennett (2000) may be right, however, if branch lengths used to calculate PD are based on phylogenies calibrated to give absolute times since divergence from a common ancestor, such as when dealing with the supertrees that have been published recently (Bininda-Emonds et al. 1999, 2002; for a recent application, see Sechrest et al. 2002).

When neutral genetic variation is conserved, PD calculated with branch lengths estimated from molecular phylogenies must reveal the correct amount of evolutionary diversity exactly, because methods to reconstruct phylogenies will take into account variations of (neutral) evolutionary rates across the phylogeny. However, assessments of genetic diversity with PD based on time-calibrated phylogenies, such as supertrees, will be biased because a constant rate of neutral divergence among lineages is assumed. For phenotypic traits, the situation is even more complex because evolutionary rates are not constant and because adaptive processes will create nonlinear relationships between phenotypic divergence and time (Hansen & Martins 1996). Thus, both phenotypic and genetic evolution will have a linear relationship with time only under a purely neutral (nonadaptive) model with constant evolutionary rates (Kimura 1983).

Previous attempts to account for the amount of phenotypic divergence to be used for establishing conservation priorities simply transformed branch lengths into amounts of divergence, expressed as the number of synapomorphies along each branch of a cladogram (Faith

1992, 1994; Williams et al. 1995). Although this strategy is in essence correct, in a more general analytical framework branch lengths can be mathematically transformed to explicitly take into account more complex patterns in phenotypic evolution, given a phylogeny with branch lengths expressed in time since divergence (for more explicit modeling, see Felsenstein 1988, Garland et al. 1992; Martins 1995, 2000; Hansen & Martins 1996; Martins et al. 2002). Under these transformations, Faith's (1992, 1994) PD is quite useful and probably the simplest strategy by which to evaluate evolutionary diversity in quantitative traits in a conservation context.

Here I discuss how branch-length transformations could be applied, in theory, to account for more complex models of phenotypic divergence based on time-calibrated phylogenies such as supertrees, showing how different models may affect PD estimates. There are practical difficulties in choosing parameters for these transformations. Therefore, I propose a simple way to incorporate patterns of quantitative divergence into Faith's (1992, 1994) phylogenetic diversity index by using methods for reconstruction of ancestral character state that must be applied to time-calibrated phylogenies. As an illustration, I applied the method to evaluation of the conservation of terrestrial Carnivora (Fissiped) in the eight New World biodiversity hotspots, based on both original branch lengths (expressed over time) and branch lengths transformed to express interspecific amounts of phenotypic evolution.

Branch Lengths and Models of Phenotypic Evolution

A purely stochastic process of phenotypic divergence among species is usually modeled with a Brownian-motion-like process in which the divergence between pairs of species (V_B) is expressed by the linear model

$$V_B = \beta t + \varepsilon,$$

where β is the evolutionary rate, t is the time (since the root), and ε is the error term. Biologically, this model can reflect a mutation-drift equilibrium neutral model or, less frequently, a directional selection process in which a trait quickly tracks random changes in environment (Hansen & Martins 1996). Evolutionary rate expressed by β is constant along the phylogeny. On the other hand, the evolution of complex quantitative traits, subject to multiple types of selection (especially stabilizing selection), may be better modeled by nonlinear models such as the Ornstein-Uhlenbeck process (Felsenstein 1988; Garland et al. 1992; Martins 1994, 1995; Hansen & Martins 1996; Hansen 1997), and in this case the relationship between divergence and time is expressed by

$$V_B = [(\sigma^2/2\alpha)(1 - \exp(-2\alpha t)] + \varepsilon.$$

Under this more complex model, the evolution of mean phenotypes generates a constrained variation in which this mean phenotype is pushed toward an adaptive peak but, at the same time, random drift causes fluctuation around it. Selection then acts like a rubber band, tending to return the population to the peak. The magnitude of this restraining force (α) can be interpreted as a measurement of stabilizing selection (Martins 1994; Hansen & Martins 1996), calibrated by the phenotypic variance (σ^2). In the Ornstein-Uhlenbeck model, V_B is related to t by an exponential decrease, which tends to zero between distantly related species. In fact, Brownian motion is a particular form of Ornstein-Uhlenbeck process in which α tends to zero.

Linking the two equations above leads to the conclusion that "time" can be distorted to account for nonlinear evolution, and in this case the time under an Ornstein-Uhlenbeck (OU) process is expressed by

$$T_{\mathrm{OU}} = [(\sigma^2/2\alpha)(\exp(2\alpha t) - 1] + \varepsilon.$$

In other words, "evolutionary time" assumes an exponential relationship with "real" time (measured in time or under a purely neutral model) if evolution of a trait occurs under stabilizing selection (Martins 1994). Inverting the reasoning, if a trait evolves faster than expected by a pure neutral model, under a strong directional selection, there would be a logarithmic relationship between evolutionary and real time (Fig. 1) (Faith 1994). In both cases, exponential or logarithmic transformations of branch lengths could then express these two general processes—stabilizing and directional selection, respectively—of phenotypic evolution (for more complex models and their biological interpretations, see Hansen & Martins 1996).

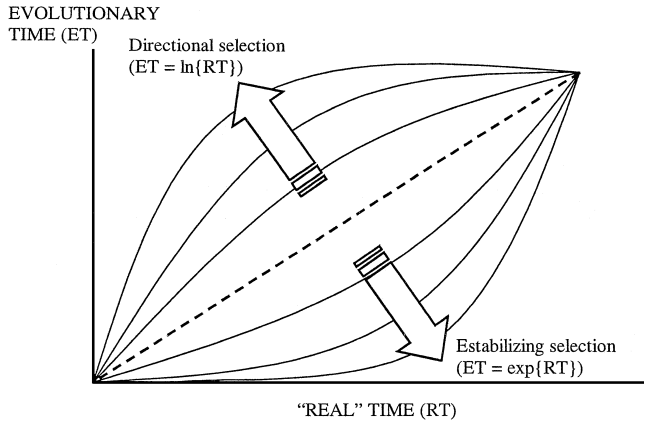

Figure 1. Models of phenotypic evolution, expressed as evolutionary time (in units of phenotypic change) against time. Different curvilinear lines express increasing magnitudes of directional and stabilizing selection, modeled by logarithmic and exponential functions, respectively.

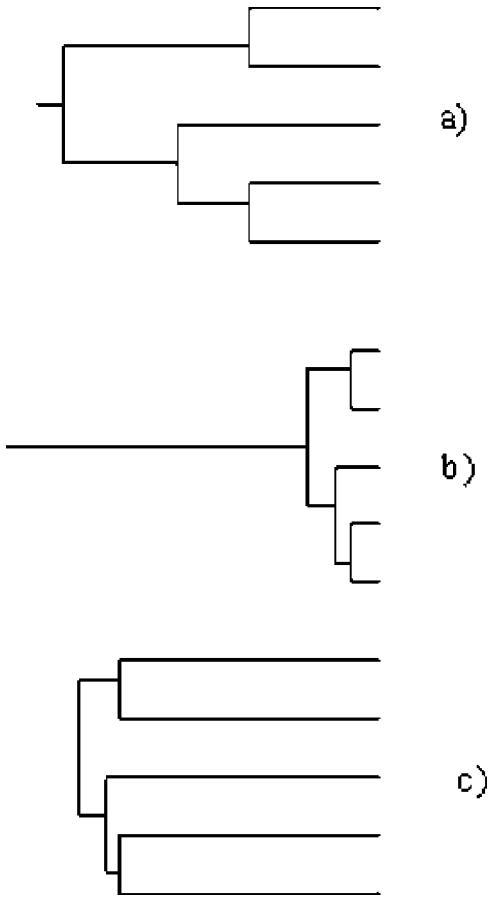

Figure 2. Short phylogenies illustrating the effect of evolutionary models on branch lengths: (a) in relation to a phylogeny with branch lengths proportional to time; (b) under stabilizing selection (branch lengths are shorter because changes are small as a result of constraints); (c) under directional selection (branch lengths are longer, expressing quick changes leading to different phenotypes in the same time).

It is easier to understand these transformations by using small phylogenies as examples (Fig. 2). Under a strong pattern of stabilizing selection, despite the fact that large original branch lengths are expressed in time (Fig. 2a), the phenotype does not change a lot because of the constraints imposed by selection. Species are quite similar, therefore, and branch lengths, expressing this phenotypic evolution, must be short (Fig. 2b). On the other hand, if evolution occurs under directional selection in the different lineages, leading each one to a new adaptive position in phenotypic space (an adaptive radiation), the branch lengths expressing this process must be larger than the "real" ones, and species tend to be independent (phenotypes cannot be predicted by phylogenetic relatedness among them) despite their short divergence in time (Fig. 2c).

Of course, these models are only crude and general approximations of reality, and in fact species must evolve under complex combinations of these processes in a macroevolutionary context, so it may be difficult to reconstruct these forces (Leroi et al. 1994). Mooers et al. (1999) pointed out the difficulties in expressing the mathematical parameters of these models in biologically meaningful terms (but see Martins et al. 2002). Many methods have been proposed to estimate the magnitude of the phylogenetic signal in data, but most of them try to measure, by different analytical strategies, only deviations from a pure Brownian-motion process (Martins 1994; Diniz-Filho et al. 1998; Abouheif 2000; Diniz-Filho 2001; Freckleton et al. 2002). Methods of quantitative evolutionary genetics (Lynch 1991) could also be used to infer whether evolution occurs under directional or stabilizing selection; but again, it must be assumed that a common process is driving phenotypic divergence across macroevolutionary time.

Despite practical difficulties in discovering the mechanisms of phenotypic evolution in different lineages (there can be no simple and unique model), the main point of the models described above is that branch lengths can be adjusted to express any model of phenotypic evolution of quantitative traits. Thus, assuming that the amount of evolutionary change should be interesting for conservation purposes, without these transformations PD will overestimate evolutionary diversity if phenotypic evolution occurs under stabilizing selection (because branch lengths that express the evolution of phenotype will be shorter than those used to calculate PD; Fig. 2b). Under directional selection, however, PD will underestimate phenotypic diversity (Fig. 2a). Of course, for conservation purposes, the last alternative is of much more concern.

If time-calibrated phylogenies or supertrees are available for organisms of interest, a simple approach would be to express branch lengths in amounts of phenotypic changes, obtained across all branches of the phylogeny and based on reconstructed ancestral states developed for comparative data analysis (for a recent review, see Martins 1999). After this transformation, PD values can be calculated in the usual way and compared with PD values based on a time-only model or with PD values obtained from molecular phylogenies (expressing neutral genetic variation with variable rates).

Time-Only and Phenotypic Diversity in Terrestrial Carnivora in New World Biodiversity Hotspots

To analyze how transforming branch lengths to amounts of phenotypic changes affects phylogenetic diversity estimates, I analyzed the species of terrestrial Carnivora living in the eight New World biodiversity hotspots (Myers et al. 2000) (Table 1). Geographic distributions for the 70 species (listed in Fig. 3) were calculated in the Worldmap grid, and species whose ranges overlapped the

Table 1. The eight biodiversity hotspots in the New World, with species richness for terrestrial Carnivora and magnitude of phylogenetic diversity.[a]

		Magnitude (%)		*Loss (%)[b]*	
Hotspots	*Richness*	PD_P	PD_N	PD_P	PD_N
Atlantic Forest	17	36.4	41.3	0.0	0.0
Cerrado	21	40.4	45.7	0.6	1.1
Chile	11	22.2	31.4	3.9	3.6
Andes	33	59.6	62.6	1.0	1.6
Ecuador	26	51.7	58.8	0.9	0.1
Mesoamerica	34	53.5	69.5	5.0	9.2
Caribe	15	41.0	47.8	0	0.0
California	20	50.8	54.8	9.4	4.7

[a] *Calculated by summing branch lengths expressed as amount of body-size evolution (PD_P, percentage of the total sum calculated for the entire species pool) and time in millions of years (PD_N, percentage of the total sum for the entire species pool).*
[b] *Amount of diversity losses, expressed as PD_P and PD_N, after excluding species that are restricted to each hotspot (in relation to the total amounts of PD_P and PD_N).*

hotspots were recorded for each hotspot (for details on the database used, see Diniz-Filho and Tôrres 2002). I used a generalized least-squares (GLS) algorithm (Martins 1999, 2000) to reconstruct the ancestral character states (and their standard errors) for log-transformed body mass for each ancestral species. I based the reconstruction on the supertree provided by Bininda-Emonds et al. (1999) (Fig. 3a) and used Compare version 2.0 to establish values for each node of the tree. I then estimated all ancestral-descendent divergences. I used body size as a surrogate variable to a model of phenotypic evolution, but other strategies should be used if more data are available (in previous research others expressed the overall amount of phenotypic divergence by counting the number of synapomorphies along each branch of a cladogram). For example, analyses should be repeated for each trait independently, and priorities should be combined a posteriori. Another strategy would be to replace original quantitative traits with a few scores derived from multivariate analyses, although this would be complicated by many missing data.

As previously discussed, PD calculated with branch lengths along the supertree is expected to express how diversity is conserved for neutral traits with constant divergence rates. Thus, here I call it time-only neutral phylogenetic diversity (PD_N). After each branch length is transformed to amounts of phenotypic evolution, the diversity must express more directly the phenotypic evolutionary diversity in body size (called here PD_P). I summed the branch lengths (transformed and untransformed; Table 1) for the Carnivora species present in the eight hotspots and expressed each sum as a percentage of the total PD_N and PD_P values for the 70 species. Following Sechrest et al. (2002), I also calculated the amount of evolutionary diversity restricted to a given hotspot in relation to all the other hotspots, which furnished a measure of the species' relative importance in terms of complementarity rather than richness.

Although the basic topology remained, there was a clear distortion after all branch lengths were transformed to amount of phenotypic changes (Fig. 3b). Although evolutionary rates of phenotypes across the phylogeny are usually slow, suggesting stabilizing selection, there were some clear peaks of strong directional selection that led to large differences in body size for closely related taxa.

Geographic ranges of only five species did not overlap the area of the eight hotspots, which accounts then for 94.2% and 95.7% of PD_P and PD_N, respectively, of the New World species. The PD_N values were higher than PD_P values (Table 1) in all hotspots, in such a way that standard PD overestimated the diversity of a non-neutral trait evolving at constant rates, as expected if a stabilizing selection drives body-size evolution. This overestimation was described recently by Diniz-Filho and Tôrres (2002), who showed that phylogenetic autocorrelation analyses of body mass in New World Carnivora corroborates an Ornstein-Uhlenbeck stabilizing selection process with a relatively small α parameter (see also Diniz-Filho 2001).

Based on PD_N, the most diverse region in the New World was Mesoamerica, which accounted for almost 70% of the evolutionary history of the species on the continent. Mesoamerica was followed by the Andes, with around 63%. With 31.4% of the evolutionary history, Chile was the poorest hotspot. Ranks based on PD_P were similar to those based on PD_N, and the two estimates were highly correlated ($r = 0.944$; $p < 0.01$), as expected, because both measure are intrinsically dependent on species richness ($r = 0.877$ for PD_P and $r = 0.922$ for PD_N; both $p < 0.01$). With PD_P, however, the Andes became the most diversified hotspot, accounting for around 60% of phenotypic evolutionary history. Thus, ranks for areas of conservation priority based on both measures of evolutionary diversity were similar and correlated with ranks based simply on variation in species richness.

It is also interesting, however, to evaluate the amount of PD restricted to a given hotspot. Out of the 65 species found in the eight New World hotspots, 20 were found in only one of them. Although the values of diversity loss are usually low (see Sechrest et al. 2002), the two estimates were not correlated ($r = 0.454$; $p = 0.259$), so PD_N was not usually higher than PD_P, and neither were intrinsically dependent on species richness ($r = -0.050$ for PD_P and $r = 0.390$ for PD_N; both $p > 0.05$). For PD_N, Mesoamerica was still the most important region, followed by Chile (which was previously considered a less important region, probably as a by-function of its low species richness). For PD_P, however, California became the most important hotspot because it accumulates a few species

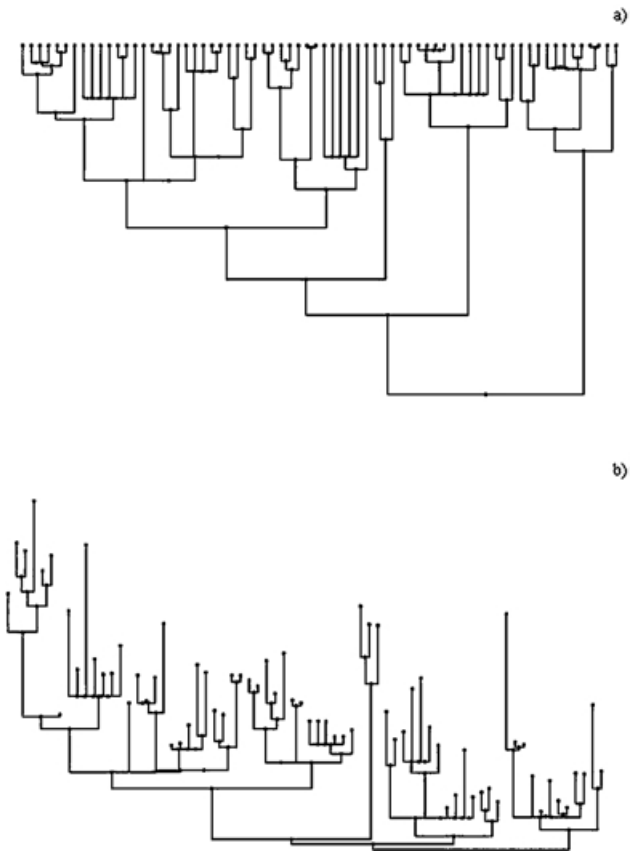

Figure 3. Phylogeny (supertree) of the 70 species of New World terrestrial Carnivora (based on Bininda-Emonds et al. 1999; see also Diniz-Filho & Tôrres 2002), with branch lengths expressed in (a) time and (b) amount of body size evolution. Species analyzed as shown (from left to right): Mustela nigripes, Mustela erminea, Mustela frenata, Mustela nivalis, Mustela africana, Mustela felipei, Mustela vison, Martes americana, Martes pennanti, Gulo gulo, Eira bárbara, Galictis cuja, Galictis vittata, Lyncodon patagonicus, Taxidea taxus, Lontra provocax, Lontra longicaudis, Lontra canadensis, Pteronura brasiliensis, Conepatus chinga, Conepatus leuconotus, Conepatus mesoleucus, Conepatus humboldtti, Conepatus semistriatus, Mephitis macroura, Mephitis mephitis, Spilogale putorius, Spilogale pygmaea, Procyon cancrivorus, Procyon lotor, Nasua narica, Nasua nasua, Nasuella olivacea, Bassariscus astutus, Bassariscus sumichrasti, Bassaricyon alleni, Bassaricyon beddardi, Bassaricyon gabbii, Bassaricyon lasius, Bassaricyon pauli, Potos flavus, Ursus arctos, Ursus americanus, Tremarctos ornatus, Canis lupus, Canis latrans, Pseudalopex culpaeus, Pseudalopex griséus, Pseudalopex gymnocercus, Pseudalopex sechurae, Pseudalopex vetulus, Atelocynus microtis, Cerdocyon thous, Chrysocyon brachyurus, Speothos venaticus, Vulpes vulpes, Vulpes velox, Urocyon cinereoargenteus, Panthera onca, Lynx Canadensis, Lynx rufus, Leopardus tigrinus, Oncifelis geoffroyi, Oncifelis guigna, Oncifelis colocolo, Oreailurus jacobita, Leopardus pardalis, Leopardus wiedii, Herpailurus yaguaroundi, Puma concolor.

with large amounts of phenotypic diversification (such as *Martes americana, Gulo gulo*, and *Ursus arctus*) (b).

Conclusion

The analyses I performed show that PD values estimated based on amounts of body-size evolution across the New World Carnivora phylogeny are smaller than the PD values estimated based on time only, although ranks were similar among hotspots. This is expected because, at least on a broad-scale evolutionary basis, body mass is probably driven by stabilizing selection with small restraining forces, which closely matches a neutral evolution process (Diniz-Filho & Tôrres 2002). However, part of the similarity between the two estimates of PD can be explained by their richness component. After this is taken into account by analyzing species restricted to a given hotspot, the ranks for conservation priorities changed and revealed that in some hotspots (such as California and Chile) high evolutionary diversity measured by PDP or PDN is not a simple consequence of species richness.

Because a low phylogenetic pattern is found in many ecological and life-history traits (Freckleton et al. 2002), as a result of both plasticity (or lability; sensu Gittleman et al. 1996) and strong stabilizing selection (Diniz-Filho 2001), my proposed method becomes important when dealing with phenotypic diversification based on supertrees or time-calibrated phylogenies. Indeed, in the example presented here, PD slightly overestimates phenotypic diversity because phenotypes are usually driven by stabilizing selection and fixed in adaptive peaks to evolve slowly under environmental changes, thus evolving slower than purely neutral traits with constant rates of changes among different lineages.

In theoretical terms, if evolution under a stabilizing selection were a common process for phenotypes (see Lynch 1991; Hansen 1997), conservation efforts and resources would be reduced and/or targeted to a few more distinct species with high evolutionary rates, reflecting new adaptive peaks (Owens & Bennett 2000). It is important, however, to consider whether accounting for these more complex models of phenotypic evolution is not a very liberal conservation strategy, considering the current biodiversity crisis. It is still necessary to understand how adaptive and neutral processes are involved in phenotypic evolution at different time scales, and the absolute need to incorporate phenotypic evolution into conservation priorities clearly depends on this balance.

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