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Contributed Paper

Selectivity in Mammalian Extinction Risk and Threat Types: a New Measure of Phylogenetic Signal Strength in Binary Traits

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Abstract: *The strength of phylogenetic signal in extinction risk can give insight into the mechanisms behind species' declines. Nevertheless, no existing measure of phylogenetic pattern in a binary trait, such as extinction-risk status, measures signal strength in a way that can be compared among data sets. We developed a new measure for phylogenetic signal of binary traits,* D*, which simulations show gives robust results with data sets of more than 50 species, even when the proportion of threatened species is low. We applied* D *to the red-list status of British birds and the world's mammals and found that the threat status for both groups exhibited moderately strong phylogenetic clumping. We also tested the hypothesis that the phylogenetic pattern of species threatened by harvesting will be more strongly clumped than for those species threatened by either habitat loss or invasive species because the life-history traits mediating the effects of harvesting show strong evolutionary pattern. For mammals, our results supported our hypothesis; there was significant but weaker phylogenetic signal in the risk caused by the other two drivers (habitat loss and invasive species). We conclude that* D *is likely to be a useful measure of the strength of phylogenetic pattern in many binary traits.*

Keywords: extinction risk, habitat loss, harvesting, phylogenetic selectivity, phylogenetic signal

Selectividad en el Riesgo de Extinción y Tipos de Amenaza en Mamíferos: una Nueva Medida de la Intensidad de la Señal Filogenética en Atributos Binarios

Resumen: *La intensidad de la señal filogenética en el riesgo de extinción puede proporcionar perspectivas acerca de los mecanismos subyacentes en la declinación de las especies. Sin embargo, ninguna medida existente del patrón filogenético en un atributo binario, como el estatus de riesgo de extinción, cuantifica la intensidad de la señal de modo que pueda ser comparada entre conjuntos de datos. Desarrollamos una nueva medida de la señal filogenética para atributos binarios,* D*, que en simulaciones proporciona resultados robustos con conjuntos de datos de más de 50 especies, aun cuando la proporción de especies amenazadas sea baja. Aplicamos* D *a la lista roja de aves británicas y de mamíferos del mundo y encontramos que el estatus de amenaza para ambos grupos mostró un agrupamiento filogenético moderadamente fuerte. También probamos la hipótesis de que el patrón filogenético de especies amenazadas por la cosecha estará agrupado más estrechamente que las especies amenazadas por la pérdida de hábitat o por especies invasoras porque los atributos de la historia de vida que intervienen en los efectos de la cosecha muestran un fuerte patrón evolutivo. Para mamíferos, nuestros resultados soportaron nuestra hipótesis; hubo señal filogenética significativa pero más débil en el riesgo causado por los otros dos factores (pérdida de hábitat y especies invasoras). Concluimos que* D *es una medida útil de la intensidad del patrón filogenético en muchos atributos binarios.*

Palabras Clave: cosecha, pérdida de hábitat, riesgo de extinción, selectividad filogenética, señal filogenética

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Introduction

Analyses of comprehensive assessments of species extinction risk reveal that risk is often not spread randomly across taxonomy or phylogeny. Rather, there is usually a significant tendency for risk to be concentrated within some major branches of a phylogeny, and for close relatives to share the same risk status. This nonrandom phylogenetic pattern in extinction risk holds true for many taxa, globally and within regions (e.g., Bennett & Owens 1997; Russell et al. 1998; Schwartz & Simberloff 2001; Stuart et al. 2004). Extinctions in the fossil record are also mostly nonrandom with respect to phylogeny (Mc Kinney 1997; Purvis 2008; Roy et al. 2009).

Phylogenetic pattern in extinction risk can give insight into the mechanisms of extinction or decline. A phylogenetically random risk pattern implies that species' fates are not largely determined by traits that show a strong tendency to take similar values among closely related species (e.g., body size or reproductive rate). Rather, extinction risk must then be shaped primarily by characteristics that do not show strong phylogenetic signal, such as the intensity of threat processes where species live. Conversely, a very strong phylogenetic pattern, in which threatened species are prevalent in some clades but not in others, implies high intrinsic susceptibility for those clades. Biological traits then play a direct or indirect role in determining species' extinction risk. Phylogenetic selectivity at smaller spatial scales, where geographical variation in threat intensity tends to be reduced, provides strong evidence for this scenario (Bielby et al. 2006; Davies et al. 2008).

Although the aim of many studies is to detect evidence of phylogenetic pattern by testing for significance, measuring the pattern's strength can additionally indicate what types of biological traits may be involved in determining risk. Considering different threat types and their phylogenetic signal strength may help separate the processes behind extinction risk. For example, in vertebrates, hunting pressure and species' ability to compensate for extra mortality are likely to reflect body size and reproductive rates, respectively (Bodmer et al. 1997); both these traits tend to show strong evolutionary pattern (Freckleton et al. 2002). On the other hand, susceptibility to a general driver of risk, such as habitat loss, may not depend strongly on life-history traits, but on ecological traits such as habitat specialization (Owens & Bennett 2000). These may be more evolutionarily labile, so their effects might show less phylogenetic signal.

Therefore, the strength of phylogenetic pattern is more useful than its significance for indicating which biological traits might successfully predict extinction risk for species or clades of unknown risk status (Kotiaho et al. 2005; Corey & Waite 2008) or for future scenarios of anthropogenic drivers (Cardillo et al. 2006; Bielby et al. 2008; Willis et al. 2008). Similar considerations apply to the study of invasion success, where success in each of the stages of invasion (arrival, establishment, and spread) might be caused by different traits with different levels of phylogenetic signal (Lockwood 1999).

For these reasons a statistically reliable measure of phylogenetic signal strength in variables such as extinction-risk status would be valuable. Most previous studies of phylogenetic pattern in extinction risk have concentrated on assessing the significance, rather than the strength, of phylogenetic signal (e.g., Bennett & Owens 1997; Purvis et al. 2000; Schwartz & Simberloff 2001; Bielby et al. 2006). Good measures of phylogenetic pattern in continuous traits such as body size are available (Freckleton et al. 2002; Blomberg et al. 2003), but these cannot readily be applied to binary traits such as risk status (threatened and nonthreatened). None of the existing methods applicable to binary traits provide a measure of signal strength that can be readily compared across data sets because they are sensitive to the prevalence of threat (Lockwood et al. 2002) or depend on phylogeny shape and the size of the data set (Webb et al. 2002).

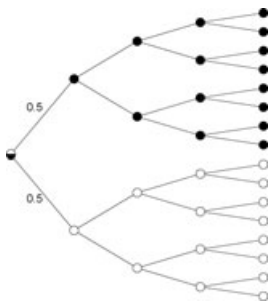
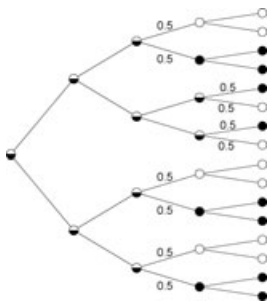
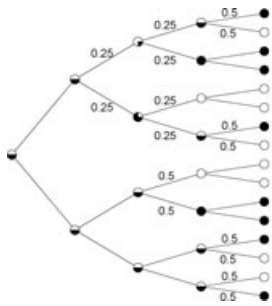
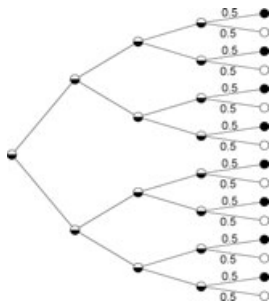
Because comparing the strength of phylogenetic selectivity among different threat types is of interest, as is testing for significance, our first aim was to introduce and test a new measure for phylogenetic signal strength in a binary trait such as risk status. We used simulations to assess performance of our new measure for phylogenetic signal strength, D, and compared significance testing of D with previously published results describing phylogenetic patterns in British birds of conservation concern (Thomas 2008). Our second aim was to use D to compare the signal strength in mammalian extinction risk caused by the three main types of current threat (habitat loss, harvesting, and invasive species) as recorded by the Global Mammal Assessment (IUCN 2008). We tested the hypothesis that extinction risk caused by harvesting shows stronger phylogenetic signal than risk from the other two main types because susceptibility to harvesting should be more strongly correlated to traits with strong evolutionary pattern, such as body size and reproductive rates (Bodmer et al. 1997; Owens & Bennett 2000).

Methods

Derivation of *D*

Our proposed measure for phylogenetic signal strength in a binary trait was based on the sum of sister-clade differences in a given phylogeny. Whereas a maximally clumped trait will be in the same character state in related species (at the tips of the phylogeny), an overdispersed trait may never be (Table 1). Consequently, the sum of sister-clade differences will be lowest for strongly clumped traits and highest for strongly overdispersed ones, everything else being equal. The actual amounts

Table 1. The calculation of *D* for different types of phylogenetic pattern in binary traits.

	Phylogenetic pattern[a]			
	extremely clumped	*clumped (Brownian)*	*random*	*overdispersed*
Phylogeny[b]				
Σd_{obs}[c]	1	5	6.5	8
D[d]	−2.4	0.0	1.0	1.9

[a] *The phylogenetic patterns shown are two extremes (phylogenetically extremely clumped and phylogenetically overdispersed), and two examples of the scaling expectations that were used to compute* D *(Brownian and random phylogenetic pattern). The Brownian phylogenetic pattern was generated under a threshold model (see Methods for details). Phylogenetically random patterns were generated by shuffling the tip values along the phylogeny.*

[b] *All branch lengths are set to 1 and trait prevalence is set to 0.5. Pie diagrams at the tips and nodes indicate species data and nodal values for the binary character in question, representing values between 0 (completely empty) and 1 (completely filled). We estimated nodal values as the weighted mean of descendant node or tip values (all weights are 1 in this example due to the chosen branch lengths). The sister-clade differences are then the differences between nodal values at each end of the branch. Branches are labeled with these values, unless their value is 0.*

[c] *Observed sum of sister-clade differences across the entire phylogeny.*

[d] *Observed sum of sister-clade differences minus the Brownian expectation divided by the difference between the random expectation and the Brownian expectation (see Methods for details). Expectations used in the calculation of* D *values are mean values from 1000 permutations (Brownian expectation: 4.93, random expectation: 6.58).*

will depend on the prevalence of the binary trait (the proportion of species in character state 1) and the size and shape of the phylogeny; these effects need to be removed to make the measure comparable among data sets.

At each internal node in the phylogenetic tree, nodal values for the binary trait were estimated, and the differences between each pair of sister clades were then summed across the whole tree to give the observed sum of sister-clade differences, Σd_{obs} (Table 1). Each nodal value was estimated as the mean of the values at its descendant nodes inversely weighted by the lengths of the branches leading to them (Felsenstein 1985); Σd_{obs} can also be computed as the sum of absolute differences between the two ends of each branch in the phylogeny. To place Σd_{obs} on a common scale comparable among data sets, we scaled it with the sum expected if the trait were phylogenetically random and the sum expected under a particular model of evolution.

Both expectations used to scale Σd_{obs} were generated with permutations based on the trait prevalence and the phylogeny of interest, which makes the scaled Σd_{obs} comparable between data sets (Table 1). Shuffling the species-trait values along the tips of the tree generated a distribution of sums of sister-clade differences expected for a random phylogenetic pattern, Σd_r (see Table 1 for an example). To generate the expectation under an evolutionary model, we simulated many continuous traits evolving along the given phylogeny independently under Brownian motion (i.e., in a random walk with constant trait variance over time [Felsenstein 1985]). For each such trait, we used a very simple threshold model to produce a binary trait with the same prevalence as seen in the observed data: species whose continuous trait value was below the threshold were scored as 0 and those above as 1, with the threshold chosen to give the required prevalence (see Felsenstein 2005 for discussion of a similar threshold model). From these many binary traits, we generated the distribution of sums expected under Brownian evolution, Σd_b. Clearly, extinction risk is not an evolved trait, but it is correlated with species traits that are, and our threshold model provides a way to scale our measure of phylogenetic signal strength under a specified evolutionary hypothesis.

We computed our measure of phylogenetic signal (or character dispersion on a phylogeny), D, by scaling the observed sum of sister-clade differences with the mean values of the two expected distributions as follows:

$$D = [\Sigma d_{obs} - \text{mean}(\Sigma d_b)]/[\text{mean}(\Sigma d_r) - \text{mean}(\Sigma d_b)].$$

The D statistic is equal to 1 if the observed binary trait has a phylogenetically random distribution across the tips of the phylogeny and to 0 if the observed trait is as clumped as if it had evolved by Brownian motion under our threshold model (Table 1). Values of D can fall outside this range. An analogy is the degrees-centigrade scale, which is also defined on the basis of two meaningful points (the freezing and boiling point of water, 0 °C and 100 °C)

that are not at either end of the possible range of values. Increasing phylogenetic clumping in the binary trait is indicated by values of D decreasing from 1. Our method also tests D for significant departure from 0 (Brownian expectation) and 1 (random expectation) by seeing where Σd_{obs} lies within the two expected distributions (Σd_b and Σd_r).

The sum of sister-clade differences has been used previously in assessments of phylogenetic pattern in extinction risk. Sjöström and Gross (2006) compare Σd_{obs} with Σd_r to test for phylogenetic nonrandomness in risk status. Davies et al. (2008) develop Σd_{obs} into a precursor of D, scaled such that a value of 1 corresponds to phylogenetic randomness. Nevertheless, neither of these approaches permit a direct comparison of phylogenetic signal strength among data sets.

We used functions from the package GEIGER (Harmon et al. 2008) in the statistical computing language R (R Development Core Team 2008) for our simulations. Our program to compute D in the R environment is publicly available as the function phylo.d, which is part of the Comparative analyses using independent contrasts (CAIC) package (Orme et al. 2009). We recommend 1000 permutations for computing both underlying D parameters because a small number of permutations affected the resolution of p values and the estimates of the Brownian expectation (data not shown).

Testing the Behavior of *D* with Simulated Data Sets

Using 1000 permutations throughout, we ran two sets of simulations. First, we evaluated the behavior of D within a range of known, underlying phylogenetic signals by investigating the relationship of D with Pagel's λ (Pagel 1999) for the underlying continuous trait in our threshold model. Pagel's λ estimates phylogenetic signal strength in a continuous trait; a λ of 0 indicates a trait is random with respect to phylogeny (i.e., there is no phylogenetic signal), whereas a λ of 1 is consistent with a trait that has evolved according to the Brownian motion model (Freckleton et al. 2002). We generated 100 random tree topologies of 100 extant species with the growTree function in CAIC (speciation rate 0.9, extinction rate 0.1 [Orme et al. 2009]) and used functions from the GEIGER package (Harmon et al. 2008) to simulate continuous characters with a given range of phylogenetic signal along those phylogenies. We varied values of λ from 0.0 to 1.0 in steps of 0.1. To convert the continuous traits to binary ones according to the threshold model, we set the trait prevalence to 0.3 to reflect the proportion of species at risk commonly found in real data sets.

To investigate how tree resolution affects D, we subsequently introduced polytomies (i.e., nodes with >2 descendants) into each simulated tree by collapsing internal branches picked at random until the resolution reached the desired level (0.9–0.5 in steps of 0.1). Resolution was calculated as the ratio of the number of nodes in the phylogeny to the number in a completely resolved phylogeny. For each resolution and each tree, we simulated traits with no ($\lambda = 0$) and strong ($\lambda = 1$) phylogenetic signal as above.

The second set of simulations investigated how D performed with tree topologies reflecting those that might be typically available (which are often more asymmetric than randomly grown trees [Mooers & Heard 1997]). We randomly sampled defined numbers (10, 25, 50, 75, 100, and 150) of mammalian species from a global list and obtained their topology and branch lengths from a published phylogeny of 5020 extant species (Bininda-Emonds et al. 2007; Fritz et al. 2009). Continuous traits with no ($\lambda = 0$) and strong ($\lambda = 1$) phylogenetic signal were simulated along these trees and converted to binary traits through the use of different levels of prevalence (from 0.1 to 0.9 in steps of 0.1). For each tree size, prevalence and λ, we computed D for 100 replicates.

Application of *D* to Red-List Status of British Birds and the World's Mammals

Thomas (2008) tested whether bird species in different categories of conservation concern (from Gregory et al. 2002) show phylogenetic signal according to their mean phylogenetic distance (MPD, see Webb et al. 2002). The MPD is the mean of the phylogenetic distances between each pair of species in the phylogeny that are ranked as character state 1, and its significance is assessed through randomizations. We estimated D for the maximum-credibility tree and the data on 181 bird species supplied by Thomas (2008) and compared significance results with MPD p values for the same maximum-credibility tree in order to test performance of D in detecting the presence of phylogenetic signal. Thomas (2008) uses the median MPD from a posterior distribution of phylogenies estimated with Bayesian phylogenetic methods, so our MPD results differ slightly from those reported by him.

We also used D to measure phylogenetic signal in extinction risk, threat, and risk status knowledge across the entire mammalian phylogeny, on the basis of data from the recently published Global Mammal Assessment (GMA, IUCN 2008). To compute D for threat status, we excluded species ranked as data deficient (Bielby et al. 2006) and defined at-risk species in two ways: species in the three threatened categories only (vulnerable, endangered, and critically endangered) and all species ranked above least concern (near-threatened and threatened categories [IUCN 2008]). Phylogenetic signal in knowledge of extinction-risk status was also assessed (species ranked as data deficient in the GMA vs. any other category). Additionally, we measured phylogenetic signal in the following threats as classified by the GMA: human-caused habitat loss or degradation, harvesting (hunting/gathering),

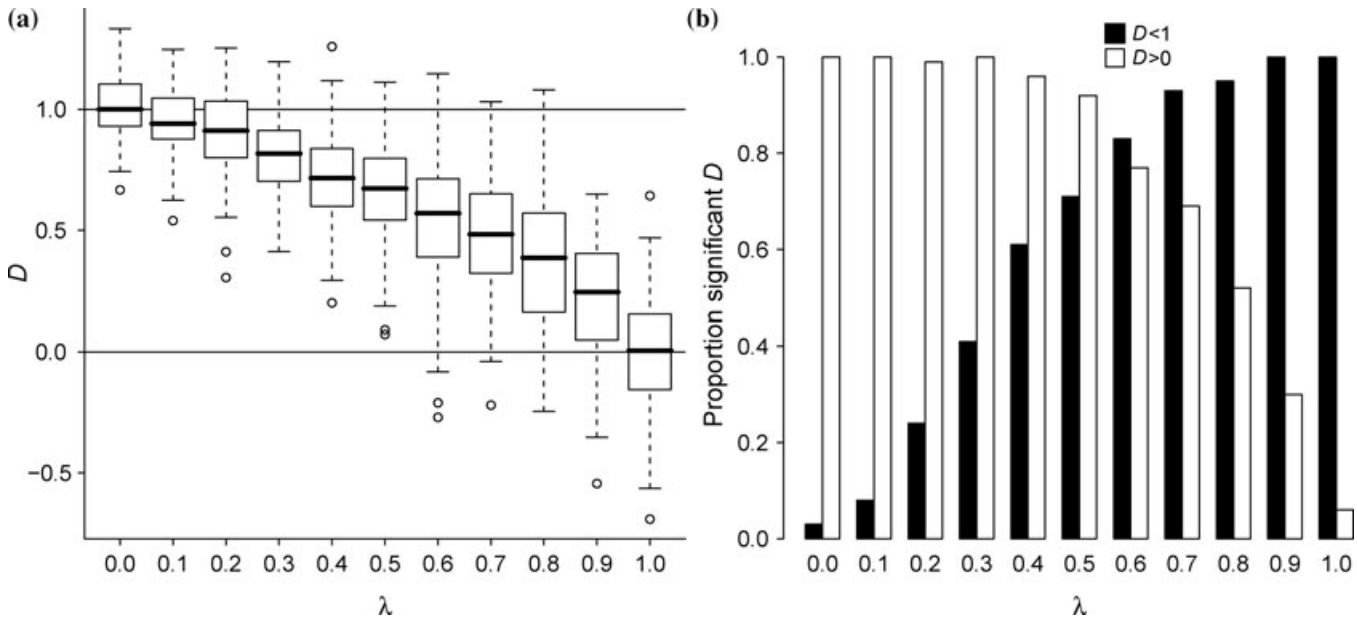


Figure 1. Behavior of D *(our new measure of phylogenetic signal) for a binary trait with different values of Pagel's* λ *(1999) for the underlying continuous trait: (a)* D *for different values of* λ *(long horizontal lines, expectations for* D*: 1 for a phylogenetically random trait [*λ *= 0] and 0 for a trait evolved under the Brownian model [*λ *= 1] [see Methods]); lines inside bars, medians; bottom and top of the boxes, first and third quartiles respectively; whiskers extend to either the maximum value or 1.5 times the interquartile range, whichever is smaller [circles outside these ranges are outliers]) and (b) proportion of significant* D *values for different values of* λ *(black, proportion of* D *values significantly <1 [i.e., significant phylogenetic signal]; white, proportion of* D *values significantly >0 [i.e., significant departure from Brownian threshold model]). Data were simulated with random tree topologies of 100 species. We simulated evolution of continuous characters with set* λ *values along these and ranked the top 30% of their values as state 1 for the binary character of interest.*

invasive alien species, unknown threats, and no threats. We tested each of these across all species (excluding only species with unknown threats where applicable) because the GMA lists threats for nonthreatened species as well. Because the threat types affecting threatened species might be better known or more faithfully recorded, we also assessed each threat-type pattern within the set of species ranked in any of the three threatened categories for overall extinction risk.

Results

The values of D for a binary trait and λ for its underlying continuous trait were strongly negatively correlated (Fig. 1a). The proportion of D values significantly <1 increased sharply with strength of the phylogenetic signal in the underlying continuous trait (Fig. 1b). The degree of tree resolution did not bias D in any consistent direction (Supporting Information). Nevertheless, when tree resolution was poor (60% or 50% resolved), variation in D estimates increased, and the proportion of falsely significant D values for both expectations was slightly elevated (to 7% and 8%, respectively; Supporting Information).

The D estimate was independent of tree size and trait prevalence if tree size was 50 tips or above (Fig. 2). Estimated D generally varied around 1 for a phylogenetically random trait and around 0 for a phylogenetically clumped one, although D was highly variable for small trees. Type I error rates for D were generally acceptable (Table 2), and D's power to detect phylogenetic signal was reduced only by a very low number of species and extreme prevalence.

Results of significance tests with D for 14 categories of conservation concern in British birds were very similar to those based on MPD (Table 3). Under a significance level of 0.05, MPD but not D indicated significant phylogenetic signal in green-listed species and species with a moderate decline in the U.K. breeding population. Neither of these show significant signal when calculating average MPD from the posterior distribution of trees, which is also the case for red-listed species ($p < 0.1$ for all three; Thomas 2008). Our D statistic showed that phylogenetic signal was strongest in species where most of the U.K. breeding population is concentrated in a few sites, followed by red-listed species and species showing rapid population

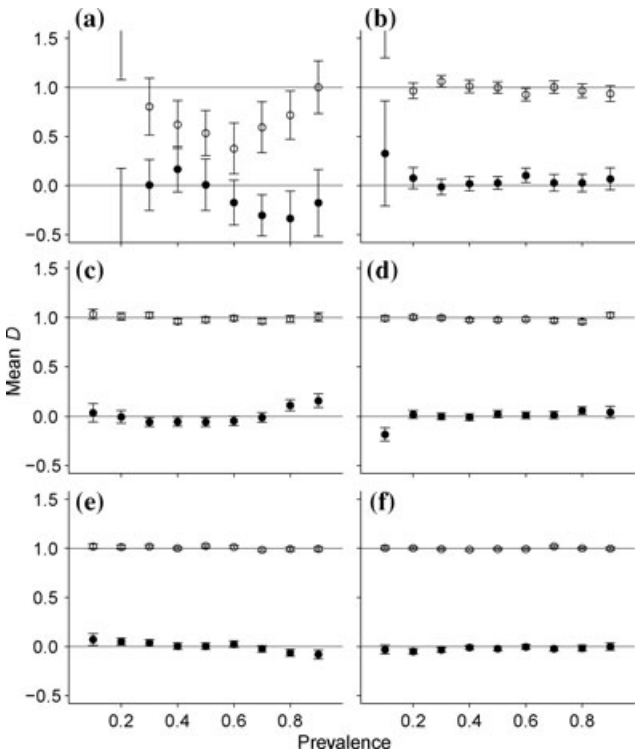


Figure 2. Performance of D *(our new measure of phylogenetic signal) for simulated binary traits with different tree sizes ([a] 10, [b] 25, [c] 50, [d] 75, [e] 100, [f] 150 species) and levels of prevalence. Means and standard errors of 100 replicates each are shown for simulated binary traits with no ($\lambda = 0$, unshaded) and very strong phylogenetic signal ($\lambda = 1$, shaded) in the underlying continuous trait (horizontal lines, expectations for* D*). All plots are scaled to the same y-axis extent for ease of comparison, so extreme means may lie outside the plot area. We ran simulations by picking the specified number of species at random from a phylogeny of most extant mammals, simulating continuous traits with set λ values along this tree, and computing* D *for binary traits scored on the basis of these continuous traits with the given prevalence.*

decline (Table 3). The signal for species breeding at few sites was so strong that it was indistinguishable from the Brownian threshold model (i.e., D was not significantly different from 0).

All tested extinction-risk categories and threat types in mammals were significantly phylogenetically clumped (Table 4). The D value was similar for species ranked above least concern and those ranked in any of the three threatened categories. The distribution of data deficient species showed weaker signal. Among known threat types, harvesting produced the highest degree of phylogenetic clumping as hypothesized; D was not significantly >0, indicating a signal as strong as if threat depended solely on an underlying continuous Brownian trait. Habitat loss produced the weakest signal of known threat types. Species categorized as not affected by any threat and species threatened by unknown threats also showed significant phylogenetic signal. These results were similar whether assessed across all evaluated species or only within species ranked as threatened.

Discussion

Statistical Performance of *D*

The simulations showed that our proposed measure for phylogenetic signal strength in a binary trait, D, performs well under the assumptions of the threshold model. The relationship between D for a binary trait and λ, the measure of phylogenetic signal for the underlying continuous trait (Pagel 1999), was much as expected from construction of the binary traits in the simulation process. Significance testing with D also worked well, and false positives were rare. The performance of D was not strongly affected by phylogenetic resolution, unless resolution fell below 70%. Our D statistic was not powerful for trees with fewer than 25 tips, and was only powerful for trees below 50 species if prevalence was not extreme. These limitations are comparable to the findings for λ in Freckleton et al. (2002) and were expected given the coarseness of the binary signal and the low number of tips involved. Above these thresholds, the value of D itself was independent of tree size and structure and trait prevalence, making it comparable across widely different data sets. Our new measure therefore improves on the conceptually similar one of Davies et al. (2008).

Our comparison of D and MPD for British birds highlighted the advantages of estimating signal strength as opposed to just testing its significance. Although p values derived from MPD and D agreed well overall, indicating presence or absence of phylogenetic signal, D additionally provided a measure of signal strength. For example, the D value for red-listed bird species indicated that clumping was moderately strong ($D = 0.56$), which fits well with global bird studies (Bennett & Owens 1997; Russell et al. 1998). Use of MPD on the same maximum-credibility tree rejected the null hypothesis of randomness, but not very strongly ($p < 0.05$), and provided no information on signal strength (although MPD could probably be standardized with randomizations as we did for Σd_{obs}). Interestingly, the median MPD for red-listed bird species from the posterior distribution of trees is marginally nonsignificant ($p < 0.1$), which leads Thomas (2008) to conclude that different threat types show conflicting phylogenetic patterns, making the overall pattern of extinction risk phylogenetically random. This difference between our and his conclusions serves as a reminder that slight changes in tree topology

Table 2. Results of the simulation of binary traits under our threshold model[a] that demonstrate significance testing with *D* (our new measure of phylogenetic signal in a binary trait).

	$\lambda = 0^b$						$\lambda = 1^b$					
Prevalence	*10*	*25*	*50*	*75*	*100*	*150*	*10*	*25*	*50*	*75*	*100*	*150*
D<1												
0.1		5	4	2	4	6		14	47	78	80	98
0.2	12	3	6	4	8	6	12	29	74	93	97	100
0.3	8	4	3	4	2	2	14	42	85	98	100	100
0.4	9	9	6	5	3	1	12	46	90	99	99	100
0.5	11	7	9	5	4	5	22	48	90	97	100	100
0.6	8	9	1	6	4	6	24	39	86	98	100	100
0.7	11	8	2	6	6	3	15	46	83	96	100	100
0.8	7	6	6	6	9	5	19	40	68	92	98	100
0.9	6	8	6	2	4	1	19	26	52	76	94	99
D>0												
0.1		14	38	58	82	96		11	7	1	5	4
0.2	13	21	69	89	96	100	17	5	7	1	4	1
0.3	6	40	82	97	100	100	4	4	2	2	5	2
0.4	12	46	82	100	100	100	9	4	5	4	5	5
0.5	13	52	84	98	100	100	4	2	6	6	4	2
0.6	18	40	88	99	100	100	4	6	5	5	8	6
0.7	13	44	76	96	99	100	4	5	8	5	2	3
0.8	14	29	67	89	96	100	5	6	8	6	3	4
0.9	12	17	50	73	88	100	4	7	6	6	2	4

[a] *We simulated binary traits for different* λ *values, different tree sizes (10, 25, 50, 75, 100, and 150 species; column labels), and different levels of trait prevalence (i.e., the proportion of species ranked as 1; row labels), as explained for Fig. 2, and we ran 100 replicates for each parameter combination. The table shows the counts of* D *values that were significantly different from 1 (*D *< 1) and 0 (*D *> 0) for each combination.*
[b] *In simulated traits with* $\lambda = 0$*, there was no phylogenetic signal, so* D *should not be significantly <1 (*D *= 1 for a randomly distributed binary trait) but should be significantly >0 (*D *= 0 for a binary trait under our Brownian threshold model). Simulated traits with* $\lambda = 1$ *have strong phylogenetic signal, so* D *should be significantly <1 but not significantly >0.*

may change phylogenetic patterns for binary traits quite dramatically.

The *D* statistic is useful because it considers all available information for each data set and is independent of trait prevalence and phylogeny size and shape. A similar measure of phylogenetic signal strength in a binary trait, Moran's *I*, is dependent on trait prevalence: Lockwood et al. (2002) suggest rarefaction methods as a solution, but these discard threatened species from the data set until the trait prevalence of all considered data sets is equal.

Table 3. Phylogenetic signal in different categories of conservation concern for 181 British birds tested with mean phylogenetic distance (MPD) from Thomas (2008) and *D* (our new measure of phylogenetic signal in a binary trait).

Conservation category[a]	N[b]	D	p *(*D *> 0)*	p *(*D *< 1)*	p *(MPD)*[c]
All red-listed species	32	0.56	<0.05	<0.01	<0.05
All amber-listed species	121	0.86	<0.001	n.s.	n.s.
All green-listed species	60	0.86	<0.001	<0.1	<0.05
Historical population decline[d]	8	0.95	<0.05	n.s.	n.s.
Historical population decline[d], includes recovering	13	0.70	<0.05	< 0.1	n.s.
Rapid decline in U.K. breeding population[e]	22	0.58	<0.05	<0.01	<0.01
Moderate decline in U.K. breeding population[e]	49	0.88	<0.001	n.s.	<0.05
Rapid contraction in U.K. breeding range[e]	6	1.26	<0.01	n.s.	n.s.
Moderate contraction in U.K. breeding range[e]	16	1.12	<0.001	n.s.	n.s.
Population size of 1–300 breeding pairs[f]	21	0.95	<0.001	n.s.	n.s.
≥50% of U.K. breeding population in ≤10 sites[g]	28	0.25	n.s.	<0.001	<0.05
≥20% of European breeding population in U.K.	14	0.76	<0.05	<0.1	n.s.
Lowest decile of population size	18	1.01	<0.001	n.s.	n.s.
Lowest decile of geographic range size	18	0.75	<0.05	<0.1	n.s.

[a] *Following Gregory et al. (2002).*
[b] *Number of species in the category in question (coded as state 1 for the binary trait).*
[c] *The MPD* p *values are from our reanalysis in which we used the maximum credibility tree from Thomas (2008).*
[d] *During 1800–1995.*
[e] *Rapid declines or contractions were ≥50%, moderate ones ≥25%; all were measured over the last 25 years.*
[f] *On the basis of a 5-year mean.*
[g] *Excludes rare breeders.*

Table 4. Phylogenetic patterns of extinction risk and threat in mammals as indicated by *D* (our new measure of phylogenetic signal in a binary trait).

	N[a]	*Prevalence*[b]	D	p *(D > 0)*	p *(D < 1)*
Risk rankings[c]					
above least concern	4275	0.31	0.637	<0.001	<0.001
threatened	4275	0.23	0.653	<0.001	<0.001
data deficient	5019	0.15	0.831	<0.001	<0.001
Threat classifications[c]					
habitat loss					
all species	4315	0.52	0.600	<0.001	<0.001
within threatened spp.	978	0.91	0.606	<0.001	<0.001
harvesting					
all species	4208	0.22	0.076	ns	<0.001
within threatened spp.	950	0.46	−0.006	ns	<0.001
invasive alien species					
all species	4204	0.07	0.464	<0.001	<0.001
within threatened spp.	952	0.17	0.527	<0.001	<0.001
unknown					
all species	4911	0.15	0.775	<0.001	<0.001
within threatened spp.	999	0.05	0.637	0.001	<0.001
no threats	4268	0.46	0.538	<0.001	<0.001

[a] *Total number of species with data and in the phylogeny.*
[b] *Proportion of species ranked as 1 for the binary trait.*
[c] *IUCN (2008).*

Moran's *I* is useful in investigations of taxonomic patterns of extinction risk, but *D* is a more comprehensive measure if a phylogeny is available. Cladistic approaches (e.g., tree-length distribution skewness and relative apparent synapomorphy analysis [RASA]) test for clearcut patterns, such as whole clades having the same trait values (Huelsenbeck 1991; Lyons-Weiler et al. 1996). Nevertheless, extinction risk usually shows more equivocal patterns; for example, *D* was nearly always significantly different from the Brownian expectation in both our bird and mammal results. Finally, Ives and Garland's (2009) phylogenetic logistic regression can be used to estimate phylogenetic signal in binary traits. Nevertheless, they assume a different underlying model, in which the probabilities of transitions between character states are constant throughout the whole phylogeny. The threshold model we used is likely to be more appropriate for binary characteristics, such as extinction risk and invasion success, that depend on continuous underlying traits.

Generally, *D* can be used as a measure for phylogenetic signal strength in any binary trait of interest, but users should be aware of the assumptions of the particular underlying threshold model (i.e., the binary trait of interest did not evolve itself, but its pattern across the phylogeny is based on one or more evolved, continuous traits). Although we developed *D* in the context of extinction risk, analogous considerations apply in other conservation issues. Invasion success, for example, depends on colonization, establishment, and spread, each of which may be underpinned by traits having different phylogenetic signal strength. Analysis of *D* might facilitate identification of the most important steps in the invasion process and traits associated with these (Lockwood 1999; Procheş et al. 2008).

Global Extinction Risk and Threat Patterns in Mammals

In agreement with previous studies (Russell et al. 1998; Purvis et al. 2000), we found highly significant phylogenetic selectivity in global mammalian extinction risk. We also found large differences in the strength of phylogenetic signal caused by different threat types. These differences confirm that different threats affect species via different processes and emphasize the importance of different threat types for understanding extinction-risk processes (Owens & Bennett 2000). They also support the suggestion that analyses of extinction-risk correlates should correct for phylogenetic effects with methods that can take variable amounts of phylogenetic signal into account (Freckleton et al. 2002; Purvis 2008; Fritz et al. 2009).

Threat caused by harvesting showed the strongest phylogenetic signal. In fact, the signal was indistinguishable from the phylogenetic clumping shown by a trait that evolved under Brownian motion according to the threshold model. This extreme signal is unlikely to be caused purely by spatial pattern in harvesting intensity; instead, it strengthens the hypothesis that hunting causes disproportionate declines in large, slowly reproducing species (Bodmer et al. 1997; Isaac & Cowlishaw 2004; Fa et al. 2005), given that body mass and life-history traits often fit the Brownian model of evolution (Freckleton et al. 2002). This suggests that intrinsic susceptibility to harvesting is more readily predicted from phylogenetic position alone than susceptibility to habitat loss or invasive species. If

trait information is lacking, phylogeny can therefore be used to predict, for example, risk from future harvesting for species in wilderness areas on the basis of their relatives' risk from current harvesting in more utilized regions. Such predictions may be useful when attempting to choose conservation targets where infrastructure is growing rapidly (e.g., Soares-Filho et al. 2006).

Contrary to expectations from previous studies in birds (Owens & Bennett 2000; Thomas 2008), all other types of threats tested were also phylogenetically patterned in mammals. Of the threats we examined, threat caused by habitat loss was least phylogenetically clumped, but its clumping was still as strong as for overall threat. These results may imply that even a general driver, such as habitat loss, targets certain biological traits, leading to disproportionate extinction risk for some clades. Previous studies of biological extinction-risk correlates in mammals that have separated different types of threats have been of narrow taxonomic or spatial focus or have concentrated on the effects of hunting (Isaac & Cowlishaw 2004; Price & Gittleman 2007). Habitat loss is the greatest current threat to biodiversity and will probably continue to have large effects, although climate change may cause more species extinctions in the future (Mace et al. 2005). Therefore, gaining an understanding of the biological traits that make species susceptible to habitat loss may help conservation efforts be effective.

The phylogenetic clumping of species threatened by habitat loss, invasive species, and unknown threats is likely to be partly due to geographical differences in the degree of habitat loss because of spatial clustering of related species and clades (Bielby et al. 2006; Davies et al. 2008). Similarly, species not currently affected by any known threat could be intrinsically less susceptible to ongoing threats or live in places that are currently "safe"—either could cause phylogenetic pattern. Studies on smaller geographic scales could resolve the respective roles of biological traits and geography, but are often impeded by small sample size. A different approach is to estimate the strength of phylogenetic and spatial signal in extinction risk in a single analysis in order to separate the relative contributions of both. A recently published study (Freckleton & Jetz 2009) introduces a new method to perform this kind of analysis, but this is currently only applicable to continuous traits.

Our results show that our new measure for phylogenetic signal strength in a binary trait, *D*, performs well with reasonable sample sizes, takes the whole phylogeny into account, and is comparable across different sizes of phylogeny and levels of trait prevalence. Strong phylogenetic signal in both British birds of conservation concern and global mammalian extinction risk and threat types confirms that biological traits directly or indirectly determine species' fates. The traits that increase susceptibility differ among threat types in mammals, with risk from habitat loss being much less dependent on traits with strong phylogenetic signal than risk from hunting.

Our results highlight a need to investigate the phylogenetic signal caused by different threat types at smaller spatial scales in order to disentangle the respective roles of biological and geographical variation. Also, future studies trying to predict species, clades, or areas of conservation concern from biological traits and anthropogenic threats should consider different threat types where possible and use phylogenetic methods that account for varying amounts of phylogenetic signal. We conclude that *D* will be a useful tool for studying the significance and strength of phylogenetic signal in many kinds of binary traits, but especially those that are likely to show equivocal phylogenetic patterns, such as extinction risk, invasion success (Lockwood 1999), or presence and absence in a community (Cavender-Bares et al. 2009).

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Supporting Information

A figure showing the relationship of our new measure for phylogenetic signal, *D*, with tree resolution (Appendix S1) is available as part of the online article. The authors are responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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