

REVIEW

Ecometrics: The traits that bind the past and present together

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Abstract

We outline here an approach for understanding the biology of climate change, one that integrates data at multiple spatial and temporal scales. Taxon-free trait analysis, or “ecometrics,” is based on the idea that the distribution in a community of ecomorphological traits such as tooth structure, limb proportions, body mass, leaf shape, incubation temperature, claw shape, any aspect of anatomy or physiology can be measured across some subset of the organisms in a community. Regardless of temporal or spatial scale, traits are the means by which organisms interact with their environment, biotic and abiotic. Ecometrics measures these interactions by focusing on traits which are easily measurable, whose structure is closely related to their function, and whose function interacts directly with local environment. Ecometric trait distributions are thus a comparatively universal metric for exploring systems dynamics at all scales. The main challenge now is to move beyond investigating how future climate change will affect the distribution of organisms and how it will impact ecosystem services and to shift the perspective to ask how biotic systems interact with changing climate in general, and how climate change affects the interactions within and between the components of the whole biotic-physical system. We believe that it is possible to provide believable, quantitative answers to these questions. Because of this we have initiated an IUBS program iCCB (integrative Climate Change Biology).

Key words: community structure, ecometrics, integrative Climate Change Biology, Taxon-free, trait distribution.

INTRODUCTION

Increasing public awareness of anthropogenically induced climate change is creating an urgency which, in

turn, is driving a political demand for rapid and practical countermeasures. Climate change is on the agenda, both scientifically and at the highest political levels, both nationally and internationally. With this urgency, a “golden age” of climate modeling has emerged. Climate modeling answers questions we all want answers to: What kind of climate will we face in 50 or 100 years (e.g. Meehl *et al.* 2007)? What consequences will this climate change have for our physical, biological and social environment (e.g. Rosenzweig *et al.* 2007; Schneider *et al.* 2007)? Modelers

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have become the augurs of our modern times, they are the masters of the future and – like the augurs of ancient times – they are often consulted by the highest decision making bodies. But there is a weakness, even a danger, in relying solely on climate modeling for information on how our environment adapts during climate change: the historical dynamics of climate, biota, and the earth system are largely neglected. We need a “golden age” of history to complement the “golden age” of climate modeling – geological, paleontological and evolutionary analyses need to be integrated into our considerations about climate and biological change.

History matters on all scales, both temporal and spatial. The past tells us about the natural variability of the climate and earth system and thus serves as a reference point for measuring anthropogenic impact. For good reasons, this historical aspect has been developed to a greater extent in the latest Intergovernmental Panel on Climate Change than in previous editions (IPCC 2007). Management efforts for sustainable development require a historical perspective. The classic problem of conservation biology, what to preserve and protect, is a fundamentally historical one – a historical approach is needed to distinguish for a given region between indigenous and alien or invasive species. But a historical perspective blurs these categories, even as it sharpens them: Where does the boundary lie between preserving a species from becoming locally extinct, reintroducing a species that was locally exterminated in the 19th or 20th centuries, and “rewilding” a megafauna that disappeared in the Late Pleistocene extinctions, in part due to human hunting pressure (Donlan *et al.* 2006)? Public dispute about the possibilities and limits of geoengineering, notably the LOHAFEX experiment to sequester carbon on the ocean floor by stimulating the productivity of planktonic algae at the surface with iron fertilization (Kintisch 2007), falls into the same category because whether such seafloor sequestration is “natural” may have different answers depending on the depth of historical perspective.

While many people agree that historical considerations are relevant to discussions about the future of our planet, a historical perspective is more than just relevant, it is fundamental because earth systems and climate dynamics are historical processes. Climate change biology is still lacking a deep-time perspective; most data used in ecological studies are at most hundreds of years long. A deep-time perspective requires data that are only available from paleontological and paleoecological studies (Willis & Birks 2006). Our knowledge of climatic and evolutionary change in the geological past is much better than is generally

appreciated (e.g. Fortelius *et al.* 2002; Jernvall & Fortelius 2002, 2004; Mosbrugger *et al.* 2005; Eronen *et al.* 2009) and the methods developed for study of the past are readily available for study of the present. These methods, we argue, also offer a promising approach to modeling the behavior of the biotic–abiotic system. We refer in particular to the set of taxon-free trait analysis methods that we call “ecometrics” and which we introduce below. There is an urgent, practical need to recognize that the whole system of climate, earth, and biota evolves historically. Integration across time scales is clearly necessary to make effective use of existing or potentially existing knowledge about climate change in the past, the present, and the future. Instead of extrapolating into the future either from a trend observed over an ecological time frame or from a longer trend observed paleontologically across multiple such time frames that have been reduced by time-averaging to their mean values, we need to relate these scales to each other and use the combined understanding to explore future perspectives. This is not an unrealistic goal.

ECOMETRICS: TRAITS, SCALE, AND SYSTEMS

Integration across scales has arguably been most successful in the study of global temperature, where stable-isotope ratios are used as proxies that can be measured globally and locally, in the present as well as the past (Hobson & Wassenaar 1999; Holmes *et al.* 2008). Integrating biotic data across temporal and spatial scales is a challenge because no such universal, scale-free common denominator exists for organisms so that the present can be compared with the past, the local with the global.

The most common biotic metrics are tabulations of the origin and extinction of individual species (e.g. Alroy 2008) and measures of the expansion and contraction of their geographic ranges (e.g. Warren *et al.* 2001). These metrics suffice for many problems, but standing diversity is a rather coarse tool for some purposes because so many climatic, biotic, and other abiotic factors influence it. An alternative, but less widely practiced method for measuring biotic systems and their interactions is taxon-free functional trait analysis, which attempts to capture direct links between biotic communities and specific climatic, biotic, or environmental factors (Box 1981, 1996; Damuth *et al.* 1992; Steffen *et al.* 1992; McIntyre *et al.* 1999).

Taxon-free trait analysis, or “ecometrics,” is based on the idea that the distribution in a community of ecomorphological traits such as tooth structure, limb proportions, body mass, leaf shape, incubation

temperature, claw shape, and any aspect of anatomy or physiology can be measured across some subset of the organisms in a community. Because we focus on biotic interactions with the environment, our traits are easily-measured phenotypes whose structure is closely related to their function and whose function interacts directly with the local environment (see Fig. 1–3). To be useful for our purpose, the trait must be statistically correlated through its functional relationships to environmental properties such as temperature, precipitation or dominant vegetation (Fig. 1–3). At any one time, distributions of such functional traits are controlled proximately by the geographic ranges of individual species; the ways in which the traits and environment interact influence the geographic distribution of the species. For example, coat length and density influence the temperature tolerance, and, therefore, the geographic distribution of a mammal species. The geographic ranges of many species determine the makeup of local communities and, therefore, the distribution of environmentally functional traits within that community. The distribution of ecometric traits is ultimately controlled by evolutionary change that generates new traits and changes the distribution of existing ones. Even though the ecometric approach is not as widely practiced as we think it should be, the importance of functional traits for studying the interactions of biota and climate has been recognized for decades and is fairly well-established in the study of macro-vegetation dynamics, stimulated in part by recommendation from the International Geosphere–Biosphere Programme (Steffan *et al.* 1992).

Regardless of temporal or spatial scale, traits are the means by which organisms interact with their environment, biotic and abiotic. The physical and biotic environments influence traits through selection, sorting and other mechanisms, and traits can feed back to change the environment by changing the composition of atmospheric gasses, altering the nutrient composition of the soil, or maintaining savannah parklands in what would otherwise be dense forest, for example. Traits are also directly involved in coevolutionary interactions between species, regardless of whether the teeth of a predator, the rootlets of an epiphyte or the hooks of a parasite; traits evolve to facilitate such interactions and the interactions change as the traits do. Traits influence the geographic distribution of species, which in turn affect community composition, both of which affect the distribution of traits in a community (see Fig. 1–3). Traits can thus be used as a central point with which to measure biotic interactions with the environment.

Functional traits are more scalable than species occur-

rences as a measure of the biotic component of earth systems dynamics. Traits can be measured in individuals, populations, species, communities or metacommunities, rendering them able to quantify any taxon-free system, regardless of whether it is a fossil assemblage or a living community. Traits can thus be used to measure the ecophenotypic plastic response of an individual organism to changes in its environment, to characterize the common features of a plant biome, or to measure the rate of escalation in predator–prey defenses over geological time, whereas the occurrences of species cannot be used for any of these purposes.

Ecometric trait distributions are thus a comparatively universal metric for exploring systems dynamics at all scales. Over annual or decadal time scales, an individual trait, such as leaf shape, can be considered to be constant in relation to its environment over space and time. Ecological, conservation and environmental data on the modern world and recent past are usually collected at the resolution of these short time scales. Over millennial or epochal time scales, the traits themselves evolve, as does their functional relationship with the environment. Paleontological, archaeological and drill-core data are usually collected at the resolution associated with these longer timescales. The mapping between inferences drawn from short and long timescales is complicated, as we have discussed. We anticipate that metapopulation dynamics (Hanski 1998) is a conceptual link between spatial patterns observed over ecological time scales and those observed over geological ones, as spatial “sorting” of species (Vrba & Gould 1986; Lloyd & Gould 1993). The ecometric approach provides a fruitful mechanism for linking data across scales because traits can be decoupled from specific taxa, allowing trait distributions to be mapped across space and through time, regardless of evolution or extinction.

Importantly, traits are also the interface between organisms and society. The long-term resilience of ecosystems and the substitutability of ecosystem goods and services are one central theme in climate change science. As the mechanism through which the environment interacts with organisms, traits are key to how climate change will affect the plants and animals around which our societies and cultures are built (Salik *et al.* 1997). Likewise, traits are what we value or despise in organisms – the structural traits of woods, the chemical traits of herbs, the locomotor traits of work animals, the disease carrying traits of pests, the terrifying traits of large carnivores – thus influencing the cultural priorities we place on conserving, protecting or extinguishing them. The interrelationships between

ecological reality, human views of ecosystems, and social responses to actual and perceived ecological change are complicated. As we modify the traits and geographic distributions of species whose traits resonate with ours, we are in turn modifying the mosaic of coevolutionary interactions, community compositions and geographical distributions, generating feedback loops that are a dominant part of the dynamics of the climate and biotic systems existing in the world today (Salik 1995). Just as individual organisms, populations and communities have different phenotypic traits, individual humans and societies have different cultural traits that will cause them to interact and react differently as biotic and climate systems change (Salik & Ross 2009).

Perhaps the most promising aspect of the ecometric approach is its taxon-free nature. Instead of being forced always to investigate some given set of species and to grapple with the controversies of what is meant by a community, ecometric studies can proceed entirely by analysis and modeling of trait distributions. Operational entities corresponding to taxa and communities can be created post hoc, and the assembly of entities at higher hierarchic levels from lower-level units can be achieved independently of taxonomic nomenclature and ecological conventions. In a spatially resolved model, such a framework will lend itself to the study of multi-entity interactions, perhaps even to a dynamic model of local sources and sinks that depend on the changing interactions of the biotic–abiotic system as a whole.

The ecometric approach offers a natural, robust and quantitative framework for validating models using information from the geological past and the ecological present, it allows rephrasing of old questions by applying them across scales and, most importantly, it allows a systems approach to climate change biology. Instead of asking how predicted climate change will affect the geographic distribution of species X, Y and Z, we can ask how the entire biotic–abiotic system evolves, how trait distributions change in populations, species and communities, how the changes feed back into the system, and how system-level characteristics such as stability, resilience and interaction complexity change. By allowing data to be quantitatively synthesized from scales ranging from the individual, through the ecological to the paleontological, ecometrics provides a tool that can cope with uniqueness, key events, lack of equilibrium, memory effects and self-organized criticality in studying the dynamics of the biotic and climate system and better forecasting the consequences of current anthropogenic climate change for the biotic system.

SCALING AND DATA QUALITY

Rapid ecological processes, such as the ones related to anthropogenic environmental change, include changes in community composition and structure. These rapid changes will influence interactions within populations, the “natural cooperation” that is often considered the third fundamental principle of evolution after mutation and natural selection (Nowak 2006). Change in the species that coexist in a community thus influences the geographic mosaic of coevolution (Thompson 2005). If we are to understand ecosystems and anticipate the nonlinear changes in the systems, we must take both into account and understand them at local and global scales, over short and long periods of time. According to Kerkhoff and Enquist (2007), resilience highlights the unpredictability of the ecological systems, whereas other concepts, like scaling laws, highlight the predictable characteristics of the systems. Therefore, scaling must be taken into account when studying the ecosystem changes.

Merely having a scalable metric with which to quantify biotic properties does not by itself solve the problem of comparing systems at different temporal and spatial scales. Trait data collected from an ecological field study may be extremely precise in their spatial and temporal resolution, whereas data collected from a single fossil sample may represent an average over a time and space greater than all the data in the ecological study combined. This kind of sampling problem requires care if inferences are to be drawn regarding whether the same processes act at different scales. Rarefaction, randomization and bootstrapping approaches provide one avenue for making cross-scale comparisons (e.g. Manly 1991; Smith *et al.* 2004). Modeling processes at fine-scale resolution and testing the predictions of those models against data taken from larger temporal and geographic scales is also key to integrating across disciplines and scales (e.g. Maurer 1999; Guisan & Zimmermann 2000).

A desirable corollary of applying methods from paleontology to living systems is that they necessarily reduce the complexity of the data, making synthesis more feasible. In contrast to the evolutionary ecologist, who struggles with the daunting complexity of living systems, the paleontologist famously faces the abominable incompleteness of the fossil record. Not only are fossil samples very small compared with what once existed, but they also come with biases that are very difficult to estimate. Fortunately, the randomness of fossil preservation favors on average the most abundant species, which means that many community properties carry through into the fossil sample. A major

recent advance in paleobiology has been the realization that this sampling bias can be used deliberately as a tool through what has become known as occupancy (Damuth 1982; Hadly & Maurer 2001; Jernvall & Fortelius 2002, 2004; Vermeij & Hebert 2004). The frequency at which a species is found in a group of fossil sites is its “commonness,” which is related to a combination of its original local abundance and geographic range, conceptually held together by the well-known species–area relationship of present-day ecology. Although the details of the “natural rarefaction” that has produced the fossil record might never be completely known, imposing artificial sampling filters on living communities has little effect on observed patterns compared to complete data (Heikinheimo *et al.* 2007). If this consistency across scales can be generalized, it suggests that incomplete sampling is not necessarily a major concern and that unwieldy (and uneven) ecological datasets can be simplified without punitive loss of information to a level where large-scale analyses become possible.

TRAITS AS PROXIES

Ecometrics for climate and environment

Integrated studies of climate and biotic systems using ecometrics are still in their infancy, with their potential far from realized. Nevertheless, the ecometric approach has been applied to an increasingly large number of systems for the study of many kinds of biotic–environmental interaction. These existing studies (e.g. Wolfe 1979; Wiemann *et al.* 2001; Fortelius *et al.* 2002; Janis *et al.* 2004; Wright *et al.* 2004; Traiser *et al.* 2005; Rodriguez *et al.* 2008; Eronen *et al.* 2010b; Polly 2010) illustrate how ecometrics can be used to integrate data to better understand biotic dynamics on many spatial and geographic scales.

Perhaps the most common use of ecometrics has been as a proxy for climate or environmental factors. In these studies, the correlation of trait to environment is used to estimate the environment from traits, especially ones observed in the fossil record. Both plant and animal traits have been used as a proxy for precipitation. Leaf shape is the classic indicator of precipitation and temperature (see Fig. 3). Leaf shape has been used as an indicator of past climates since the 1900s (Bailey & Sinnot 1915) and is increasingly used as a paleoclimate indicator today. The proportion of species in a flora whose leaves have more teeth, proportionally larger teeth and a higher perimeter-to-area ratio is greater the colder and moister the climate (Wolfe 1979, 1993; Wilf 1997; Wiemann *et al.* 2001; Green

2006), something that is also true of these same features among geographically varied populations within a species (Royer *et al.* 2009). Traiser *et al.* (2005) investigate in detail what features of leaf shape correlate to different climatic conditions. There are number of investigations using these methods for fossil leaf assemblages (e.g. Wilf *et al.* 1998; Jacobs 2002; Royer *et al.* 2005). The physiology of leaves and the traits that describe the metabolism has been studied intensively (e.g. Wright *et al.* 2004, 2005). Wright *et al.* (2004) identifies a worldwide “economic” spectrum of correlated leaf traits that affects global patterns of nutrient cycling and primary productivity. Shipley *et al.* (2006a,b) use these relationships to predict the distribution and diversity of plants in communities. The mapping of the physiology of leaf traits opens up opportunities for integrating these relationships to climatic variables in the past.

Mammal tooth traits in herbivores can also be correlated with precipitation (see Fig. 1). Herbivores use plants as their foodsource. The structure of vegetation locally and the distribution of plants regionally are both influenced by climate. The structural and nutritional properties of available plants in turn determine the demands placed on functional traits of herbivores. For example, the average height of the molar tooth crown, or hypsodonty, is greater in drier regions with fibrous, low-quality forage (Eronen *et al.* 2010b), allowing it to be used as a proxy for precipitation in fossil mammal sites to study changing patterns of regional aridity in the Miocene (Fortelius *et al.* 2002; Janis *et al.* 2004). The detailed description of the tooth crown height proxy for precipitation is given in Eronen *et al.* (2010b), and the application to fossil data is available in Eronen *et al.* (2010a). Rodriguez *et al.* (2008) describe the geographical pattern of mean body size of the non-volant mammals in the New World. They find that body size and temperature are nonlinearly correlated. According to their results, mean body size is negatively correlated with temperature, and in the Nearctic it increases towards the north. This suggests that body size could be used as an ecometric variable to describe temperature once the relationship has been quantified in detail. The size of ectothermic animals is also correlated with mean ambient temperature (Makarieva *et al.* 2005), allowing the body size of animals such as snakes to be used as “paleothermometers” (Head *et al.* 2009).

The dominant macro-vegetation of a region can also be estimated from the average traits of the animals that live there. The “cenogram” method for interpreting habitat structure on a closed–open axis from the distribution of body masses of the mammal species living in that habitat

is one that has been founded on data from modern faunas and applied to the interpretation of paleoenvironments (Valverde 1964; Legendre 1986; Brown & Nicoletto 1991; Millien *et al.* 2006; Travouillon & Legendre 2009). The proportions of carnivore feet that are associated with different types of locomotion and substrate use are also significantly correlated with habitat type (see Fig. 2) and have similar potential as a proxy for the macro-vegetation environment (Polly 2010).

Other ecometric properties have been used as proxies for many other environmental factors, either climatic or individual. Dental wear patterns, dental structure and tooth crown complexity have been used to estimate diet in mammals (Fortelius & Solounias 2000; Evans *et al.* 2007). Leaf stomatal counts have been used to estimate CO₂ concentrations in the atmosphere (Pagani *et al.* 1999; Pearson & Palmer 2000; Kürschner 2008). Propagule size has been used to measure plant dispersal (Bullock *et al.* 2006).

Perhaps the most illuminating example of how we can use ecometrics at the moment comes from Miocene and Pliocene (23 to 2 Ma) fossil mammal assemblages of Eurasia, a period during which environments changed from closed forests to more open woodlands and grasslands. Using the ecometric of mean hypsodonty (mean plant-eater molar crown height), first introduced by Fortelius *et al.* (2002) and significantly developed by Eronen *et al.* (2010a) as

briefly described above, it has been possible to map the spatial and temporal development of open-adapted mammal assemblages during this time in considerable detail. Such assemblages first appeared in Central Asia around 15–14 Ma, spreading from Central Asia into Europe 10–8 Ma. The open-adapted assemblages had their origins in the central part of the continent, where the effects of the mid-latitude drying that subsequently engulfed most of Eurasia during late Miocene were first apparent (Bernor 1983; Fortelius *et al.* 2002; Eronen *et al.* 2009). As the open habitats spread, so did the mammals adapted to it, until the process culminated in westernmost Europe in the extinction event known as the Vallesian Crisis, when much of the last lingering forest-community finally disappeared (Agusti *et al.* 2003; Eronen *et al.* 2009).

The ecometric approach, as in the hypsodonty analysis just described, relies on verification and calibration based on modern biotas to determine the basic relationship between the trait values and whatever aspect of climate or environment they relate to (see Fig. 1–3). It must be emphasized that the ecometric trait distributions in space primarily reflect population and dispersal dynamics in ecological time (“sorting” in the sense of Vrba & Gould 1986), and that in any one place their distribution expresses an aspect of community structure. The evolutionary processes that adjust and give rise to new ecometric traits, in

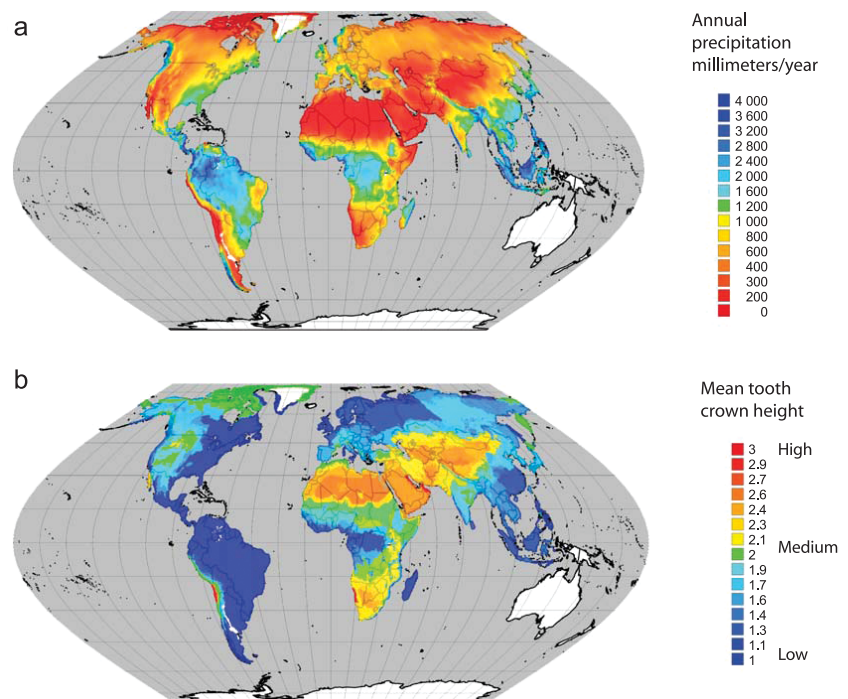


Figure 1 Ecometric traits related to community’s mean tooth crown height in herbivorous large mammals are strongly associated with precipitation ($R^2 = 0.66$; Eronen *et al.* 2010b): (a) Global annual precipitation (mean for 1950–2000) data from Hijmans *et al.* 2005; and (b) mean tooth crown height in herbivorous large mammals (after Eronen *et al.* 2010b).

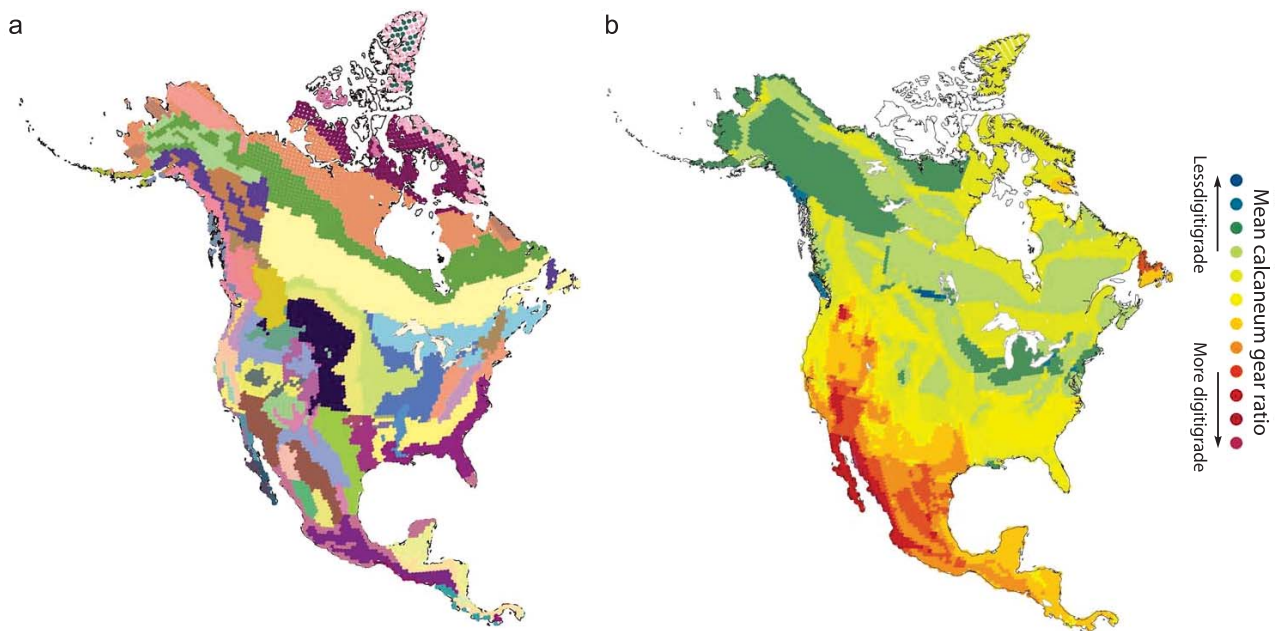


Figure 2 Ecometric traits related to digitigrady in mammalian Carnivora are strongly associated with ecological provinces ($R^2 = 0.70$; Polly 2010): (a) Ecoregion provinces (Bailey 1998), with an arbitrary shading scheme; and (b) mean calcaneal gear ratio (calcaneum length/sustentacular position) for the carnivoran species sampled with 50-km grid points (after Polly 2010).

contrast, typically operate on much longer (geological) time scales. The ecometric pattern measured in communities spread across time and space thus results from both geographic reshuffling of faunas through migration and from evolutionary adaptation of lineages to changing conditions. The level at which ecometric traits are used is coarse relative to within-species variation and, therefore, is largely unaffected by it. For example, the use of molar tooth height as a proxy for rainfall is based on a classification of tooth crown height into 3 values: low, medium and high (see Fortelius *et al.* 2002; Eronen *et al.* 2010b). Although crown height varies within a species, and has a direct Darwinian relationship to rainfall (King *et al.* 2005), we are not aware of a single species (and only very few genera) where these class boundaries would be crossed. Presumably, within species variation would contribute to the ecometric “signal” if local populations are adapted to local environmental conditions, although to date this supposition has not been tested.

Although some uncertainty remains as to how well ecometrics can resolve the past if the modern relationship of trait to environment has changed, as it no doubt has, the performance of ecometric proxies in the present is very well documented. If a methodological connection between the present and the past is needed, ecometrics seems a

promising candidate.

Persistence and dissolution of community structure

A classic and still largely unanswered question in ecology is why do communities appear to persist for long periods of time despite the fact that species appear to respond individually to climate change (Connell & Sousa 1983; Graham *et al.* 1996; Lyons 2005)? Taxonomic issues have made this question difficult to address satisfactorily in the fossil record where the temporal dimension is best represented, but it can be rephrased in a more answerable form in a trait-based framework.

With paleontological data we can determine whether general rules of community assembly and disassembly exist on longer timescales, at different time intervals and non-analogous situations. We know from fossil records that similar types of communities re-assemble after major disturbances, and that there is some degree of inertia in communities (e.g. McGill *et al.* 2005). There are also some studies on how much constant perturbations of the environment affect the community assembly (e.g. van der Meulen *et al.* 2005), but how do these mechanisms work and what are the underlying biotic and abiotic processes?

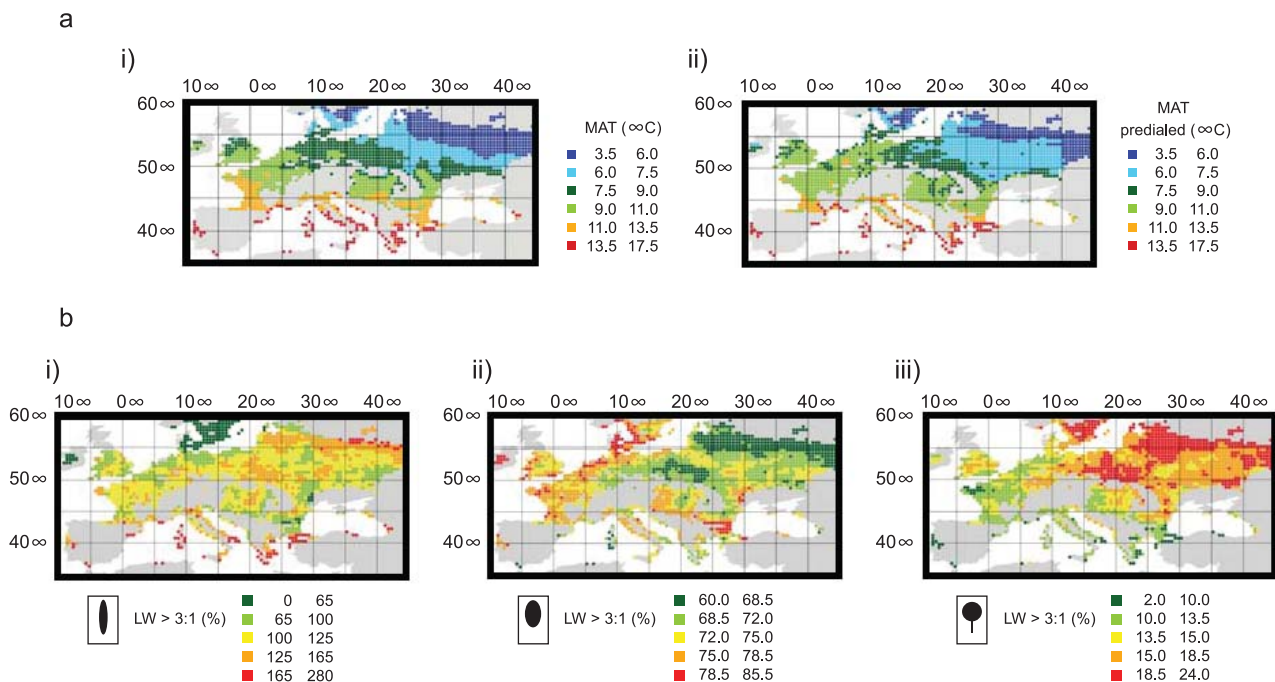


Figure 3 Ecometric traits related to leaf shape are strongly associated with mean annual temperature (Traiser *et al.* 2005). (a) Distribution pattern of mean annual temperature (MAT): (i) actual MAT (data from New *et al.* 1999); (ii) predicted MAT from the MLR transfer function, $R^2 = 0.89$, standard error = 0.9°C (figures i and ii modified from Traiser *et al.* 2005). (b) Distribution patterns of 3 leaf shape (length : width ratio) classes: (i) narrow leaves; (ii) medium L : W ratio leaves; and (iii) broad leaves (figures i and iii modified from Traiser *et al.* 2005).

Although still grounded in a taxonomic framework, the observation that species and genera wax and wane in a regular manner during their history in geological time offers support for the view that community persistence is a function of the dynamics of individual species. Individual species and genera of fossil mammals (Jernvall & Fortelius 2004), molluscs (Foote *et al.* 2007) and marine microflora (Liow & Stenseth 2007) have been found to have a strongly unimodal occupancy distribution, with most taxa waxing to a peak at which they are at their most geographically widespread and then waning to extinction without secondary increase. This pattern appears to be inconsistent with community persistence because it suggests that the history of species that inhabit communities are independently stochastic of one another. However, are these paleontological taxa comparable to one another? Could persistent communities as might be observed in the living world be masked by taxonomic artefacts that agglomerate many species as they would be recognized based on observations in the living world into single “species” as they are recognized morphologically in the fossil record?

An ecometric approach applied equally to living and extinct communities would provide a common point of comparison with which to address this problem. Regardless of taxonomic splitting or lumping, variation in functional traits can be measured equally accurately in systems at all scales. One such ecometric analysis of trophic relationships has shown that unimodality in occupancy is strongest for primary consumers and weakest for omnivores, suggesting that climate change, mediated by food and habitat, is a main causal factor (Jernvall & Fortelius 2004). So far, only speculation has been offered for explaining the strong pattern of unimodality (Jernvall & Fortelius 2004; Foote *et al.* 2007; Liow & Stenseth 2007), which contrasts so dramatically with the strong fluctuations that characterize populations observed at ecological time scales. This is an obvious challenge for integrative research. Climate change biology badly needs to integrate observations from time scales that cover the entire history of taxa. There has been recent advancement in this regard concerning biogeography and niche modeling (see Wake *et al.* 2009). We propose that the link between

the past and the present is most naturally made using taxon-free entities based on functional traits.

Taxonomic and functional diversity in ecosystems

Further questions that are ripe for an ecometric approach are: what is the relationship between taxonomic and functional richness in ecosystems, and how does it depend on climatic conditions and change? In a concrete application of taxon-free analysis, Jernvall *et al.* (1996) use both taxic and taxon-free approaches to look at the history of diversity (richness of taxa) and disparity (richness of traits) of land mammals over 65 Myr. They show that although the 2 largely went hand in hand during the Eocene warming 40 Ma, the rising taxonomic richness in the Neogene was not accompanied by a corresponding rise in disparity, suggesting a different relationship between resource use and functional capability in the younger and harsher world.

NICHE MODELING

Part of the climate change science is the niche modeling of species. Most of the approaches for reconstructing or estimating past or future climates using taxa depend upon a species' geographic range being correlated with one or more climate parameters such as temperature, precipitation or seasonality. This is usually referred to as the climate envelope of the species. The climatic envelope of a species is a multivariate space: its axes are climatic variables; its boundaries are the upper and lower values of those variables that occur across the species' geographic range; and its purpose is to describe the climatic limits experienced by the species. When climate envelopes are projected to a map, or used to estimate its potential geographic range otherwise, the approach is called niche modeling. Many studies equate the climate envelope with a species' niche, but it is only when the factors that limit the existence of the species are, in fact, climatic that the climate envelope is a good proxy for the fundamental niche in the Grinnellian sense (Grinnell 1917; see also Soberón 2007). In other words, one can equate the climate envelope with species niche only when the envelope describes the full range of climate conditions that permit a species to live (Hutchinson 1957; Soberón & Peterson 2005; Soberón 2007). Niche modeling is widely used in climate change biology studies. Our approach of mapping traits can be integrated to the niche modeling studies relatively easily. As a taxon free approach, the ecometrics could be used to build climate envelopes for trait combinations. Alternatively, we can combine traits to species, although the taxon-free na-

ture of the ecometric approach is then lost.

A recent approach with great potential for integrating ecometrics with niche modeling is the mechanistic niche modeling proposed by Kearney and Porter (2009), where species distribution models are combined with physiological traits to predict the future ranges of species based on modeled climate change. This functional, trait-based approach is closely related to ones in botany that use "plant functional types" to model the interaction of communities to climate (Box 1981, 1996; McIntyre *et al.* 1999). This axis of integration is especially promising because it includes known functional relationships, and could, therefore, provide a basis for an interactive systems approach to the biology of climate change. All of the systems used as environmental proxies described above could be used with this type of mechanistic modeling to generate predictions that cross temporal and geographic scales and can, therefore, be used to test and integrate data drawn from many sources.

INTEGRATED CLIMATE CHANGE BIOLOGY

The main challenge now, as we see it, is to shift the perspective, to ask not only what the effects of future climate change will be on the distribution of organisms and biomes, or what its impact will be on ecosystem services, but how biotic systems interact with changing climate in general, and how climate change affects the interactions within and between the components of the whole biotic-physical system, and not only to ask, which has always been possible in principle, but to provide believable, quantitative answers, which we argue here is entirely possible. The challenge is to describe complex interactions and feedback loops within abiotic-biotic systems and changing ecological networks and their resulting feed-forward mechanism (Kerr *et al.* 2007), recognizing that interactions might change as a result of change in the climate or biotic components of the earth system. Our emphasis on "integrative climate change biology" is thus on the first and last words. It must be integrative in the full sense of the word, as lucidly described by Wake (2008); that is, provide a hierarchical exploration of the issue, including processes at the individual, population and community levels. The need to integrate data across geographic and temporal scales is widely recognized by climate change biologists (Carpenter 2002; Willis & Birks 2006; Kerr *et al.* 2007). Nearly a decade ago, Thompson *et al.* (2001) already saw ecological research as entering a new era of collaboration and integration; nevertheless,

such integration remains a challenge because researchers from varied areas of expertise must collaborate to attack problems, they must combine empirical, experimental, theoretical and modeling components from all scales, and they must develop research frameworks in which to conduct their work (Wake 2008). Under the initiative of the International Union of Biological Sciences, we have brought together a working group of ecologists, paleontologists, paleoanthropologists, modelers, climatologists and computer scientists to meet these challenges and focus on geobiological aspects of “integrated climate change biology” (iCCB).

In thinking about the interaction between the biotic and climate systems it is helpful to recall that climate is not a fundamentally hierarchical phenomenon. “Climate” simply means regional weather conditions added over some period of time, in other words a set of frequency distributions of physical parameters, not fundamentally different if the period is a decade, a century or a million years. However, at least 2 aspects of climate are scale-dependent. The first is cyclic climate change (e.g. Milankovitch cycles), where the cycles interact differently with biotic systems depending on their scale, especially regarding speciation and extinction (e.g. Barnosky 2001). The second is the occurrence of exceptional events, whose probability increases cumulatively as a function of time (e.g. Van Valen 1973). Rare disasters, which may serve to reset biotic systems, periodically pruning them of susceptible populations, may not be observed over short time scales, but are frequently seen over longer time periods where their consequences range from range shifts and local replacement of one community by another to global mass extinctions (Roopnarine 2006; Erwin 2008). The larger-scale aspects of climate change cannot be addressed simply by study of living organisms but their effects are commonplace in the fossil record; scale-dependent data such as these must be integrated from sources at many scales to fully understand how biotic systems are interacting with anthropogenic climate change today.

CONCLUSIONS

We summarize our key points as follows.

1. The main challenge in climate change biology today is to describe complex interactions and feedback loops within the abiotic-biotic system in such a way that it can be applied to changing ecological networks, including their resulting feed-forward mechanisms.
2. It is important to provide believable, quantitative answers to how biotic systems interact with changing climate in general, and how climate change affects the interactions within and between the components of the whole biotic–physical system.
3. We need to integrate data across geographic and temporal scales, including the future scenarios as well as the deep past, into a single continuum.
4. The larger-scale aspects of climate change on biota cannot be addressed simply by the study of living organisms. Rather, climatic effects are commonplace in the fossil record. If we are to fully understand how biotic systems interact with anthropogenic climate change today, scale-dependent data such as these must be integrated from sources at many scales.
5. The climate is not a fundamentally hierarchical phenomenon. It is a set of frequency distributions of physical parameters, not fundamentally different whether the period is a decade, a century or a million years. However, at least 2 aspects of climate are scale-dependent: cycles and rare events. These might not be observed over short time scales, but are frequently seen over longer time periods.
6. History matters: the past tells us about the natural variability of the climate and earth system and, therefore, serves as a reference state to measure the anthropogenic impact. Without knowledge of the past it is very hard to understand climate change.
7. We feel that the ecometrics approach is a promising one for studying climate and biological change across different geographic and temporal scales.

What we have outlined here is essentially an approach and a research program for understanding the biology of climate change, making use of integration and the fact of extraordinary climate change in progress. We believe that integrated climate change biology has the potential to go beyond this goal, into the demanding arena of forecasting future states of the system, including such critical aspects as ecosystem services. The mechanistic modeling of niches and habitats using functional types (Box 1981, 1996; Kearney & Porter 2009) is designed explicitly for prediction purposes, and our broader integration of functional elements across temporal scales should only make the task more feasible. This is not to say that it will be easy, or that reliable forecasts would be the first result of integrated climate change research. Rather, we believe that the framework we propose is one where it is reasonable to expect concrete answers to crucial questions about forecasting and prediction in general. Which aspects of the system are, and which are not predictable? What are time-persistent patterns, and what processes produce them?

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