IDEA AND PERSPECTIVE

When should species richness be energy limited, and how would we know?

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Abstract

Energetic constraints are fundamental to ecology and evolution, and empirical relationships between species richness and estimates of available energy (i.e. resources) have led some to suggest that richness is energetically constrained. However, the mechanism linking energy with richness is rarely specified and predictions of secondary patterns consistent with energy-constrained richness are lacking. Here, we lay out the necessary and sufficient assumptions of a causal relationship linking energy gradients to richness gradients. We then describe an eco-evolutionary simulation model that combines spatially explicit diversification with trait evolution, resource availability and assemblage-level carrying capacities. Our model identified patterns in richness and phylogenetic structure expected when a spatial gradient in energy availability determines the number of individuals supported in a given area. A comparison to patterns under alternative scenarios, in which fundamental assumptions behind energetic explanations were violated, revealed patterns that are useful for evaluating the importance of energetic constraints in empirical systems. We use a data set on rockfish (genus *Sebastes*) from the northeastern Pacific to show how empirical data can be coupled with model predictions to evaluate the role of energetic constraints in generating observed richness gradients.

Keywords

Diversification, evolution, latitudinal gradient, niche conservatism, phylogenetic structure, simulation, species richness, species-energy theory, zero sum.

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INTRODUCTION

The idea that the number of species coexisting in a region might be limited by the energetic capacity of that region to support life was first proposed explicitly by G. Evelyn Hutchinson in his seminal Homage to Santa Rosalia (Hutchinson 1959). Prior to that, explanations for geographical gradients of species richness had emphasised historical factors – such as Wallace's (1878) observation that in temperate regions evolution had not 'had a fair chance' to diversify owing to periodical disturbances – or to differences in rates of diversification between the tropics and temperate zone (Dobzhansky 1950; Fischer 1960). Certainly, many scientists going back to Forster, Wallace and von Humboldt invoked variation in climate as a potential cause of richness gradients, but usually in the sense that harsh climates provided a filter with respect to species' abiotic tolerances.

Hutchinson (1959) summarised his view for how energetic constraints might limit the number of species in a region by arguing that '[i]f the fundamental productivity of an area is limited…to such a degree that the total biomass is less than under more favourable conditions, then the rarer species in a community may be so rare that they do not exist' (p. 150). In other words, his argument was not about energy in a kinetic, temperature-related sense, as was hypothesised subsequently (Rohde 1992), but in the potential energy sense related to resource availability and the productivity of the environment. It is this sense in which the term 'energy' will be used hereafter.

Hutchinson (1959) did little more than suggest the importance of energetic constraints, but his ideas were re-vitalised and expanded upon in Jim Brown's homage to the Homage two decades later (Brown 1981). Brown (1981) advocated for a 'top down' understanding of community structure and dynamics based on system-level constraints, rather than attempting to model all species and their interactions separately from the 'bottom up'. System-level constraints, or in Brown's terminology, 'capacity rules', were one major ingredient of a general equilibrium theory of diversity. Brown was heavily influenced by the heuristic success of MacArthur & Wilson's (1967) theory of island biogeography, which also attempted to explain variation in species richness using system-level constraints of island isolation, and especially, area. Larger areas were hypothesised to support more individual organisms and higher mean population sizes. In addition to reducing average extinction rates, an increase in the total number of individuals was expected to result in an increase in

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the number of species based on theoretical arguments about species abundance distributions (Preston 1962; May 1975). Recognising that area alone was a crude predictor of overall abundance, Wright (1983) substituted total resource availability (resource density times area) into the mathematical machinery of Preston (1962) and May (1975), and 'species-energy theory' was born.

Over the past three decades, numerous studies have demonstrated relationships between species richness and environmental variables that might reflect the availability of resources. At large geographical scales, commonly used proxies for resource availability include net primary productivity (Kaspari *et al.* 2000b), actual evapotranspiration (Currie 1991) and annual precipitation (O'Brien 1993). Environment-richness relationships have been shown to hold through time as well as across space (Hurlbert & Haskell 2003), lending additional support to explanations based on top-down constraints. Finally, a number of lab and field studies have also documented positive energy-richness relationships using more direct measures of resource availability than these climate-based and remotely sensed proxies (Srivastava & Lawton 1998; Hurlbert 2006).

Nevertheless, support for positive energy-richness relationships over broad geographical extents is far from universal. For a variety of taxa, especially ectotherms, temperature is often a stronger predictor of species richness than estimates of productivity (Buckley *et al.* 2012). For some groups richness peaks in areas of low to moderate productivity (Kouki *et al.* 1994; Stevens & Enquist 1998). Furthermore, the vast majority of the literature on species-energy relationships has been based on correlations, and few studies have evaluated the hypothesised intermediate relationships with abundance (but see Srivastava & Lawton 1998; Kaspari *et al.* 2003; Currie *et al.* 2004; Hurlbert 2006), or developed in more detail specific mechanisms leading to a positive energy-richness relationships and secondary predictions of those relationships (but see Evans *et al.* 2005). The slow progress in rigorously testing and advancing these ideas coupled with the increasing availability of phylogenetic information and subsequent interest in historical explanations for species richness gradients has led to increased scepticism regarding the importance of energy-based explanations (Wiens 2011; Cornell 2013). For example, niche conservatism alone could result in low species richness in non-ancestral environments because of the reduced chance of successful colonisation of such environments and the reduced time for diversification relative to ancestral environments once colonised (Wiens & Donoghue 2004).

Our goal here was to more fully develop the logic and assumptions behind species-energy relationships and explore subsequent implications for patterns beyond richness gradients. Specifically, we discuss some of the contexts in which energetic constraints are expected to be most relevant, and identify several secondary patterns beyond environment-richness correlations that would be predicted to arise due to energetic constraints. Some patterns are testable with a strong fossil record that provides information on extinct lineages and clade dynamics over time. However, because the fossil record is incomplete for most taxa, we focus on lines of evidence that are possible in the absence of such data. We develop a simulation model that examines how the presence

of an energetic constraint is expected to affect the diversification and spatial distribution of a clade over evolutionary time, considering patterns of phylogenetic structure as well as species richness.

While many simulation models of diversity dynamics have been developed in recent years (Appendix S1), none has incorporated energetic constraints on regional community size while tracking both phylogenetic and functional diversification over a spatial gradient. We use the simulation model to evaluate the extent to which commonly examined spatial and phylogenetic patterns are reliable indicators of the presence of energetic constraints, and make recommendations for the type of empirical analyses that are most likely to be diagnostic. As an example of how to couple the model's predictions to empirical systems, we compare model predictions to patterns derived from the rockfish genus *Sebastes* distributed across the northeastern Pacific. The temperate origin of this group makes it a useful test case, and this model-data comparison illustrates how a particular set of spatial and phylogenetic patterns can provide new insight into the importance of energetic constraints.

THE LOGIC OF ENERGETIC CONSTRAINTS

Energetic constraints are a fundamental principle of both ecology and evolution. All living organisms transform energy from light or stored in chemical bonds in order to perform the basic tasks of growth, maintenance and reproduction. As collections of individuals, species can then be thought of in terms of the amount of energy sequestered in biomass or abundance, an amount which fluctuates over both ecological and evolutionary time (Maurer 1989). The limited availability of chemical, or trophic, energy has necessary consequences then for ecological systems, and geographical gradients in energy availability could help drive geographical gradients in ecosystem properties such as species richness (Liow *et al.* 2011). The simplest argument that available energy limits species richness is based on three assumptions and a number of corollaries. We summarise and discuss each of these assumptions and corollaries in turn.

Assumption 1: Extinction probability is most proximately a function of population size.

Assumption 2: The focal assemblage operates under a zero-sum resource constraint.

Corollary 2a: Regions with more resources will support more individuals, assuming no systematic variation in body size or individual energy requirements.

Corollary 2b: As the number of species present in a region increases (through speciation or immigration) under a fixed total number of individuals, mean population size goes down and hence average extinction rate will increase. As such, extinction rate is richness-dependent.

Corollary 2c: If extinction rate is richness dependent, then species richness will tend to be regulated around some equilibrial value.

Assumption 3: Sufficient time has passed without major intervening disturbances such that equilibrium has emerged.

Assumption 1: Extinction probability is most proximately a function of population size.

Many factors might influence the extinction risk of a particular species, but of these, population size is the most direct (Lande *et al.* 2003). While various life history and ecological traits – slow population growth rate, small geographical range, large body size – may contribute to overall extinction risk and may be important for making predictions about the relative success of clades over large periods of time (e.g. Cardillo *et al.* 2008), the effects of demographic and environmental stochasticity that proximately lead to extinction are felt most directly through population size. This is the assumption that is perhaps most broadly applicable across taxa and regions.

Assumption 2: The focal assemblage operates under a zero-sum resource constraint.

The idea that energy use integrated over some broadly defined biota is roughly equal to energy availability through time is known as a zero-sum game (Van Valen 1973; Hubbell 2001). One implication of such a constraint is that any increase in abundance by one species must be offset by a collective decrease in all other species. While zero-sum dynamics are today most widely associated with Hubbell's (2001) neutral model, they are simply an assumption of his model and are agnostic about the importance of ecological niches. Justification for this assumption comes from the observation from a wide range of systems that the community is collectively up against some overall space or resource constraint (Connell 1961; Frost *et al.* 1995; Ernest *et al.* 2009).

Energetic constraints are least controversial when considering ecosystems and the entire suite of organisms contained within them. Early work by Lindeman (1942) and later Odum (1969) emphasised the importance of energetic constraints on the biomass and productivity of distinct trophic levels as a way of explaining Elton's (1927) classical pyramid of numbers. The inefficiency of trophic energy transfer sets an upper limit on the amount of productivity possible in higher trophic levels. Hairston *et al.* (1960) argued that the rate of accumulation of organic matter ('fossil fuels') through time on the planet is very low compared to the rate of energy fixation through photosynthesis, implying that 'all organisms taken together' are using up nearly all of the biologically available energy (i.e. net primary productivity) at a rate close to its production. Given a zero-sum game, a number of consequences follow.

Corollary 2a: Regions with more resources will support more individuals.

Given a zero-sum constraint, regions with more resources will have more individuals than regions with fewer resources. Empirically, this has been shown for a diverse array of animals (Kaspari *et al.* 2000a; Pettorelli *et al.* 2009), plants (Enquist & Niklas 2001), and microbes (Xu *et al.* 2013).

Historically, this corollary has been invoked in the context of species-area relationships (Preston 1962) and island biogeography theory (MacArthur & Wilson 1967). If resource density is constant, then larger areas are expected to support more individuals all else being equal (Wright 1983).

A positive relationship between resources and number of individuals should hold assuming there is no systematic variation in mean per-individual energy requirements along the resource availability gradient. Indeed, a zero-sum constraint should most directly apply to overall energy use rather than number of individuals, allowing potential tradeoffs between individual metabolic rate and abundance (White *et al.* 2004; Ernest *et al.* 2009). If organisms in high resource environments tended to be larger in body size, and hence had greater energetic requirements, then such regions could potentially consist of fewer, larger individuals. However, Bergmann's rule suggests that within species, individuals should be larger in cooler, low resource environments than warmer, tropical ones (Mayr 1956). This result holds for birds using mean assemblage-level body sizes (Olson *et al.* 2009), while in other groups the relationship between body size and latitude or net primary productivity is idiosyncratic (Hawkins & Lawton 1995). Given this evidence, we expect that the number of individuals should vary as expected with resource availability to first approximation, and that any variation in body size will not systematically weaken this trend.

Corollary 2b: Extinction rate is richness-dependent.

The most important consequence of a zero-sum game in the context of limits on species richness is that, given a fixed number of individuals that could be supported in a region (J), the number of species in that region (S) will be inversely proportional to the average population size ($\bar{N}$)

$$\bar{N} = J/S \tag{1}$$

If the number of species within a region were to increase through either immigration or *in situ* speciation, the average population size of species within the region would be reduced, and hence average extinction rate would rise (MacArthur & Wilson 1967; Hubbell 2001; Allen *et al.* 2006). Thus, under a zero-sum game, extinction rate is richness dependent. This should be true at any spatial scale, although at smaller scales immigration will play a larger role than speciation in counterbalancing extinction.

Corollary 2c: Richness will be regulated around some equilibrial value.

If extinction rate is richness dependent, then assuming some fixed, non-zero rate of speciation or immigration of new species, the number of species in the region will approach an equilibrial level at which the rate of appearance of new species is balanced by the extinction of existing species. We note that richness-dependent speciation rates could also contribute to equilibrial richness dynamics; however, they are not a necessary consequence of energetic constraints and so we do not focus on them here.

Assumption 3: Time has been sufficient for equilibrium to emerge.

Richness is expected to increase through time in a region until it reaches equilibrium. Therefore, a critical assumption for the role of energetic constraints in limiting richness is that sufficient time has passed to achieve equilibrium. The amount of time that is 'sufficient' will depend on the regional diversification rate, the equilibrium level of richness and the frequency of major disturbances, all of which may be difficult to ascertain. While richness equilibria over ecological timescales have been widely observed (Brown *et al.* 2001) and experimentally demonstrated (Simberloff 1976), evidence over evolutionary timescales is mixed (Wiens 2011; Cornell 2013; Rabosky 2013).

ENERGETIC CONSTRAINTS AND TAXONOMIC SCALE

Nearly all life on Earth relies on energy ultimately derived from sunlight and photosynthesis. Regions with higher rates of net primary productivity (NPP) should support a greater diversity of life forms according to the arguments above. But what about for more narrowly defined taxonomic groups – tenebrionid beetles, hummingbirds, hylid frogs – for which we are most likely to have relevant data sets? Several studies have demonstrated that richness patterns for subsets of assemblages – individual families or foraging guilds – are variable and are not necessarily congruent with the richness pattern for the assemblage as a whole (Currie 1991; Buckley *et al.* 2010). While some have argued that such findings are inconsistent with arguments based on energetic constraints (e.g. Buckley *et al.* 2010), this variability is to be expected from an energetic perspective for several reasons.

First, the narrower the taxonomic delimitation, the less likely that conditions for a zero-sum game will be met. Even if resource availability is defined specifically to the clade in question, something that is difficult to do in broad geographical scale analyses, a zero sum constraint may not apply if that clade represents a minority of organisms consuming those resources (Cornell 2013). If many consumers exist outside the focal clade, then a change in energy availability may have no effect on the abundance of individuals within the clade itself, resulting in a failure of *Corollary 2a*.

In addition, the narrower the taxonomic delimitation, the greater the possibility that factors other than resource availability may be limiting over broad spatial gradients. For example, some groups have phylogenetically conserved physiological tolerances preventing them from accessing available resources over parts of a gradient. Other species may be limited by other phylogenetically conserved constraints such as the availability of nest sites or redox conditions. In general, variability in resource availability may be expected to have inconsistent effects on population densities and species richness of small clades. However, broadly defined clades are more likely to encompass a wider portfolio of niches (e.g. thermal optima) such that the non-resource related factors constraining particular subclades will not necessarily govern richness patterns of the larger clade.

The implication of these issues is that species-energy relationships should be strongest for broader, more taxonomically inclusive clades, while relationships for smaller clades should be variable in strength depending upon the suitability of the zero-sum assumption and the extent to which actual resource availability is correlated with the energetic proxy used.

SIMULATION MODEL

Spatial richness gradients can arise from many different processes, which has led to the proliferation of hypotheses of which few have been eliminated. Secondary patterns and predictions are therefore of increasing importance because they provide additional dimensions by which to evaluate proposed explanations for such gradients. Examples of secondary predictions include patterns of phylogenetic tree shape, the variation in tree shape along spatial and environmental gradients, and variation in the strength of richness gradients with clade age or size. Simulation models can be an important tool in generating both qualitative and quantitative expectations under different underlying processes that might govern observed spatial gradients in species richness (Stegen *et al.* 2012). Here, we describe a model that examines diversification of a clade along a spatial gradient while simultaneously considering trait evolution and assemblage-level carrying capacities.

The goal of the model was to illustrate some of the patterns in species richness and phylogenetic structure expected when a spatial gradient in energy availability determines the number of individuals that can be supported across regions. We then evaluate the patterns that are expected under two alternative scenarios – when *Assumptions 2* (zero sum) and *3* (sufficient time) are violated – and identify which patterns are diagnostic of an overarching energetic constraint.

Basic simulation dynamics

We used a one-dimensional spatial gradient with twelve discrete spatial bins across which an environmental variable changes directionally. For simplicity, we conceptualise the environmental variable as temperature, which varied linearly from a warm 'tropical' region to a cooler 'temperate' region, although the model could be used to simulate a variety of environmental gradients in natural systems. Each bin was meant to represent a large region size of $\sim 10^5$–10^6 km^2 in area in which species might coexist without interacting directly, as in most evolutionary range dynamics models. While we did not explicitly model a coexistence mechanism, doing so would be a fruitful area for further development.

An ancestral species was assumed to originate at one end of the gradient (both temperate and tropical origins are modelled, see below) with an environmental optimum matching the environment in that region. Speciation occurred at a constant per individual rate. During a speciation event an extant species produced a descendant within the same region with a different, but probabilistically similar, environmental optimum. New species were assigned a population size based, in part, on their match to the region's environment, were able to disperse to adjacent regions, and went extinct with a probability based on their population size (Fig. 1). Details of these components are described in Box 1.

Box 1. Simulation model

Species' traits and niche conservatism
Each species was assigned an environmental optimum based on the optimum of its ancestor plus some deviation chosen from a Gaussian distribution (McPeek 2008). The standard deviation of the Gaussian (σ_E) reflects the strength of niche conservatism. Simulations were run with σ_E values ranging from 1 to 11, but we focused on results in which $\sigma_E = 1$, reflecting highly conserved niches. Larger values of σ_E had minimal effects on key results (Figure S2).

Regional carrying capacity and species' population sizes
Regional carrying capacity (K_j) increased 10-fold along the spatial gradient in parallel with temperature. Rather than directly modelling population dynamics over ecological time, we assumed that a species' long-term population size varied as a function of the match between the species' environmental optimum and the regional environment. We assumed that as the difference between a species' optimum and its environment grows, the species' resource use efficiency, and hence the maximum abundance the species can achieve, declines as a Gaussian function (as in McPeek 2007, 2008) from a maximum of K_j (Figure 1). The standard deviation of this Gaussian, ω, reflects the strength of environmental filtering. Simulations were run for ω values ranging from 1 to 11, but we focused on simulations in which $\omega = 3$, reflecting a moderately strong effect of environmental selection on abundance. Values of σ_E and ω lower than used here resulted in clades that did not diversify across the spatial gradient.

Our simulation did not explicitly account for local-scale coexistence mechanisms. As such, the model implicitly assumed that the existence of a species in a region is primarily the result of speciation, extinction and dispersal dynamics. The time step over which population size estimates were updated was assumed to span many (~ 10–100) generations such that species achieved relative abundances dictated by the match to their environment. If only a single species was present in a region, its population size was given by the product of the region's carrying capacity and the species' resource use efficiency, as given by the Gaussian environmental filtering function (Fig. 1). Thus, even in the absence of competitors, a species poorly matched to the environment had a small population size due to inefficient conversion of resources to individuals. When multiple species were present, population sizes were assigned proportionally based on species' resource use efficiencies such that the sum over all populations was no more than the regional carrying capacity (Fig. 1). Thus, as species that were better suited to the environment arose in a region via speciation or dispersal, all population sizes were updated to reflect the new hierarchy in resource use efficiency.

We also examined a 'no zero sum' scenario in which *Assumption 2* was violated, where species' population sizes were limited only by the match of their environmental optima to the regional environment. The addition of a new species to a region, even one that was better adapted, did not reduce the population sizes of any existing species. The maximum population size attainable by any one species did not vary across the gradient, as expected when energy does not constrain abundance.

Speciation, dispersal and extinction
Speciation, dispersal and extinction were modelled as stochastic processes that varied with population size. Speciation was modelled as a binomial process, where every individual had the same probability of spawning a mutated daughter species and each population produced no more than one daughter per time step. As such, species with larger population sizes had a greater chance of producing daughter species (Hubbell 2001; Allen *et al.* 2006; but see Butlin *et al.* 2012). While a descendant arose in the region of its ancestor, the regions are assumed to be large enough to be consistent with either allopatric or sympatric speciation and such differences are not a focus of the model. We made the simplifying assumption that the mode of speciation did not vary systematically across the spatial gradient. Once a new species arose, it reached an equilibrium population size based on its match to the environment within the time step. The model therefore ignores species that may have arisen briefly and gone extinct within the multi-generation timescale of a single simulation time step, and thus differs from pure point mutation models of speciation.

Dispersal was also modelled as a binomial process with a constant per-individual rate, and thus larger populations were more likely to send propagules to adjacent regions. The probability of extinction for a population varied as a negative exponential of population size.

Running simulations

Both the zero sum energy gradient scenario and the non-zero sum alternative were run starting with either a temperate or tropical ancestor, and we conducted 100 replicate simulations of each scenario-origin combination. Simulations were stopped after reaching either 100 000 time steps or 10 000 species, whichever came first. The zero-sum scenario consistently reached equilibrium prior to 100 000 time steps at richness levels below 10 000 species, while the non-zero sum alternative consistently reached 10 000 prior to 100 000 time steps. We do not focus on the specific number of species produced by a simulation or the number of time steps to equilibrium as these both depend on the specific values chosen for regional carrying capacities and speciation rate. All relevant simulation parameters are described in Table S1.

Evaluation: baseline patterns

Preliminary analysis suggested that the extreme tropical and temperate regional bins experienced boundary effects because
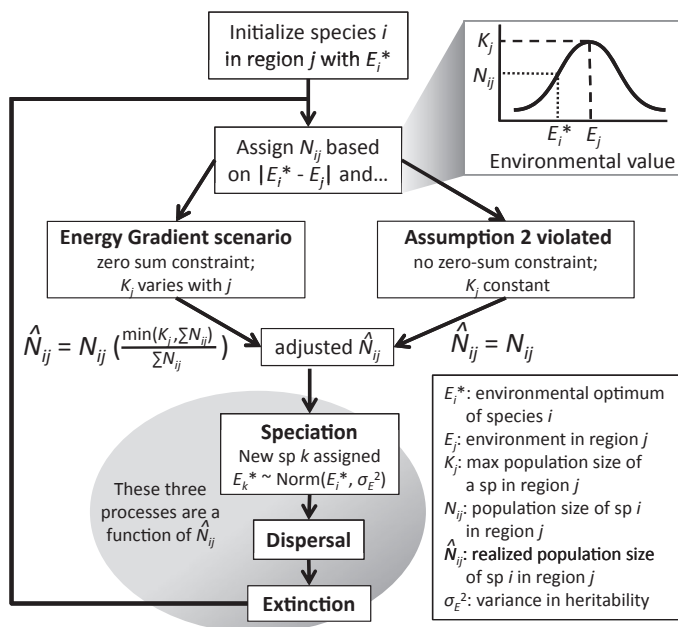
Figure 1 Flow chart illustrating the simulation of two different eco-evolutionary scenarios. Population size of a species varies with the match of a species to its environment based on a trait characterising the environmental optimum. For the baseline Energy Gradient scenario in which a zero-sum constraint exists, population size is modified by the presence of other species in the region and their relative fitness such that the maximum regional abundance does not exceed K_j. To test the importance of Assumption 2, the simulation is also conducted without a zero sum constraint in which species abundances are independent of the presence of other species.

they only received dispersing propagules from one adjacent region. Because these boundary effects are not the focus of this study, and because they were restricted to the two extreme regional bins, we focused our analyses on the ten internally distributed spatial bins. We evaluated the following patterns of richness and phylogenetic structure arising from the simulation through time.

(1) We calculated Pearson's correlation coefficient between regional richness and latitude across the gradient. In our simulation, latitude is an exact proxy for energy availability.

(2) We evaluated two related metrics of phylogenetic structure of the regional assemblages from across the spatial gradient: mean root distance (MRD; Kerr & Currie 1999), and phylogenetic species variability (PSV; Helmus *et al.* 2007). MRD reflects how evolutionarily derived species are (*sensu* Hawkins *et al.* 2006), based on the average number of nodes separating species from the root, while PSV is a measure of phylogenetic clustering with low values indicating high clustering. The relationships between PSV, MRD and species richness should reflect the relative importance of pure niche conservatism and time for generating richness patterns (Algar *et al.* 2009). When niche conservatism is strong and the primary reason for low richness in non-ancestral environments, PSV should decrease and MRD should increase along the gradient as richness decreases, whereas these relationships should be weak if the richness gradient is due to factors other than niche conservatism (Algar *et al.* 2009). We quantified MRD

(scaled by the maximum root distance in the phylogeny so that MRD varied between 0 and 1) and PSV within each region and examined how these metrics varied with regional species richness across space.

(3) We also measured β, a purely topological measure of tree symmetry or balance, following Blum & François (2006). Trees with β > 0 are more balanced or symmetrical than those generated from a Yule model, whereas trees with β < 0 are more imbalanced. β does not require information about branch lengths.

(4) Lastly, we evaluated phylogenetic tree shape using the γ statistic developed by Pybus & Harvey (2000). γ values close to zero are consistent with branching patterns from a constant rate birth–death model. Negative values of γ are thought to imply an early burst of diversification with a deceleration in rate, while positive values have been suggested to imply an increasing rate of diversification with the balance of nodes occurring closer to the tips (Pybus & Harvey 2000).

Evaluation: violation of assumptions

The consequences of violating the zero-sum constraint (*Assumption 2*) were examined in two ways. First, we evaluated the four patterns above for the alternative simulation in which the zero-sum constraint was turned off and for which no energy gradient existed. Second, we examined latitude-richness correlations for all possible subclades nested within the overall phylogeny that had at least 30 species and that were distributed across at least five spatial bins. Because the simulated energetic constraint applies to all organisms in aggregate, the zero-sum assumption becomes less appropriate as subclade size decreases. We also examined whether this relationship between clade size and latitude-richness correlation was diagnostic of the zero sum constraint.

The consequences of violating the time-for-equilibrium assumption (*Assumption 3*) were examined by evaluating the baseline patterns described above for the zero-sum energy gradient simulations before equilibrium had been reached. In this case, species were diversifying and dispersing in a universe in which energetic constraints existed, but in which richness was still below carrying capacity in all regions. Ultimately, we would like to know whether this pre-equilibrial scenario is distinguishable from one in which no zero sum constraints exist.

Evaluation: empirical analysis

We examined empirical data for a clade of 66 rockfish species (genus *Sebastes*) distributed across the eastern Pacific from Alaska to Baja California that is known to have first colonised the region from Asia via the Aleutian Islands between 7 and 8 MYA (Hyde & Vetter 2007). The reliance on coastal habitats makes it straightforward to characterise the richness pattern in a single latitudinal dimension, and the known temperate origin of this clade makes it a useful test case because a pure time-for-speciation effect would predict an inverse latitudinal gradient. Finally, while the clade has only 66 species, rockfish often comprise more than 90% of the fishes found in the rocky reef and kelp forest habitats off the Pacific coast

(Butler *et al.* 2012). We quantified latitude-richness correlations, slopes of MRD and PSV vs. species richness, β and γ statistics, and compared these results to the patterns generated by our simulation model. We used the *Sebastes* phylogeny and latitudinal distributions described in Ingram (2011).

Source code for running and analysing the simulation model described here are provided in an online repository at https://github.com/ahhurlbert/species-energy-simulation.

RESULTS

Spatial richness gradients

The most obvious difference between zero sum and non-zero sum simulations was the bounded vs. unbounded nature of richness dynamics (Fig. 2a). When the ancestor was of tropical origin, neither the zero-sum assumption nor the assumption that an equilibrium had been reached was critical for generating a classical latitudinal richness gradient (Fig. 2b). When the ancestor was of temperate origin, however, a violation of either assumption resulted in qualitatively different patterns. A temperate origin and the absence of a zero-sum constraint resulted in an inverse latitudinal gradient (Fig. 2b, dashed blue line). Under the zero sum scenario with a temperate origin, the relationship between richness and latitude ranged from positive to negative depending on how far the system was from equilibrium (Fig. 2b, solid blue line; Fig. S1).

We also examined the strength of the latitude-richness relationship for increasingly smaller and more recently derived subclades nested within the overall phylogeny (Fig. 3). Without zero sum constraints subclades representing as little as 1–2% of the total phylogeny exhibited strong correlations with latitude with the sign determined by region of origin (Fig. 3b). Under the zero sum scenario, while the oldest and largest clades exhibited strong negative latitude-richness correlations (i.e. richness increased with energy), there was increasing variant in correlation coefficients as clade size and age declined (Fig. 3c, d). Once subclades fell below 20–25% of the total clade richness, latitude-richness correlations were frequently quite weak (Fig. 3d). For smaller and more recently derived clades, diversification was still governed by spatial gradients in available energy, but the energy gradient experienced by newly arising clades did not necessarily parallel the overall energy gradient. For simulations with a tropical origin, as richness increased in tropical regions the opportunity for diversification (as measured by the fraction of equilibrial richness in a region that was available at the time of colonisation) became greater towards the unoccupied temperate end of the gradient leading to positive latitude-richness correlations in more recently derived subclades (Fig. 3e, grey subclade).

After species had diversified across the entire gradient, extinction rates and the opportunity for further diversification varied less through space such that newly arising clades were equally likely to diversify in either direction and to accumulate species where they arose. This is exemplified by the black subclade in Fig. 3e, for which no latitudinal gradient in opportunity existed. By the time it colonised regions beyond its region of origin, those regions were close to equilibrial richness and had high extinction rates. As such, these smaller,
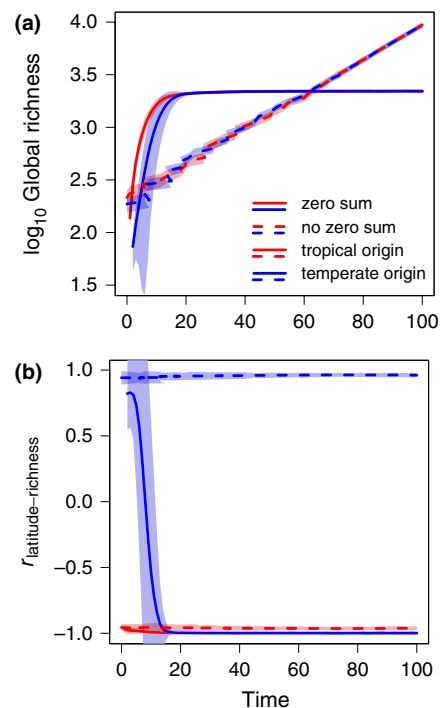

Figure 2 Temporal trajectories of (a) species richness and (b) the strength of the latitude-richness correlation over the course of zero sum (solid lines) and non-zero sum (dashed lines) simulations. Simulations in which the ancestor arose in the tropics are in red, while simulations in which ancestors arose at the temperate end of the gradient are in blue. Envelopes represent ± 2 SDs based on 100 replicates of each simulation scenario. Time is measured in the percentage of the simulation duration over which there was analysable output, which differed between zero sum (~ 10^5 time steps) and non-zero sum (~ 10^2 time steps) scenarios. As such, the emphasis is on comparing the shapes of these curves rather than comparing values at a specific point in time.

more recently derived clades exhibited weak latitudinal gradients and form the cloud of points centred around a latitude-richness correlation coefficient of 0 (Fig. 3c, d).

Rockfish richness increased from Alaska to Point Conception, California and then declined to Baja California (Fig. S3). Point Conception is a geographical boundary, south of which upwelling and primary production decrease while sea surface temperature increases (Longhurst 2010). As such, we examined latitude-richness correlations within the Pacific rockfish for all subclades with at least five species for the entire gradient (23–66 °N) and for the gradient north of Point Conception only (34–66 °N, Fig. 3c). Especially for the latter gradient over which richness monotonically declined with latitude, the latitude-richness correlation for the entire phylogeny and for larger subclades was close to −1, while it was more variable for subclades smaller than 25% of the overall clade richness (Fig. 3f).

Inference from phylogenetic structure

Aspects of phylogenetic tree structure were also sensitive to violations of the two assumptions tested. We first examined the γ statistic, which describes the tendency of branching events to be more concentrated towards the root (negative) or
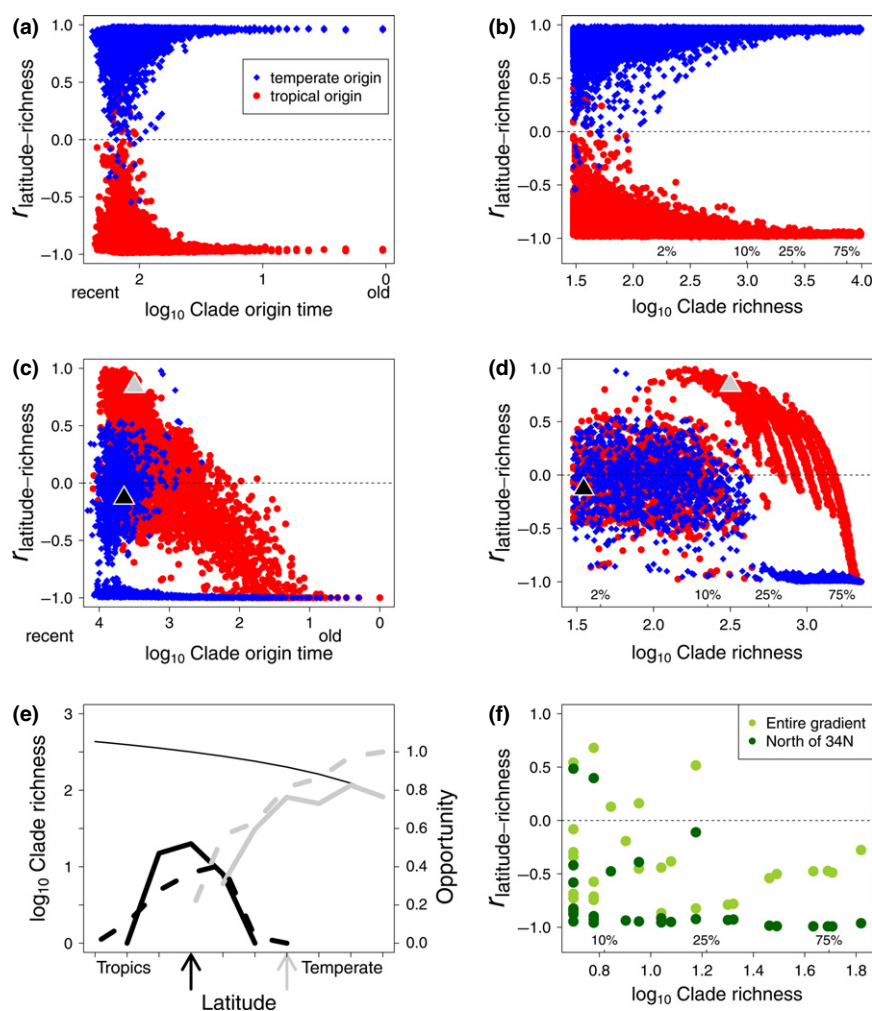
Figure 3 For each nested subclade in a simulation, latitude-richness correlations are plotted as a function of (a, c) clade origin time, and (b, d) clade size for simulations without (a, b) and with (c, d) energetic constraints. Clades of temperate origin, blue, tropical origin, red. Two example subclades from a tropical simulation highlighted as triangles (black subclade: 35 species, time of origin 5272; grey subclade: 317 species, time of origin 3656). (e) Richness patterns (thick solid lines) for the two highlighted subclades in (c) and (d). The thin solid line represents the equilibrial richness gradient, while dashed lines reflect the fraction of equilibrial richness in each region that was available when the subclade first colonised. Arrows indicate the region of origin for each subclade. (f) Latitude-richness correlations for subclades within the 66 species phylogeny of northeastern Pacific rockfish. Correlations across the entire gradient (23–66 °N), light green, correlations for the gradient north of Point Conception (34–66 °N), dark green.

the tips (positive). Consistent with naive expectations about how γ should behave under a diversity-dependent process, γ became quite negative under the zero sum scenario (Fig. 4a). However, as was demonstrated by Quental & Marshall (2010), post-equilibrial species turnover led to increasingly positive γ (Fig. 4a). Given the wide range of values possible under the zero sum scenario, γ cannot be used to reliably diagnose the presence or absence of zero sum constraints and is not discussed further.

The metric of tree imbalance, β, was diagnostic of *Assumption 2* and this diagnostic power was generally robust to violation of *Assumption 3*. β was negative when zero sum dynamics were imposed and positive in their absence (Fig. 4b). Furthermore, under the zero sum scenario, trees were similarly unbalanced pre- and post-equilibrium, suggesting that β might be useful in evaluating the role of energetic constraints even if a clade has not yet reached equilibrial richness.

Linear slopes relating species richness to MRD and PSV were also potentially diagnostic of the zero-sum energy gradient scenario. The PSV-richness relationship was only useful during a transient period prior to and immediately after equilibrium for clades of temperate origin only (Fig. 4c). MRD-richness slopes were much more useful, however, with slopes differing depending on whether *Assumptions 2* and *3* were met (Fig. 4d). Violation of *Assumption 2* (zero sum) resulted in slopes close to 0, while given a zero sum constraint the slope was distinctly positive (for temperate clade origin) or negative (for tropical origin). For tropical origin simulations, the negative slope was independent of whether the clade had reached equilibrium with the energy gradient, while for temperate origin simulations the pre-equilibrium slopes spanned a wide range of values overlapping predictions for tropical origin and non-zero sum scenarios (Fig. 4d).
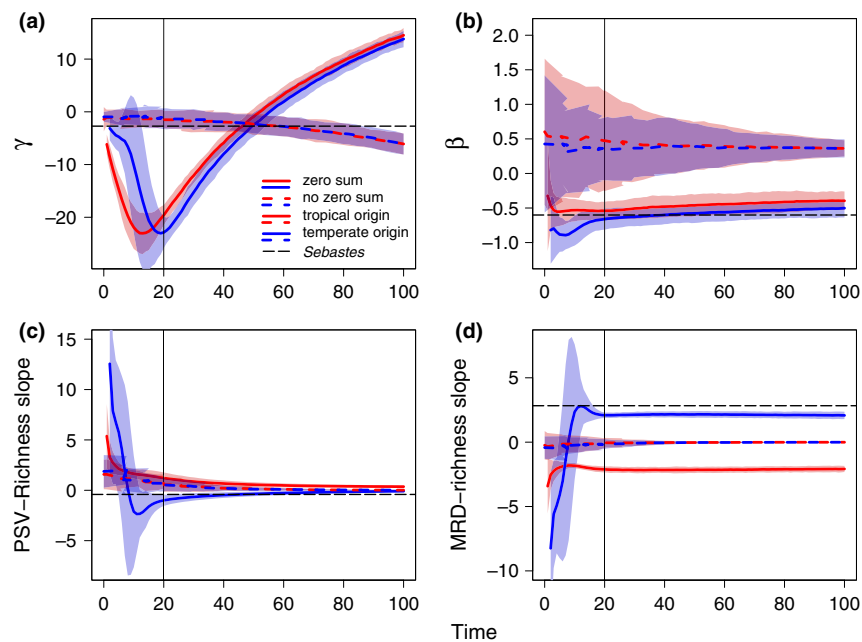
Figure 4 Temporal trajectories of four metrics of phylogenetic structure over the course of diversification simulations: (a) Pybus & Harvey's (2000) γ statistic, (b) Blum & François' (2006) measure of tree imbalance, β, (c) the slope of the relationship between species richness and phylogenetic species variability (PSV; Helmus *et al.* 2007) across spatial bins, and (d) the slope of the relationship between species richness and mean root distance (MRD; Kerr & Currie 1999) across spatial bins. Legend and *x*-axis as in Fig. 2. Dashed black lines indicate empirical values for the rockfish genus *Sebastes*. Vertical lines denote the approximate point in time by which zero sum scenarios achieved equilibrial richness gradients and facilitate comparison of values pre- and post-equilibrium.

Empirically observed values for the rockfish data set were generally consistent with the temperate origin, zero sum scenario with β = −0.60, a PSV-richness slope of −0.0004, and a scaled MRD-richness slope of 0.0028 (Fig. 4).

DISCUSSION

When should richness be energy-limited?

Energetic limits impose fundamental constraints on various aspects of ecosystems. While researchers have conceived of several ways by which increased energy availability might lead to higher species richness (Evans *et al.* 2005), we focused on three assumptions which, if met, logically imply such a relationship. These are that (1) extinction probability is foremost a function of population size, (2) the focal assemblage operates under a zero-sum constraint, and (3) sufficient time has passed for an equilibrium to emerge. The first assumption is straightforward and was not investigated here. However, testing *Assumptions 2* and *3* directly or identifying patterns that are indicative of those assumptions being met will provide stronger tests of the energetic constraint hypothesis than evaluating richness-environment correlations alone.

How would we know? Phylogenetic evidence

While it is difficult to prove that energetic constraints govern observed spatial variation in species richness, our simulation model reveals several metrics that allow the hypothesis of energetic constraints to be tested and rejected. First, the measure of tree imbalance or asymmetry, β, should be negative if

a clade arose under a zero sum energy gradient, and this should be true even if the clade has not yet reached equilibrium. Davies *et al.* (2011) found that under Hubbell's (2001) zero sum neutral model, β took on a range of negative values depending on speciation rate, migration rate and mode of speciation. Only in cases of extremely limited migration under one particular mode of speciation (fission with equal splits) were β values strongly positive for this zero sum scenario (Davies *et al.* 2011). A large number of empirical phylogenies have been found to exhibit negative β values below what would be expected from an equal rates birth–death process (Davies *et al.* 2011; Purvis *et al.* 2011). Unbalanced trees are expected to result in our simulation given that lineage-specific probabilities of diversification are not equal across the tree under a zero sum constraint. As lineages colonise novel portions of the spatial gradient, they are able to achieve greater population sizes and hence experience lower extinction rates and higher probabilities of producing daughter species than the sister lineages they left behind, and this pattern of imbalance will persist throughout the colonisation of the gradient. Nevertheless, more work is needed to identify other common macroevolutionary processes that might result in imbalanced trees (e.g. Purvis *et al.* 2011).

The MRD-richness slope provides similar inference to β, and allows for additional insight. The similarity in inferences drawn from the two metrics is expected because an unbalanced tree in which the spatial distribution of species is phylogenetically conserved – as must be the case under niche conservatism and a spatially autocorrelated environment – will necessarily exhibit differences in MRD across the gradient. Regions far from the region of origin for the entire clade

will be composed of evolutionarily derived species (*sensu* Hawkins *et al.* 2006), while the region of origin itself may potentially include older basal species. Thus, one difference between the inferential ability of the MRD-richness slope and β is that the sign of the slope should indicate where the clade originated relative to the existing richness gradient. In the case of our empirical example, the sign is in agreement with what is known about the way *Sebastes* colonised the northeast Pacific. Conversely, Hawkins *et al.* (2006) showed that MRD varies negatively with species richness for birds in the western hemisphere, consistent with a tropical origin under zero sum constraints. A second difference between the utility of the two metrics is that under zero sum constraints the MRD-richness slope for clades of temperate origin is often zero or negative prior to equilibrium. These values are consistent with other scenarios such that MRD-richness slopes at or below zero should be combined with β and non-phylogenetic analyses (see following section) to infer the region of origin and the presence or absence of zero sum constraints.

While γ has been suggested to reflect the slowdown in diversification rate expected under diversity dependence (Pybus & Harvey 2000; McPeek 2008), others have noted that γ is subject to bias from various sources (e.g. Revell *et al.* 2005; Brock *et al.* 2011) and that both positive and negative values may arise through multiple processes (see Table 1 in Quental & Marshall 2010). We confirmed that γ is not a reliable indicator of energetic constraints because it is strongly dependent on when it is estimated relative to when equilibrium is achieved (Liow *et al.* 2010; Quental & Marshall 2010), although strongly negative values would appear to reject a constant diversification rates hypothesis and could be indicative of a zero sum system.

Both β and the MRD-richness slope are metrics that reflect tree topology and do not rely on branch lengths, unlike γ and PSV. As such, they are not susceptible to the many sources of error associated with knowing true branch lengths, such as missing extinct species and assumptions about heterogeneity of molecular rates of evolution. The properties of these metrics and the contexts in which they provide important information about the role of energetic constraints certainly deserve further investigation.

How would we know? Richness patterns and taxonomic scale

Given a strong richness gradient for a particular clade, the degree to which the various nested subclades exhibit similar richness gradients might also be useful in assessing the existence of an energetic constraint for the clade overall. Buckley *et al.* (2010) argued intuitively that if a richness gradient were the result of a gradient in carrying capacity then all subclades should exhibit roughly parallel richness patterns, whereas subclade patterns should be highly variable if phylogenetic niche conservatism in the absence of constraints were important in their generation (see their Fig. 1). Our simulation results show that their intuition does not hold up under the range of conditions we examined, and that richness-environment relationships across nested subclades are expected to be more variable when diversifying under energetic constraints than when such constraints are absent. The energy gradient

that a subclade actually experienced depended on the presence and abundance of organisms from outside the focal clade that also utilised those resources, and this 'opportunity gradient' frequently differed from the overall gradient in energetic constraints. When the root clade was of tropical origin, some subclades even exhibited strong reverse richness gradients, as Buckley *et al.* (2010) found empirically within the mammal phylogeny. In general, clades that were more recently derived and that made up less than 25% of the overall clade exhibited increased variation in latitude-richness correlations, centred on 0. In the absence of zero sum constraints, the diversification and spread of any particular subclade was independent of other subclades. Since the majority of subclades arose near the region of origin of the overall clade ancestor and shared similar thermal optima, richness gradients paralleled that of the root clade even for subclades making up 1–2% of the entire phylogeny.

This pattern of subclade variation in the strength of richness gradients is another line of evidence, albeit a qualitative one, that can be used in conjunction with the other lines mentioned previously. In our empirical analysis of rockfish, small clades exhibited a broad range of richness patterns and the largest clades were characterised by strong latitude-richness relationships, especially when analyses were restricted to latitudes north of Point Conception (34 °N) where species richness varied monotonically. This result supports the idea of this clade diversifying under energetic constraints and matches what we know about its temperate origin. While objective measures of resource availability for this group are unavailable, the evidence accumulated from both phylogenetic and non-phylogenetic analyses suggests that richness is indeed energy-limited and therefore the overall rockfish richness pattern presents a testable hypothesis for how those resources vary over the gradient. Although marine net primary productivity is spatially variable, the fact that it peaks off of Point Conception (Fig. S3) is consistent with the idea that NPP may be a coarse proxy for rockfish resource availability.

How would we know? Fossil evidence

Above we have focused on lines of evidence that could be evaluated with the types of data most frequently available: geographical distributions and phylogenetic relationships among extant taxa. However, in the presence of a strong fossil record, several additional and often more direct lines of evidence regarding equilibrial diversification dynamics in general and energetic constraints in particular become testable. (1) Equilibrial dynamics imply that the number of taxa should fluctuate around some constant level through time rather than exhibiting an unbounded increase (Cornell 2013; Rabosky 2013). (2) A subsequent prediction of energetic constraints is that compensatory dynamics are observable in the waxing and waning of sizes of competing clades (Sepkoski 1996), and that origination and extinction rates are observed to be diversity-dependent (Alroy 1998, 2010). (3) With data on the relative abundances of fossil taxa through time, compensatory dynamics of the species themselves may be evaluated in the manner used for ecological time series (e.g. Gonzalez & Loreau 2009).

(4) Spatial and temporal variation in energy availability, when a reasonable proxy is available for the group of interest, can be used to predict how taxonomic richness should vary through either space or time. The idea that energy availability broadly defined has varied over the earth's history with variation in atmospheric or ocean chemistry, climate and net primary productivity implies that more complex predictions than those expressed in (1) may frequently be possible (e.g. Payne & Finnegan 2006). Empirical evidence for the above patterns is either underexplored or mixed (Cornell 2013). With improvements in the spatial and temporal resolution of fossil data (e.g. the Paleobiology Database) and in the quality of environmental and climatic reconstructions, we expect further pursuit of these questions to be productive. Nevertheless, for the many groups lacking a strong fossil record, the comparison of observed spatial and phylogenetic patterns to those generated from simulations will continue to be a promising approach.

Diversity dependence in the context of energetic constraints

Evolutionary models of diversity-dependent diversification assume that per-lineage rates of speciation decrease and/or per-lineage rates of extinction increase as richness accumulates (Rabosky & Lovette 2008; Quental & Marshall 2010; Etienne et al. 2012). The former assumption has typically been discussed in the context of niche space saturation (e.g. Walker & Valentine 1984), while the latter derives from island biogeography theory (MacArthur & Wilson 1967). Energetic constraints are a useful framework for conceptualising either of these possibilities by exploring the consequences of average population sizes for diversification. With respect to the saturation of niche space, an energetic perspective formalises the idea implicit to these models that resources are ultimately limited, regardless of whether they can be divided among various distinct niches. Traditional arguments about reduced 'ecological opportunity' for speciation when richness is high may be reframed as reduced per-lineage probability of speciation assuming a constant per-individual rate (Hubbell 2001; Wang et al. 2013). In our simulation framework, modelling speciation as a constant per-lineage rate rather than a constant per-individual rate would eliminate the diversity dependence of speciation. The extent to which this decision alters perceived differences between zero sum and non-zero sum patterns deserves further study.

Perhaps, the most critical consequence of zero sum dynamics is that per-lineage extinction rate should be diversity-dependent (Hubbell 2001). While several studies have found evidence of diversity-dependent extinction (Foote 2000; Quental & Marshall 2013), many have not (Alroy 1998; Rabosky & Lovette 2008). However, diversity-dependent extinction may be difficult to detect if the majority of extinction events involve incipient species that never achieved high abundance or broad geographical ranges and are largely absent from both the phylogenetic and fossil record, as proposed under a 'ephemeral speciation model' (Rosenblum et al. 2012). Further modelling studies are needed to reconcile a high frequency of ephemeral incipient species with empirically observed extinction and speciation rates.

CONCLUDING REMARKS

The processes by which clades have diversified and spread out across the globe are inarguably complex. Our simulation model captured several features of interest that had not previously been investigated within a single framework. Specifically, it is the first attempt to track regional diversification across a spatial environmental gradient in which (1) species exhibit niche conservatism for traits that affect relative fitness along the gradient, and (2) a spatial gradient in energy availability imposed a constraint on the total number of individuals across species that may be supported in different regions. The aim of our simulation model was not to include all mechanisms thought to be important in generating spatial richness gradients. Rather, we included the basic components necessary for modelling diversification under an energetic constraint, and asked how sensitive resulting spatial and phylogenetic patterns were to two key assumptions of energy-based explanations. In using our model for empirical comparisons, we encourage the adjustment of model parameters to match any existing knowledge of the system of interest (e.g. range of the energy gradient, strength of niche conservatism). We also highlight the need for continued model development to determine whether mechanisms not examined here are expected to produce patterns indistinguishable from the patterns generated under energetic constraints in our model. The frequency at which a system is displaced from equilibrium by disturbance, or at which effective energy availability increases due to major evolutionary innovations are particularly important scenarios for further consideration.

While our conceptual discussion of energetic constraints and of the simulation model outputs have been primarily framed around latitudinal species richness gradients in multicellular taxa, the central ideas apply broadly across taxonomic groups and types of spatial gradients. For example, the model could be equally well applied to variation in soil microbial diversity along elevational or chemical gradients. To date, microbial diversity gradient studies have largely ignored variation in absolute cell density (e.g. Fierer et al. 2011), whereby diversity is a per-individual quantity instead of a per-area quantity. Incorporating cell density would allow for stronger comparisons between microbial and non-microbial richness patterns, and would provide an important evaluation of the generality of energetic constraints.

When the assumptions of diversity-dependent extinction rates, a zero-sum resource constraint, and sufficient time for equilibrium are met, we should expect energy availability in a region to play a role in determining both the number of species present, as well as the phylogenetic structure of those species. Even prior to equilibrium, energetic constraints are expected to influence diversification patterns and, in turn, phylogenetic structure of regional assemblages. Key challenges for future work are (1) to directly model the effects of a resource competition trait and the impact of key innovations; (2) the simultaneous modelling of additional mechanisms hypothesised to govern richness gradients; and (3) extension of the modelling framework to groups, such as microbes, for which species energy theory has not historically been considered.

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STATEMENT OF AUTHORSHIP

AH and JS performed simulations, analysed output and wrote the manuscript.

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SUPPORTING INFORMATION

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Table S1. Parameter values used in simulations, as well as the range of alternative values explored (in brackets) but not presented in this analysis. Values that are listed as a range refer to the values at the "temperate" and "tropical" ends of the spatial gradient, and all gradients were linear. Z, zero sum energy gradient, and NZ, non-zero sum scenarios.

Parameter	Value [range evaluated]	Units
Environmental gradient	0 - 40	˚C
Regional carrying capacity, K_{max}	Z: 4,000 - 40,000 NZ: 40,000	individuals
Strength of environmental selection, ω	3 [1 - 11]	˚C, standard deviation units
Strength of niche conservatism, σ_E	1 [1 - 11]	˚C, standard deviation units
Per individual speciation probability	10^{-6} [10^{-7} - 10^{-5}]	probability
Per individual dispersal probability	10^{-4} [10^{-6} - 10^{-2}]	probability
Extinction rate parameter (governing negative exponential decline of extinction vs abundance)	0.1	individuals^{-1}

Maximum number of species	10,000	species
Maximum number of time steps	100,000	time steps
Region of origin	tropical-most bin, temperate-most bin	spatial bin (1-10)

Supplementary Figure Legends

Figure S1. Latitudinal gradient in species richness for zero-sum energy gradient simulation with a temperate origin (region 10) illustrated every 3,000 time steps.

Figure S2. Simulation metrics over the first 30,000 time steps for a tropical origin, zero sum energy gradient scenario as a function of the strength of niche conservatism, σ_E. Weaker niche conservatism (blue) primarily results in a longer time to equilibrium, as evidenced by patterns of global richness and γ. Behavior of other simulation metrics is qualitatively similar.

Figure S3. Latitudinal richness gradient for 66 species of rockfish (genus *Sebastes*) in the northeastern Pacific, as well as variation in mean root distance (MRD, blue) and phylogenetic species variability (PSV, red) based on distributional and phylogenetic data in Ingram (2010). Mean annual net primary productivity (NPP, green) over a 5° latitude moving window was derived from the updated CbPM model for the year 2011 from Westberry et al. (2008). The shaded region marks the latitude of Point Conception, California, a biogeographical boundary. Note that MRD is scaled by the maximum root distance to vary between 0 and 1.

Sim 3345 , Origin = temperate , w = 3 , sigma = 1 , disp = 1e−04 , specn = 1e−06 , K gradient present