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Journal

Frontiers of Biogeography, 4(1)

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Publication Date

2012

DOI

10.21425/F5FBG12562

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perspective



Losing time? Incorporating a deeper temporal perspective into modern ecology

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Abstract. Ecologists readily acknowledge that a temporal perspective is essential for untangling ecological complexity, yet most studies remain of relatively short duration. Despite a number of excellent essays on the topic, only recently have ecologists begun to explicitly incorporate a historical component. Here we provide several concrete examples drawn largely from our own work that clearly illustrate how the adoption of a longer temporal perspective produces results significantly at odds with those obtained when relying solely on modern data. We focus on projects in the areas of conservation, global change and macroecology because such work often relies on broad-scale or synthetic data that may be heavily influenced by historic or prehistoric anthropogenic factors. Our analysis suggests that considerable care should be taken when extrapolating from studies of extant systems. Few, if any, modern systems have been unaffected by anthropogenic influences. We encourage the further integration between paleoecologists and ecologists, who have been historically segregated into different departments, scientific societies and scientific cultures.

Keywords: climate change, conservation, macroecology, paleoecology, palaeoecology, woodrat

The pronghorn (*Antilocapra americana*) is a quintessential symbol of the Great Plains. As the fastest land mammal in the Americas, it can reach close to ~100 km/h and can sustain speeds of 45 km/h for long distances (Byers 1997). Much of its physiology, morphology and life history reflect an optimization for being swift; pronghorn have oversized hearts and lungs, a 320° field of vision, hollow hair and overlong gestation for their size (Byers 1997). Understanding the selective pressures that led to such specialized adaptations is difficult without the knowledge that the pronghorn co-evolved with a suite of now extinct predators, including the American cheetah (*Micracinonyx trumani*) (Byers 1997, Barlow 2001). As the only surviving member of the once speciose North American family Antilocapridae, the pronghorn no longer has effective natural predators. Consequently, many of its social, morphological and physiological traits have little apparent modern selective value (Byers 1997).

Ecologists recognize the anachronistic

nature of animals like the pronghorn, but more as a curiosity rather than as a concrete example of the substantial alteration of ecosystems that occurred in the late Quaternary. Although work investigating the ecology and life-history characteristics of tropical and temperate plants has proposed that numerous adaptations for dispersal or regrowth arose in response to foraging by now-extinct megafauna (Janzen and Martin 1982, Wing and Tiffney 1987, Barlow 2001), in general, the implications of the prehistoric loss of megafauna in the late Pleistocene have been overlooked. Yet, these animals undoubtedly played key roles in terms of ecosystem structure and function; their abrupt disappearance some 11,000 years ago must have profoundly influenced ecosystem dynamics (Martin 1967, Donlan et al. 2005). How many other life-history, ecological or distributional features of extant animals and plants are due in some part to now-extinct components of the ecosystem?

As ecologists increasingly turn from ‘explaining the present’ to ‘anticipating the future’, there has been renewed interest in bringing a historical perspective into ecology (Botkin et al. 2007, Gavin et al. 2007, Williams and Jackson 2007). While earlier workers illustrated the insights a wider temporal window yields (e.g., Schoonmaker and Foster 1991, Herrera 1992, Delcourt and Delcourt 1998), the contemporary focus on anthropogenic climate change has galvanized efforts. After all, the late Quaternary provides abundant examples for examining the influence of changing abiotic conditions on organism distribution, ecology and evolution (Clark et al. 2001, Botkin et al. 2007, Gavin et al. 2007, Williams and Jackson 2007). Evidence from fine-scale paleoclimate reconstructions (e.g., pollen, cross-dated tree-ring chronologies, ice cores, and other indicators) suggests abrupt climate shifts occurred with regularity in the past (Schoonmaker and Foster 1991, Allen and Anderson 1993, Dansgaard et al. 1993, Bond and Lotti 1995, Alley 2000). Some, such as the Younger Dryas, were significant events, with temperature warming of as much as 5–10°C reportedly occurring within a decade (Alley et al. 1993, Alley 2000), a rate of change higher than that expected under most scenarios of anthropogenic climate change (IPCC 2007). Virtually all species extant today were present and successfully coped with the Younger Dryas. Thus, it has been recognized as a particularly useful analog for studying the likely effects of anthropogenic climate change. Indeed, the most recent IPCC report now contains sections on paleoclimate.

The *de facto* standard traditionally used by ecologists to set ecological baselines is to replicate experiments across space. The implicit assumption is that if the spatial extent is sufficient it encompasses the possible range of natural variation. However, more than 20 years ago it was recognized that conceptual problems occur if ecologists use “*short-term experiments to address long-term questions*” (Tilman 1989, pg 139). Although the incorporation of a broader spatial perspective clearly increases the natural range of variation expressed in both abiotic and biotic

conditions, space is not necessarily an adequate substitute for time. Simply put, ecological history matters. This disparity may occur because of non-analog climatic conditions found in the past, leading to assemblages of mammal or vegetative communities not found together today (e.g., Huntley 1990, Schoonmaker and Foster 1991, Overpeck et al. 1992, Graham et al. 1996, Williams et al. 2001, Williams and Jackson 2007), or because the type or magnitude of change in the past dwarfs that represented along a modern spatial gradient (Jackson 2007).

Here, we provide several concrete examples of how the adoption of a deeper temporal perspective can sometimes provide more complete and often divergent insights into modern ecology. These are drawn largely from our own work or that of close colleagues because it was otherwise difficult to obtain the original data that would allow us to redo the analyses. Our first examples demonstrate how limiting macroecological studies to extant taxa may yield skewed interpretations of broad-scale geographic patterns. The second set of examples demonstrates the added utility that a longer temporal perspective can provide for conservation biology. Both paleontologists and conservation biologists are interested in extinction, and understanding past events could aid in the understanding of current risk for many taxa. Finally, we focus on studies of the likely effect of anthropogenic climate change on organisms and ecosystems. Climate scientists have traditionally used forward-projected models with baselines established using modern conditions. Given the likelihood of non-analog climatic regimes in the future, models that are parameterized based only on modern conditions are likely to fail to accurately predict ecological responses to novel climates. Here, a historical perspective can be particularly useful. Our intent is to demonstrate the need to integrate both paleontological *and* ecological approaches in developing a synoptic understanding of ecological systems.

Ecological examples

Body size distributions in macroecology

Macroecology was developed in the late 1980s as an effort to understand patterns underlying the local abundance, distribution and diversity of species (Brown and Maurer 1989). As a complementary approach to experimental ecological research, it has been remarkably successful at illuminating large-scale spatial and statistical patterns (Smith et al. 2008 and references therein). Body size is often used as a variable of interest in macroecological studies because it is tightly related to many fundamental physiological, ecological and evolutionary characteristics, and moreover, is relatively easy to characterize even for fossil forms (Peters 1983, Damuth and MacFadden 1990). But what if the underlying body-size distribution used in an analysis is biased or incomplete? The use of body size as a dependent variable could potentially lead to misleading results if portions of the biota are selectively missing.

In 1991, Brown and Nicoletto reported that the shapes of mammalian body-size distributions in North America change with spatial scale. The continental-level body-size distribution was unimodal and right skewed, but as spatial scale decreased, regional distributions became progressively flatter until they were nearly uniform for local communities. Brown and Nicoletto's results had important implications in terms of community assembly and structure and the paper has been highly cited. Because species found at local scales were not a random subsample of the regional scale (differing in median, mean, skew and range of size), they argued there were 'rules' influencing the assembly of communities and a limit to the number of species of each body size that could co-exist locally. Distributions became peaked as sites were aggregated over space because of higher taxonomic turnover in smaller-bodied species. Numerous authors have debated the validity of both the patterns and underlying mechanisms since this seminal paper was published; for example, mammalian communities in South American tropical forests reportedly show more

peaked distributions than those in other habitats (Marquet and Cofré 1999, Bakker and Kelt 2000) and the body-size distributions of bats are not flat at the local level across a wide range of latitudes (Willig et al. 2008).

To what extent were the macroecological patterns described by Brown and Nicoletto (1991) influenced by the use of extant North American mammals? The contemporary distributions of both North and South American mammals were heavily impacted by the human-mediated late Pleistocene megafaunal extinction (Martin 1967, Surovell and Waguespack 2009). This event was extremely size biased; although 'only' 12.8% of the North American mammal fauna were extirpated, they were mostly the largest species present (Lyons et al. 2004). To address the sensitivity of these macroecological patterns, we reanalyzed the results reported by Brown and Nicoletto (1991) at the local, regional and continental level, using a global database of body size in late Quaternary mammals (Smith et al. 2003). As an example, we present the mammalian body-size distribution of a county in New Mexico nested within the western grasslands biome of North America. For each of these areas we determined the likely presence of extinct species based on FAUNMAP range reconstructions and local fossil evidence (Harris 1970, Graham et al. 1996, Wilson and Ruff 1999, NPS 2007).

Our analysis suggests little sensitivity to inclusion of extinct species at the local level (Fig. 1); although the range of mammalian body size at sites was underrepresented (e.g., the local area supported larger animals than the maximum present today), the shape of the distribution was not significantly different. At coarser spatial scales, however, both the range of body size *and* the shape of the distribution changed significantly (Kolmogorov–Smirnov two-sample tests, regional: $P < 0.05$, continental: $P < 0.01$). The body size distribution at both the regional and continental levels contains a second mode of larger-bodied mammals (Fig. 1). Recent work by Lyons et al. (2004) suggests that such multimodality is typical of all continents when extinct late-Pleistocene megafauna are included.

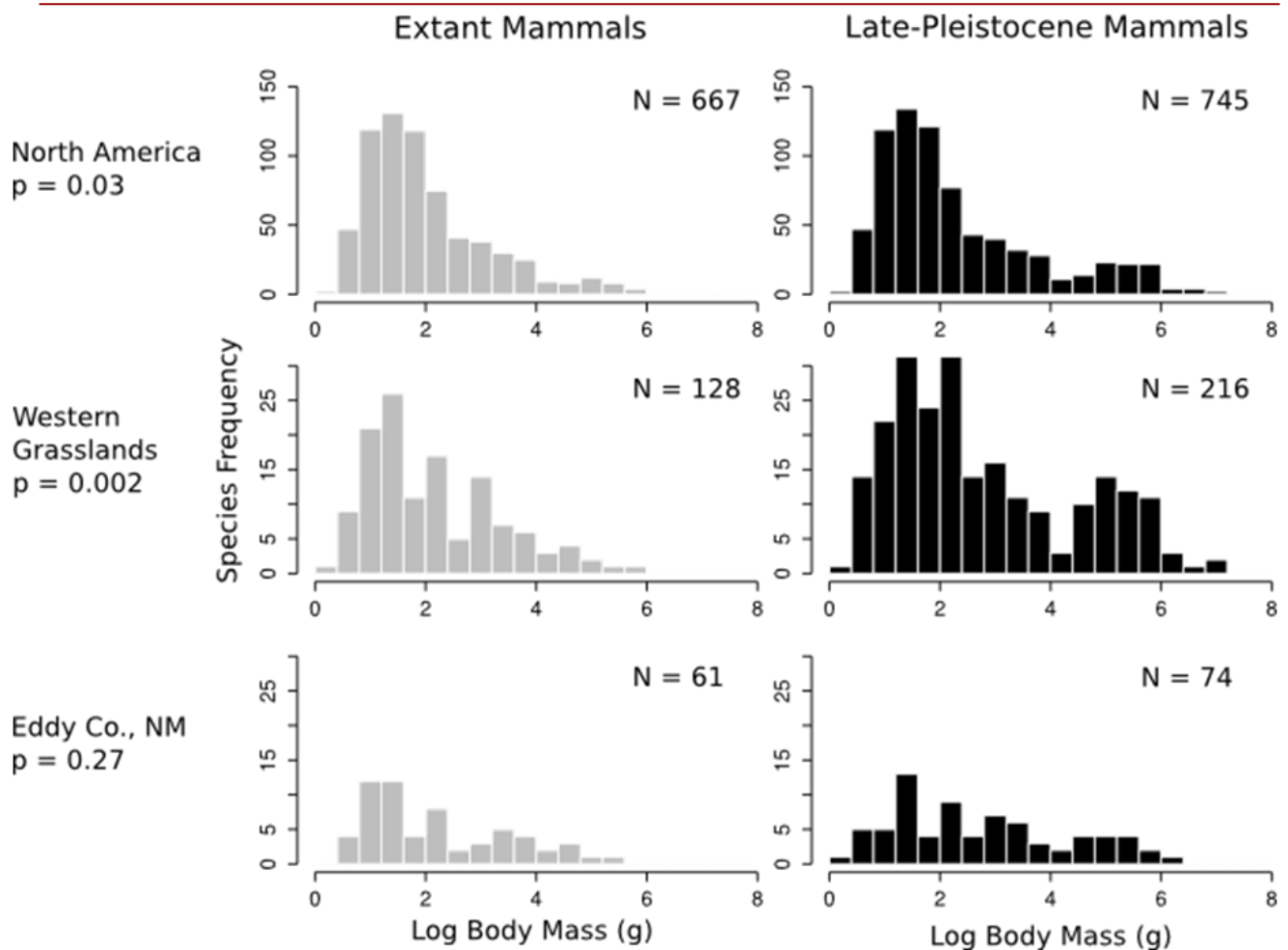


Figure 1. Body size frequency distributions of North American mammal species before (black shading) and after (grey shading) late-Pleistocene extinctions. Distributions are shown at three different scales: the continent of North America (top), regional (a western grassland biome; middle), and local (Eddy County, New Mexico; bottom). While significant differences between past and present body size distributions are observed at the continental and regional scales, patterns were statistically indistinguishable at the local scale.

What does this mean in terms of ecosystem function? Macroecologists routinely use patterns in the body-mass distributions of animals as a basis for understanding the structure, assembly and persistence of ecological communities. Many hypotheses have been proposed to explain body-size distributions at various levels, including ones based on energetics, ecology, phylogeny, biogeography and habitat or textural discontinuities. However, a longer temporal perspective reveals the influence of the size-biased extinction on the shape of contemporary body-size distributions. Clearly large animals have pivotal roles in ecosystems (e.g., Owen-Smith 1987, Pringle et al. 2007), and integrative paleoecological studies are beginning to reveal the profound effects of megafaunal extinction on

vegetation structure, composition, and dynamics, both in North America (Gill et al. 2009), and elsewhere (Hansen and Galetti 2009, Johnson 2009).

Scaling of landmass area and body size

Space use in animals is strongly linked to body size and has been a focal point of much macroecological research (Brown and Maurer 1989, Brown 1995, Gaston 2003, Jetz et al. 2004). Marquet and Taper (1998), and later Burness et al. (2001), observed that the size of the largest mammal on a given landmass increases with land area. To explain this pattern, they noted that large mammals are characterized by both low population densities and large home ranges. Recent studies of mammalian (Okie and Brown

2009) and avian (Boyer and Jetz 2010) body size on islands also found robust scaling relationships between maximum size and island area. These effects imply that to persist large species require large areas to sustain viable population sizes, and important concept in reserve design and conservation of large-bodied mammals (Kelt and Van Vuren 2001). However, Jetz et al. (2004) found a high degree of home range overlap in large mammal species, suggesting that population density rather than home range size is the better measure to use in quantifying individual area needs for conservation purposes. Since many islands experienced extinctions during the late Pleistocene (Alcover et al. 1998), and these extinctions may have affected the local body-size distribution (Lyons et al. 2004, Boyer and Jetz 2010), we re-examined the scaling of maximum size with land area before the influence of human-mediated extinctions.

We gathered data on the largest mammal species found today and in the late Pleistocene on 30 islands and landmasses around the world. Mammal data were limited to herbivorous and

omnivorous species, owing to differences in the scaling of population density and space use between carnivores and herbivores (Peters 1983, Jetz et al. 2004). Island area was based on present-day measurements. Because island mammals would have experienced a dynamic land area due to eustatic sea-level changes during the late-Pleistocene, and because the extinct taxa in our dataset also differ in their dates of last appearance, we found it difficult to assign a single late-Pleistocene value for land area to each island. However, because sea levels in most areas were over 100m lower than present levels during the last glacial maximum (Fleming et al. 1998), the land area of many islands would have been substantially larger during the late-Pleistocene and some islands were connected to nearby continents by exposed land bridges. To control for these issues, we excluded all land-bridge islands and islands where extinction occurred when sea levels were substantially lower than current levels (ca. 7000 years before present, Fleming et al. 1998). For comparison to the island data, we also included late-Pleistocene and modern body mass

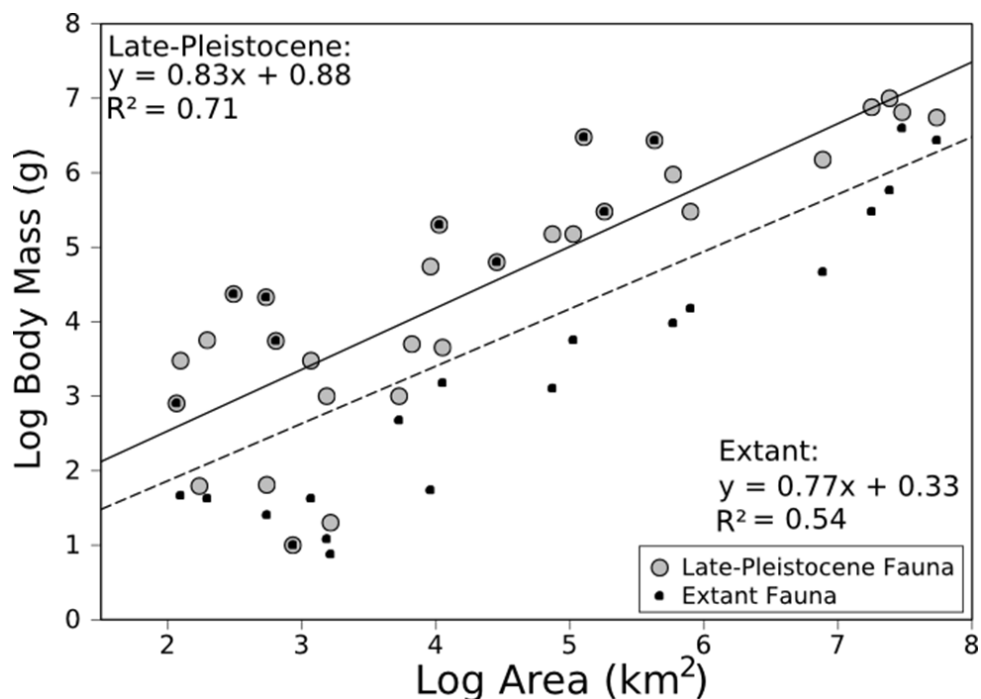


Figure 2. Relationship between maximum body size and area of landmass for extant (open circles, $N = 28$) and late Pleistocene (closed circles, $N = 30$) mammals. Modern data are missing for two islands, Barbuda and East Falkland, due to the extinction of all terrestrial, non-carnivorous, mammals. Both body size and area were \log_{10} -transformed prior to analysis. Slopes were indistinguishable between the two time periods, but the intercept for late-Pleistocene mammals was significantly larger (ANOVA; $p < 0.01$) than for extant species, suggesting that islands supported larger animals in the past.

values and modern land area for six continental landmasses (Australia, New Guinea, South America, North America, Africa, and Eurasia). Body size (g) and area (km²) were log₁₀-transformed prior to analysis. We compared the size of the largest mammal species on each island before and after the extinction, and plotted these body size maxima against land area (Fig. 2).

The strength and direction of the scaling between maximum body size and area in extant species was not significantly altered by the inclusion of extinct species, but the intercept was significantly higher when late-Pleistocene species were included (ANOVA, $P < 0.01$, $df=1,54$, $F=7.4$) than for extant species (Fig. 2). This translates to an order of magnitude *decrease* in the size of the largest mammal supported by a given land area since the late Pleistocene. For example, according to the modern data, the largest mammal that an island of 1000 km² would be expected to support is about 431g, however, in the late-Pleistocene fauna, this maximum size was 2291g.

In order to compare the scaling of body size with area to other studies, we computed the slope of the relationship with body mass as the independent variable (late-Pleistocene: slope = 0.86, extant: slope = 0.71). Late-Pleistocene faunas were statistically consistent with previous studies of both the scaling of maximum body size with area in extinction-structured communities (slope = 0.79, Marquet and Taper 1998) and the body-size scaling of population density in mammals (slope = 0.76, Jetz et al. 2004), suggesting that late-Pleistocene island faunas accurately represent the ecologically constrained scaling of maximum body size with area. It is beyond the scope of this study to determine the ecological mechanisms that allowed larger species to inhabit smaller areas in the past than that observed today; differences in scaling intercept may relate to the allocation of land area and resources for use by humans and their commensals (Boyer and Jetz 2010). However, it is clear that macroecological studies based solely on extant species, especially those conducted in areas known to be affected by recent extinctions, may offer an incomplete picture of these ecosystems.

Temporal perspective in conservation studies

A central goal of conservation biology is to understand the extinction process in order to mitigate current and future anthropogenic biodiversity losses. Extinction risk analyses, like many other predictive ecological studies, are often based on current distributions of extant species (Cardillo 2003, Jones et al. 2003). Longer temporal records, however, can provide an alternative perspective on how conservationists view extinctions. From this perspective, near-time fossil data can be invaluable for identifying general patterns of extinction risk (McKinney 1997, Willis et al. 2007, Boyer 2010). The inclusion of fossil data has several advantages: unlike data on extant endangered species, fossil data provide direct information on the extinction process itself. Rarity and extinction do not always result from the same processes. Second, fossil data represent an independent dataset of extinction probability on which to build predictive models. This avoids the circularity inherent in building a model and testing it on the same dataset (such as the IUCN Red List). Not only can paleoecological data provide a comparison of prehistoric (>500 years) and historic (past 500 years) extinctions, but such data may also aid in determining baseline conditions for conservation and restoration, and help predict future extinction risk.

As a conservation-oriented case study, we turn to the Holocene extinction of birds on Pacific islands. In the Hawaiian islands, the arrival of Polynesian colonists about 1200 years ago corresponded with the extinction of about 50% of indigenous land bird species (56/111 species; Olson and James 1982, 1991). In comparison, historic losses of Hawaiian birds amount to about 40% of the historically observed species (23/55 species; Boyer 2008). To put global Holocene avian extinctions in context, Pimm et al. (2006) estimated extinction rates for pre-European and historic timescales, and compared these to the generic background of ~1 extinction per million species per year (E/MSY). Historic rates were around 26 E/MSY, but after accounting for pre-European extinctions, the estimate rose to ~100 E/MSY. The vast majority of recorded extinctions

before the 20th century were on islands. If the most vulnerable species were lost quickly after human colonization, we may expect rates on islands to slow down over time (Pimm et al. 1994). However, human impacts on island environments have intensified through time, so how do prehistoric and historic extinctions compare in Hawaii?

In the Hawaiian islands, the influence of humans on natural environments differed between the two time periods. Consequently, prehistoric and historic extinction waves may have had different causes resulting in contrasting patterns of extinction risk (see Boyer 2008). Prehistoric extinctions showed a strong bias toward larger body sizes and flightless and ground-nesting species, even after accounting for fossil preservation bias. Many small, specialized species also disappeared, implicating a wide suite of human activities including hunting and destruction of habitat. In contrast, the highest extinction rates in the historic period were in medium-sized nectarivorous and insectivorous birds. Although the most vulnerable species may have disappeared first, changing human activities led to continued extinctions through time.

Currently endangered species are only the most recent victims of a human-caused biodiversity crisis that began thousands of years ago (Steadman 1995). Despite the crucial information the past can provide, paleoecological data are not always incorporated in studies of extinction risk (Blackburn et al. 2004, Trevino et al. 2007). To illustrate the difference this might make, we examined correlates of extinction risk for Hawaiian birds using decision tree models (Boyer 2008). We compared the results of two models: one including only extinctions that occurred since European colonization of Hawaii (ca. 1800 AD), and one incorporating all known prehistoric and historic extinctions (cumulative). The addition of older data to the model produced a substantial increase in explanatory value (7.3 Δ% DE; Fig. 3). When the recent extinctions alone were considered, extinction predictors included body mass and diet, but the cumulative tree expanded the list to include endemism and

flightlessness as significant risk factors as well. While these traits may have been most important during the prehistoric extinction, they remain important for modern birds. As well as identifying traits associated with past extinctions, the two models were used to predict extinction risk for extant Hawaiian birds. Predictions from the cumulative model were a better match to current IUCN Red List status for extant Hawaiian birds than predictions from the historic model, but the difference between the two models was not significant (ANOVA, cumulative $r^2=0.15$, recent $r^2=0.09$; $P >0.85$; $df = 4, 56$; $F=0.33$). Extant Hawaiian birds have already been through a strong extinction filter (Pimm et al. 2006) and these past extinctions have relevance for the conservation of the remaining species.

Although human environmental impacts on birds and their habitats have changed over time, modern endangered birds within the Pacific region share many of the same ecological characteristics as victims of previous extinctions (Boyer 2010). It seems logical that conservation and restoration policies should incorporate

Prehistoric & Historic Extinctions: 43.9%DE

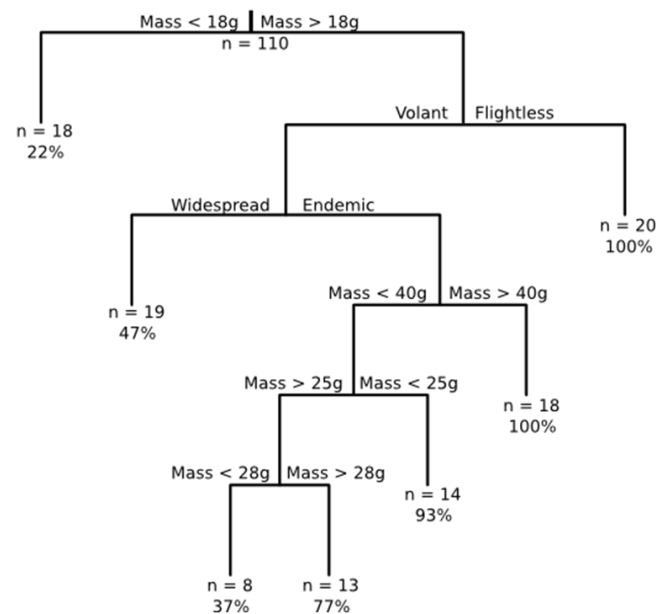


Figure 3. Classification tree model of extinction risk among Hawaiian birds. Extinction probability increases to the right of each branch point. Terminal nodes provide number of species and estimated probability of extinction. See text for details. %DE = percent deviance explained.

paleoecological information about bird species' ranges and island ecosystems. Fossil evidence suggests that many species currently limited to a single island were much more widespread before human contact (Steadman 2006). Thus, Steadman and Martin (2003) argued that future extinctions may be partially offset by selectively translocating birds to islands where they once occurred. The Marquesas Lorikeet (*Vini ultramarina*) and the Polynesian Megapode (*Megapodius pritchardii*) have been reintroduced to well-forested islands in their former range; in New Zealand, similar island sanctuaries have been quite successful (Birdlife International 2004). Steadman and Martin (2003) provided examples of five more species that could benefit from such translocations. Proactive conservation strategies present opportunities for paleoecology to step outside its traditionally retrospective role.

Ecological history and climate change

A better understanding of ecological history can enhance our understanding of how organisms respond to climate change in several ways. Fine-scaled paleoclimate reconstructions of the late Quaternary indicate that climate variability over the past 100 years does not adequately represent the full range of climate changes that occur in ecosystems and, further, that we tend to underestimate the degree of climatic 'teleconnections' (Schoonmaker and Foster 1991, MacDonald et al. 2008). Given that many researchers have employed forward projected models to predict future climate and ecosystem responses, such models parameterized based only on modern conditions are likely to be misleading (Botkin et al. 2007, Williams and Jackson 2007). For some organisms the paleorecord provides us with multiple examples of responses to climate shifts of varying magnitude and frequency. For example, pollen records can provide well-resolved information on regional shifts in abundance, and distributional movements of plants over the late Quaternary (Schoonmaker and Foster 1991, Davis and Shaw 2001, Williams et al. 2001, Williams et al. 2002). Similarly, there are detailed records for animals (Graham 1986, Graham and Grimm 1990,

Graham et al. 1996, Hadly 1996). Of particular interest is the woodrat paleomidden record, which allows fine-grained study of morphological adaptation to climate shifts of varying intensity.

Woodrats (genus *Neotoma*) are small rodent herbivores found throughout much of North America. They are unique in creating middens or debris piles consisting of plant fragments, fecal pellets and other materials held together by evaporated urine ("amberat"). When sheltered in a rock crevice or cave, the contents form an indurated conglomerate, which can be preserved for thousands of years (Betancourt et al. 1990). Microscopic identification and radiocarbon dating of the materials yields estimates of diet and vegetation over time. Moreover, the width of the pellets is highly correlated with body mass, thus allowing estimates of morphological change of populations over time; ancient DNA can also be extracted (Smith et al. 1995, Smith and Betancourt 2006). Middens are ubiquitous across rocky arid regions of the western United States; a well-sampled mountain region may yield upwards of 50–100 discretely dated samples spanning 20,000 years or more. Thus, paleomidden analysis yields a fine-grained characterization of both morphological and genetic responses of woodrat populations to climate fluctuations over thousands of years.

We have used the woodrat paleomidden record to investigate the response to late Quaternary climate change over the western United States. We find that in most instances woodrats readily adapted *in situ*, although there were intervals when temperature alterations apparently exceeded species' thermal tolerances (Smith and Betancourt 2006, Smith et al. 2009). Overall, woodrats follow Bergmann's rule: within a region the body size of woodrat populations was larger during cold temporal intervals and smaller during warmer episodes. As might be expected, sites located near modern range boundaries where animals approach physiological and ecological limits demonstrate more complicated responses. At range boundaries, elevation matters. Populations at higher elevations adapt, while those low-elevation sites may become extirpated, depending

on the severity of environmental shifts.

Note that our interpretations of the ecological history of woodrats are firmly rooted in modern ecology. The robust relationship between the body sizes of woodrat populations and ambient environmental temperature is also seen spatially with modern populations of multiple woodrat species (Brown 1968, Brown and Lee 1969, Smith et al. 1998). We are able to attribute the underlying mechanism to physiology because both laboratory and field studies have demonstrated that maximum and lethal temperature scale inversely with body mass (Brown, 1968, Brown and Lee, 1969, Smith et al. 1995, Smith and Charnov 2001). Moreover, lab studies have yielded estimates of high heritability for woodrat body mass, suggesting that the morphological shifts observed probably include both a genetic and phenotypic component (Smith and Betancourt 2006).

Does analysis of paleomiddens provide additional insights over studies of modern animals? Given the extreme sensitivity of woodrat body mass to temperature, could we predict how woodrats would respond to environmental change without recourse to the paleomidden record? We argue no. In recent work, we investigated the influence of late-Quaternary climate change along a steep elevational and environmental gradient in Death Valley, California. Today, this is the hottest and driest area in the Western Hemisphere with temperatures of 57°C (134°F) recorded. During the late Quaternary, however, pluvial Lake Manly covered much of Death Valley and climate was probably 6–10°C cooler (Mensing 2001, Koehler et al. 2005). Two species of woodrats live in this area today: *N. lepida*, the desert woodrat, found from the valley floor to elevations of ~1800 m on the surrounding mountains and *N. cinerea*, the bushy-tailed woodrat, restricted to elevations above 1800–2000 m in the Panamint Mountains on the east side of the valley.

Over the past few years, we have collected and analyzed a series of 74 paleomiddens recovered from a 1300 m elevational transect along the Grapevine Mountains on the west side of the valley. These span 24,000 years and

indicate a complicated ecological history (Fig. 4). Although *N. cinerea* are currently extirpated on the east side of Death Valley, they were ubiquitous throughout this area from late Pleistocene to middle Holocene. They adapted to climate shifts by phenotypic changes in body

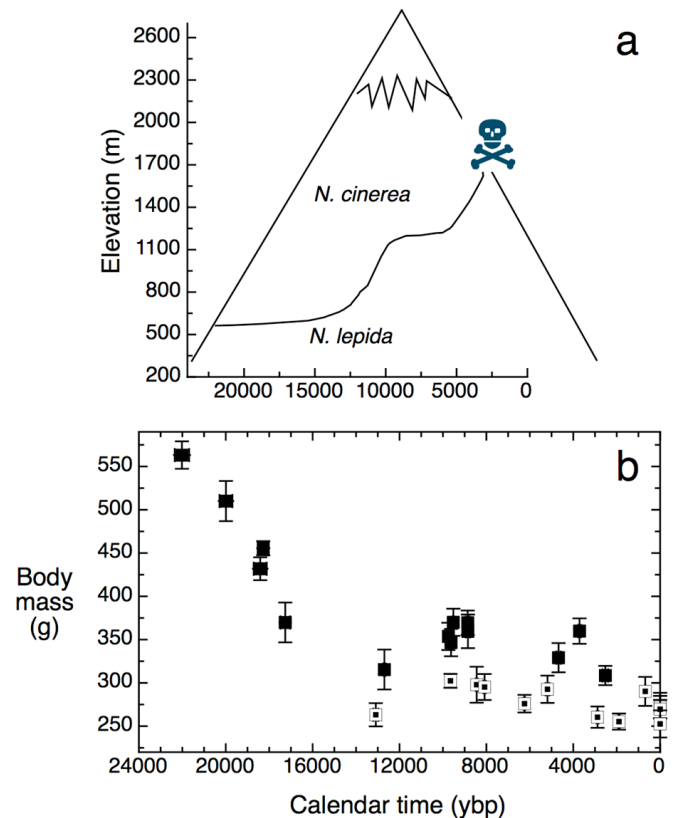


Figure 4. Elevational displacement and evolutionary response of two species of woodrat to late-Quaternary climate change in Titus Canyon, Death Valley National Park, California. Filled squares: *Neotoma cinerea* (bushy-tailed woodrat); open squares with dots: *N. lepida* (desert woodrat). The two species vary considerably in habitat requirements, body mass and thermal niche dimensions; see text for details. a) Elevational displacement over the past 24,000 years. Note that *N. cinerea* was widespread at lower elevations during much of the late Pleistocene, but retreated upslope as climate warmed during the early to middle Holocene; it was eventually completely extirpated on the east side of Death Valley. As the larger and behaviorally dominant *N. cinerea* retreated, *N. lepida* expanded its elevational range upwards until eventually reaching the limits of its cold tolerance at ~1800m, a limit maintained into modern times. b) Body mass over time. Error bars are 95% confidence intervals. Note the remarkable and rapid dwarfing of body mass of *N. cinerea* populations from the full glacial (~21,000 calendar ybp) to the Holocene; for much of this time, the animal occupied the same elevational range, but adapted to climate changes *in situ*. Panel b redrawn from Smith et al. (2009).

mass; during colder episodes they were larger, and during warmer intervals, animals were smaller (Fig. 4b). Their presence may have been tied into a much more widespread historical distribution of juniper (*Juniperus spp.*); we document a downward displacement of ~1,000 m relative to juniper's modern extent in the Amargosa Range. These results suggest a cooler and more mesic habitat association persisting for longer and at lower elevations than previously reported. As climate warmed during the Holocene, *N. cinerea* adapted and retreated upslope; populations were eventually completely extirpated on the east side of Death Valley, despite the presence of what would appear to be enough high-elevation habitat (Fig. 4a; Smith et al. 2009). Moreover, the range retraction of the larger and behaviorally dominant *N. cinerea* led to a range expansion of *N. lepida*, which eventually reached the limits of its cold tolerance at ~1800m, an upper elevational limit maintained into modern times. Of particular interest is the remarkable and rapid dwarfing of body mass of *N. cinerea* populations from the full glacial (~21,000 calendar ybp) to the Holocene (Fig. 4b); for much of this time, they occupied the same elevational range, but adapted to climate changes *in situ*. Similar patterns are seen in other parts of the range (e.g., Smith et al. 1995, Smith and Betancourt 2006). Note that a modern ecologist would detect the presence of only one species (*N. lepida*) in the area today, occupying an elevational range from -84 to 1800m, with a maximum body mass of ~250g. Analysis of present distributions provides a limited perspective when trying to evaluate the potential response of these species to anthropogenic warming; clearly considerable *in situ* evolutionary adaptation occurred along with extensive distributional/elevational migrations. Our paleomidden work highlights just how dynamic and sensitive body size and range are to thermal shifts, and suggests that both are likely responses to future anthropogenic climate shifts.

Finding time

As Herrera (1992) stated, "*Ecologists study thin temporal slices of historically dynamic systems.*"

Certainly, the examples we have provided all underscore this point. The conclusions drawn by each study were markedly different without the incorporation of a longer temporal perspective in the analysis. In each of these instances, the "missing perspective" was biased in a way that compromised the results. Flightlessness, for example, did not come out as a factor predisposing insular birds to extinction in our analysis based on modern data, because the flightless birds had already gone extinct. Yet, if such an analysis was extended to predict extinction risk and direct conservation efforts in another archipelago, the absence of flight ability as a factor in the analysis could have very damaging real-world results. Similarly, given that macroecological studies are often dependent on large-scale distributional information, how much validity do we give studies aiming to tease apart factors influencing the structure and function of ecological systems if major components of the system are missing?

Our message is not novel; a number of workers have emphasized the importance of incorporating a longer-term perspective in modern ecology (Schoonmaker and Foster 1991, Herrera 1992, Delcourt and Delcourt 1998, Botkin et al. 2007). And progress is ensuing. Certainly, ecologists increasingly recognize the importance of long-term studies; a number of important field projects have now been running for many decades (e.g., Paine 1994, Brown et al. 2001). Yet, as Tilman (1989) noted, non-linear dynamics and new equilibrium states can complicate interpretations from even the best-designed and longest-running ecological studies. Here, we have provided examples where the temporal scale required was much longer than that achieved by *any* ecological study. Our purpose in doing so was not to criticize modern ecology, but rather to clearly illustrate why paleoecology is relevant. By providing concrete examples, we hope we have clearly demonstrated the utility of incorporating a historical perspective. There are many resources available to do so; numerous comprehensive databases provide paleo distribution and abundance information for pollen, mammals, and

other fossils, making it possible to imbed modern ecological work into a deeper context.

The extent to which time matters clearly depends on the questions ecologists ask. In some cases, a millennial-scale temporal perspective may not be relevant. But for many of the most pressing ecological issues facing society, an appreciation of past history is imperative. Along with earlier workers (e.g., Schoonmaker and Foster 1991, Herrera 1992, Delcourt and Delcourt 1998, Botkin et al. 2007), we encourage better integration between paleoecologists and ecologists, who are often interested in the same questions. Effective communication between these disciplines remains complicated by the traditional structuring of universities and funding agencies into the physical and natural sciences, which have physically and philosophically segregated paleoecology from ecological or evolutionary disciplines. Yet, progress on some of the most topical issues requires that we integrate across both macro- and micro-evolutionary and ecological theory and combine both theoretical and empirical perspectives. In much the same way that understanding the specialized running abilities of pronghorn antelope requires an understanding of the context in which they evolved, there may be many more ecological features of extant animals and plants that are due in some part to now-extinct components of ecosystems.

Acknowledgements

We thank members of the Smith and Brown labs for many helpful discussions; S.K. Lyons kindly provided data and assistance. This is contribution number 5 from the NSF sponsored *Research Coordination Network: Integrating Macroecological Pattern and Process across Space*. Funding provided by NSF grants BIO-0541625 and BIO-DEB-0344620 to FAS. AGB was supported by a Smithsonian Postdoctoral Fellowship and a NSF Postdoctoral Research Fellowship in Biological Informatics (DBI-0805669).

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Edited by Daniel Gavin