LINEAGES THAT CHEAT DEATH: SURVIVING THE SQUEEZE ON RANGE SIZE

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Evolutionary lineages differ greatly in their net diversification rates, implying differences in rates of extinction and speciation. Lineages with a large average range size are commonly thought to have reduced extinction risk (although linking low extinction to high diversification has proved elusive). However, climate change cycles can dramatically reduce the geographic range size of even widespread species, and so most species may be periodically reduced to a few populations in small, isolated remnants of their range. This implies a high and synchronous extinction risk for the remaining populations, and so for the species as a whole. Species will only survive through these periods if their individual populations are "threat tolerant," somehow able to persist in spite of the high extinction risk. Threat tolerance is conceptually different from classic extinction resistance, and could theoretically have a stronger relationship with diversification rates than classic resistance. I demonstrate that relationship using primates as a model. I also show that narrowly distributed species have higher threat tolerance than widespread ones, confirming that tolerance is an unusual form of resistance. Extinction resistance may therefore operate by different rules during periods of adverse global environmental change than in more benign periods.

KEY WORDS: Climate change, diversification, extinction, fragmentation, geographic range size.

The diversity of species is the product of extinction and speciation in evolutionary lineages. A classic puzzle is why some lineages (e.g., families) are so much more species-rich than others (Stanley 1979; Marzluff and Dial 1991; Barraclough et al. 1998; Jablonski 2007). When two lineages are of the same age, differences in their species-richness must indicate differences in their extinction and speciation rates. It follows that any heritable trait influencing extinction or speciation might help to explain lineage diversity.

Large geographic range size has been extensively associated with reduced extinction risk, and more recently with a high diversification rate (Jablonski 1995; Gaston and Blackburn 1997; McKinney 1997; Owens et al. 1999; Purvis et al. 2000; Cardillo et al. 2003). However, range sizes fluctuate enormously over short evolutionary time periods, especially in response to cycles of global climate change (Overpeck et al. 1992; Webb and Bartlein 1992; Cronin et al. 1996; FAUNMAP Working Group

1996; Davis and Shaw 2001). During environmentally adverse periods of change such as glaciations, species can be reduced to small remnant areas of habitat that are themselves broken up into even smaller fragments (Vrba 1992; Webb and Bartlein 1992; FAUNMAP Working Group 1996; Haffer 1997; Dynesius and Jansson 2000; Davis and Shaw 2001; Bonaccorso et al. 2006), with classic glacial "refugia" being an extreme example of this process (Haffer 1997). However, fragmentation of geographic range and confinement to small areas can commonly occur outside of glacial maxima as well (Vrba 1992; Jansson and Dynesius 2002).

Although refugial remnants were originally posited as oases against extinction for the species occupying them (Haffer 1997), species reduced to a few populations in small remnants during periods of global environmental change must face significant extinction pressures. Species are generally range-restricted at such

moments, whatever their time-averaged or time-point range sizes, and range restriction increases extinction risk (Jablonski 1987; McKinney 1997). In addition, it is now known that populations confined to remnant habitat areas face a high risk of extinction in ecological time, due to increased vulnerability to environmental stochasticity and local catastrophes (especially when restriction to a small area also implies reduction to a small population size) (MacArthur and Wilson 1967; Diamond 1984; Gilpin and Soule 1986; Simberloff 1986b; Lande 1993; Lawton et al. 1994; Newmark 1995; Cowlishaw 1999; Harcourt and Schwartz 2001). Indeed, island biogeography theory (MacArthur and Wilson 1967) has clearly demonstrated that if an area of habitat such as forest is reduced in size and fragmented, then the remnant piece of habitat must lose species over time in a process known as "relaxation" (Brown 1971; Diamond 1972; Simberloff and Abele 1975; Terborgh and Winter 1980; Diamond 1984). Very small populations in remnants may even be at risk of extinction from loss of genetic variation if the isolation is prolonged (Gilpin and Soule 1986).

The set of extinction pressures described above may occur repeatedly as species' distributions wax and wane, and so the ability to survive temporary periods of high risk, here abbreviated to "threat tolerance," may have a significant influence on species' longevity, and so on lineage diversity.

THREAT TOLERANCE AND CLASSIC EXTINCTION RESISTANCE

Threat tolerance is conceptually different from the well-studied type of extinction resistance associated with a widespread geographic distribution. In particular, the two types of extinction resistance imply different relationships between population extinction and species extinction, and large differences in population-level susceptibility. In a widespread species, it is unlikely that all populations will be simultaneously threatened. The species as a whole then persists because at least one population somewhere escapes from each threat (remains untouched by it) (Simberloff 1986a). Temporary population losses can later be replaced by immigration from other populations in nonthreatened areas (Brown and Kodric-Brown 1977; Lomolino 1986). Individual populations can therefore be highly susceptible to threat, but this is unimportant to species persistence. I will refer to this type of extinction resistance as "escape" or "classic extinction resistance." Threat tolerance, on the other hand, means that a population is under direct extinction pressure in situ but persists in the face of the danger, rather than because it is far away from the danger. The species persists because its individual populations have a surprisingly low susceptibility to direct extinction threats.

For example, if widespread species A consists of 20 populations and narrowly distributed species B consists of two populations, then classic extinction resistance makes A less likely to go extinct than B. However, if global change reduces both A and B to a single small population in a limited area, then the species better able to directly tolerate the consequently high extinction threat will have the higher probability of persisting.

EXTINCTION RESISTANCE AND LINEAGE DIVERSITY

Intuitively, one might expect any mechanism that lowers extinction to lead to high species diversity in a lineage. But this is not necessarily a robust assumption. Lineages that have low rates of extinction also tend to have low rates of speciation (Stanley 1979), and there is therefore no a priori reason to believe extinction-resistant lineages should be more diverse than high-turnover lineages. In general, no consistently strong link has been found between classic extinction resistance and lineage diversity. Indeed, the traits associated with classic extinction resistance, such as large geographic range size and generalism, are often found in species-poor, slowly diversifying lineages (Stanley 1979; Vrba 1992; Jablonski and Roy 2003; Hernandez Fernandez and Vrba 2005b). This is perhaps because the very traits that make species extinction-resistant also potentially sabotage the speciation process; for example, high dispersal (characteristic of widespread species) and the occupation of many habitat types can make it difficult for one population to become reproductively isolated from the rest of the species.

Tolerance could potentially have a much stronger relationship to lineage diversity than classic extinction resistance does, because it lowers extinction rates without a compensatory sabotaging of speciation rates. Reproductively isolated populations that could become new species will often be small and (by definition) spatially isolated. But if they are to achieve full species status, these isolates must first survive thousands of years of the very extinction risks implied by smallness and isolation (Stanley 1979; Glazier 1987; Allmon 1992). Tolerance will therefore raise the effective rate of speciation (defined as the rate of creation of reproductively isolated populations, multiplied by the rate at which these reach full species status), by reducing population extinction rates. Indeed, tolerance should be seen as an extension of the Stanley–Glazier–Allmon theory of selection on small founder populations.

SCOPE OF THIS STUDY

Theoretically, there may be several types of tolerance to various different extinction threats. I chose here to study tolerance of periodic contraction and fragmentation of geographic range, because this is one of the more widely documented extinction pressures over prehistoric time and so likely to strongly influence extinction in lineages (Vrba 1992; Webb and Bartlein 1992; FAUNMAP Working Group 1996; Haffer 1997; Dynesius and Jansson 2000; Davis and Shaw 2001; Bonaccorso et al. 2006); because several decades of ecological literature have made advances in working

out the extinction responses of populations in such a situation (Brown 1971; Diamond 1972, 1984; Simberloff and Abele 1975; Terborgh and Winter 1980); and because of its current relevance to the anthropogenic climate change crisis.

This aspect of threat tolerance has been frequently addressed at the population level by island biogeographers and conservation ecologists (Diamond 1984; Henle et al. 2004). To my knowledge, however, there has been no test for an evolutionary relationship between tolerance and lineage diversity, and I test that relationship in primates here. Nor has much attention been paid to the large conceptual difference between the mechanisms of classic extinction resistance and the mechanisms of tolerance. I also show that surprisingly, tolerance is higher in geographically rare species than in widespread species, implying the underlying mechanisms are indeed very different. The rules of extinction may therefore change dynamically as planetary climate fluctuates, creating a shifting balance in the selective advantages enjoyed by different lineages.

Methods

As described above, threat tolerance is likely to be a population-level attribute, even though its effects may be detectable at the level of species and lineages. As a model system to test threat tolerance in species that have been reduced to small habitat remnants by climate change, I studied primate populations trapped on small islands of habitat ("landbridge islands") that became cut off from the mainland coastal habitat ~10,000 years ago, when climate change caused the extensive melting of planetary ice and raised sea levels over 100 m (Rohling et al. 1998). In other words, the islands are small fragments of the formerly continuous mainland coastal habitat that have suffered ~10,000 years of isolation. The trapped populations have been subjected to the multiple extinction threats associated with limited range size and reduced population size up to the present day (Lande 1993; Lawton et al. 1994), and would also have been unable to migrate in response to environmental change. I assume these extinction threats are reasonably analogous to the threats faced by refuge or isolate populations during other periods of range reduction and fragmentation, especially that associated with climate change.

ASSESSING SPECIES' POPULATION-LEVEL TOLERANCE

I used primates as a model because global primate distributions on both mainland and islands are well known. Also, postisolation recolonization of islands from the mainland would obscure patterns of tolerance by reviving failed populations (Brown and Kodric-Brown 1977; Lomolino 1986). Primates rarely cross ocean gaps, and so minimize this potential confound (Heaney 1986; Abegg

and Thierry 2002). Finally, a complete, dated, modern phylogeny exists for the primates (Vos and Mooers 2006), allowing comparison of lineage tolerance with lineage diversification rates.

I searched the literature for landbridge islands that contain at least one primate species (or that contained a species that has recently been extirpated by man). Where one source recorded a species on an island and another did not, I treated the species as being present on the island. *Macaca fascicularis* was omitted because it has been widely observed to cross ocean gaps, mixing island and mainland populations (Abegg and Thierry 2002). The decision as to whether *Macaca assamensis* and *Hylobates concolor* were present on islands depends on a very limited number of fairly old historical records (from early in the 20th century), and so analyses were run with and without these two species' lineages. I discarded any islands that lay close to river deltas, because they probably do not have isolated populations (primates would cross the intervening ocean on vegetation rafts swept downstream). I also discarded any islands less than 3 km offshore, to further ensure that the islands contained well-isolated populations. I omitted the very large islands of Sri Lanka and Hainan: Sri Lanka is so large as to have endemic species different from mainland congeners, complicating assessment of extinction, and Hainan (34,000 km^2) was subjectively judged too large to represent meaningful range restriction. After these discards, a total of 62 primate-occupied landbridge islands remained (Table S1 and Supporting Information).

It can reasonably be assumed that for a non–sea-crossing taxon such as primates, species currently on the island today must also have been present at the island's moment of isolation from the mainland, and have survived the intervening period. The island's modern-day species are therefore classified as "tolerant" of the extinction pressures associated with prolonged restriction to a small habitat remnant created by climate change. The next step is to define the "intolerant" species that were originally trapped on the islands but have since gone locally extinct and are no longer found there today.

HOW MANY EXTINCTIONS OCCURRED ON EACH ISLAND?

For most taxa including primates, fossil evidence is too incomplete to assess either the exact number or the identity of the species that went extinct following landbridge island formation, and so a model of local extinctions must be used instead (Diamond 1984; Harcourt and Schwartz 2001). The pioneering and still widely used model assumes that any species found on the mainland opposite the landbridge island, but not found on the island itself, has gone extinct from the island (Brown 1971; Diamond 1984; Harcourt and Schwartz 2001). However, critics have often pointed out that a small area of land (the proto-island in this case) is unlikely to have held every species present on the much larger

mainland (Simberloff and Abele 1982; Haila and Jarvinen 1983; Bolger et al. 1991).

I therefore took two approaches. The first, which will be referred to as the "full species set analysis," took the traditional approach of assuming that all missing mainland species represent local extinctions. The second, the "reduced species set analysis," sought to incorporate criticisms of this approach and assumed that only some of the missing mainland species represent true local extinctions. The reduced species set model calculates a reduced number of extinction events for each island, by estimating the initial species richness on each island and subtracting the current-day species richness. A reasonable first approximation of an island's initial species richness (at the moment it was cut off from the mainland) is the number of species found in an island-sized area of the mainland coast (Haila and Jarvinen 1983).

Unfortunately, however, surveys of several local mainland plots at a scale relevant to the islands are almost never available. The species–area information available with which to estimate the original primate species richness on the island is usually limited to counting the species that coarse-scale range maps indicate should occur in the coastal area immediately opposite the island. Even where the species richness of a few mainland communities is known, the slope of the species–area relationship derived from these communities may be subject to considerable uncertainty, limiting its usefulness as a rigid model parameter (Simberloff and Abele 1982; Boecklen and Simberloff 1986).

I therefore assumed that the unknown number of species in an island-sized area of mainland coast can be estimated from the known species richness of the region by using the established mathematical species–area model, $S = cA^z$ (Preston 1962; MacArthur and Wilson 1967; Soberon and Llorente 1993; Leitner and Rosenzweig 1997). S is species richness, A is the area sampled in square kilometers, and z is a coefficient typically taking values between 0.10 and 0.20 (Preston 1962; MacArthur and Wilson 1967; Leitner and Rosenzweig 1997).

The number of species statistically expected in a small area S_i can then be estimated as

$$S_i = N \times (A_i/M)^z, \qquad (1)$$

where S_i is the number of species on the island at the moment of isolation, A_i is the area of the island, and N is the number of species whose range maps overlap the mainland coastal point opposite the island. In sampling on the ground, a small area sample at the coastal point will not contain all N species even though their range maps suggest they should all be present. As one samples an increasingly large area, the probability of all N species being contained in the sample increases. M represents how big a sampling quadrat would need to be empirically to be reasonably sure that it included of all N species.

N and A_i are known (A_i is assumed to be similar to the value in the present day), and I fitted models using z-values of 0.10, 0.12, 0.14, 0.16, and 0.18. If M were known for certain, equation (1) would reduce to the equation developed by Pimm and Askins (1995) to calculate expected species losses in a reduced area. However, the size of quadrat M needed to capture all N species is uncertain, and may be quite large because of the existence of large "holes" of zero density in species' distributions (Hurlbert and Jetz 2007). Nevertheless, the value of M must be constrained by biological realism, and this allows limiting conditions to be set. As M becomes smaller, the model starts to predict that the island originally had more species than the mainland does today. This is highly improbable in a relaxing system, and the first condition disallows any model in which this occurs. As M increases, the model predicts that species richness has actually grown on more and more islands—"negative extinction," whereas species richness should decrease or not change in a relaxing system. (Stochastic variation in the original species richness of the island may sometimes create this artifact empirically, but it is undesirable that the model should predict it in more than a few cases.) I chose the minimum value of M, therefore, because this minimizes the number of islands on which negative extinction is predicted.

I searched in increments of 500 km^2 for the minimum value of M for each z. M values used for each z in the basic model were 6000, 6500, 7000, 7500, and 8000 km^2 (for $z = 0.10, 0.12, 0.14, 0.16$, and 0.18). This effectively means that only islands greater in size than M (such as Bangka, 11,900 km^2) can be assumed to have originally contained all the species that range maps suggest should be present in the area. For all islands smaller than M, the fraction of missing species regarded as true extinctions can be seen for each island size in Figure 1. The total number of local (island) extinctions events predicted using equation (1) varied between 35 and 75 with variation in z.

I checked the sensitivity of the number of predicted extinctions to variation in the value of M. Variability in M has little impact on model outputs, because predictions for the number of extinctions must be rounded to the nearest whole species. For example, the median size of the islands used to calculate M is 290 km^2, and the average mainland species richness (derived from rangemaps) is five species. For a z value of 0.14, any M value between 3800 and 40,000 predicts that the median-sized island once contained three species.

It is possible that species have gone extinct from both the mainland control areas and the islands (invisible extinctions). In the model, this would mean that the number of extinction events on islands was underestimated, potentially distorting the choice of M and altering predicted values overall. I tried artificially incrementing mainland species richness by 33% and recalculating M. This 33% change caused M values to be augmented by 1000 km^2, but this creates a difference of only 1–2% in the number of local
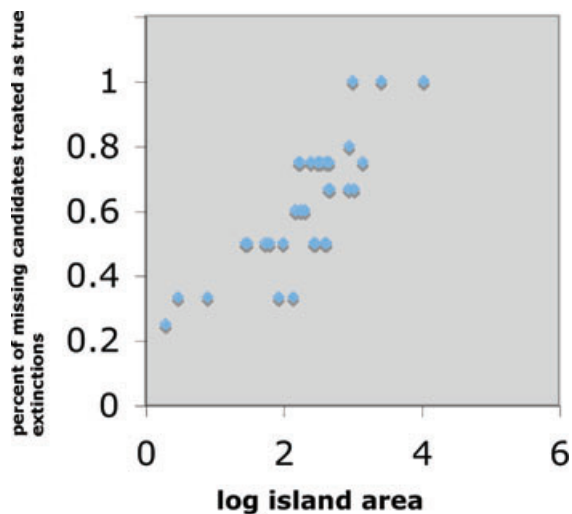
Figure 1. The proportion of missing mainland species assumed to represent true extinctions on islands, as a function of island size. The scenario shown is for $z = 0.10$. Islands where no extinctions were predicted have been omitted from the figure because a percentage of zero is undefined.

extinctions predicted (increasing to 4% for $z = 0.10$ only). Invisible extinctions will therefore have a minimal impact on predicted number of extinctions (further effects of invisible extinctions on hypothesis testing are addressed in the discussion).

The number of species predicted on an island from equation (1) is the statistical expectation only, that is, it assumes that the island would represent a point lying directly on the regression line from the species–area relationship. Microhabitat differences between areas and chance will introduce scatter about this expectation (Boecklen and Gotelli 1984). I added an error term to the above model, yielding $S = N * (A_i/M)^z + \varepsilon$, and derived a different species-richness prediction stochastically for each island in each of 1000 runs of the model. The error term ε was drawn randomly from a normal distribution with its mean set to the regression expectation, and where two standard deviations represented a 33.4% variation from the mean. This level of variation is consistent with empirical plots of error species/area sampling plots (Soberon and Llorente 1993; Hill et al. 1994) and is large enough to create variation in expected extinctions even for smaller low-diversity islands (small diversity numbers require fairly large variation to cause addition or subtraction of whole numbers of species after rounding). Where the error term caused a prediction that exceeded mainland species richness, the predicted species richness was set as equal to mainland species richness. Negative predictions were set to zero.

The overall assumption in the model is that, because landbridge islands at the moment of formation were parts of the mainland coast, then they should have had similar habitat to the coast. However, most primates are forest species, and area of forested habitat may be a better predictor of species richness in a plot than

the gross size of the island itself. There is insufficient evidence to estimate even roughly the area of forest habitat available on each island 10,000 years ago, although forested area was probably reduced in the dry late Pleistocene/early Holocene (Meijaard and van der Zon 2003; Bird et al. 2005). The larger z-values in the model reduce the primate richness expected on each island and so make the effective island size, that is, the forested area smaller.

The tendency of most primate species to use forests will create a further bias in effective island size. Small islands are typically dominated by low-lying forested habitat in this study, but large islands may have substantial areas containing habitats other than moist lowland forest. This "habitat diversity effect" means that island area generates a much greater overestimate of primate habitat area for large islands than for small islands. The model will therefore overestimate the predicted species richness of the large islands. The majority of islands in this study are small (median island area $= 290$ km^2). For islands an arbitrary >1000 km^2, where habitat area could make a difference to predicted species richness, I repeated the 1000 runs of the model three times more, reducing island area to 60%, 75%, and 90% of the total area, respectively. The precise arbitrary value is unimportant to model outcomes: predictions of island species richness are rounded to the nearest integer, and the percentage reductions in size do not alter the expected species richness for any island <1000 km^2 in size.

Which species went extinct?

Each model scenario described above produces an estimated number of species extinctions for each island. Landbridge islands by definition contain a subset of mainland species when they are formed (Brown 1971; Diamond 1972), and so extinctions are assumed to come from the species that are found on the mainland immediately opposite to each island but are missing from the island itself (Brown 1971; Diamond 1972; Wilcox 1978; Terborgh and Winter 1980; Diamond 1984; Gotelli and Graves 1990). For example, five mainland species may be missing from an island and so class as "candidates" for extinction there, but the model may suggest three extinctions. I therefore drew extinct species from the list of candidates at random. (Islands >100 km^2 offshore were excluded a priori because it was difficult to determine accurately the "candidates" for them.) The probability of a species occurring in a small area at the moment of isolation is positively related to its population density, and so I weighted the probability of drawing each species according to its population density. Some species were missing from some islands but present on others. In these cases, I classed species as intolerant if they had gone extinct on $>50\%$ of islands (this percentage can be varied widely without affecting the outcomes, see Supporting Information).

Each run of the model for each set of parameters made 1000 stochastic draws for both the number of extinctions on each island,

and the identity of the species that went extinct. Models were run 1000 times for each set of parameters (five *z*-values, each with three possible percentage size reductions to account for the habitat diversity effect). The assumption is that, if observed relationships between tolerance and species diversity, or between tolerance and geographic range size, are robust to this fairly large degree of stochastic variation in the inputs, then they can be regarded as credible despite the empirical stochastic variation that occurs in the identity and number of species found on islands.

Four possible changes of habitat may have occurred between islands and mainland coasts over the past 10,000 years, causing errors in the identification of intolerant species: (1) habitat has disappeared from the island but not the mainland, for example, due to deforestation, in which case extinction on the island is not a risk but a certainty and it is meaningless to test tolerance; (2) new habitat has appeared on the island; (3) habitat has disappeared from the mainland coast but not the island, and so species that used to be opposite to the island are no longer recognizable as candidates; (4) new habitat has appeared on the mainland coast but not on the island, causing a set of mainland species to spread to the coast and falsely appear to be candidates for former presence on the island.

To minimize potential errors under scenarios (1) or (4), I excluded a priori from the list of candidates any mainland species for which the island contained no suitable habitat (see Supporting Information). These exclusions also prevent species from being erroneously counted as candidates in cases in which the island has always had different habitat from the nearby coast. Scenario (2), under which primate habitat was not present on the island at the moment of insularization but subsequently develops there, seems fairly unlikely to affect the analysis, not least because primates could not have crossed the ocean postinsularization to take advantage of the new habitat. Analyses could be affected if the new habitat generated false candidates, especially if recent island afforestation created the false expectation that mainland forest-dwellers ought to have been present on the island since its creation. However, it seems more likely that the gross forest habitat required by nearly all primates in this study has been continuously present on the islands in most cases, perhaps because maritime effects buffered climate fluctuations and provided moisture (Cronk 1997). Any significant decrease in forest cover in the past 10,000 years on already-tiny islands would almost certainly cause the extinction of forest species, but even very small islands typically retain forest-dwelling primate species today.

Scenario (3) requires the assumption that a primate not found today on either mainland or island was once present on both. Some studies have addressed this problem by using circles of a fixed radius (ranging from hundreds to thousands of kilometers) centered on each island to define the potential source pool of species for the island (Gotelli and Graves 1990; Cardillo et al.

2008). I did not do this, because such circles would cut across major geographic boundaries such as the Sanaga River in West Africa, and would sometimes assume that species coexisted on an island when they have significant allopatric separations on the mainland. Instead, I checked each individual island to see whether any species within the biogeographic region containing the island lay near to the coastal point opposite to the island but not directly on it. Where a species might only questionably have been a candidate for one island, it was nearly always a clear and unequivocal candidates for several other islands, and so uncertainties about near-coastal distributions had a very limited effect on the overall list of intolerant species. A few widespread species today occupy no landbridge islands or coastal areas at all, but may conceivably have once been landbridge island species. I carried out sensitivity analyses to see whether these may have affected results (see Supporting Information and Discussion), but did not include them in the basic analysis.

Comparing tolerance and diversity

I tested the main hypothesis—that lineages containing tolerant species should have diversified more than lineages containing intolerant species, by mapping tolerance and intolerance onto the complete primate phylogeny (Vos and Mooers 2006). Diversification rates are often measured from phylogenetic nodes (Isaac et al. 2003). However, tolerance evolves fairly rapidly along the phylogeny—lineages older than 2.2 million years begin to contain mixtures of tolerant and intolerant species—and so it seemed inappropriate to perform comparative analyses for tolerance over branch lengths that sometimes extend to nodes several million years older than this. I therefore adapted the standard diversification rate analysis by measuring diversification rates from a consistent point in the recent past. I took a time slice through the phylogeny at 2 Myr before present (slightly younger than the minimum time for tolerance to evolve between character states), such that each branch emerging from the slice 2 Myr ago represents one lineage. Each lineage has an equal random chance of diversifying over the period between the time slice and the present. The full species set had 31 threat-tolerant lineages and 22 threat-intolerant lineages. The reduced species set, when entered into stochastic analyses, retained all 31 tolerant lineages, but removed a small number of intolerant lineages from analysis whenever a stochastic run classified all species in a candidate lineage as false extinctions. The average number of threat-intolerant lineages in the reduced species set analyses was 18.

To check robustness to the 2-Myr parameter, I removed the species that defined the date of the youngest split between tolerant and intolerant lineages (*Procolobus badius* and *P. pennantii*) and repeated the analysis for the new youngest split date of 2.8 Myr. Diversification rate was calculated as ln(number of species in the lineage/time) (Isaac et al. 2003).

Figure 2. Measuring diversification rates in threat-tolerant and threat-intolerant lineages, based on a consistent point in the recent past or "timeslice." Each branch arising from the timeslice is treated as a lineage, and the rate is calculated from how often the branches diversify between the timeslice and the present. The date of the timeslice is set so that all lineages have a single trait value (tolerant or intolerant). Dashed lines = threat-intolerant species, solid lines = threat-tolerant species. A small number of species have unknown tolerance values (gray line), and these were assumed to have the trait value common to all the known species in the lineage.

Diversification rates of tolerant and intolerant lineages could then be compared by a *t*-test. However, there was a strong phylogenetic signal in tolerance itself (see Results), indicating that a phylogenetically corrected statistic was more appropriate (Abouheif 1999). For each of the 1000 models runs, I carried out a phylogenetic regression of diversification rate on a binary variable tolerance/intolerance (Grafen 1989), equivalent to a phylogenetically corrected *t*-test, and recorded the *P*-values and direction of the relationship. I then counted how many times out of one thousand the *P*-value was significant at alpha < 0.05 (the random expectation is 50 times).

When dividing lineages into tolerant and nontolerant, it was usually possible to establish the trait value directly for every species in the lineage (e.g., this was possible in 37/53 of the 2-Myr-old lineages in the full species set). Where a lineage contained a species that was not island-associated and so had no direct measure of tolerance (usually a single species case), the tolerance trait value shared by all other members of the lineage was assigned to the nontestable species (Fig. 2). Tolerance has a significant phylogenetic signal (Supporting Information), with a strong clustering of similar trait values in large clades such as the Lorisidae (bushbabies and allies) and Hylobatidae (gibbons) (see Table S2), and so in the very young clades used here, it seemed reasonable to assume that the "unknown" species in a lineage should share the tolerance trait value of the known species.

TESTING THE RELATIONSHIP BETWEEN TOLERANCE AND GEOGRAPHIC RANGE SIZE

It is reasonably well established that large range size increases the longevity of species (Koch 1980; Jablonski 1987, 1995; McKinney 1997). If tolerance were positively correlated with large range size, or with factors that cause species to have large range size, then tolerance could appear to drive lineage diversity simply because it was cocorrelated with an existing strong predictor of extinction resistance. On the other hand, if tolerance is not positively correlated with range size, this would suggest that it is a different form of extinction resistance with a novel influence on species diversity. I compared log-transformed range sizes of tolerant and intolerant species with a phylogenetically corrected *t*-test, as before. Range sizes were calculated by digitizing published range maps and using ArcGIS utilities (ESRI 2005) to calculate the distributional area (Supporting Information).

The assumption here is that the relative range sizes of primate species have remained broadly consistent in their relationships to each other over the past 10,000 years (a period in which no speciation events have occurred in the primates used), even if the individual range sizes have fluctuated. That is to say, range sizes that are big today have generally been bigger over the past 10,000 years than range sizes that are small today, for example, the baboon *Papio*, with a modern range size of 13,460,000 km^2, has consistently had a wider distribution in the Holocene than the guenon *Cercopithecus preussi*, with a modern range size of 80,800 km^2.

POTENTIAL SOURCES OF ERROR

Population abundance has been theoretically linked with diversification (Gavrilets 1999; Hubbell 2001) and has often been identified as the major determinant of species survival in habitat remnants as well (Diamond 1984; Harcourt and Schwartz 2001; Lindenmayer 2006). Any relationship between tolerance and diversification could therefore occur because both are cocorrelated with abundance. I tested whether abundance (population density) was a correlate of diversification rate, by regressing diversification rate on the average log-transformed population density of each 2-Myr-old lineage, using the phylogenetic regression (Grafen 1989). Population densities were means of values taken from a wide search of the primate literature (see Supporting Information). Population density has a surprisingly strong phylogenetic signal (lambda = 0.87 where 1.0 indicates the strongest possible signal [Purvis et al. 2005]), and so it seems reasonable to use modern-day densities in comparative evolutionary analysis. I did not perform the same test for geographic range size: the relationship between range size and diversification is a complex topic in which the appropriate neontological methodology is still being debated (Gaston and Blackburn 1997; Owens et al. 1999; Cardillo et al. 2003; Losos and Glor 2003; Waldron 2007) and is the subject of a forthcoming study (Waldron in preparation).

The primate phylogeny will not be completely accurate and the taxonomic status of primate species is regularly debated (Groves 2001). Groves (2001) lists 348 primate species in comparison the 218 in Vos and Mooers (2006). I tested for

Table 1. Statistical relationships between tolerance and (a) lineage diversification rate in 2-Myr-old lineages; (b) rate in 2.8-Myr-old lineages; (c) geographic range size. Columns with *Z*-values show the stochastic reduced-species analysis, final column shows the all-species analysis (see text). *P*-values in reduced-species analysis are medians of 1000 simulations, with values in brackets showing the percentage of times the *P*-value fell below 0.05.

	Z=0.10	Z=0.12	Z=0.14	Z=0.16	Z=0.18	All-species
(a) Tolerance and diversification rate (2 Myr)	Positive	Positive	Positive	Positive	Positive	Positive
	$P<0.001$	$P<0.001$	$P<0.001$	$P=0.001$	$P=0.001$	$P=0.012$
	(100%)	(100%)	(100%)	(100%)	(100%)	
(b) Tolerance and diversification rate (2.8 Myr)	Positive	Positive	Positive	Positive	Positive	Positive
	$P=0.017$	$P=0.016$	$P=0.013$	$P=0.023$	$P=0.023$	$P=0.010$
	(100%)	(100%)	(99.7%)	(99.8%)	(99.2%)	
(c) Tolerance and log (range size)	Negative	Negative	Negative	Negative	Negative	Negative
	$P=0.008$	$P=0.008$	$P=0.007$	$P=0.007$	$P=0.008$	$P=0.002$
	(99.9%)	(99.8%)	(99.6%)	(99.3%)	(98.8%)	

potential sensitivity to changes in taxonomy by counting how many new species would be added to tolerant and intolerant clades, respectively, by Groves (2001). To address the possibility that changes in the phylogeny affect results, I updated the operational phylogeny with studies on individual clades that post-dated the studies used to create the supertree, so long as such studies provided a dated phylogeny of the clade (Cortes-Ortiz et al. 2003; Collins 2004; Nieves et al. 2005; Tosi et al. 2005; Chatterjee 2006; Chakraborty et al. 2007). Phylogenetic GLS-based analyses could not strictly be performed on such a large compilation of separate phylogenies without constructing a new supertree. I did, however, perform a nonphylogenetic *t*-test on the diversification rates of tolerant and intolerant clades in the updated phylogeny, and compared this with a nonphylogenetic *t*-test on the Vos and Mooers (2006) clades (see Supporting Information).

DATA SOURCES AND STATISTICAL SOFTWARE

Primate distributions on islands and mainlands were garnered from a variety of published sources (Supporting Information). Phylogenetic signal testing was carried out with Abouheif's TFSI and "Runs" programs (Abouheif 1999). Phylogenetic regressions, model simulations, and *t*-tests were carried out in the R statistical environment (R Development Core Team 2005) using APE (Paradis et al. 2004) for the phylogenetic regression.

Results

Tolerance had a strong correlation with lineage diversification rates (Table 1). For example, intolerant lineages have not diversified at all in the last 2 Myr under any stochastic model set of parameters, compared to nearly half of tolerant lineages (Fig. 3).
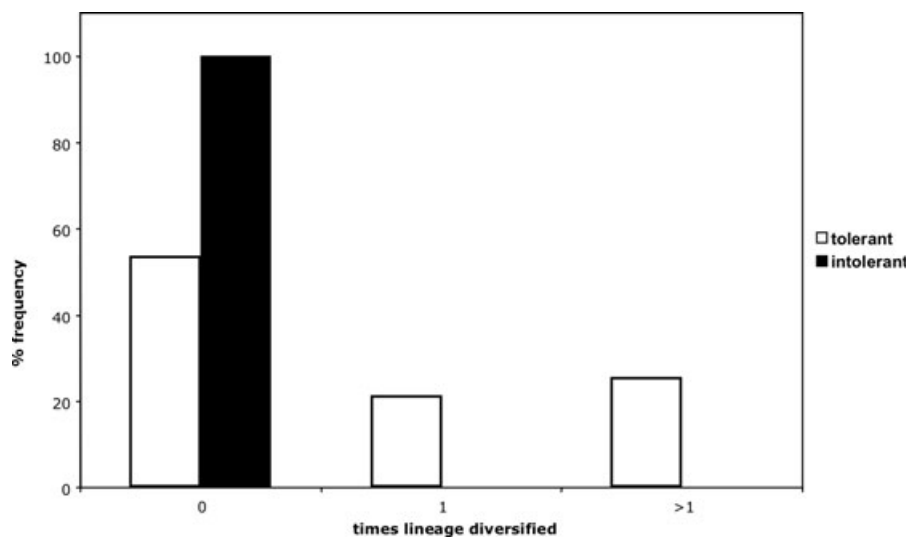

Figure 3. Diversification rates in threat-tolerant and threat-intolerant lineages. Bars show the proportional frequency of three classes of diversification rate (no diversification, one new extant species, >1 new species) over the past 2 Myr for the reduced species set analyses. Frequencies do not vary with *z*. $N = 31$ tolerant lineages and an average of 17 intolerant lineages across the stochastic analyses.
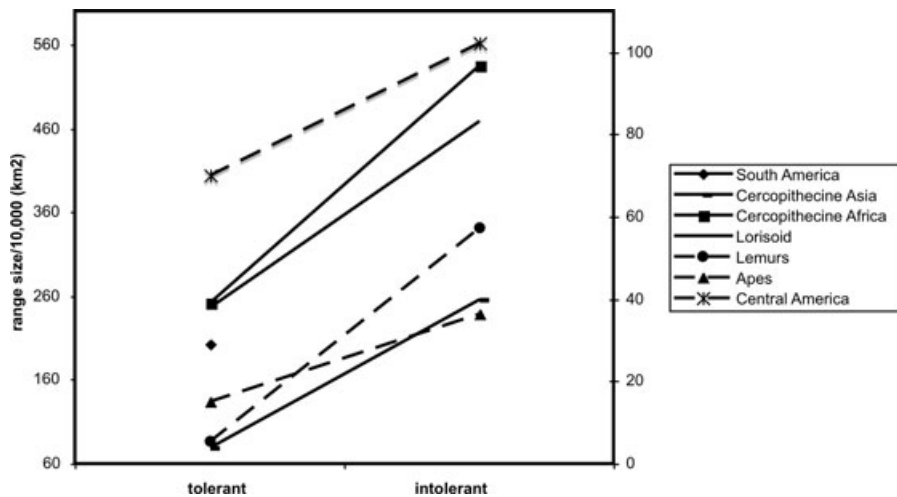
Figure 4. Average geographic range sizes of tolerant and intolerant lineages. Lineages have been grouped into broad-scale clades for illustration, although data were analyzed by taking account of all phylogenetic relationships. Apes, Central American lineages, and Lemurs (dashed lines) are on the secondary axis, because of their average small range sizes. Lemurs have tiny range sizes, and these were multiplied by 6 to fit on the graph. The single point for South America indicates that no extinctions were inferred for the islands of Trinidad and Gorgona. Error bars are omitted for clarity.

For the full species set analysis, 1/22 (5%) intolerant lineages had speciated, compared to 12/31 tolerant lineages (39%). The qualitative result was unaffected by variation in the extinction scenario used (Table 1 and Supporting Information), and held true for both time slices (2 Myr and 2.8 Myr). All results reported are for tests that omitted *Macaca assamensis* and *Hylobates concolor*. The reported outcomes are therefore conservative, because both of these omitted (and tolerant) lineages have diversified more than once in the past 2 Myr. The quantitative values are also conservative, because the time-slice method underestimates the difference between lineage diversification rates (Waldron, unpublished analysis). All figures and results given are for simulations in which the early Holocene habitat area on islands >1000 km^2 was assumed to be 75% of the total island size (see Methods). Alternative percentages (60%, 90%, and 100%) did not qualitatively affect the results.

Tolerant lineages would have more species added to them by taxonomic revisions in Groves (2001) than intolerant ones (mean 1.77 for tolerant, 0.95 for intolerant). This suggests that taxonomic revisions are unlikely to alter the analysis' conclusions, and indeed are likely to strengthen them. An exact statistical test of diversification rates cannot be made because the ages of new species and lineages are unknown. Similarly, when the Vos and Mooers supertree's diversification dates are partially updated using diversification dates from more recent, clade-specific phylogenetic studies, the observed patterns tended to strengthen (*t*-tests on the difference in diversification rate between tolerant and intolerant 2-Myr-old lineages, $t = -3.5725$ for an updated phylogeny vs. $t = -2.981$ for the original phylogeny, *P*-value $= 0.001$ vs. 0.005; Table S4 and Supporting Information).

Tolerance is negatively associated with geographic range size. In other words, lineages with small range sizes are more tolerant than related lineages with large ranges (Table 1, Fig. 4). This result was also robust to variation in the extinction scenario used: the percentage of significant results across all stochastic variations and across all parameter variations is approximately 99% or more, considerably higher than would be expected at random (Table 1). There was no influence of population density on rate of diversification (median $P > 0.93$ in all stochastic scenarios).

Tolerance, ln-transformed geographic range and ln-transformed population density all showed phylogenetic signal (Abouheif's (1999) method, $P = 0.026$ for tolerance, $P = 0.003$ for range size, $P = 0.001$ for population density) (Table S3).

Discussion

This study argued that when all populations in a species, or all individuals in a population are affected by an extinction threat, then the species or population will only persist if it has sufficient threat tolerance to survive in spite of the high level of danger. I studied the common set of threats implied by geographic range contraction, restriction and fragmentation, especially when these are associated with periods of environmental and climate change. I found that tolerance to these threats at the level of populations correlates with species diversity at the level of evolutionary lineages. Tolerance is heritable, and will therefore have consistent effects on diversification over evolutionary time.

TOLERANCE AND CLASSIC EXTINCTION RESISTANCE

I also found that tolerance was unexpectedly correlated with small range size. This suggests that tolerance represents a different type of extinction-resistance from the resistance conferred by having a large range size. Widespread species probably have low extinction risk because threats are nearly always circumscribed in area, and so some groups of individuals will lie outside the scope of each passing threat (they "escape" threat). The implied mechanism is that persistence occurs when threat levels are low, and threat levels are always low for some population in a widespread species. For tolerance, on the other hand, the implied mechanism is that populations are surprisingly resistant when directly exposed to threat, that is, when threat levels are high.

Tolerance and escape imply different relationships between population extinction rates and species extinction risk. For escape, individual population extinctions are largely irrelevant to the overall persistence of the species, because other, unthreatened populations exist elsewhere. For tolerance, population-level and species-level persistence must be highly correlated, because it is only the tolerance of populations that keeps the species afloat.

The link observed in this study between population persistence and lineage diversity is most easily explained by a strong correlation between the persistence of populations and species. Global periods of hostile environmental change are likely to tighten the relationship between population-level and species-level persistence, because large numbers of species are reduced to a few small and simultaneously threatened populations. During more benign periods, the average global influence of escape on species persistence may increase, and the influence of tolerance may decrease.

High degrees of threat tolerance in rare lineages probably represent the outcome of an evolutionary filter. Lineages that have small (and fluctuating) range sizes will have been repeatedly exposed to the dangers of range restriction throughout most of their history. Geographically rare species also tend to consist of several discrete populations (Maurer and Nott 1998) and to have poor dispersal (Gaston 1994). Small populations, isolation, and inability to migrate will therefore have been important parts of the selective pressures experienced by most rare species, and rare species unable to withstand these pressures should be pruned from the tree of life. (See Stanley (1990) and Jablonski (2001) for a similar idea that clades become more extinction-resistant over time as more susceptible species are progressively pruned).

The precise ecological adaptations that allow rare species to tolerate geographic restriction and isolation would be a topic for future research. It seems possible that widespread, usually generalist species have high dispersal ability (Brown 1995) because they must range widely in time and space to acquire resources. Dispersal may also be an adaptive strategy responding more generally to unstable population dynamics, as has been shown in bee-

tles (Boer 1970; Glazier 1987). Species that experience extreme variation in resource availability may be "obligate dispersers," in the sense that individuals must travel widely in ecological time in order for the population to persist. Obligate dispersal may also occur at the species level if species with unstable local populations depend upon high levels of dispersal in a metapopulation structure to persist. Isolation in a small area would cause local extinction in obligate-dispersing species.

DIVERSITY, LONGEVITY, AND EXTINCTION

Geographically rare species are short-lived in comparison to widespread species (Jablonski 1987, 1995; Hunt et al. 2005). Although tolerance must increase longevity, the small range size of tolerant species therefore suggests that they are unlikely to represent the longest-lived species in a taxon. However, species diversity is the net difference between speciation events and extinction events, and so biological attributes that reduce extinction rates relative to speciation rates will cause increases in lineage diversity, whatever species life spans are in absolute terms. Geographical rarity is often associated with high speciation rates, both for raw range size (Mayr 1963; Jackson 1974; Vrba 1980; Stanley 1986; Vermeij 1987; Jablonski and Roy 2003), and for the number of biomes used under Vrba's resource-use hypothesis (Vrba 1987, 1993; Hernandez Fernandez and Vrba 2005a; Bofarull et al. 2008). However, the effect of this rapid speciation on diversity may be nullified by the equally high species extinction rates associated with rarity (Stanley 1979; Stanley 1986; Vrba 1992; McKinney 1997). A major impact of tolerance could be in reducing extinction rates in rare lineages, so that their high speciation rates can become translated into high species diversity.

More generally, tolerance of geographic restriction during environmental change may allow species to persist long enough to become widespread in the first place. Species tend to start out with small range sizes (Vrba and DeGusta 2004; Liow and Stenseth 2007; Waldron 2007). Species can later occupy large geographic areas (Vrba and DeGusta 2004; Foote et al. 2007; Liow and Stenseth 2007; Waldron 2007), but will need to survive their potentially vulnerable early years to do so.

TOLERANCE AND THE SPECIATION PROCESS

Tolerance can bestow extinction resistance not only on newly created species, but also on small, reproductively isolated populations that may go on to become new species. Peripatric speciation involves the isolation of small populations as a mechanism of speciation (Mayr 1963), and Stanley (1979), Glazier (1987), and Allmon (1992) used the term "isolate selection" to describe the idea that peripatrically speciating ancestor species would only leave behind daughter species if those daughters could survive the initial threat implied by smallness and isolation.

The overall importance of peripatric speciation to the accumulation of species diversity in lineages may be limited (Barraclough and Vogler 2000). However, recent work suggests that even the apparently dominant mode of allopatric speciation (Barraclough and Vogler 2000; Phillimore et al. 2008) often splits ancestral range so asymmetrically that it creates a daughter species with a very small range size (Waldron 2007). The same is likely to be true for sympatric speciation (Waldron 2007). Glazier's and Allmon's ideas therefore apply to speciation in general. Indeed, many modern species are thought to have arisen when species became split into two small, isolated populations in fragmented habitat refugia either during the Neogene (Vrba 1980, 1992, 1993; Klicka and Zink 1997; Avise and Walker 1998; Weir and Schluter 2004).

Jansson and Dynesius (2002) have argued that range fluctuations due to climate change are too short to trigger speciation, because isolated populations will be reunited quickly when further climate change causes the reexpansion of their ranges. Similarly, Vrba (1992, 1995) indicates that full reproductive isolation does not occur in all Milankovitch cycles, but only in the longest ones. It is interesting to note that tolerance is associated here with rare, probably low-dispersal species. Populations of low-dispersal species may have so little gene flow between them that they remain isolated long after a glacial maximum ends and their ranges begin to reexpand, as has been shown in birds (Price et al. 1997). In addition, reproductive isolation can be the cumulative result of repeated geographic isolations (Avise and Walker 1998), suggesting that the frequency of the cycles and the rate at which species reexpand their populations between cycles may be as important as the duration of a single Milankovitch cycle.

POTENTIAL CONFOUNDS

The apparent link between tolerance and lineage diversity could be artifactual, if tolerance were correlated with other factors that independently increase diversification rates. However, the traits generally believed to increase diversification in mammals—generalism, high dispersal rates, and large range size itself are positively correlated with geographic range size (Brown 1995; Rosenzweig 1995; Gaston and Blackburn 1997; Owens et al. 1999; Cardillo et al. 2003; Isaac et al. 2003; Phillimore et al. 2006; Jablonski 2008). Tolerance, on the other hand, is negatively correlated with range size in spite of its strong positive correlation with diversification rate, suggesting its effect is independent of other common factors that influence lineage diversity. In addition, the strongest general predictor of tolerance in the literature, population abundance (Brown 1971; Diamond 1984; Laurance et al. 2002; Lindenmayer 2006) has no relationship here with diversification rate.

It is possible that some species populations go extinct from landbridge islands for reasons that are unrelated to the extinction pressures postulated here. For example, ground-nesting birds may suffer higher rates of nest predation on the newly created island that they did on the mainland (Karr 1982). These idiosyncratic effects are unlikely to be consistently correlated with a low rate of diversification across all species, and so would most probably appear as error terms in the relationship between diversification rate and tolerance.

A number of widespread species may have been on both coast and island in the past, but have modern-day range limits a few hundreds of kilometers short of the coast. If they had gone extinct on islands, this would be undetectable from their present-day distribution, and they would be wrongly omitted from the list of intolerant species. Examples are *Gorilla* and *Miopithecus* for Bioko, *Symphalangus* and *Pongo* for several of the Sunda Shelf islands, *Phaner* and *Avahi laniger* in Madagascar (Harcourt and Schwartz 2001; Meijaard and van der Zon 2003; Ganzhorn et al. 2006). Although there is not enough evidence to confidently state which of these species should and should not be included as intolerants in formal analysis, none of these lineages have diversified at all in the past 2 Myr (and some of them are indeed among the slowest-diversifying of all primate lineages). Their inclusion would only strengthen the conclusions found in this study.

The geographic range size of species today may have been dramatically altered by human influences, distorting the relationship of range size and tolerance. For the observed patterns to be an artifact of anthropogenic habitat reduction, human impacts would need to universally cause dramatically bigger range collapses in tolerant species than in intolerant species (see Fig. 4). This seems an unlikely assumption, especially given that many documented range collapses have occurred in intolerant species such as gibbons and orangutan (this may in itself by an outcome of their populations' intolerance of reduced, fragmented habitat) (Harcourt 1999; Geissman et al. 2000).

The phylogeny is not likely to be completely accurate, either in its arrangement of species or in its diversification dates. This could affect both the diversity of lineages, and the accuracy of the timeslice method. However, modern taxonomic and phylogenetic revisions in species arrangement seem likely to strengthen the diversity patterns observed (see Results and Supporting Information). As regards dating errors, the diversification events for most lineages occur millions of years away from the timeslice dates chosen, especially in intolerant clades, and so the timeslices for these lineages are likely to be robust to considerable error. When dates do lie close to the timeslices, shifting those dates will increase or decrease diversity almost exclusively in tolerant lineages. Date-shifted tolerant lineages will still have more diversity on average than the universally monospecific intolerant lineages, and so the overall conclusions are highly robust to dating errors.

It may be argued that large islands do not represent an extinction risk to all populations. Some populations may naturally occupy areas less than, for example, the 11,900 km^2 of the largest island, and so insularization causes a mild threat at best via isolation. There is surprisingly little information on the geographic extent of primate populations that would permit measurement of how much each population on each island has been truncated, but the median size of islands is 290 km^2, suggesting probable truncation in many cases. I retested the correlations using only islands of 2000 km^2 or less, and again for 500 km^2 or less, and found no difference in the qualitative results. Nor are the tolerant species somehow "island specialists": they all have the great majority of their distribution on the mainland.

Nevertheless, an alternative hypothesis to why some populations persist in fragments is that these populations are less truncated, and so suffer a lower level of threat (instead of having a higher tolerance of threat). If the spatial extent of a species correlates with the spatial extent of its individual populations (as seems to be the case [Maurer and Nott 1998]), then geographically rare species will have less truncated populations in remnants than widespread species. Rare species still have higher odds of survival in remnants, but the main attribute causing differential survival would be the natural geographic extent of a species' populations.

RARITY HAS POSITIVE AND NEGATIVE EFFECTS ON EXTINCTION RISK

A major implication of this study is that geographic rarity can have both positive and negative effects on extinction risk. These effects will depend on the severity and geographical extent of threats themselves, and on the timescales involved. Rare species tolerate range shrinkage better than common species (a positive impact of rarity). On the other hand, tolerance can have no influence when all habitat is wiped out, and such catastrophic destruction will be experienced more often by rare species than by widespread species (a negative impact of rarity). One implication is that tolerance may be a weaker influence at higher latitudes, where habitat loss is more often catastrophic (Bennett et al. 1991; Jansson and Dynesius 2002). I studied primates, whose tropical distribution means they should often suffer habitat shrinkage rather than habitat obliteration during climate change.

Similarly, it seems likely that few environmental changes will be so widespread as to envelop every last population in a widespread species. Species with large ranges therefore have their tolerance tested only rarely, but may prove extinction-prone at the population level when they are so tested. If environmental change has been sufficiently severe to reduce a generally widespread species to a few isolated populations, then the entire species has a high risk of extinction because of its populations' intolerance of threat. Rare species, on the other hand, will frequently be enveloped by an extinction threat, but may prove extinction-resistant so long as the threat is noncatastrophic.

Overall, the positive impacts of rarity on persistence seem likely to operate over shorter timescales than the negative effects. The results of this study suggest that the short-term effects last long enough to leave a signature over the evolutionary timescales associated with speciation and extinction. This is in keeping with the observed periodicity of climate change over the past few million years, with Milankovitch cycles occurring every 100,000 or 41,000 years, and as often as every 19,000–23,000 years (Berger 1988). Mammal species on average experience about 20 periods of major climate change over their lifetimes (Vrba 1992), and it would seem that this periodicity would certainly be rapid enough to accord a significant role to tolerance.

The difference between the mechanisms of tolerance and classic extinction resistance also suggests that as climate and environment cycles, there may be a shifting balance of selective pressures on species. When habitat is widespread and continuous, populations are much less fragmented, and generalists can disperse in response to adverse local fluctuations. Classic extinction resistance will have a strong influence on species persistence, and widespread and generalist species will have low extinction risks. But when climate change reduces habitat to small, isolated fragments, tolerance becomes more important to species persistence, and rare species may gain the persistence advantage (at least those that lie within distributional reach of an environmental refuge).

Measurements of tolerance would also have clear usefulness today in predicting the extinctions likely to result from anthropogenic habitat loss, fragmentation, and climate change. Human land use conversion has already caused habitat loss and fragmentation to become the number one threat to species survival today (Diamond 1984; Wilcove et al. 1998; Secretariat of the Convention on Biological Diversity 2006). Climate change will worsen this situation, both because it will reduce some habitats further, and because populations in isolated fragments cannot migrate in response to environmental change. Tolerance will be a key determinant of survival under such circumstances. But its unexpected link with small range size suggests that some widely used predictors of extinction risk may be poor predictors of populations' extinction risk in a hotter, more fragmented world.

LITERATURE CITED
Abegg, C., and B. Thierry. 2002. Macaque evolution and dispersal in insular south-east Asia. Biol. J. Linn. Soc. 75:555–576.
Abouheif, E. 1999. A method for testing the assumption of phylogenetic independence in comparative data. Evol. Ecol. Res. 1:895–909.

Allmon, W. D. 1992. A causal analysis of stages in allopatric speciation. Pp. 219–258 *in* D. J. Futuyma and J. Antonovics, eds. Oxford surveys in evolutionary biology. OUP, Oxford.

Avise, J. C., and D. Walker. 1998. Pleistocene phylogeographic effects on avian populations and the speciation process. P. R. Soc. Lond. B Biol. 265:457–463.

Barraclough, T. G., and A. P. Vogler. 2000. Detecting the geographical pattern of speciation from species-level phylogenies. Am. Nat. 155:419–434.

Barraclough, T. G., A. P. Vogler, and P. H. Harvey. 1998. Revealing the factors that promote speciation. Philos. T. R. Soc. B. 353:241–249.

Bennett, K. D., P. C. Tzedakis, and K. J. Willis. 1991. Quaternary Refugia of North European Trees. J. Biogeogr. 18:103–115.

Berger, A. 1988. Milankovitch theory and climate. Rev. Geophys. 26:624–657.

Bird, M. I., D. Taylor, and C. Hunt. 2005. Environments of insular Southeast Asia during the Last Glacial Period: a savanna corridor in Sundaland? Quaternary Sci. Rev. 24:2228–2242.

Boecklen, W. J., and N. J. Gotelli. 1984. Island biogeographic theory and conservation practice – species-area or specious-area relationships. Biol. Conserv. 29:63–80.

Boecklen, W., and D. Simberloff. 1986. Area-based extinction models in conservation. Pp. 247–276 *in* D. K. Elliott, ed. Dynamics of extinction. John Wiley and Sons, New York.

Boer, P. J. D. 1970. On significance of dispersal power for populations of Carabid-Beetles (Coleoptera, Carabidae). Oecologia 4:1–28.

Bofarull, A., A. Royo, M. Fernandez, E. Ortiz-Jaureguizar, and J. Morales. 2008. Influence of continental history on the ecological specialization and macroevolutionary processes in the mammalian assemblage of South America: differences between small and large mammals. BMC Evol. Biol. 8:97.

Bolger, D. T., A. C. Alberts, and M. E. Soule. 1991. Occurrence patterns of bird species in habitat fragments – sampling, extinction, and nested species subsets. Am. Nat. 137:155–166.

Bonaccorso, E., I. Koch, and A. T. Peterson. 2006. Pleistocene fragmentation of Amazon species' ranges. Divers Distrib. 12:157–164.

Brown, J. H. 1971. Mammals on mountaintops – nonequilibrium insular biogeography. Am. Nat. 105:467–478.

———. 1995. Macroecology. University of Chicago Press, Chicago.

Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58:445–449.

Cardillo, M., J. S. Huxtable, and L. Bromham. 2003. Geographic range size, life history and rates of diversification in Australian mammals. J. Evol. Biol. 16:282–288.

Cardillo, M., J. L. Gittleman, and A. Purvis. 2008. Global patterns in the phylogenetic structure of island mammal assemblages. P. R. Soc. B. 275:1549–1556.

Chakraborty, D., U. Ramakrishnan, J. Panor, C. Mishra, and A. Sinha. 2007. Phylogenetic relationships and morphometric affinities of the Arunachal macaque Macaca munzala, a newly described primate from Arunachal Pradesh, northeastern India. Mol. Phylogenet. Evol. 44:838–849.

Chatterjee, H. J. 2006. Phylogeny and biogeography of gibbons: a dispersal-vicariance analysis. Int. J. Primatol. 27:699–712.

Collins, A. C. 2004. Atelinae phylogenetic relationships: the trichotomy revived? Am. J. Phys. Anthropol. 124:285–296.

Cortes-Ortiz, L., E. Bermingham, C. Rico, E. Rodriguez-Luna, I. Sampaio, and M. Ruiz-Garcia. 2003. Molecular systematics and biogeography of the Neotropical monkey genus, Alouatta. Mol. Phylogenet. Evol. 26:64–81.

Cowlishaw, G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. Conserv. Biol. 13:1183–1193.

Cronin, T. M., M. E. Raymo, and K. P. Kyle. 1996. Pliocene (3.2–2.4 Ma) os-tracode faunal cycles and deep ocean circulation, North Atlantic Ocean. Geology 24:695–698.

Cronk, Q. C. B. 1997. Islands: stability, diversity, conservation. Biodivers. Conserv. 6:477–493.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

Diamond, J. M. 1972. Biogeographic kinetics – estimation of relaxation-times for avifaunas of southwest pacific islands. Proc. Natl. Acad. Sci. USA 69:3199–3203.

———. 1984. 'Normal' extinctions of isolated populations. Pp. 191–246 *in* M. H. Nitecki, ed. Extinctions. University of Chicago Press, Chicago.

Dynesius, M., and R. Jansson. 2000. Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proc. Natl. Acad. Sci. USA 97:9115–9120.

ESRI. 2005. ArcGIS 9.2. Environmental Systems Research Institute, Redlands, CA.

FAUNMAP Working Group. 1996. Spatial response of mammals to late Quaternary environmental fluctuations. Science 272:1601–1606.

Foote, M., J. S. Crampton, A. G. Beu, B. A. Marshall, R. A. Cooper, P. A. Maxwell, and I. Matcham. 2007. Rise and fall of species occupancy in Cenozoic fossil mollusks. Science 318:1131–1134.

Ganzhorn, J. U., S. M. Goodman, S. Nash, and U. Thalmaan. 2006. Lemur biogeography. Pp. 229–254 *in* S. M. Lehman and J. G. Fleagle, eds. Primate biogeography. Springer, New York.

Gaston, K. J. 1994. Rarity. Chapman and Hall, London.

Gaston, K. J., and T. M. Blackburn. 1997. Age, area and avian diversification. Biol. J. Linn. Soc. 62:239–253.

Gavrilets, S. 1999. A dynamical theory of speciation on holey adaptive landscapes. Am. Nat. 154:1–22.

Geissman, T., X. D. Nguyen, N. Lormee, and F. Momberg. 2000. Vietnam primate conservation stauts review 2000: part 1, Gibbons. Fauna and Flora International, Indochina Programme, Hanoi.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: the porcesses of species extinctions. Pp. 19–34 *in* M. Soule, ed. Conservation biology: the science of scarcity and diversity. Sinauer Associates, Sunderland, MA.

Glazier, D. S. 1987. Toward a predictive theory of speciation – the ecology of isolate selection. J. Theor. Biol. 126:323–333.

Gotelli, N. J., and G. R. Graves. 1990. Body size and the occurrence of avian species on land-bridge islands. J. Biogeogr. 17:315–325.

Grafen, A. 1989. The phylogenetic regression. Philos. T. R. Soc. B. 326:119–157.

Groves, C. 2001. Primate taxonomy. Smithsonian Institute Press, Washington.

Haffer, J. 1997. Alternative models of vertebrate speciation in Amazonia: an overview. Biodivers. Conserv. 6:451–476.

Haila, Y., and O. Jarvinen. 1983. Land bird communities on a Finnish Island – species impoverishment and abundance patterns. Oikos 41:255–273.

Harcourt, A. H. 1999. Biogeographic relationships of primates on South-East Asian islands. Global Ecol. Biogeogr. 8:55–61.

Harcourt, A. H., and M. W. Schwartz. 2001. Primate evolution: a biology of Holocene extinction and survival on the southeast Asian Sunda Shelf islands. Am. J. Phys. Anthropol. 114:4–17.

Heaney, L. R. 1986. Biogeography of mammals in Se Asia – estimates of rates of colonization, extinction and speciation. Biol. J. Linn. Soc. 28:127–165.

Henle, K., D. B. Lindenmayer, C. R. Margules, D. A. Saunders, and C. Wissel. 2004. Species survival in fragmented landscapes: where are we now? Biodivers. Conserv. 13:1–8.

Hernandez Fernandez, M., and E. Vrba. 2005a. Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. Evol. Ecol. 19:199–219.

———. 2005b. Macroevolutionary processes and biomic specialization: testing the resource-use hypothesis. Evol. Ecol. 19:199–219.

Hill, J. L., P. J. Curran, and G. M. Foody. 1994. The effect of sampling on the species-area curve. Global Ecol. Biogeogr. Lett. 4:97–106.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, NJ.

Hunt, G., K. Roy, and D. Jablonski. 2005. Species-level heritability reaffirmed: a comment on "On the heritability of geographic range sizes". Am. Nat. 166:129–135.

Hurlbert, A. H., and W. Jetz. 2007. Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. Proc. Natl. Acad. Sci. USA 104:13384–13389.

Isaac, N. J. B., P. M. Agapow, P. H. Harvey, and A. Purvis. 2003. Phylogenetically nested comparisons for testing correlates of species richness: a simulation study of continuous variables. Evolution 57:18–26.

Jablonski, D. 1987. Heritability at the species level – analysis of geographic ranges of cretaceous mollusks. Science 238:360–363.

———. 1995. Extinction in the fossil record. Pp. 25–44 in R. M. May and J. H. Lawton, eds. Extinction rates. Oxford University Press, Oxford.

———. 2001. Lessons from the past: evolutionary impacts of mass extinctions. PNAS 98:5393–5398.

———. 2007. Scale and hierarchy in macroevolution. Palaeontology 50:87–109.

———. 2008. Species selection: theory and data. Annu. Rev. Ecol. Evol. S 39:501–524.

Jablonski, D., and K. Roy. 2003. Geographical range and speciation in fossil and living molluscs. Proc. R. Soc. Lond. B. Biol. 270:401–406.

Jackson, J. B. C. 1974. Biogeographic Consequences of Eurytopy and Stenotopy among Marine Bivalves and Their Evolutionary Significance. Am. Nat. 108:541–560.

Jansson, R., and M. Dynesius. 2002. The fate of clades in a world of recurrent climatic change: milankovitch oscillations and evolution. Annu. Rev. Ecol. Syst. 33:741–777.

Karr, J. R. 1982. Avian extinction on Barro-Colorado Island, Panama – a Reassessment. Am Nat 119:220–239.

Klicka, J., and R. M. Zink. 1997. The importance of recent ice ages in speciation: a failed paradigm. Science 277:1666–1669.

Koch, C. F. 1980. Bivalve species duration, areal extent and population-size in a Cretaceous Sea. Paleobiology 6:184–192.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. Am. Nat. 142:911–927.

Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. Conserv. Biol. 16:605–618.

Lawton, J. H., G. Daily, and I. Newton. 1994. Population-Dynamic Principles. Philos. T. R. Soc. B 344:61–68.

Leitner, W. A., and M. L. Rosenzweig. 1997. Nested species-area curves and stochastic sampling: a new theory. Oikos 79:503–512.

Lindenmayer, D. B. A. F. J. 2006. Habitat fragmentation and landscape change. Island Press, Washington, DC.

Liow, L. H., and N. C. Stenseth. 2007. The rise and fall of species: implications for macroevolutionary and macroecological studies. Proc. R. Soc. B. 274:2745–2752.

Lomolino, M. V. 1986. Mammalian Community Structure on Islands – the Importance of Immigration, Extinction and Interactive Effects. Biol. J. Linn. Soc. 28:1–21.

Losos, J. B., and R. E. Glor. 2003. Phylogenetic comparative methods and the geography of speciation. Trends Ecol. Evol. 18:220–227.

MacArthur, R. H., and E. O. Wilson. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, NJ.

Marzluff, J. M., and K. P. Dial. 1991. Life-History Correlates of Taxonomic Diversity. Ecology 72:428–439.

Maurer, B. A., and M. P. Nott. 1998. Geographic range fragmentation and the evolution of biological diversity. Pp. 31–50 in M. L. McKinney and J. A. Drake, eds. Biodiversity dynamics: turnover of populations, taxa and communities. Columbia University Press, New York.

Mayr, E. 1963. Animal species and evolution. Harvard University Press, Cambridge, MA.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annu. Rev. Ecol. Syst. 28:495–516.

Meijaard, E., and A. P. M. Van Der Zon. 2003. Mammals of south-east Asian islands and their Late Pleistocene environments. J. Biogeogr. 30:1245–1257.

Newmark, W. D. 1995. Extinction of Mammal Populations in Western North-American National-Parks. Conserv. Biol. 9:512–526.

Nieves, M., M. S. Ascunce, M. I. Rahn, and M. D. Mudry. 2005. Phylogenetic relationships among some Ateles species: the use of chromosomic and molecular characters. Primates 46:155–164.

Overpeck, J. T., R. S. Webb, and T. Webb. 1992. Mapping Eastern North-American Vegetation Change of the Past 18 Ka – No-Analogs and the Future. Geology 20:1071–1074.

Owens, I. P. F., P. M. Bennett, and P. H. Harvey. 1999. Species richness among birds: body size, life history, sexual selection or ecology? Proc. R. Soc. Lond. B Biol. 266:933–939.

Paradis, E., J. Claude, and K. Strimmer. 2004. APE: analyses of Phylogenetics and Evolution in R language. Bioinformatics 20:289–290.

Phillimore, A. B., R. P. Freckleton, C. D. L. Orme, and I. P. F. Owens. 2006. Ecology predicts large-scale patterns of phylogenetic diversification in birds. Am. Nat. 168:220–229.

Phillimore, A. B., C. D. L. Orme, G. H. Thomas, T. M. Blackburn, P. M. Bennett, K. J. Gaston, and I. P. F. Owens. 2008. Sympatric speciation in birds is rare: insights from range data and simulations. Am. Nat. 171:646–657.

Pimm, S. L., and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern north-america. Proc. Natl. Acad. Sci. USA 92:9343–9347.

Preston, F. W. 1962. Canonical Distribution of Commonness and Rarity.1. Ecology 43:185–215.

Price, T. D., A. J. Helbig, and A. D. Richman. 1997. Evolution of breeding distributions in the old world leaf warblers (genus Phylloscopus). Evolution 51:552–561.

Purvis, A., M. Cardillo, R. Grenyer, and B. Collen. 2005. Correlates of extinction risk: phylogeny, biology, threat and scale. Pp. 295–316 in A. Purvis, J. L. Gittleman, and T. Brooks, eds. Phylogeny and Conservation. Cambridge University Press, Cambridge.

Purvis, A., K. E. Jones, and G. M. Mace. 2000. Extinction. Bioessays 22:1123–1133.

R Development Core Team. 2005. R: 2.2.1: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.

Rohling, E. J., M. Fenton, F. J. Jorissen, P. Bertrand, G. Ganssen, and J. P. Caulet. 1998. Magnitudes of sea-level lowstands of the past 500,000 years. Nature 394:162–165.

Rosenzweig, M. L. 1995. Species diversity in space and time. CUP, Cambridge.

Secretariat of the Convention on Biological Diversity. 2006. Global Biodiversity Outlook. Montreal.

Simberloff, D. 1986a. The proximate causes of extinction. Pp. 259–276 in D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Springer-Verlag, Berlin.

———. 1986b. The proximate causes of extinction. Pp. 259–276 *in* D. M. Raup and D. Jablonski, eds. Patterns and processes in the history of life. Springer-Verlag, Berlin.

Simberloff, D. S., and L. G. Abele. 1975. Island biogeography theory and conservation practice. Science 191:285–286.

Simberloff, D., and L. G. Abele. 1982. Refuge design and island biogeographic theory – effects of fragmentation. Am Nat 120:41–50.

Soberon, J., and J. Llorente. 1993. The use of species accumulation functions for the prediction of species richness. Conserv Biol 7:480–488.

Stanley, S. M. 1979. Macroevolution. Freeman, San Francisco.

———. 1986. Population-size, extinction, and speciation – the fission effect in Neogene Bivalvia. Paleobiology 12:89–110.

———. 1990. Delayed recovery and the spacing of major extinctions. Paleobiology 16:401–114.

Terborgh, J., and B. Winter. 1980. Some causes of extinction. Pp. 119–133 *in* M. E. Soule and B. A. Wilcox, eds. Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, MA.

Tosi, A. J., K. M. Detwiler, and T. R. Disotell. 2005. X-chromosomal window into the evolutionary history of the guenons (Primates: Cercopithecini). Mol. Phylogenet. Evol. 36:58–66.

Vermeij, G. J. 1987. The Dispersal Barrier in the Tropical Pacific – Implications for Molluscan Speciation and Extinction. Evolution 41:1046–1058.

Vos, R. A., and A. O. Mooers. 2006. A new dated supertree of the primates. Inferring large phylogenies: the big tree problem. PhD thesis. Simon Fraser University.

Vrba, E. S. 1980. Evolution, species and fossils – how does life evolve. S. Afr. J. Sci. 76:61–84.

Vrba, E. 1987. Ecology in relation to speciation rates; some case histories of Miocene-Recent mammal Clades. Evol. Ecol. 1:283–300.

Vrba, E. S. 1992. Mammals as a key to evolutionary-theory. J. Mammal 73:1–28.

———. 1993. Turnover-pulses, the red queen, and related topics. Am. J. Sci. 293A:418–452.

———. 1995. On the connections between paleoclimate and evolution. Pp. 24–45 *in* E. S. Vrba, G. H. Denton, T. C. Partridge, and L. H. Burckle (eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven.

Vrba, E. S., and D. DeGusta. 2004. Do species populations really start small? New perspectives from the Late Neogene fossil record of African mammals. Philos. T. R. Soc. B 359:285–292.

Waldron, A. 2007. Null models of geographic range size evolution reaffirm its heritability. Am. Nat. 170:221–231.

Webb, T., and P. J. Bartlein. 1992. Global changes during the last 3 million years – climatic controls and biotic responses. Annu. Rev. Ecol. Syst. 23:141–173.

Weir, J. T., and D. Schluter. 2004. Ice sheets promote speciation in boreal birds. Proc. R. Soc. Lond. B. Biol. 271:1881–1887.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. Bioscience 48:607–615.

Wilcox, B. A. 1978. Super-saturated island faunas – species-age relationship for lizards on post-pleistocene land-bridge islands. Science 199:996–998.

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Supporting Information

The following supporting information is available for this article:

Table S1. Islands used, primates associated with them, and number of extinctions.
Table S2. Tolerance and biology of island primate species.
Table S3. Phylogenetic signal in traits used in this study.
Table S4. The effect of incorporating modern phylogenetic revisions on the outcome of a *t*-test comparing diversification rates between tolerant and intolerant clades (full species set model).

Supporting Information may be found in the online version of this article.

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