Processes of ecometric patterning: modelling functional traits, environments, and clade dynamics in deep time

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Ecometric patterning is community-level sorting of functional traits along environmental gradients that arises historically by geographic sorting, trait evolution, and extinction. We developed a stochastic model to explore how ecometric patterns and clade dynamics emerge from microevolutionary processes. Strong selection, high probability of extirpation, and high heritability led to strong ecometric patterning, but high rates of dispersal and weak selection do not. Phylogenetic structuring arose only when selection intensity, dispersal, and extirpation are all high. Ancestry and environmental geography produced historical effects on patterns of trait evolution and local diversity of species, but ecometric patterns appeared to be largely deterministic. Phylogenetic trait correlations and clade sorting appear to arise more easily in changing environments than static ones. Microevolutionary parameters and historical factors both affect ecometric lag time and thus balance between extinction, adaptation, and geographic reorganization as responses to climate change. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **118**, 39–63.

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INTRODUCTION

Earth systems – atmospheric composition, climate, ocean chemistry, sea level, and tectonics – have been changing since life began (Haq, 1991; Webb & Bartlein, 1992; Berner *et al.*, 2003; Patzkowsky & Holland, 2012). Biotic communities, which are defined here as assemblages of co-occurring species, have been transformed along with Earth systems as their members have tracked optimal climatic or environmental conditions, adapted through natural selection or environmental plasticity, diversified through speciation, or succumbed to extinction (Simpson, 1944; Levins, 1968; Jablonski, 1991; Lynch & Lande, 1993; Lister, 2004; Barnosky, 2005; McPeek, 2007). These modes of response are seldom exclusive, and the balance between geographic reorganization, adaptive change, speciation, and extinction has varied tremendously in Earth's history as documented by the rich store of examples from the fossil record (Vrba, 1993; Cerling *et al.*, 1997; Fortelius *et al.*, 2002; Barnosky, Hadly & Bell, 2003; Lieberman, 2005; Liow & Stenseth, 2007; Blois & Hadly, 2009; Carrasco, Barnosky & Graham, 2009; Lyons, Wagner & Dzikiewicz, 2010; Barnosky, Carrasco & Graham, 2011a; Barnosky *et al.*, 2011a; Hannisdal & Peters, 2011; Lawing & Polly, 2011; Willis & MacDonald, 2011). Extinction dominated the balance five times during Earth history's mass extinctions (Raup & Sepkoski, 1982), and appears to dominate biotic change today in the Anthropocene's sixth extinction (Barnosky *et al.*, 2011b). A better understanding of what controls the balance between these modes of response is desirable.

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The mechanism by which communities respond to changing environments is through the functional traits of the species that make up the communities (Ricklefs & Travis, 1980; Chapin, 1993; Poff, 1997; Wright *et al.*, 2005; McGill *et al.*, 2006; Webb *et al.*, 2010; Violle *et al.*, 2014; Jønsson, Lessard & Ricklefs, 2015; Morales-Castilla *et al.*, 2015). Species vary in their integument cover, gas exchange surfaces, locomotor morphology and masticatory mechanics and therefore respond differently to factors like ambient temperature, oxygen concentration, physical topography, predator abundance, and food quality. Functional traits are the tangible features of organisms that are coupled with particular environmental factors. Any particular state of the trait will perform better in some environments than others, and thus play a part in the overall fitness of an organism in a particular environment. Selection and local extinction will therefore tend to optimize functional trait states along environment gradients, ceteris paribus. Environmental factors that are limiting like resource availability will tend to assemble communities with diverse functional traits for acquiring resources (character displacement), whereas factors like aridity will tend to assemble communities with similar functional traits for osmoregulation. Non-limiting environmental factors will therefore have a tendency to assemble communities with average trait states that co-vary geographically with environmental gradients across space and time, such as with mean annual temperature and body mass in Bergmann's rule (e.g., Meiri & Dayan, 2003).

We refer to the geography of functional traits as ecometric patterning and we refer to the spatial correlation between the ecometric pattern and its associated environmental factor as ecometric correlation (Eronen *et al.*, 2010a; Polly *et al.*, 2011). The stronger the ecometric correlation, the more the traits in local communities co-vary with the functional requirements of their local environments. However, a strong ecometric correlation merely demonstrates that the traits co-vary with the environmental factor, it does not necessarily imply that their performance is optimal. We therefore refer to the mismatch (anomaly) between traits and their performance optimum as the ecometric load, analogous to the genetic loads of populations, which are the mismatches between local allele frequencies and fitness optima (Haldane, 1937). A high ecometric load indicates that many communities have members whose traits are performing suboptimally in their local environments, which may indicate a failure to adapt, a failure to sort, or a failure to succumb to extirpation and it implies increased risk to current or changing conditions (unless the change is in a direction that increases trait fitness). Ecometric load is thus an indicator of the 'fitness' of the overall biota. All things being equal, sub-optimal trait performance will lower fitness in local populations and drive biotic change through natural selection, dispersal, extirpation, and extinction until the ecometric load is lowered and the trait-environment relationship equilibrates.

One of the clearest examples of dynamic ecometric patterning in response to changes in Earth systems comes from the fossil record of the geographic and temporal spread of hypsodonty (high-crowned cheek teeth) in large herbivorous mammals, including horses, in response to the global spread of aridity and grasslands that resulted from the Himalayan uplift, continental reconfiguration, and changes in atmospheric and oceanic circulation (Fig. 1; Fortelius *et al.*, 2002, 2014; Eronen *et al.*, 2010b,c). This change occurred through a complex combination of geographic range changes, evolution, extinction, and clade sorting (MacFadden, 1985, 1992; Hulbert, 1993; Vrba, 1993, 1995; Lister *et al.*, 2005; Wolf, Bernor & Hussain, 2013; Fortelius *et al.*, 2014). Community means of other functional traits such as leaf shape in plants, hind limb posture in mammals, and body proportions in snakes are also known to be sorted ecometrically at continental scales (Wolfe, 1993; Polly, 2010; Lawing, Head & Polly, 2012).

Because ecometric patterning emerges at the community level from trait-environment interactions in many species, it potentially involves both microevolutionary population-level processes and macroevolutionary clade dynamics (Ricklefs, 1987; Webb *et al.*, 2002; Emerson & Gillespie, 2008; Graham & Fine, 2008; Cavender-Bares *et al.*, 2009). Microevolutionary factors include evolvability of the traits, the effect of mismatch between trait and environment on reproductive fitness, intensity of selection, geographic isolation and gene flow, dispersal ability, and population extirpation (Lande, 1976; Hanski & Gilpin, 1991; Lynch & Lande, 1993; Holt, 1997a,b). Macroevolutionary factors that emerge from microevolutionary processes include convergent evolution of functional traits in independent lineages that share the same local environment, parallel evolution in independent lineages that experience the same long-term environmental changes, clade-level sorting of species into communities based on functional trait states shared by common ancestry, and clade turnover by extinction of one clade and radiation of another based on functional traits shared by common ancestry (Damuth, 1985; Webb *et al.*, 2002, 2010; Ackerly & Cornwell, 2007; Jablonski, 2008; Hunt & Rabosky, 2010). Indeed, it is a matter of ongoing controversy whether functional traits shared by species in the same environment should be expected to have evolved independently or to arise
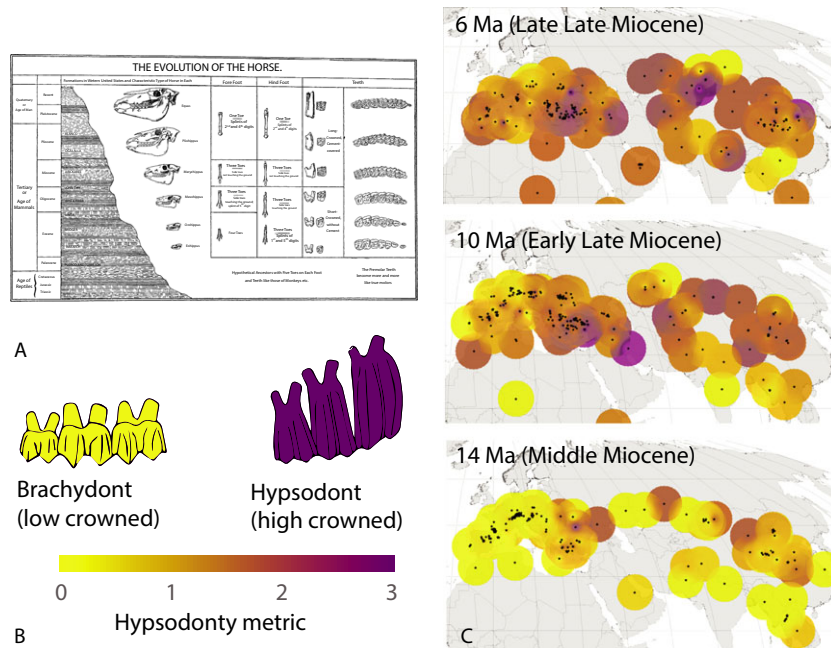
Figure 1. Hypsodonty in time and space. (A) Hypsodonty (cheek tooth crown height) increased on average in mammalian ungulates through the Miocene and Pliocene as global climates became more arid and grasslands spread, as shown here in a classic diagram of horse evolution from five-toed browsers in the Eocene to single-toed grazers in the Pliocene (from Matthew, 1926). (B) Tooth crowns range from low brachyodont forms to high hypsodont forms, quantified from 0 to 3 (yellow to purple; colour scale used throughout figures this paper). (C) Geographic and temporal ecometric changes in mean crown height in fossil assemblages from the Middle to Late Miocene (after Fortelius *et al.*, 2002).

by clade sorting based on functional trait states that are shared by common ancestry (Westoby, Leishman & Lord, 1995; Little, Kembel & Wilf, 2010; Lawing *et al.*, 2012). It is also a matter of ongoing controversy whether ecological processes such as community assembly are deterministic, arising predictably from fundamental principles like energy budgets and nutrient availability, or whether they are historically contingent on the ecology of ancestors and the quirks of geography (Ricklefs, 1987, 2006). Clade-level macroevolutionary processes, such as modes of trait evolution (e.g., Brownian motion, stabilizing selection, directional selection), phylogenetic trait correlation, lineage extinction and tree balance, and geographic and temporal sorting of clades, are thus important to how communities respond to Earth system changes.

To better understand how ecometric patterns and clade dynamics arise from microevolutionary processes we developed a general simulation model (Gotelli *et al.*, 2009) in which species originate, populations disperse and become extirpated, functional traits evolve in response to environmental selection and drift, and communities are assembled in an environmentally heterogeneous environment. The microevolutionary factors in our model are derived from quantitative genetic and metapopulation theory: heritability, phenotypic variance, selection intensity, extirpation probability, dispersal probability, and population size. Our overarching goal is to determine how the balance between these parameters at the population level affects ecometric outcomes at the community level and phylogenetic patterns of trait evolution and community assembly at the clade level. Our specific aims are: (1) to explore the range of ecometric patterns that arise from variation in microevolutionary parameters; (2) to determine which combinations of parameters produce ecometric patterns that match the pattern expected from the functional relationship between trait and environment; (3) to determine the balance of parameters that produce species sorting, clade turnover, and phylogenetic patterns of trait evolution and community assembly; (4) to determine how microevolutionary parameters affect the balance between geographic range changes, extinction, and adaptive evolution as responses to environmental change (as discussed below, our conclusions about responses to change are inferences because our models were run in a heterogeneous but static environment); and (5) to assess whether ecometric patterning arises deterministically from the interaction between model

parameters and environmental gradients or whether stochastic and historically contingent events play a role. Our modelling approach allows us to derive general principles about ecometrics and clade dynamics because, not only can we control microevolutionary parameters, we can control the trait-environment relationship and the geography of performance optima, all of which are challenging to estimate in real-world examples.

MODEL AND METHODS

We modelled the evolution of hypsodonty, or tooth crown height (Fig. 1). Herbivores with high-crowned teeth can tolerate a lifetime of abrasion from diets of silicaceous grasses or grit-covered vegetation, whereas low-crowned teeth, which are less mineralogically expensive to produce, are adequate for less abrasive diets (Janis & Fortelius, 1988; Damuth & Janis, 2011). Crown height thus influences whether herbivore species are able to flourish in regions with particular environmental conditions and, therefore, the geographic distribution of species and clades (Eronen *et al.*, 2010b,c). Reciprocally, the regional environment exerts selection on crown height and the evolutionary response of trait evolution to environment.

Antecedents of our modelling approach include the theoretical models of phenotypic evolution in heterogeneous environments developed by Levins (1968) and Endler (1977); the work by Lande (1976) and Arnold, Pfrender & Jones (2001) on evolution of quantitative phenotype traits; the concepts of metapopulation dynamics developed by Hanski (1999), Holt (1997a), and others; and the 'taxon-free' functional concepts of community assembly advanced

by Damuth *et al.* (1992), Fortelius *et al.* (2002), McGill *et al.* (2006), and others. It shares many common components with the geographically and phylogenetically explicit models implemented by Bokma, Bokma & Mönkkönen (2001), Rangel & Diniz-Filho (2005), Rangel, Diniz-Filho & Colwell (2007), and Roy & Goldberg (2007). See Gotelli *et al.* (2009) for a review of the history of macroecological modelling.

GEOGRAPHY OF HUMBOLDTLAND

Our model was set in a virtual world with two continents, Humboldtland, which are respectively heterogeneous and homogeneous for the environmental variables that are relevant to hypsodonty (Fig. 2). The homogeneous continent provides an experimental control, because ecometric patterning is expected to arise only from geographically heterogeneous environments (Levins, 1968; Endler, 1977; Fortelius *et al.*, 2002).

The continents were gridded into cells spaced at 50 km to approximate the maximum spatial averaging expected in terrestrial fossil sample due to the combination of movements of living animals, predator accumulation, and fluvial transport (Voorhies, 1969; Polly, 2010). The model's mechanics are scale-free so the scale has no effect on outcomes. Each cell has an associated value for five environmental variables: elevation, mean annual temperature, annual precipitation, biome, and grit. The distributions of four vegetative biomes (tundra, desert, grassland, or forest) are determined by mean annual temperature and precipitation (Whittaker, 1967, 1975). The proportion of grit in a cell (0–1) is determined by downwind distance from high elevation mountain regions.
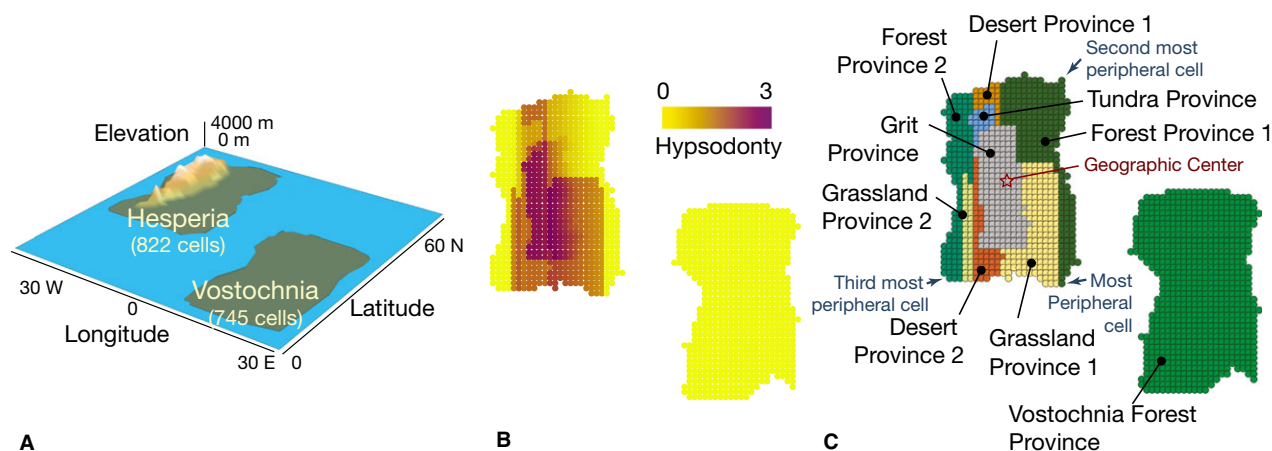

Figure 2. The ecometric geography of Humboldtland. (A) Topographic overview. (B) Selective optimum for molar crown height (function of precipitation, biome, and grit). (C) Ecometric zones (derived from selective optimum).

The western continent, Hesperia (Latin, 'western land'), is situated at mid to high latitudes and is bordered along its western margin by a high mountain range, and thus has steep latitudinal and altitudinal temperature gradients and an east-west precipitation gradient. The area of Hesperia is about 2.06 million km^2 (822 grid cells), about two-thirds the size of Australia. Areas downwind (east) of Hesperia's highest elevations are blanketed with airborne grit. Hesperia is environmentally heterogeneous with elevations ranging from 55 to 4405 m, mean annual temperatures (MAT) from −9 to 19.5 °C, precipitation from 10 to 199 cm per year, grit ranging from 0% to 100%, and all four biomes. The eastern continent, Vostochnia (Russian, 'eastern land'), is situated at low latitudes, has little relief and, therefore, weak temperature and precipitation gradients. Vostochnia's area is about 1.86 million km^2 (745 grid cells). Vostochnia has a comparatively uniform environment with elevations ranging from 5 to 986 m, MAT from 9.2 to 25 °C, annual precipitation from 194 to 300 cm, no grit, and is completely forested.

Maps of the geographic distribution of environmental variables in Humboldtland are presented in Supporting Information, Fig. S1 and database tables for its gridded geographic and environmental variables are provided in Supporting Information, Table S2.

MODEL ALGORITHM

Each run of the model was 400 steps long, starting with a single local population whose trait value was set to its local selective optimum. The model's parameters affect the width of local adaptive peaks (selection intensity), genetic variance, dispersal probability, and extirpation probability for the entire model run (see below and Supporting Information, Data S1).

The model simulates the functional evolution of a single trait, molar crown height, which has values that range from 0 (lowest crowned, brachyodont) to 3 (highest crowned, hypsodont) (Fig. 1B). The trait value in each local population of each species is tracked and is influenced by a combination of ancestry, local selection, gene flow, and drift. Trait values were averaged over all local populations to determine the species mean trait value. Trait values were averaged in each grid cell over the local populations of the species occupying it to determine the local ecometric mean.

The phylogenetic framework was a balanced, dichotomous tree with 16 terminal tips (Fig. 3A). Each lineage was composed of a number of local populations and is, thus, what Hanski & Gilpin (1991) call a geographical scale metapopulation (Fig. 3D). Local populations could disperse, be extirpated (become locally extinct), undergo drift, respond to selection, and receive gene flow via dispersal of other populations of the same species into the same grid cell.

The fitness of local populations depended on their mean molar crown height relative to the selective optimum of the local grid cell (Fig. 3C). High-crowned teeth perform better in arid, gritty environments with tough vegetation, while low-crowned teeth perform better in moist, clean environments with tender vegetation (Janis & Fortelius, 1988; Damuth & Janis, 2011). A function of annual precipitation, grit, and biome was used to determine the selective optimum for each cell. Direction and magnitude of selection on the local population were derived from an adaptive peak model (Simpson, 1944; Lande, 1976; Arnold et al., 2001) (Fig. 3C). Tooth crown height was allowed to evolve freely in response to local selection, regardless of whether higher or lower-crown heights were favoured. Empirical data suggest that evolution from low to high crowns has been much more common than the reverse (Damuth & Janis, 2011; Mushegyan et al., 2015), but it is not known whether this is because development or genetic constraints make transitions easier in one direction than in reverse, because selection for high crowns is more intense than selection for low crowns, or because environmental circumstances have on average favoured selection toward higher crowns. Our modelling does not incorporate either of the first two possibilities, but the third could emerge from the model runs. Each local population was also subject to neutral genetic drift, which is a function of the heritable phenotypic variance and population size (Lande, 1976).

Dispersal of local populations was stochastic, with separate chances for each population to disperse at each step of the model into each nearby grid cell (Fig. 3D). If a population dispersed into a cell that was already occupied by that species, then the phenotypes of the incumbent and dispersing populations were averaged to simulate gene flow.

Extirpation of local populations was also stochastic, with a higher probability the farther the population's trait value was from the local selective optimum (Fig. 3C). In nature, extirpation occurs when a population's mean fitness is too low to maintain a stable size (Holt, 1997a,b).

Speciation by peripheral isolation occurred in every species at fixed points (Fig. 3A). We used a simplified version of the peripheral isolates model of speciation, not because it is arguably common in nature (Mayr, 1942, 1963; Bush, 1975; Coyne & Orr, 2004; Vrba & DeGusta, 2004; but cf. Lynch, 1989), but because (1) we wanted the founding populations of new species to be influenced by geographic variation in the trait of the parent species; and (2) we wanted our model to have opportunities for species
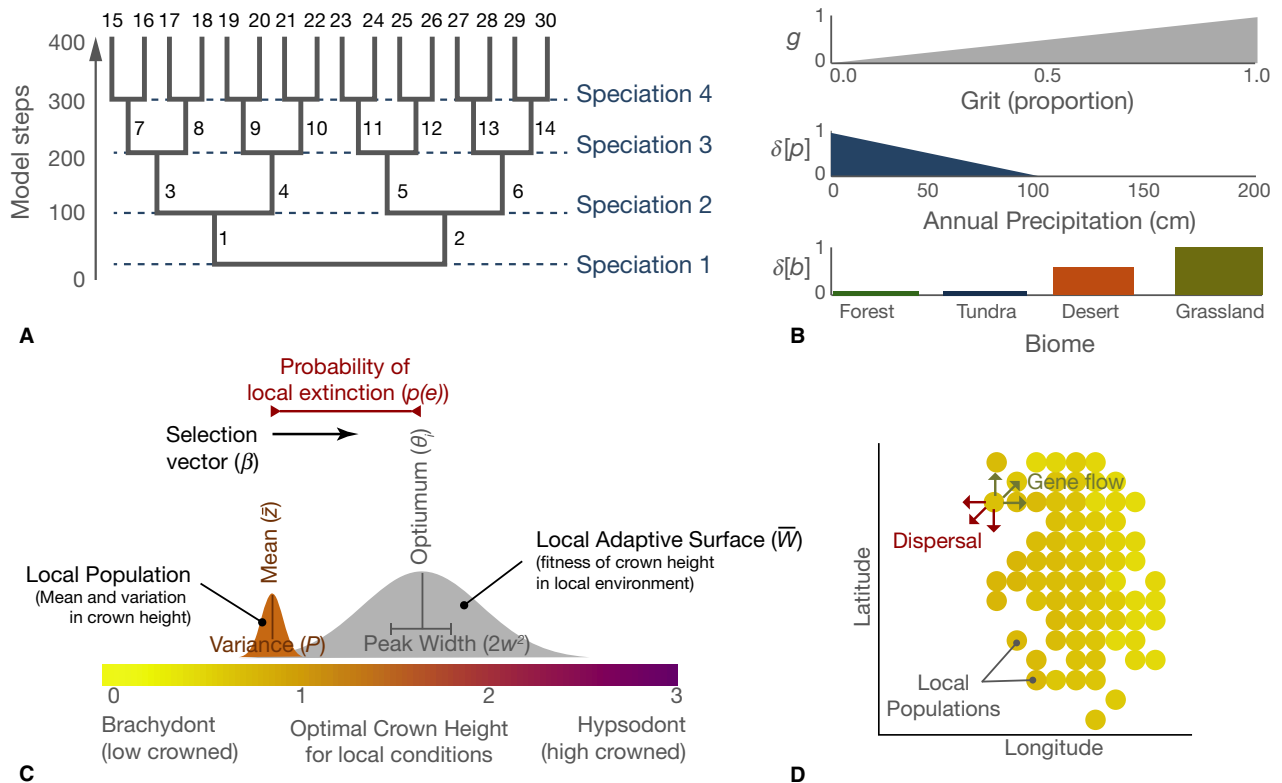
Figure 3. Components of the ecometric model. (A) Phylogenetic topology and branch identification numbers. (B) Calculation of the selective optimum (θ_i) for each grid cell (Fig. 2B) is based on the sum of three performance functions for the cell's grit proportion, annual precipitation, and vegetation. (C) For each grid cell, an adaptive peak centered at θ_i is used to calculate a selection vector that moves the local population toward the optimum and to determine the probability of extirpation. Local populations occupying a same grid cell that belong to different species undergo independent selection and extirpation. (D) Each species is composed of a set of local populations that can disperse into new cells or into cells already occupied by the species, in which case trait values are averaged to simulate gene flow.

to diverge in morphology. Peripheral isolation accomplishes both these goals because populations along the periphery of the species range are likely to have outlying trait values because they receive less gene flow than populations in the centre and because the small founding populations of the peripheral isolate descendants have a greater chance of diverging due to selection or drift than the large, geographically widespread parent population (Dobzhansky, 1941; Mayr, 1963; Bush, 1975; Eldredge & Cracraft, 1980). As discussed below, the peripheral isolate mode of speciation had important consequences for the patterns that emerged from our model.

For reference, the odd numbered branches of the phylogenetic tree were always founded by a single peripheral isolate population and the even numbered branches, except Lineage 2, are always founded by the remainder of the local populations of the parent species (Fig. 3A). Thus, half of the species in the model demonstrate the effects of founder bottlenecks and the other half do not. This dichotomy also has

important consequences on the model's outcomes, which are discussed below.

A complete description of the model's algorithms and parameters are presented in Supporting Information, Data S1. *Mathematica* code for a generic model run is given in Supporting Information, Data S3.

MODELLING EXPERIMENTS

To explore the effects of individual parameters on clade dynamics and ecometric patterns we ran five series of models in which one parameter was systematically varied and the others held constant at intermediate values. The full set of starting parameters for all model runs is reported in Supporting Information, Table S1.

Experiment 1: Adaptive Peak Width
In this experiment, four runs were performed on each continent in which adaptive peak width (w^2)

was assigned values of 0.5, 1.0, 1.5, and 2.0 respectively. The width of the adaptive peak affects the intensity of selection: narrower peaks have steeper slopes and therefore more intense local selection. The width parameter is analogous to the variance of a Gaussian (normal) distribution and is expressed in squared hypsodonty units (Fig. 3C). A value of 2.0 therefore equals a 'standard deviation' of about 1.4 units on the hypsodonty scale, which means that almost the entire range of crown heights are near the peak and have high fitness. This is very weak selection. In contrast, a value of 0.5 encompasses only about 0.7 hypsodonty units near the fitness peak, which translates into very strong selection toward the local optimum. Note that in this paper the term 'adaptation' refers to trait values that are at or near their local selective optimum because of trait-environment selection.

Experiment 2: Dispersal

In this experiment, four runs were performed on each continent in which the probability of dispersal was varied from 0.5 to 2.0 in 0.5 increments. Probabilities of 1.0 or greater meant 100% probability of dispersal into each adjacent cell.

Experiment 3: Extirpation

In this experiment, five runs were performed on each continent in which the extirpation scaling factor was assigned values of 0.0, 0.5, 1.0, 1.5, and 2.0 respectively. A factor of 0.0 means that local populations are never extirpated, a factor of 1.0 means that the probability of extirpation is exactly proportional to the distance of the local population mean from the selective optimum relative to the width of the adaptive peak.

Experiment 4: Phenotypic Variance

In this experiment, four runs were performed on each continent in which the phenotypic variance was assigned values of 0.01, 0.05, 0.09, and 0.13 respectively. In our model, the phenotypic variance parameter controls the amount of genetic variance, and therefore the response of the local population to selection and the rate of genetic drift, because heritability (h^2) is held constant at 0.5. The phenotypic variance parameter therefore behaves similarly to the rate parameter in macroevolutionary models such as Brownian motion. A population with a small phenotypic variance changes less in response to selection than one with a large variance, and the same for drift.

Experiment 5: Start Point

In this experiment, the starting grid cell was randomly varied. Ten runs were conducted on Hesperia

to sample a reasonable range of starting environments (including three out of the four biomes), and five were conducted on Vostochnia (where there is virtually no environmental variance to sample).

Post-hoc experiments

A second round of experiments was run to deliberately try to produce examples of phylogenetic correlation in the trait value and clade turnover, neither of which emerged from the five core experiments. In these four experiments, three out of four key parameters (dispersal, adaptive peak width, extirpation scaling factor, and phenotypic variance) were fixed (1.0, 0.3 2.0, 0.2 respectively) and the other one was varied.

ANALYTICAL METHODS

Ecometric zones

We divided Humboldtland into discrete ecometric zones based on the continuous geographic distribution of selective optima (Fig. 2). Ecometric zones are contiguous geographic patches analogous to ecological zones (*sensu* Ricklefs, 2006), but are defined by environmental parameters that relate directly to local performance of a functional trait (Arnold, 1983) instead of general environmental conditions, such as temperature, precipitation, and elevation. Boundaries between ecometric zones may be gradational or sharply defined (Whittaker, 1967; Endler, 1977; McGill *et al.*, 2006). In our study, the combined effects of precipitation, vegetation cover, and ambient grit define hypsodonty ecometric zones because these three factors affect the durability of teeth and therefore the relative fitness of individuals in different environments (King *et al.*, 2004, 2012). Zones help distinguish effects of local adaptation from dispersal and clade sorting from parallel adaptation because zones with the same selective optimum may be separated by a sub-optimal barrier (such as the two forest zones in our model), and zones with different selective optima may be geographically contiguous (such as between forest and grit in our model). The order of spread of expanding species and clades between ecometric zones helps determine whether ecometric specialization has a phylogenetic component (Ricklefs, 2006; Ackerly & Cornwell, 2007; Webb *et al.*, 2002). Delineating ecometric zones in nature may be difficult because it requires an understanding of functional performance relative to the geography of environmental gradients that affect its performance.

Ecometric load

Ecometric load is a measure of how well an ecometric pattern matches the pattern expected from

environmental selection. Ecometric load is analogous to genetic load, which is the difference between actual fitness of a population and its maximum fitness in a particular environment (Haldane, 1937). We calculated ecometric load as the average difference between the mean trait value in local communities relative to the corresponding optimal trait value:

$$n^{-1} \sqrt{\sum_{i=1}^{n} \left(\bar{z}_C - \theta_i \right)^2}, \qquad (1)$$

where $\bar{z}_C$ is the mean trait value of the community, θ_i is the selective optimum for the trait in geographic grid cell i, and n is the total number of grid cells. Ecometric load is related to ecometric correlation (R^2) between an observed ecometric pattern and another geographic variable (Polly, 2010; Lawing *et al.*, 2012; Polly & Sarwar, 2014), but load is a more direct goodness-of-fit statistic because it does not scale with ecometric variance.

Ecometric equilibrium

Ecometric equilibrium is the ecometric load converged upon by a model with a particular combination of parameters. Ceteris paribus, the ecometric pattern in each model reaches an equilibrium whose distance from the selective optimum depends on the intensity of selection, gene flow, distribution of environments, and ancestry. Equilibrium is attained faster with some combinations of parameters than others, which has implications for ecometric tracking of changing environments.

Phylogenetic signal and evolutionary rate

Phylogenetic signal is a measure of the congruence between the distribution of trait values of lineages and their shared evolutionary history. We used Pagel's λ (Pagel, 1999) to assess how much variation in hypsodonty could be explained by phylogenetic relationships among the species extant at the end of the simulations. Note that this assumes a simple Brownian motion model of trait evolution. Calculations were performed in R (R Core Team, 2014) using the geiger package (Harmon *et al.*, 2008). Lineages that went extinct during the simulation were pruned from the phylogeny prior to calculating Pagel's λ.

Rates of evolutionary change could be summarized directly from our models because each step change was recorded for all branches in the tree. Because peripheral isolation frequently causes punctuated bursts of change, rates of change along branches (anagenetic) and at speciation events (cladogenetic) were calculated separately. Mean and variance were calculated for each set of anagenetic and cladogenetic changes respectively. The variance is equivalent to a standard phylogenetic rate parameter (e.g.,Felsenstein, 1985; Martins & Hansen, 1997; Revell, Harmon & Collar, 2008), and the mean is an indicator of directionality (e.g., Butler & King, 2004; Polly, 2004; Hunt, 2006). The rate statistics are reported in Supporting Information, Table S1.

Geographic summary statistics

Geographic variance is the intraspecific variance in trait values among local populations; mean geographic variance is its average across all species at the end of the model run. Range size is calculated as the number of grid cells a species occupies in proportion to the total number of grid cells in the continent; mean range size is averaged across all species at the end of the model run. Species richness is the total number of species occupying a grid cell at the end of the model run, and mean richness is the average across all grid cells.

Phylogenetic community patterns

Phylogenetic structure of species composition in local communities can be an important clue to the clade dynamics of community assembly (Webb *et al.*, 2002; Ricklefs, 2006; Emerson & Gillespie, 2008; Cavender-Bares *et al.*, 2009) and by extension to the historical processes underlying ecometric patterns. Phylogenies were mapped onto ecometric zones as one method for assessing phylogenetic structuring (e.g., third column of Fig. 4). We measured community relatedness for each grid cell as the evolutionary branch lengths

Figure 4. Examples of five ecometric patterns arising from the model experiments. (A–D) Pattern 1. Adaptive peak experiment, w^2=2.0 (2013-10-25-18-39-15-Hesperia). (E–H) Pattern 2. Phenotypic variance experiment, $\sigma^2 = 0.13$ (2013-10-25-18-21-39-Hesperia). (I–L) Pattern 3a. Start location experiment, start zone = grit (2013-10-25-22-02-06-Hesperia). (M–P) Pattern 3b. Variable peak, high dispersal and extirpation experiment, $w^2 = 1.0$, disp = 1.0, extirp = 2.0 (2014-06-10-10-47-02-Hesperia). (Q–T) Pattern 4. Extirpation experiment, extirp = 1.0 (2013-10-25-19-24-20-Hesperia). First column shows the ecometric pattern at step 400 of each model; the second column shows changes in the trait mean of each species; the third column shows phylogenetic pattern of geographic spread through ecometric zones (layout of branches follows Fig. 3A); and the fourth column shows change in the ecometric load (average difference per grid cell between ecometric pattern and the selective optimum shown in Fig. 2B) as blue line, equilibrium load as horizontal grey line, and the time at which equilibrium is reached as broken vertical line.
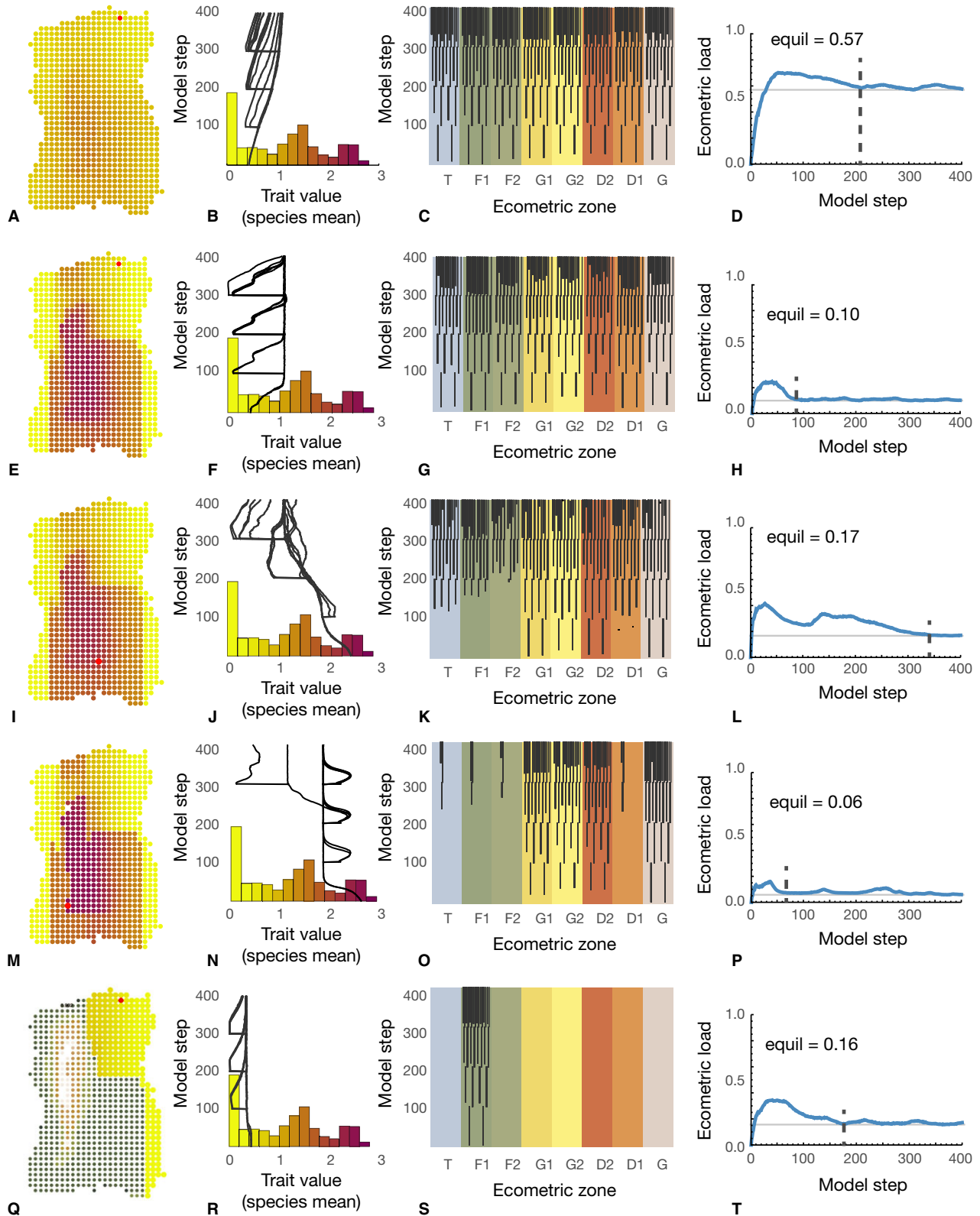
spanned by species present in a community proportional to total length of the tree (Supporting Information, Fig. S1.2), which is similar to other metrics

commonly used in phylogenetic community ecology (Webb, 2000; Webb *et al.*, 2002; Graham & Fine, 2008; Cavender-Bares *et al.*, 2009), especially Faith's

original phylogenetic diversity metric (Faith, 1992). To correct for chance sampling, the proportion is reported as the *P*-value that is higher or lower than a randomly selected group of species of the same number. Note that *P*-values were calculated relative to the complete tree (Fig. 3A) regardless of branches that became extinct during the model. A community can have higher or lower relatedness than expected by chance because of either geographic exclusion or extinction, which are quickly distinguished by inspection of extinction patterns. These results are presented in map form in Supporting Information, Data S2.

GUIDE TO MODEL OUTPUT

A summary of key statistics from the core model runs on Hesperia is reported in Appendix and a full summary of statistics is reported in Supporting Information, Table S1. Graphic output of ecometric patterns, species ranges, species richness patterns, phylogenetic change in trait means, and geographic patterns of community relatedness are presented in Supporting Information, Data S2. Graphs showing the change in ecometric load and the final ecometric equilibrium of each model are shown in Supporting Information, Fig. S2. Phylogenetic diagrams showing the history of ecometric zone occupation are shown in Supporting Information, Fig. S3. Animations showing the development of ecometric pattern through the course of each model run are packaged in Supporting Information, Tables S3 and S4. It is recommended that readers refer to at least a few of the output graphics (Data S2) and animations (Tables S3 and S4) as an aid to understanding discussion of our results.

RESULTS AND DISCUSSION

ECOMETRIC PATTERNS, THEIR CAUSES, AND THEIR INTERPRETATION

Interpretation of the processes by which ecometric patterns arise and the trade-offs between different mechanisms of achieving them requires understanding of which patterns arise in our modelling and why. Trait differences can arise when communities are composed of different combinations of species that are sorted by the trait-environment relationship (interspecific variation in the trait) or when communities have the same species-level composition but their local populations are selectively optimized for differences in environment (intraspecific variation). Environmental impediments to species dispersal is required for communities to differ in membership (Gaston, 2003), strong local selection that overwhelms the homogenizing effects of gene flow without local extirpation or other barriers to dispersal (Kirkpatrick & Barton, 1997; Lenormand, 2002) is required for communities to differ in their trait composition yet still have the same species-level membership. When species compositions differ between communities, the shared trait values within each community may have evolved independently in response to the local environment (homoplasy) or the local trait values may be shared by common ancestry (clade sorting based on phylogenetically correlated functional trait states). The same overall ecometric pattern can, in principle, arise from any of these sources, which implies that the same biotic response to ecometric load can be achieved through different evolutionary and ecological processes. Our modelling experiments produced four out of five ecometric patterns, as classified based on the source of the trait differences between communities (Table 1).

Table 1. Classification of ecometric patterns and associated properties

	Pattern	Ecometric pattern	Ecometric load	Range size	Intraspecific trait variation	Interspecific trait variation	Species richness	Gene flow	Selection
1	No ecometric pattern	Absent	High	Large	Low	Low	High	High	Weak
2	Intraspecific variation	Present	Low	Large	High	Low	High	Low	Strong
3	Ecometric mosaic	Present	Low	Intermediate	Intermediate	Intermediate	Variable	Variable	Strong
4	Ecometric endemics	Present	Low	Small	Low	High	Low	Variable	Strong
5	Intra-community variation	Present	Intermediate	Variable	Low	High	Variable	High	Strong

Ecometric pattern weak or absent (Pattern 1)

This pattern is characterized by low ecometric correlation, high ecometric load, and lack of spatial differentiation. Weak ecometric patterns indicate that the traits of the biota are not at functional equilibrium with the environment. Lack of ecometric patterning can result from a variety of causes, including lack of environmental heterogeneity, high gene flow across ecometric zones, low selection intensity, or substantial neutral drift. This pattern arose in our models only when local fitness did not depend heavily on trait value, either because selection was weak (wide adaptive peaks) or the probability of extirpation was low (Fig. 4A-D; Appendix). Strong local selection overwhelms gene flow to produce an ecometric pattern by local differentiation of conspecific populations in different ecometric zones, whereas high extirpation probability excludes unfit species from local community membership. When either of these factors is relaxed, species became pangeographic (their ranges filled the entire continent), species richness was uniformly high across the continent (because all species were pangeographic), each species evolved in parallel toward the same mean trait value (trending toward the mean selective value of the continent, which was 1.08), and each species had low intraspecific variation because gene flow homogenized each species faster than local selection could cause them to become differentiated (Table 1).

Lack of ecometric patterning, lack of inter- and intraspecific functional trait differentiation, and large, overlapping species ranges may therefore be real-world indicators of forgiving environmental conditions with respect to the trait of interest. But the same outcomes can also arise for very different reasons when the environment is geographically homogeneous (Levins, 1968; Endler, 1977; Gaston, 2003; McPeek, 2007), as they did in our Vostchnia models (Appendix, Supporting Information, Table S1, Data S2 and Fig. S2). In Vostchnia, environmental conditions relevant to molar crown height vary only a little and the entire continent forms a single ecometric zone (Fig. 2). Therefore, regardless of selection intensity or extirpation, all model runs resulted in a homogeneous ecometric distribution of traits, pangeographic species ranges, and little differentiation in traits, superficially like ecometric Pattern 1. But in Vostchnia ecometric homogeneity is the environmentally optimal pattern and, unlike Hesperia, it carries a low ecometric load and is best classified as a special example of Pattern 4 (strong ecometric pattern arising from species endemic to each ecometric zone; see below). The apparent lack of ecometric patterning in modern or fossil data therefore requires understanding of the functional trait-environment relationship and knowledge of the distribution of the relevant environmental factors in order to interpret it.

Intraspecific variation creates ecometric pattern (Pattern 2)

Within-species geographic variation in trait values can produce an emergent community-level ecometric pattern without any differences in community composition at the species level. Low ecometric loads, large pangeographic species ranges, little or no variation of the mean trait value across species, but strong geographic variation within species characterize this pattern. Pattern 2 is an end member that grades to Patterns 3 and 4 based on the size of species ranges.

Pattern 2 occurred only once in our modelling experiments when the parameter for phenotypic variance in local populations was set very high (Fig. 4E–H; Appendix). Phenotypic variance is the parameter in our models that controls response to selection. Selection acts on the heritable or genetic component of variance (Equation 7 in Supporting Information, Data S1), and in our simulations heritability (h^2) was held constant at 0.5. Selection was therefore able to move the traits of local populations to their local environmental optimum despite the counteracting effects of gene flow. Consequently, every species was able to adapt locally to all environments, which meant that they were all able to spread across the entire continent and were essentially identical to one another in having the same overall trait mean and the same geographic pattern of trait variation (Supporting Information, Data S2, p. 18). In principle, strong local selection could also overcome gene flow and move trait values to the optimum, but the a narrow adaptive peak required to do that increases the risk of extirpation by narrowing the range of viable local phenotypes and thus produces ecometric patterns in which species composition differs among communities instead of patterns that arise from intraspecific variation.

Pattern 2 could plausibly arise by plastic response to local environments. Plastic responses are non-genetic (ecophenotypic) changes in traits in response to environmental conditions that can maintain fitness in a population without selective adaptation (West-Eberhard, 1989). If the plastic component of the trait (the non-genetic component of phenotypic variance) is able to take on optimal values for local environments, then species will be able to spread across all ecometric zones regardless and maintain fitness regardless of gene flow (which affects only the genetic component of trait variance). Indeed, many authors have argued that plastic response was an important mechanism for surviving Quaternary climate cycles thus might be common in species in the

modern world (Lister, 2004; Hof *et al.*, 2011). While we did not specifically include plastic responses in our models, it could be done by increasing the environmental component of phenotypic variance, which would result in ecometric Pattern 2 similar to strong response to selection.

Pattern 2 cannot occur without parallel evolution because local populations of different species have to independently evolve traits that fit the environmental optimum for each local community. In our model, phylogenetic correlation in trait values was low in the simulation with high phenotypic variance as indicated by Pagel's λ (Table 1). Furthermore, it logically precludes clade sorting because each local community has the same member species.

Whether ecometric Pattern 2 is found in nature is unclear. Intraspecific geographic variation in those traits that have been studied ecometrically, such as leaf shape, body mass, molar crown height, and locomotor morphology, appears to be small relative to between-species variation within local communities (Dolph & Dilcher, 1979; Legendre, 1986; Brown & Nicoletto, 1991; Polly, 2010), but within-species environment clines have been documented in body size in many taxa and in locomotor morphology of reindeer and carnivores (Klein, Meldgaard & Fancy, 1987; McLellan, 2000; Murray & Larivière, 2002; Meiri & Dayan, 2003; Makarieva, Gorshkov & Li, 2005). The current balance of evidence suggests that real ecometric patterns are formed primarily by species sorting (Patterns 3–5) with a secondary contribution from local within-species variation. The contribution of intraspecific variation to ecometric patterning needs further investigation.

Interspecific variation and mosaic of ranges produces ecometric pattern (Pattern 3)

In this pattern ecometric load is low, geographic ranges are intermediate in size, each species occupies some but not all ecometric zones, intraspecific variation is low, and variation between species is high. A key feature of this pattern is that all species within a single local community take on approximately the same functional trait value; we discuss patterns in which coexisting species take on different values of the same functional trait below under Pattern 5. This pattern arises from partial sorting at the species level rather than local intraspecific adaptation within the species. Sorting of species is partial because the traits of species that span more than one ecometric zone cannot be perfectly adapted to all of them because each zone has a different optimum and gene flow will create an ecometric load for that species in one or more of the zones. In principle, species could span zones and be locally adapted to all of them through intraspecific variation, but conditions

that permit that to happen would normally allow species to spread into all ecometric zones (Pattern 2). In Pattern 3, species richness is lower and more variable than Patterns 1 or 2 because each species is confined to a subset of the continent. Parallel evolution can produce this pattern (Pattern 3a) when several species must converge on the selective optimum of an ecometric zone, but it could also arise from clade sorting (Pattern 3b) if a single lineage colonizes a new ecometric zone then speciates within it. Patterns 2 and 4 are opposite end members of Pattern 3 when species ranges either extend over all ecometric zones or are confined to just one.

Pattern 3 arose frequently in our models (in 19 out of 27 of the core models), occurring whenever selection strength was not too low and extirpation and phenotypic variance were not too high (Fig. 4I–P; Appendix). Interestingly, in our core experiments this pattern always arose from parallel evolution (Pattern 3a), never clade sorting (Pattern 3b), as discussed in detail below. Many real ecometric patterns have most of the features of Pattern 3 (species ranges that span several ecometric zones, variable species richness, more variation between species than within species), but trait differences between species in local communities are frequently quite variable as in Pattern 5 (e.g., Polly, 2010; Lawing & Polly, 2011).

Endemics confined to single ecometric zones produces ecometric pattern (Pattern 4)

In this pattern, ecometric patterning is strong and ecometric load is low, but species are each confined to only one ecometric zone. Range sizes are necessarily small (equal to the sizes of the ecometric zones), within-species variation is low or non-existent because all populations are adapted to the optimum of a single ecometric, and variation between species inhabiting different zones is high (equal to variation among ecometric zone optima).

This pattern occurred in our models when species were prevented from crossing ecometric zone boundaries because extirpation was high (immigrant populations are immediately extirpated because their traits are optimized for their ancestral zone and are too far from their new local adaptive peak) or phenotypic variance was low (immigrant populations cannot respond to selection quickly enough to adapt to the new optimum before they are extirpated) (Fig. 4Q–T; Appendix). All of the *Vostochnia* models resulted in Pattern 4 because that continent only has one ecometric zone. In principle, this pattern could arise by parallel evolution (Pattern 4a) if species inhabiting the same ecometric zone are distantly related, or by clade sorting (Pattern 4b) if they are closely related; however, the distinction could not be

made in our models because the entire clade always remained confined to its ancestral zone. Indeed, the only way a monophyletic clade could have species that occupy several ecometric zones yet are individually confined to only one would be if the balance between parameters was just right to make colonization of new zones improbable but possible and if the jump between zones was made with speciation events.

Marked differences in trait values within communities (Pattern 5)

This final ecometric pattern differs from others in that trait values vary substantially among the members of a local community, yet the average trait value of the communities covaries with the associated environmental variable. In other words, ecometric correlation is high at the community level, but the species within a community have trait values distributed widely around the community mean. In principle, Pattern 5 could involve widespread species or ones that are confined to individual ecometric zones (c.f., Patterns 3 and 4). This pattern is characterized by strong variation between species, little intraspecific variation, intermediate or small geographic range sizes, and heterogeneity in trait values within local communities.

None of our models produced Pattern 5. Within-community trait differences were never larger on average than geographic variation within species or even the differences between species in their overall trait means (Appendix). In other words, all species cohabiting the same local community had traits that were similarly optimized to the local environment. In contrast, ecometric traits often vary substantially between the members of local communities in the real world. Variation within communities is common in mammalian body mass (Legendre, 1986; Brown & Nicoletto, 1991), ungulate molar crown height (Damuth & Janis, 2011), carnivoran locomotor morphology (Polly, 2010), snake locomotor morphology (Lawing et al., 2012), and plant leaf shape (Dolph & Dilcher, 1979; Givnesh, 1984).

That our models did not result in intra-community trait differentiation indicates that additional factors affect real-world ecometrics. One way in which this pattern can arise is when species traits are optimized for one ecometric zone, but their range extends into other zones where gene flow prevents local adaptation (Endler, 1977; Kirkpatrick & Barton, 1997; Lenormand, 2002). In principle, Pattern 5 could have arisen this way from our models if the balance of parameters controlling gene flow, selection, and extirpation was right. Intra-community variation can also arise when local environments are heterogeneous and support several optimum trait values instead of just one (MacArthur, 1972; Endler, 1977). Mixed savannah vegetation, for example, can support both browsing and grazing herbivores and thus a combination of low and high-crowned teeth (Damuth & Janis, 2011). Competition between species can, in principle, result in within-community differentiation by creating community assembly rules that filter membership based on functional traits, and competitive character displacement can reinforce differentiation between species coexisting in a local community (Cody & Diamond, 1975). Finally, we suspect that historical contingencies (discussed in more detail below) would add to intra-community variation when clades with deep divergences in ancestry are mixed after long periods of confinement to different continents or past environments (Linder et al., 2014; Jønsson et al., 2015). Periodic connections between North America and Eurasia, for example, have iteratively mixed clades into the respective communities of the two continents, such as the effects on carnivoran locomotor ecometrics that immigration of felids into the New World ca. 18 Ma, the migration of canids into Eurasia ca. 9 Ma, and the immigration of crown-group ursids from Eurasia ca. 4.5 Ma must have had (Hunt, 1998; Martin, 1998; Tedford, Wang & Taylor, 2009). These clades have evolved characteristically distinct locomotor indices since their last common ancestor (ca. 42 Ma) that are now mixed in modern faunas and account for most of the community-level heterogeneity in functional traits (Polly, 2010). Our current models are too short and static to allow these kinds of deep phylogenetic dynamics to emerge. All of these processes are frequent in the real world and, had they been built into our models, it is likely that many of the runs that produced Pattern 3 would have produced Pattern 5.

EFFECTS OF MICROEVOLUTIONARY MODEL PARAMETERS ON ECOMETRIC PATTERNS

Adaptive peak width, which controls the intensity of local selection, had the largest effect on the emergence of patterning than any single parameter (Appendix; Supporting Information, Data S2, Fig. S2). When the adaptive peak was narrow (w^2=0.5), the ecometric load dropped to 0.05, the lowest value in any of the models our five core experiments (i.e., mean hypsodonty in each grid cell was on average only 0.05 units from the selective optimum across the entire continent, which is nearly perfect). Narrow adaptive peaks increased the difficulty in crossing ecometric zone boundaries (where these are sharp), because immigrant populations will tend to have a greater distance from the selective optimum, which effectively increases the probability of extirpation. Consequently, species-range sizes and

the number of ecometric zones occupied by each species was on average lower when peak width was narrower. Note, however, that narrow peaks were not as effective at limiting dispersal as raising the extirpation probability. Narrow adaptive peaks encouraged interspecific differences among species if they occupied different ecometric zones, but encouraged similarity among species if they were endemic to the same zone or were pangeographic across all zones. As peak width increased ($w^2 \geq 1.5$), ecometric load increased, species ranges tended toward being pangeographic, and ecometric patterning disappeared because local selection weakened enough that gene flow swamped any differentiation – all populations of all species converged on the continent's average selective optimum (1.01 for Hesperia).

Dispersal probability, which is the probability of a local population expanding into a nearby cell, affected the time required for a new species to spread and the rate of gene flow (Appendix; Supporting Information, Data S2). The effects of dispersal were most obvious in the post-hoc experiments where dispersal probability was varied from 0.2 to 1.0 (VarDispHExtMedAPW; see below), which demonstrated that range size and species richness both increase as dispersal becomes more probable. The lowest dispersal probabilities were associated with low intraspecific geographic variance, which is arguably counterintuitive because one would expect that low gene flow would allow local selection to cause differentiation across the geographic range; however, low dispersal probability also decreased the likelihood that populations would cross ecometric zone boundaries and thus confined them to a more homogeneous environment, which produced less geographic variation despite lack of gene flow (Kirkpatrick & Barton, 1997) (see for example Experiment VarDispHExtMedAPW, Model 2014-06-10-08-20-20-Hesperia).

Extirpation probability had largely the opposite effect of adaptive peak width: when the extirpation scaling factor was low, species tended to be pangeographic with little ecometric differentiation (Pattern 1), but as it increased traits became more locally differentiated and species tended to be more geographically restricted (Pattern 3), ultimately being confined to a single ecometric zone (Pattern 4) (Appendix; Supporting Information, Table S1). Extirpation and peak width have subtle but important differences though, because weak extirpation allows unfit populations to survive without being selected toward the local adaptive optimum, for example when gene flow counteracts local selection, even though selection may be intense, whereas wide adaptive peaks produce less intense selection because a wider range of phenotypes are fit.

Phenotypic variance within a local population increases its response to selection in our models because it has the effect of increasing genetic variance because we held heritability (h^2) constant. A population with higher genetic variance thus responded more to local selection in our models than one with low variance. Low phenotypic variance prevented populations from crossing ecometric zone boundaries because they could not adapt quickly enough to avoid extirpation, resulting in species with ranges confined to a single ecometric zone (pattern 4), but with a relatively high ecometric load (similar to pattern 1) (Appendix; Supporting Information, Table S1, Data S2). When phenotypic variance was low species were frequently excluded from some ecometric zones, in large part because the inability to respond to selection caused drift and gene flow to become more important in carrying populations away from the local selective optimum and making them more vulnerable to extirpation (Supporting Information, Fig. S3) (see Kirkpatrick & Barton, 1997; Lenormand, 2002). As phenotypic variance increases, average range size and intraspecific variation increase and ecometric load and between-species differentiation decrease (grading through Pattern 3 to 2).

Start location had perhaps the most interesting effect because it affected the frequency of global extinction, species richness, and the time to reach ecometric equilibrium more than any other parameter, but it had little effect on final ecometric load, average number of ecometric zones occupied by a species, or between-species differentiation (Fig. 4I–L, 5; Appendix; Supporting Information, Table S1, Data S2, Fig. S3). In this experiment the only thing that varied was the start location, which was chosen at random (the other four experiments all started in the northern part of the Forest 1 ecometric zone); all other parameters were equal. As discussed in more detail below, the effect of start location is influenced by the ancestral value of the trait and the geography of the ecometric zones and their ecotones, as well as from the interaction between that geography and the peripheral isolate mode of speciation.

SPECIATION, CLADE DYNAMICS, AND ECOMETRIC PATTERNING

Peripheral isolate speciation strongly influenced clade dynamics by creating punctuated jumps in phenotypes and by influencing the distribution of extinction events on the tree, but it only weakly affected ecometric patterning. In our models, speciation occurred by peripheral isolation in which the population that was most geographically distant from the species' centre became the founder of a new species.
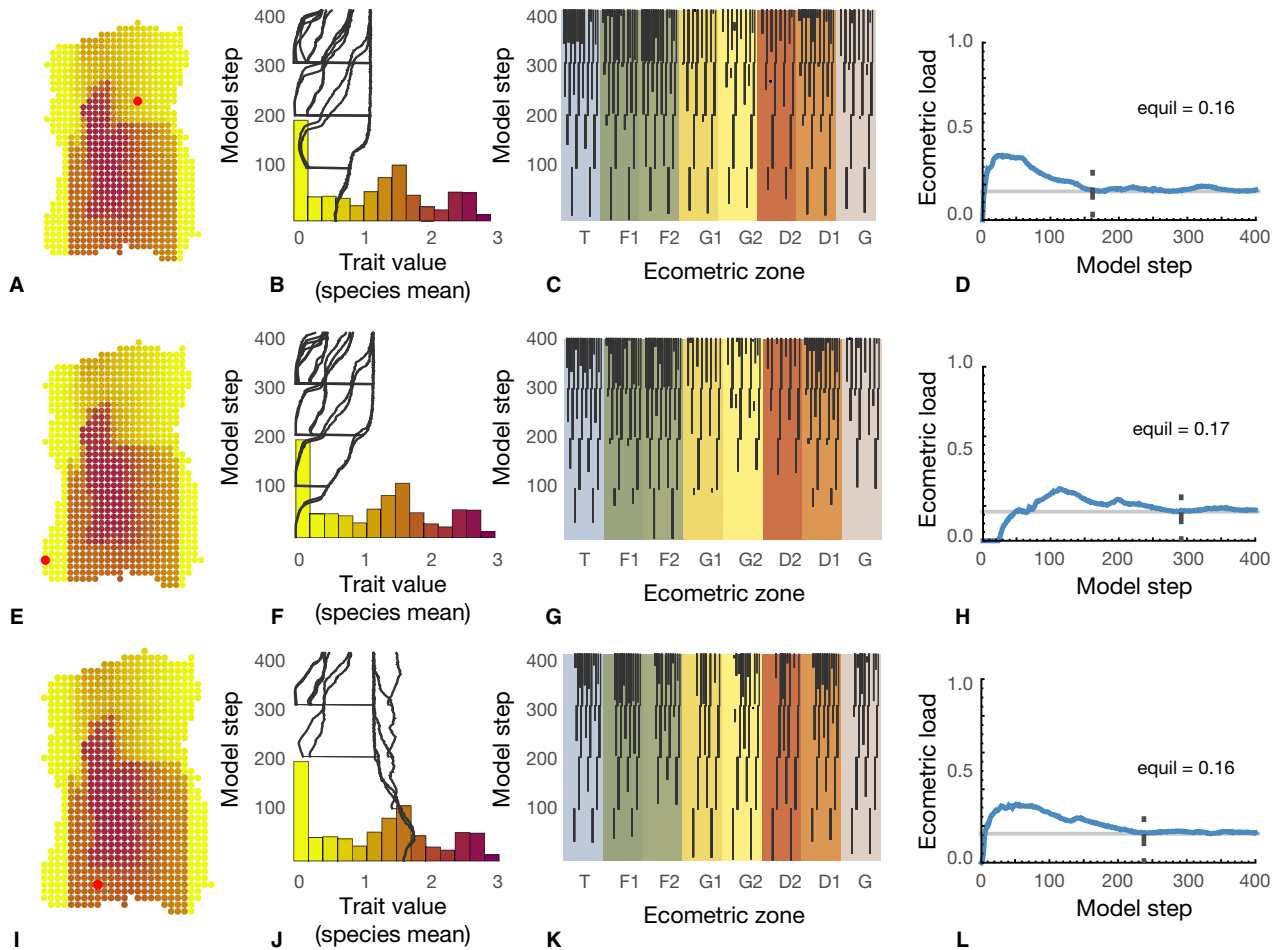
Figure 5. Comparison of start location models. (A–D) Start location in Forest 1 ecometric zone (2013-10-25-17-54-16-Hesperia). (E–H) Forest 2 (2013-10-25-16-35-58-Hesperia). (I-L) Desert 2 (2013-10-25-20-52-17-Hesperia). See also Fig. 4I–L for start location in the Grit zone. Panels as in Fig. 4.

We used a Hennigian concept for species nomenclature (*sensu* de Queiroz, 2007) in which both the peripheral isolate and the remainder of the parent populations were classified as new reproductively isolated offspring species, the latter of which was usually widespread and nearly identical to the parent. Because the new isolate species consists of a single population with what will frequently be an outlying phenotype, the early history of the new species is more affected by drift, more prone to extinction, and frequently phenotypically different from the majority of populations in the parent species. This mode of speciation therefore affects macroevolutionary patterns because it generates a highly unbalanced split in which the peripheral isolate species may, depending on circumstances, undergo rapid expansion and differentiation until it reaches an equilibrium (balance between gene flow, environmental selection, and environmental, ecological and physical barriers

to expansion) and the widespread offspring species may remain roughly unchanged if the parent had already achieved evolutionary stability (Mayr, 1963; Bush, 1975).

The initial rate of evolutionary change (change in the mean trait of the species per step) in the isolate species is likely to be much higher than in the widespread species. Indeed, this effect was invoked by Eldredge & Gould (1972) as the mechanism punctuated change at speciation events in their punctuated equilibrium model of evolution. Their hypothesis prompted much investigation of the frequency of peripheral isolate speciation and its effects on evolutionary change, geographic ranges, and other aspects of ecology and evolution (e.g., Glazier, 1987; Lynch, 1989; Frey, 1993; Gaston, 1998). Peripheral isolation produced noticeable punctuation in our models (Figs 4, 5). Across all models, cladogenetic rates of evolution (the change in mean trait value between

the last generation of the parent species and the first generation of the offspring species) were about three orders of magnitude greater than rates of anagenetic evolution (Supplemental Information S3).

The magnitude of punctuated change and the subsequent evolution in the trait mean differed markedly between models. For example, the average cladogenetic change was only −0.326 hypsodonty units (meaning that, on average, the trait value decreased by −0.326 units at speciation) and lineages subsequently increased in parallel when adaptive peaks were wide (Fig. 4B), but cladogenetic change was three times greater at −0.975 and lineages subsequently converged on the ancestral trait value when phenotypic variance was high (Fig. 4F). This difference in behaviour was tied to the overall ecometric pattern. In the wide adaptive peak model, ecometric load was high because there was very little geographic variation within species and all populations had phenotypes near the continental mean optimum hypsodonty value (1.08) (model 2013-10-25-18-39-15-Hesperia in Appendix; Supporting Information, Data S2). Peripheral populations in this model were not very different from the species mean, so there was less punctuation. Each new species slowly spread across the continent as local selection and gene flow interacted to slowly pull its trait mean toward the mean continental optimum, hence the parallelism. Ecometric load therefore remained high and equilibrium was achieved slowly (Fig. 4D). Conversely, in the high phenotypic variance model, geographic variation within species was high because the traits of local populations were always near the local selective optimum (model 2013-10-25-18-21-39-Hesperia in Appendix; Supporting Information, Data S2).

Crown height in peripheral isolate populations was always much lower than the continental mean because the periphery of Hesperia is covered in moist forests and therefore favours populations with brachyodont teeth (Fig. 2B and C). After their punctuated origin, species quickly spread across the entire continent with each local population being efficiently selected to the local optimum, which caused the mean value of the trait across the entire species to converge quickly on the mean continental optimum. Ecometric load was low and equilibrium was achieved quickly (Fig. 4H). Microevolutionary parameters and mode of speciation thus simultaneously affect geographic range size, geographic variation in traits, and species-level rates and patterns of trait evolution (García-Ramos & Kirkpatrick, 1997; Kirkpatrick & Barton, 1997; McPeek, 2007), which in turn affect ecometric load. The net result of this configuration was that crown height usually started low and became higher in most lineages. Probably by

coincidence, crown height has more frequently changed from brachyodont to hypsodont in the evolution of mammals (Damuth & Janis, 2011; Mushegyan et al., 2015). In our model this pattern arose specifically because of the configuration of environments on the continent. The periphery of Hesperia, which was usually the location of speciation events, favours low crowns and the interior, into which species then expanded, favours high crowns; however, in the real world this pattern may occur because selection for low crowns is likely to be driven by the metabolic cost of mineralization, which may not be high, whereas selection for high crowns is likely to be driven by the detrimental effects of dentitions wearing away.

The geographic layout of ecometric zones interacts with peripheral isolate speciation to produce patterns of trait evolution. In Hesperia, the most peripheral population of a pangeographic species will always be found in a forest biome and will have a brachyodont phenotype with a smaller hypsodonty index than its parent species (which systematically produces negative changes in trait value at speciation) because of the coincidence of Hesperian geography (Fig. 2B and C). A continent with moist, forested central highlands and coastal deserts would conversely produce punctuated trait changes in the positive direction at speciation, whereas a continent in which the selective optimum at the periphery was near the continental mean selective optimum would produce little or no punctuation.

The effect of peripheral isolate speciation is different for species that are confined to a small number of ecometric zones. Consider, for example, a species confined to the Grit Zone, which has grassland, desert, tundra, and forest on its periphery that would produce a greater variety of peripheral isolate traits than a pangeographic species (Fig. 2C). This geographic effect is overdetermined in our model because speciation is forced at specified intervals and the founder population is always the one most peripheral to the species' geographic centre. Nevertheless, the geography of environments, the frequency and distribution of ecometric zones, and the complexity of their ecotones should have similar macroevolutionary effects even when peripheral isolate speciation is more stochastically achieved through real-world processes (McPeek, 2007).

We imposed regular speciation events on our models, regardless of whether such events would be likely given the configuration of populations at the time of speciation. In reality, model runs that produced geographically widespread, phenotypically homogeneous species with high rates of gene flow would not likely result in peripheral isolate populations, which would inhibit speciation and would

result in lower diversity. Using a different modelling strategy, Fortelius *et al.* (2015) recently showed that speciation is more likely to occur under some environmental configurations than others, especially when change in the environmental gradient is considered, and the process is closely linked to the amount of within-species trait polymorphism.

PHYLOGENETIC TRAIT CORRELATION AND CLADE SORTING

An important consequence of peripheral isolate speciation was that it lowered phylogenetic trait covariance and decreased the likelihood that species sharing an ecometric zone would be closely related. Pagel's λ for traits at the tips of the phylogenies (the means trait values for each species across all of its local populations) was almost always near zero, indicating that the distribution of traits differed substantially from what is expected from their shared evolutionary history (λ = 1 when trait evolution is consistent with Brownian motion) (Appendix). Furthermore, phylogenetic correlation and clade sorting (Patterns 3b and 4b) were never important contributors to ecometric patterns. Peripheral isolate speciation interferes with phylogenetic patterning because the more widespread offspring species tend to retain ancestral trait values because their populations are numerous, closer to equilibrium with respect to selection, dispersal, and gene flow. Species that arise from peripheral isolates tend to jump in parallel to new phenotypes (e.g., Fig. 4). Furthermore, peripheral isolate species are comparatively likely to become extinct early in their history if their founding populations are extirpated. Every dichotomy in our model's phylogeny produced both kinds of offspring, the right hand (even numbered) branches being the large offspring and the left hand (odd numbered) branches being the peripheral isolates (Fig. 3A). Even and odd numbered lineages thus respectively tend to share properties that differ between the two groups, creating homoplasy in trait values, geographic distributions, range sizes, and patterns of ecometric zone occupation. Lineages 2, 6, 14, and 30 thus tended to stabilize progressively through each simulation, whereas lineages 1, 3, 7, and 15 tended to iteratively accumulate stochastic events in their chain of peripheral isolate ancestry. This systematically dimorphic behaviour in nested sets of lineage pairs resulted in macroevolutionary patterns of trait evolution in our models that depart from simple Brownian motion or OU. Thus, information derived only from lineages present at the end of our simulations (i.e. the 'extant taxa') does not yield information about these past evolutionary dynamics, especially dynamics that occurred deeper in the phylogeny.

Other modes of speciation, such as peripatric (vicariant events that split the parent species into two geographically subequal halves) would result in quite different dynamics in which the entire clade behaved like the right hand branches in our models. Brownian motion patterns with less pronounced punctuated speciation events would be much more likely if speciation divided the parent species into two subequal offspring, each with similar effective population sizes. Because speciation by founder population can have such a profound effect on trait evolution, founder events can, in principle, be identified using macroevolutionary model fitting (Bokma, 2002, 2008; Pagel, Venditti & Meade, 2006; Hunt, 2014), although the effects of extinctions complicate the inferences that can be made from extant taxa alone (Rabosky & Lovette, 2009; Rabosky, 2010; but see Silvestro, Schnitzler & Zizka, 2011; Beaulieu & O'Meara, 2015).

Because phylogenetic trait correlations and species sorting both appear to occur frequently in the real world in association with ecometric patterns (Ackerly & Cornwell, 2007; Jablonski, 2008; Little *et al.*, 2010; Polly, 2010; Lawing *et al.*, 2012), we conducted a second series of modelling experiments with combinations of parameters that are most likely to produce strong phylogenetic signature. Phylogenetic trait correlations and clade sorting are most likely to arise when a single lineage crosses into a new ecometric zone, adapts to the new trait mean, and then speciates within that zone. Intense selection and high probability of extirpation tend to prevent species from expanding across zone boundaries, whereas high dispersal probability increases the number of attempts at crossing. Low phenotypic variance also lowers the chance of populations establishing themselves in new ecometric zones. Thus, we set extirpation probability high and varied the other parameters (Appendix, Supporting Information). In one experiment, dispersal and extirpation probabilities were constantly high and adaptive peak width was constantly narrow (HDispHExtNAPWPV); in another, dispersal probability was systematically varied from low to high and adaptive peak width was intermediate (VarDispHExtMedAPW); and in the third, dispersal and extirpation probabilities were constantly high and adaptive peak width was systematically varied (HDispHExtVarAPW). Start location was chosen randomly in all three experiments.

Only three out of 31 of the models in these new experiments resulted in strong phylogenetic trait correlations (Appendix). One was in the variable dispersal experiment and occurred when dispersal probability was high and start location was in the Desert 2 ecometric zone (2014-06-10-14-46-36-Hesperia) and two were in the variable adaptive

peak experiment and occurred when it was relatively wide, which would increase the chance that a boundary-crossing population was fit, starting in Forest 1 and Grit zones respectively (2014-06-10-05-05-59-Hesperia, 2014-06-10-10-47-02-Hesperia). These examples unfolded as expected, as illustrated in Fig. 4M-P based on the third case. The clade started in the Grit Zone with a high-crowned phenotype. The initial two lineages spread in the first 100 steps into three other high-crown zones (Desert 2 and Grassland 1&2), but the clade failed to cross into the lower-crown zones until a single peripheral isolate lineage (L-09) did so just after the speciation event at step 200 and became pangeographic. It speciated in Forest 1 to give rise to one large pangeographic species (L-20) and a peripheral isolate species (L-19) that remained confined to the low-crown zones (Tundra and Forest 1&2) (Fig. 4M-P, Supporting Information, Data S2). These three cases showed that clade sorting and phylogenetic trait correlation can arise from our models, but it is nevertheless unlikely given that it occurred in fewer than 10% of the models where parameters were chosen to maximize its chances. Furthermore, it should be noted that estimates of phylogenetic signal from small trees need to be interpreted with caution due to increased Type I error rates (Blomberg, Garland & Ives, 2003).

STATIC VS. CHANGING ENVIRONMENTS ARE LIKELY TO AFFECT CLADE DYNAMICS DIFFERENTLY

The static environment of our models is likely to be an important factor in why phylogenetic sorting was rare and trait diversity within communities was low. Even though the environment of Hesperia is heterogeneous, it did not change during the course of the models. The geographic spread of taxa across a heterogeneous environment is partially analogous to what happens to taxa during environmental change because the colonization of new ecometric zones is similar in many respects to adaptation to a changed environment. Nevertheless, the connections between dispersal, adaptive evolution, and environmental selection are different in a changing environment (Table 2). In a stable environment, a species requires neither dispersal nor evolution to maintain its status quo in an ecometric zone to which it is already adapted; however, in a changing environment a species is more likely to track the geographic translocation of its preferred environment if dispersal and extirpation probabilities are both high enough to allow it to move into areas that acquire the preferred environment and to keep it from persisting in ancestral areas where the environment is changed. Conversely, evolutionary adaptation to a changing

Table 2. Dispersal and evolution as responses to environmental differences in stable and changing worlds

	Stable environments		Changing environments	
Geographic tracking of one environment	Dispersal	No	Dispersal	Yes
	Evolution	No	Evolution	No
Evolutionary adaptation to a new environment	Dispersal	Yes	Dispersal	No
	Evolution	Yes	Evolution	Yes

environment is more likely if dispersal and extirpation probabilities are both low, thus increasing the chance that the species remains in the ancestral area long enough for its traits to adapt. Changing environments are thus likely to alter speciation outcomes by shifting where isolation is likely to occur, to change the steepness of environmental gradients, and to modify the likelihoods of extinction and species expansion when zone boundaries are difficult to cross.

Consider the models in which extirpation was high and the entire clade remained confined to just one ecometric zone (Fig. 4Q–T) vs. the one in which both dispersal and extirpation were high and one clade colonized a set of derived ecometric zones (Fig. 4M–P). The latter example suggests that with some reasonable probability the clade in the former example could have lineages that colonize the other ecometric zones. If the ancestral ecometric zones disappeared to be replaced by expansion of the other ecometric zones, the entire ancestral paraclade would most likely become extinct and subsequent speciation would occur entirely in the offshoot clade in the derived ecometric zones. Clade turnover, strong phylogenetic trait correlation, and strong phylogenetic structuring in ecometric zones would be the result.

Phylogenetic turnover was common in mammals in response to the rapid expansion of open habitat grasslands in the Late Miocene followed by global temperature downturn and closing of many habitats in the Quaternary (DeSantis *et al.*, 2012; Liow & Finarelli, 2014; Fraser, Gorelick & Rybczynski, 2015). Borophagine canids, for example, were diverse in North American during the Miocene, but became extinct and were replaced by the global radiation of the Caninae, which is the only extant clade of canids, after the end of the Miocene (Tedford *et al.*, 2009). While such phylogenetic structuring was rare in our static models, the behaviour of traits and species in connection with the dispersal, selection intensity, and extirpation parameters of our models is consistent with phylogenetic turnover in changing

environments. Modelling in changing environments is needed to confirm this hypothesis.

ECOMETRIC EQUILIBRIUM MATTERS FOR RESPONSE TO ENVIRONMENTAL CHANGE

The time required to reach ecometric equilibrium has profound implications for the response of communities to climatic change. Ecometric equilibrium is the stable pattern of community trait values that emerges in our models, each with a characteristic ecometric load. Typically ecometric load increases early in the model and then gradually drops to its equilibrium value (Fig. 4, 5). Both the equilibrium load and the time required to reach it vary depending on model parameters, on the stochastic effects of start location, and on the environmental configuration of the continent. Higher ecometric loads arise when more populations of more species have trait values that perform suboptimally in their local environment. All things being equal, high ecometric loads correspond to many populations being near their extirpation thresholds.

Changing environments will likely result in higher ecometric loads and thus increase the chance of extirpation of populations and extinction of species. If equilibrium is reached slower than the environment is changing, then the chances of extirpation should be greater than when equilibrium is reached quickly. A similar argument was made by Lynch & Lande (1993) for the response of single populations to climatic change. Combinations of parameters that result in low ecometric loads being reached quickly are thus more likely to produce faunas that are robust to extinction from climate change. High phenotypic variance did this in our models (Fig. 4E–H), consistent with the hypothesis that high phenotypic variance within local populations makes them more robust to extinction from climate change (Lynch & Lande, 1993). Interestingly, high probability of extirpation and dispersal are also parameters that could make communities more robust to climate change (Fig. 4M–T). The winnowing effects of extirpation along ecometric clines may therefore be associated with adaptability to changing climates, a possibility that is also consistent with observations that phylogenetic turnover often accompanies climate change. Historical contingency is also likely to be a factor in robustness to climate change based on the results of the start location experiment: models whose ancestor started in forest ecometric zones (Fig. 5A–D) reached equilibrium almost twice as quickly as one that started in the Grit Zone (Fig. 4I–L), even though all other parameters were the same. Historical effects on ecosystem dynamics (Ricklefs, 1987, 2006) seem likely to be important in changing climates based on our modelling.

Based on a different modelling strategy, a similar conclusion was reached by Fortelius *et al.* (2015), wo found that the rate of environmental change relative to the rate at which populations are able to reach an evolutionarily stable state has a substantial effect on extinction, speciation, and trait polymorphism. They showed that the opening of new niches (equivalent to our ecometric zones) and the loss of existing ones affect patterns of extinction and speciation. They also showed that the amount of trait variation in the species affects the probability that populations will be able to speciate into newly opened niches.

CONCLUSIONS

Ecometric patterns in the functional traits of communities are a useful tool for studying biotic response to climate change because they are taxon-free and can therefore be used to compare responses to past changes that are documented in the fossil record with cursrent anthropogenic change (Eronen *et al.*, 2010a; Polly *et al.*, 2011). Most of the work that has been done on trait-environment community assembly on continental and palaeontological scales has been empirical (e.g., Wolfe, 1993; Fortelius *et al.*, 2002, 2014; Eronen *et al.*, 2010b,c; Polly, 2010; Lawing *et al.*, 2012), with only a few attempts to systematically examine how ecology, evolution, and phylogeny interact to produce ecometric turnover in response to climate change (e.g., Lister, 2004; Barnosky, 2005; Blois & Hadly, 2009; DeSantis *et al.*, 2012). We used stochastic modelling to explore the links between the evolutionary theory of quantitative traits, ecological processes, and clade dynamics in the formation of ecometric patterns in static environments.

We found that the combination of evolutionary parameters in our models had significant effects on ecometric patterning, ecometric load, phylogenetic trait covariances, and the time required to reach ecometric equilibrium. Phylogenetic trait covariances and geographic clade sorting rarely arose in our static-environment models, only occurring when the probabilities of dispersal and extirpation were both high and selection intensity was strong. But the outcomes of our models suggest that phylogenetic structuring of both traits and communities is more likely to occur when environments are changing. The modern and fossil records suggest that clade sorting between contemporaneous environments and turnover between changing environments have been common effects of trait-environment dynamics.

We also found that history matters. The ancestral starting point of our models, both in terms of the ancestral trait value and the ecometric zone in which it originated, had substantial effects on clade dynamics and

the time to reach ecometric equilibrium, but not on the equilibrium point itself. Furthermore, the differences between our models, including the differences between the environmentally heterogeneous continent Hesperia and the homogeneous Vostochnia, demonstrate that the historical contingencies of the geography of environments has an overarching effect on the dynamics of trait evolution such that different evolutionary rates, modes of evolution, and frequency of trait values among tip taxa are expected even if the phylogenetic topology, mode of speciation, and population-level evolutionary parameters are the same. Differences due to start location and the interaction between speciation and environmental geography that arose in our models are examples of how clade history and physiography impact ecological systems in historically contingent ways (Ricklefs, 1987, 2006; Linder *et al.*, 2014; Jønsson *et al.*, 2015). Nevertheless, the convergence of ecometric patterns on an equilibrium determined by microevolutionary parameters in all models indicates that some deterministic outcomes are likely regardless of the historical pathways by which they arise.

Finally, the variety of equilibrium points reached by ecometric systems under different combinations of parameters, and with different historical contingencies, suggests that robustness of ecosystems may be closely related to its overall ecometric load. Systems in which the equilibrium load is greater or takes longer to achieve may be more vulnerable, ceteris paribus, to changing Earth systems, including anthropogenic climate change. This hypothesis is based on simple modelling of the dynamics that arise between the interactions between a single functional trait and a static environment, on which the effects of multiple traits, pleiotropy, and species interactions have not yet been explicitly explored leaving open crucial avenues for continued investigation of the importance of functional trait ecology, clade dynamics, and ecometrics to biotic change.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article:

Figures S1. S1.1 Geography of Humboldtland. S1.2 Phylogenetic community metrics.
Figure S2. Ecometric equilibrium graphs.
Figure S3. Phylogenetic occupation of ecometric zones.
Table S1. Model output summary statistics.
Table S2. Database of Humboldtland's geography and environment
Table S3. Animated ecometric maps for models in Fig. 4.
Table S4. Animated ecometric maps for models in Fig. 5.
Data S1. Detailed explanation of the ecometric model and parameters.
Data S2. Model output summary graphics.
Data S3. *Mathematica* code for the ecometric model.

APPENDIX
SUMMARY OF KEY MODEL RESULTS

Model run	Parameter setting	Ecometric load	Mean range size (proportion)	Mean number of ecometric zones	Mean species richness (16 max)	Interspecific trait variation (SD)	Mean intraspecific trait variation (SD)	Mean within community trait variation (SD)	Pagel's lambda	Interpretation
Adaptive peak experiment										
2013-10-25-16-40-13-Hesperia	0.5	0.05	0.48	4.9	6.7	0.24	0.24	0.03	0.0	3a
2013-10-25-17-07-22-Hesperia	1.0	0.16	0.69	6.7	11.1	0.31	0.31	0.13	0.0	3a
2013-10-25-17-46-09-Hesperia	1.5	0.42	0.89	8.0	14.3	0.22	0.22	0.17	0.0	1
2013-10-25-18-39-15-Hesperia	2.0	0.57	0.93	8.0	14.8	0.18	0.19	0.17	0.0	1
Dispersal experiment										
2013-10-25-16-38-36-Hesperia	0.5	0.16	0.68	6.5	10.2	0.32	0.32	0.12	0.0	3a
2013-10-25-17-16-28-Hesperia	1.0	0.20	0.86	7.5	13.8	0.25	0.25	0.13	0.0	3a
2013-10-25-18-39-31-Hesperia	1.0	0.20	0.88	7.7	14.0	0.23	0.23	0.13	0.0	3a
2013-10-25-20-04-24-Hesperia	1.0	0.21	0.87	7.6	14.0	0.23	0.23	0.13	0.0	3a
Extirpation experiment										
2013-10-25-16-37-30-Hesperia	0.0	0.36	1.00	8.0	16.0	0.04	0.04	0.05	0.0	1
2013-10-25-17-44-23-Hesperia	0.5	0.31	0.99	8.0	15.8	0.04	0.04	0.07	0.0	1
2013-10-25-18-47-27-Hesperia	1.0	0.16	0.68	6.4	9.6	0.32	0.32	0.13	0.0	3a
2013-10-25-19-24-20-Hesperia	1.5	0.10	0.27	1.0	4.3	0.04	0.04	0.04	0.0	4
2013-10-25-19-39-54-Hesperia	2.0	0.09	0.25	1.0	3.9	0.07	0.07	0.05	0.0	4
Phenotypic variance experiment										
2013-10-25-16-35-58B-Hesperia	0.01	0.41	0.32	2.2	4.1	0.07	0.08	0.08	0.0	4
2013-10-25-16-53-42-Hesperia	0.05	0.16	0.69	6.7	11.1	0.30	0.30	0.13	0.0	3a
2013-10-25-17-32-53-Hesperia	0.09	0.12	0.85	7.8	13.6	0.23	0.23	0.10	0.0	3a
2013-10-25-18-21-39-Hesperia	0.13	0.10	0.99	8.0	13.9	0.02	0.02	0.05	0.0	2
Start location experiment										
2013-10-25-16-35-58-Hesperia	Forest 2	0.17	0.67	6.4	10.7	0.30	0.30	0.14	0.0	3a
2013-10-25-17-11-37-Hesperia	Grassland 1	0.16	0.72	7.5	9.4	0.33	0.33	0.10	0.0	3a
2013-10-25-17-54-16-Hesperia	Forest 1	0.16	0.69	6.8	10.3	0.29	0.29	0.12	0.0	3a
2013-10-25-18-33-57-Hesperia	Grit	0.18	0.81	6.2	8.1	0.36	0.36	0.09	0.0	3a
2013-10-25-19-06-50-Hesperia	Forest 2	0.16	0.68	6.6	10.2	0.31	0.31	0.13	0.0	3a
2013-10-25-19-42-40-Hesperia	Forest 2	0.16	0.64	7.2	10.3	0.32	0.32	0.12	0.0	3a
2013-10-25-20-20-59-Hesperia	Desert 1	0.16	0.65	6.0	7.8	0.30	0.30	0.13	0.0	3a
2013-10-25-20-52-17-Hesperia	Desert 2	0.16	0.73	6.9	8.7	0.36	0.36	0.12	0.0	3a
2013-10-25-21-28-02-Hesperia	Forest 1	0.16	0.66	6.5	10.5	0.30	0.30	0.14	0.0	3a
2013-10-25-22-02-06-Hesperia	Grit	0.17	0.83	6.4	12.4	0.30	0.30	0.13	0.0	3a