

1 **A resource-based conceptual model of plant diversity that reassesses causality in the**
2 **productivity–diversity relationship**

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7
8 **ABSTRACT**

9 **Aim**

10 To contribute towards an understanding of the potential mechanisms by which
11 environmental variation translates into species richness patterns, by outlining a
12 conceptual model of plant diversity that combines the putative influences of climate
13 and consumable-resource heterogeneity.

14 **Location**

15 We draw on studies from various parts of the world, encompassing both terrestrial
16 and non-terrestrial ecosystems, but with primary focus on the terrestrial.

17 **Methods**

18 The explanatory variables are gradient combinations (the number of ways in which
19 gradients of consumable resources can be combined) and gradient distance (a
20 measure of the extent and grain size of resource variation within the above-ground
21 and below-ground habitat volumes created by plants). We explore some theoretical
22 consequences of using these variables to explain variation in plant diversity.

23 **Results**

24 If our conceptual model is valid it has wide-ranging implications within the field of
25 biodiversity studies. We focus on two in particular. First, in our model the role of
26 productivity can be strictly prescribed, a feature that allows exceptions to coarse-
27 scale positive monotonic productivity–diversity correlations to be interpreted without
28 abandoning climate-based capacity models of species richness patterns. Our model
29 predicts that environments with identical resource inputs and productivities can
30 differ substantially in plant diversity at a range of spatial scales. Secondly, the
31 influence of environmental ‘harshness’ on diversity (Terborgh, 1973) is reassessed
32 within the model’s framework: most harsh environments are characterised by few

33 gradient combinations and short gradient distances, which could explain why many
34 harsh environments have relatively low species richness.

35 **Main conclusions**

36 The extent to which, and the means by which, productivity might be causally related
37 to diversity are under debate, as is the nature of the productivity–diversity
38 relationship at a range of scales. Our model may help to explain exceptions to
39 productivity–diversity relationships at all spatial scales, and may provide a potential
40 mechanism by which variation in resource inputs translates into diversity patterns.
41 Finally, the model emphasizes the importance of both photosynthetically active
42 radiation, a direct measure of the key energy resource consumed by plants, and
43 habitat volume (rather than habitat area). We think that both of these have been
44 given too little attention in the recent literature on patterns of plant species richness.

45

46 **KEY WORDS:** Diversity, species richness, latitudinal gradients, productivity–
47 diversity relationship, resource gradients, gradient combinations, gradient distance,
48 photosynthetically active radiation, water, plant functional types.

49

50 **RUNNING HEAD:** Resource gradients and plant diversity

51

52 **INTRODUCTION**

53 Progress in understanding latitudinal and other patterns of diversity has been fitful
54 over the last two centuries. Early workers believed that diversity gradients are driven
55 by climatic gradients, a view that is still widely held (O’Brien, 1993, 1998; Francis
56 & Currie, 2003; Whittaker *et al.*, 2003; Hawkins, 2004; and many others). While
57 there seems to be some convergence in the literature on the importance of climate,
58 and specifically water and energy, in determining macro-scale patterns of species
59 diversity, the causal mechanisms are arguably as obscure today as they have ever
60 been (Rosenzweig & Abramsky, 1993; Abrams, 1995; Srivastava & Lawton, 1998;
61 Groner & Novoplansky, 2003; Hawkins, 2004; Hillebrand, 2004). At finer spatial
62 grains and extents the best correlates of species richness tend to be more varied and
63 less predictable (Field *et al.*, in prep), and again the mechanisms are hotly debated.

64 In relation to climate, researchers often argue that the most likely intermediary
65 between climate and diversity is productivity (Connell & Orias, 1964; Whittaker *et*
66 *al.*, 2003) or something closely allied to it (Rosenzweig, 2003), and relate diversity
67 to productivity via linking mechanisms that collectively encompass most areas of
68 ecology and operate at a range of spatial and temporal scales (Aarssen, 2001; Francis
69 & Currie, 2003; Whittaker *et al.*, 2001; Whittaker *et al.*, 2003). This expansive
70 approach may in the end be necessary as it seems unlikely that any single
71 explanation can account for the classical patterns of diversity variation and the
72 numerous exceptions to them (Brown & Lomolino, 1998; Ricklefs, 2004), but when
73 hypotheses proliferate in such a way models that synthesise and contextualise
74 different explanatory schemes may be particularly instructive.

75 This paper outlines a conceptual model of plant diversity that combines the
76 influences of climatic variation and resource heterogeneity. According to the model,
77 the physical environment sets the capacity for diversity at all scales via its control of
78 the potential for resource heterogeneity. Within such limits, realized resource
79 heterogeneity and habitat volume provide the domains for diversification over space
80 and time, both of which are affected by a number of factors in scale-dependent
81 ways. The model does not require (but does not discount) a direct causal link
82 between productivity and diversity, a feature that allows well known exceptions to
83 the productivity–diversity correlation to be accounted for. The model predicts that
84 environments with identical inputs of water and energy and identical productivities
85 can nevertheless differ profoundly in plant diversity at a range of scales.

86

87 **RATIONALE**

88 Primary productivity and species diversity are often strongly correlated at a range of
89 scales, at least for low to moderate values of productivity (Waide *et al.*, 1999;
90 Mittelbach *et al.*, 2001; Whittaker and Heegaard, 2003; Whittaker *et al.*, 2001,
91 2003), which has led researchers to propose causal links between the two (Srivastava
92 and Lawton, 1998). However, none of the proposed mechanisms is universally
93 accepted (Srivastava and Lawton, 1998; Francis and Currie, 2003). We do not deny
94 that productivity may directly influence diversity, but the controversy prompted the

95 following line of thought. Assume that variations in water and energy influence
96 patterns of plant diversity (Smith and Huston, 1989; O'Brien, 1998; Ackerly, 2003;
97 Whittaker *et al.*, 2003). Assume further either that productivity and diversity are not
98 causally related, or that the role of productivity in influencing diversity is restricted
99 to its effect on vegetation structural complexity. Is it possible to account for spatial
100 patterns of diversity under such restrictions? What mechanisms could account for a
101 non-causal or weakly causal correlation between productivity and diversity and for
102 the numerous well known exceptions to this relationship (Terborgh, 1973; Huston,
103 1979; Brown and Lomolino, 1998; Field *et al.*, 1998; Whittaker *et al.*, 2001)? One
104 obvious possibility is that productivity and diversity are controlled by, but
105 sometimes respond differently to, some of the same underlying physical factors.
106 Usually both productivity and diversity correlate positively with these particular
107 factors, but in some circumstances, and especially at smaller spatial scales, physical
108 variables combine in such a way that values of productivity and diversity diverge. In
109 what follows we attempt to develop a conceptual model based on variations in
110 resources consumed by plants that accounts simultaneously for the productivity–
111 diversity correlation and for the general class of outliers comprising environments
112 exhibiting relatively high plant productivity and relatively low plant diversity. We
113 focus on water and light, but the framework could be applied and extended to other
114 resources.

115

116 GRADIENT COMBINATIONS AND CLIMATE

117 Figure 1 graphs the envelope of possible water–light states for a light gradient and a
118 water gradient, both arbitrarily divided into ten units. (In this paper ‘light’ refers to
119 photosynthetically active radiation, because this is the resource consumed by plants,
120 Huston, 1994. The role of temperature is not part of our model, except inasmuch as
121 it controls water availability, O'Brien *et al.*, 1998, because heat is not a consumed
122 resource, Austin and Smith, 1989; Huston, 2003; c.f. Allen *et al.*, 2002; Hawkins *et*
123 *al.*, 2003; see Discussion. The model is distinct from that of Jackson and Overpeck,
124 2000, which considers only non-resource factors; see also Ackerly, 2003.) The
125 number of potential gradient combinations increases linearly with linear increases in

126 one variable with the other held constant (light and water are interchangeable in
127 Fig.1), the slope of the relationship being dependent on the value of the constant
128 variable. The case of light and water increasing in parallel ($L = W$) is also shown.

129 Physical and biological processes modify initial inputs of light and water, and
130 the amount of each resource available in an environment can only vary between its
131 input level and zero. Thus, where inputs are low the number of potential water–light
132 combinations will be low also; where inputs are high the range of potential
133 combinations will be greater, all other things equal (Fig.1). This proposition is
134 trivially true.

135 The idealized environments depicted in Figure 2 receive varying inputs of
136 water and light. Gradient lengths are represented by the lines arbitrarily divided into
137 three units. Arrows show the range of likely realised (as opposed to potential)
138 gradient combinations.

139 In tropical rainforests the range of potential gradient combinations is great at
140 all scales because water and light gradients are long. Structurally complex forests
141 growing on topographically varied terrain (Clark *et al.*, 1999; Webb *et al.*, 1999;
142 Kubota *et al.*, 2004) may realise many combinations of drainage, shelter, aspect and
143 shading (Huston, 1994), and thus a wide range of water–light combinations. If the
144 range of realised combinations reflects potential combinations, tropical rainforest
145 regions should have the capacity to support a wide range of plant functional types
146 and a large number of species (Smith and Huston, 1989).

147 In treeless tropical swamps (Fig.2) the number of potential gradient
148 combinations is high because water and light are abundantly supplied, but the range
149 of realised combinations is relatively small because drier conditions are restricted or
150 absent (Fig.2b) (swamps with trees are easily accommodated within the model; we
151 use the structurally simplest example for clarity). Additionally, the vertical distance
152 over which light gradients operate (gradient distance) is short because vegetation is
153 low growing. The full light gradient is present in a tropical swamp in the sense that
154 incident light energy attenuates to unusable levels by some physical or biological
155 route, but low-growing vegetation offers only a fraction of the habitat volume
156 provided by a rainforest, and thus only a fraction of the volume at any given range

157 of light states created by the canopy (see Björkman *et al.*, 1972 and Björkman, 1981;
158 Huston, 1994; Wright, 2002). Species–volume–heterogeneity effects are analogous to
159 species–area–heterogeneity effects (Rosenzweig, 1995), so the relationship between
160 diversity and habitat volume should typically be positive.

161 The range of potential gradient combinations in high latitude environments is
162 relatively small because, compared with tropical regions, water and light gradients
163 are typically short (Fig.2). Even where precipitation is locally or regionally great,
164 low temperatures often restrict the availability of liquid water (O’Brien *et al.*, 1998),
165 and light energy is relatively weak and thus likely to be relatively uniform (because
166 light intensity can only vary between its input level and zero, Fig.1). In the example
167 shown in Figure 2 light gradient distances are short because vegetation is too. Lack
168 of usable water may also limit the extent to which plants can tolerate low light
169 levels, restricting the range of plant functional types at high latitudes (Smith and
170 Huston, 1989). Restriction of gradient combinations and plant functional types
171 implies that, at large spatial scales, diversity averaged over high latitude
172 environments is likely to be low, and locally is never likely to be more than
173 moderate. Similar reasoning accounts for the low diversity of plants at a range of
174 scales in hot deserts, where energy input is high, water input low, habitat volume
175 small and gradient distances short (Fig.2).

176 Tropical forests and swamps may be equally productive, yet plant diversity in
177 swamps is rarely, if ever, as high as in adjacent forests (Richards, 1969). The
178 commonly held belief that diversity increases causally with productivity (up to a
179 point) is problematic in this case, and is usually maintained by invoking arguments
180 about scale (for example, that the diversity of tropical swamps and forests combined
181 will tend to be greater than that of environments at higher latitudes sampled within
182 equivalently large spatial units; see Whittaker *et al.*, 2001, and Whittaker and
183 Heegaard, 2003, for a wide-ranging discussion). Figures 1 and 2, by contrast, predict
184 that tropical swamps and forests with identical inputs of water and light and identical
185 productivities may vary substantially in diversity over a wide range of spatial scales
186 because of differences in the range of realised gradient combinations, and
187 differences in the biologically mediated distances over which gradients operate. Thus

188 the model potentially has trans-scale applicability down at least to the level of
189 habitats within climatically homogenous areas (Auerbach & Shmida, 1987;
190 Whittaker *et al.*, 2001). Of course, for the proposed diversity mechanism to operate,
191 sufficient evolutionary time is necessary for diversification within the capacity set by
192 the realized gradient combinations. This allows a role for history to modify the
193 relationship between realised gradient combinations and plant diversity. The spatial
194 configuration and temporal variability of each gradient combination will also affect
195 the ability of evolution to ‘fill’ the gradient combinations. Note that the fineness of
196 subdivision of gradient combinations among species does not have to be constant,
197 and that the variability between species in terms of this gradient-combination width
198 (analogous to niche width) does not have to be low, for the model to work. The
199 model simply assumes that the gradient-combination widths occupied by different
200 species are not consistently smaller in environments with fewer realized gradient
201 combinations.

202

203 **GRADIENT COMBINATIONS AND PRODUCTIVITY**

204 In theory, our model allows diversity to be partially uncoupled from productivity:
205 the supply of resources such as usable light and water determines productivity, in
206 conjunction with non-resource factors such as temperature, whereas the range of
207 realized gradient combinations sets the template for diversity. High productivity may
208 generate further complexity and greater diversity (as in a vertically complex tropical
209 forest, but see Huston, 1994, 2003), but equally it may not (as in a structurally
210 simple tropical swamp) (Fig.2c). What affects the likelihood of such positive
211 feedback thus becomes an important issue, and one that is probably scale dependent
212 (Fig.3c).

213 Fig.3 represents our ideas in a series of flow diagrams. Fig 3a–b presents
214 highly simplified views of a standard productivity-based hypothesis of plant
215 diversity (see O’Brien *et al.*, 1998) and of our model for comparison. These illustrate
216 the greater dissociation in our model between productivity and the postulated causal
217 chain leading to plant diversity. Fig.3c represents our model more fully and
218 incorporates expectations of the spatial scale-dependence of each proposed causal

219 link. Each of these propositions is either testable or trivially true. An interesting
220 feature that emerges is that the chain of causation involving gradient combinations
221 (shown on the left-hand side of Fig.3c) consists mostly of links for which a much
222 stronger effect is expected at broad scales (other than those that are scale
223 independent). This would suggest the strongest overall effect at the broadest scales.
224 By contrast, the chain of causation involving productivity and structural complexity
225 (right-hand side) consists of links for which a weaker effect is expected at broad
226 scales (or that are scale independent), some of which are likely to be highly variable
227 on fine scales. This suggests that the productivity–diversity relationship is most
228 likely to be monotonic, but not necessarily very strong, at the broadest scales.

229 The form of productivity–diversity curves may also be interpreted within the
230 model’s framework (see Waide *et al.* 1999; Mittelbach *et al.*, 2001; Whittaker *et al.*,
231 2003; Whittaker and Heegaard, 2003; see also Rahbek, 2005). At fine spatial scales
232 such curves are commonly unimodal (diversity increases with productivity up to a
233 point, and declines thereafter). At coarse spatial scales the relationship is frequently
234 positive monotonic (diversity increases continuously with productivity). A possible
235 explanation for this difference is that beta diversity may correlate positively with
236 productivity at coarse spatial scales, yielding a positive monotonic relationship
237 overall (see Whittaker *et al.*, 2001, 2003, their Figs 1 and 7.3, respectively, but note
238 that the authors do not favour this explanation). The empirical work of Chase and
239 Leibold (2002) supports this hypothesis.

240 If a positive correlation between beta diversity and productivity at coarse
241 spatial scales is a general pattern (more research is required on this point), an
242 explanation of such a relationship is required. A candidate can be derived from our
243 model using the following propositions, which are either trivially true or testable:
244 productivity reflects resource inputs (testable, Fig.3c); high resource inputs equate to
245 long resource gradients (trivially true, Fig.1); long resource gradients equate to many
246 potential gradient combinations (trivially true, Fig.1, Fig.3c); realised gradient
247 combinations reflect potential combinations (testable, Fig.2, Fig.3c); beta diversity
248 reflects realised gradient combinations (testable, more on this below – Fig.5); thus,
249 productivity and beta diversity are positively correlated. (Note that high productivity

250 is not the primary cause of high beta diversity according to the model.) Differences
251 between regions in both productivity and beta diversity, therefore, may be traceable
252 back to input levels of light and water.

253 The model also suggests a response to the commonly asked question why
254 high productivity correlates with more species rather than simply more individuals
255 of the same species (Willig *et al.*, 2003, call for this key assumption of various
256 energy-based and productivity-based theories to be validated from first principles).
257 Part of the answer may be that increases in the input of water and light typically, but
258 not inevitably, raise both productivity and the range of realised gradient
259 combinations (Figs 1, 2 and 3).

260

261 **GRADIENT COMBINATIONS AND HARSHNESS**

262 Brown & Lomolino (1998) favour a causal link between productivity and diversity
263 but recognize environmental exceptions to the rule, namely marshes, estuaries, hot
264 springs, eutrophic lakes and temporary ponds (all often high productivity and low
265 diversity). They use the concept of harshness to account for these exceptions (see
266 also Terborgh, 1973; Huston, 1979; Whittaker *et al.*, 2001):

267

268 Presumably ...abiotic stresses affect diversity because progressively fewer
269 species can produce and maintain the adaptations required to persist in
270 increasingly stressful environments. [In addition,] harsh environments would
271 be those in which extinction rates are high or colonization and speciation rates
272 low, or both ...Geographic isolation and physical conditions that are very
273 different from those of the surrounding areas reduce the rate of successful
274 colonization. Small and ephemeral habitats have high extinction rates and
275 concomitantly low speciation rates. (pp. 478-9)

276

277 Harshness may explain some high productivity–low diversity environments for the
278 reasons suggested (and scale is also likely to be important, Whittaker and Heegaard,
279 2003), but restriction of gradient combinations and distances may play a role, too.

280 The environments mentioned by Brown & Lomolino are typified by short water

281 gradients all or some of the time (mangroves also fall into this category, Field *et al.*,
282 1998; Whittaker *et al.*, 2001; Clarke, 2004) and lack the vertical complexity to
283 produce light gradients over distances sufficiently great to be exploited by a wide
284 range of species. Marshes, hot springs and shallow temporary ponds are analogous
285 to swamps in that low water states are restricted or absent (Fig.2). Open water
286 environments necessarily have short water gradients and the operational distance of
287 a light gradient in water is likely to be negatively correlated with productivity (that
288 is, an extremely eutrophic lake may be more like a swamp than an oligotrophic lake
289 in that light attenuates to an unusable level over a short vertical distance, effectively
290 reducing the volume of habitat to little more than that dominated by the species
291 responsible for the attenuation; Fig.4). It is surely important that harsh environments
292 are generally rare and patchily distributed, and that the pool of species within
293 evolutionary striking distance of them is relatively small, but these factors may be
294 complementary to variation in effective gradient lengths and resource heterogeneity
295 in determining diversity.

296

297 **DISCUSSION**

298 **Gradient combinations and resources**

299 Equivalent areas at high and low latitudes do not have equivalent potential water–
300 light resource spaces, and thus may not support comparable ranges of resource
301 gradient combinations. A large resource space can be divided into a greater number
302 of equal-sized niches than a small one (the influence of increased R , MacArthur,
303 1972), and a heterogeneous environment allows more plant species to coexist than a
304 homogeneous one (MacArthur and MacArthur, 1961; Paine, 1966; Recher, 1969;
305 Connell, 1975; Levin, 1976; Huston, 1979; Tilman, 1982; 1988; Tilman & Pacala,
306 1993; Huston, 1994; Tews, 2004).

307 Productivity typically correlates positively with resource supply except where
308 inputs are extreme, which implies that over a wide range of environments and
309 latitudes plant communities do deplete light and liquid water to similarly low levels
310 from very different starting points (Fig.1). Thus the combined influence of
311 topography, aspect, drainage and vegetation commonly turns initial light–water

312 states at low latitudes into those typical of high latitudes (although temperature will
313 be different), but is unlikely to turn initial states at high latitudes into those typical of
314 low latitudes (the Russian doll effect). In terms of light and water, therefore, low
315 latitude environments typically experience more climates. Greater variability in
316 physical conditions should in turn allow the coexistence of a greater range of plant
317 functional types and a greater number of species (Smith and Huston, 1989), given
318 time and opportunity for diversification (Taylor *et al.*, 1990).

319 To what extent realised gradient combinations reflect potential combinations
320 is an empirical matter worthy of greater attention, and the answer is likely to be
321 scale dependent (Fig.3c; Pausas & Austin, 2001). Points on the earth's surface by
322 definition show no spatial heterogeneity in physical characteristics. As the sample
323 increases in physical dimensions the number of sampled gradient combinations will
324 tend to increase also. This includes the vertical dimension: an epiphyte high in a
325 forest canopy will experience very different light, water and nutrients to a plant
326 growing in the soil directly beneath it. The habitat volume sampled, then, will
327 strongly affect the number of gradient combinations sampled, at small scales. Where
328 gradient lengths are short the range of possible combinations may be exhausted at
329 relatively small grain sizes, restricting beta-diversity (Fig.5); where they are long the
330 number of realised combinations sampled should continue to increase as grain
331 coarsens via a simple sampling effect, all other things being equal. The effect of
332 increasing combinations on diversity will thus tend to plateau relatively quickly as
333 sampled area increases where gradient lengths are short, after which increases in
334 diversity will depend mainly upon increases in the area of combinations already
335 sampled (assuming area-only effects are significant; Rosenzweig, 1995). Where
336 gradient lengths are longer the transition to area-only effects will tend to be delayed.
337 Thus over a range of scales correspondences may exist between resource
338 combinations–area/volume curves and species–area/volume curves, and between
339 resource distributions and patterns of species abundance (Huston, 1994), that are
340 more than coincidental.

341

342 **Gradient combinations and plants**

343 The range of realised gradient combinations is influenced by plants on land via the
344 resource templates that determine their diversity and growth forms (Smith and
345 Huston, 1989). A hypothetical unvegetated tropical landscape would have a large
346 potential water–light resource space but a small number of realised gradient
347 combinations, because variation in light intensity and water availability would be
348 controlled by topography, aspect and drainage alone. Only in the shade of isolated
349 boulders or rocky overhangs would above-ground light intensities fall to low levels.
350 Add a 50cm-tall grass canopy and high, medium and low light conditions are
351 generated across the landscape (Smith and Huston, 1989). Below ground, plants
352 diversify water availability and nutrient supplies (Huston & DeAngelis, 1994).
353 Replace low-growing, densely packed grasses with tall, relatively widely spaced
354 rainforest trees, and the grain of heterogeneity in soil structure, water and nutrients
355 coarsens (Ricklefs, 1977), while the volume of habitat and the distance over which
356 light gradients operate may increase as much as a hundredfold (see Björkman *et al.*,
357 1972; Björkman, 1981; Huston, 1994, for examples and analysis of the bioenergetic
358 trade-offs that allow plant species to coexist at either end of such a light gradient;
359 high water availability also promotes shade tolerance in plants, effectively
360 lengthening light gradients in rainforests and other moist environments, Smith and
361 Huston, 1989; Huston 1994). The area and volume of exploitable living spaces for a
362 wide range of organisms that are characterised by different resource states thus
363 increase as plants coalesce and gain height and complexity, so the number of species
364 may be expected to increase too (Fig.5; Simpson, 1949; MacArthur, 1964; Ricklefs,
365 1977; Huston, 1994; Palmer and Maurer, 1997).

366 Although many researchers have suggested that environmental heterogeneity
367 may govern species diversity, and that the relative abundance or area of habitats may
368 determine the relative abundance of individuals (e.g. MacArthur, 1964, 1970; Levin,
369 1976; Tilman, 1982, 1988; Abrams, 1988; Tilman & Pacala, 1993; Kerr & Packer,
370 1997; Palmer & Maurer, 1997; Ricklefs & Lovette, 1999; Kassen *et al.*, 2000; van
371 Rensburg *et al.*, 2002; Kubota *et al.*, 2004), rigorous studies at coarse spatial grains
372 and extents are rare (Pausas *et al.*, 2003), usually employ measures of habitat rather
373 than resource heterogeneity (Davidowitz & Rosenzweig, 1998; see below), are

374 heavily biased towards animals, and ‘drastically’ biased towards vertebrates (Tews *et*
375 *al.*, 2004: 79). Grain is also measured almost exclusively in terms of area and not
376 volume. It is at coarse spatial scales in particular that heterogeneity is widely thought
377 to be important in controlling diversity (Kerr & Packer, 1997; Austin, 1999; Aauri
378 & de Lucio, 2001; Rey Benayas & Scheiner, 2002). It is also at such scales that
379 differences in resource heterogeneity (Fig.1) offer the most intuitive explanation of
380 different (and frequently lognormal) patterns of relative abundance (Huston, 1994,
381 pp. 90–91; Marquet *et al.*, 2003). Our understanding of diversity variation across
382 landscapes and regions may thus benefit from the development of effective ways of
383 characterising gradient lengths and resource heterogeneity.

384

385 **Gradient combinations and habitat diversity**

386 Gradient combinations relate to habitat diversity but not in a straightforward way,
387 because habitats are not delimited on the basis of resource dynamics (nor are they
388 clearly defined, Simberloff, 1976), and because different habitats sample different
389 areas of resource space (Fig.1; Whittaker, 1975). To what extent gradient
390 combinations underlie patterns of vegetation heterogeneity and diversity within and
391 between habitats as traditionally delimited is one of the key questions at issue (c.f.
392 Pianka, 1966; Davidowitz & Rosenzweig, 1998). Lowland tropical forests, for
393 example, may sample a greater area of resource space than other forest types
394 (MacDonald, 2003), and large samples of rainforest may be spatially more variable
395 than other kinds of woodland (Tuomisto *et al.*, 1995; Ojo & Ola-Adams, 1996).
396 Relating species diversity to spatial measures of habitat diversity, therefore, may not
397 always be meaningful (Tews *et al.*, 2004). It is sometimes claimed that within-habitat
398 latitudinal gradients in diversity count as evidence against heterogeneity as a primary
399 cause of diversity patterns (Davidowitz & Rosenzweig, 1998), but unless it can be
400 shown that similar habitats at different latitudes are comparable in terms of resource
401 dynamics (and other factors), what controls diversity will remain an open question.

402

403 **Scale, capacity and relationships with other theories**

404 The break-down of resource gradients into gradient combinations is expected to
405 occur mainly at local and landscape scales, and depends on heterogeneity related to
406 vegetation structure, topography, aspect and drainage. The nature of the break-down
407 is likely to be very complex, with some gradient combinations more patchily
408 distributed than others (in both space and time), so that some may be usable locally
409 by plant species while others are not. To the best of our knowledge, no empirical
410 work has yet been done on the distribution of gradient combinations in space and
411 time in ecological systems. Simple averaging suggests that the full realised break-
412 down is likely to occur at relatively broad scales for very long gradients, and at finer
413 scales for short gradients. Scale, therefore, is expected to affect the number of
414 realised gradient combinations via a sampling effect that results in an expectation of
415 different levels of differentiation diversity (turnover or ‘beta’ diversity) between
416 areas varying in resource input levels (Fig.5; e.g. mesic tropical vs. high-latitude
417 terrestrial vegetation). This does not preclude the scale effects advocated by
418 Whittaker *et al.* (e.g. 2001, 2003; Willis & Whittaker, 2002; Whittaker & Heegaard,
419 2003). In this context the model can be seen as offering a linking mechanism
420 between climatic factors and plant diversity, which operates at scales finer than the
421 macro scale, but whose effects may be very important at the macro scale.

422 Most climate-based theories of spatial species richness patterns at the macro
423 scale characterize any given site as having a single combination of climatic
424 parameters, such as energy and rainfall, and the climatic regime is seen as fostering
425 a certain level of ‘biological activity’ (productivity) (e.g. O’Brien *et al.*, 1998;
426 Whittaker *et al.*, 2003). It is usually argued that greater levels of biological activity
427 tend to result in more species at the macro scale, given time and opportunity, via a
428 wide variety of possible mechanisms (e.g. reduced extinction rates owing to larger
429 population sizes, faster recovery from disturbance, reduced competitive exclusion
430 resulting from greater predation and parasitism, etc). These ideas have received
431 mixed support (e.g. Currie *et al.*, 2004; though often the issue of scale has been
432 inadequately addressed, Whittaker *et al.*, 2001). Very relevant to this general
433 approach are debates about whether or not there is a peaked relationship at the
434 macro scale between diversity and energy, as measured by potential

435 evapotranspiration (PET) or temperature (e.g. Francis & Currie, 2003; Whittaker *et*
436 *al.*, 2003; O'Brien 1993, 1998), and between diversity and productivity (e.g.
437 Mittelbach *et al.*, 2001, Whittaker & Heegaard, 2003).

438 Our model does not contradict these ideas, nor does it deny the importance of
439 such debates. However, it does focus attention on the implicit assumption running
440 through most of the relevant literature that climate represents a combination of
441 single-value parameters (e.g. Currie, 1991; but see Begon *et al.*, 1996). In essence
442 ours is a capacity model in that it concerns differences in the capacity of the
443 environment to support plant species. We have focused mostly on productivity and
444 its relationship with plant diversity, arguing that the link between the two may be far
445 from direct. However, our model is relevant to a range of hypotheses for the
446 latitudinal diversity gradient and other species richness patterns. For example, in
447 addition to a productivity hypothesis the recent paper by Currie *et al.* (2004)
448 examines and tests tolerance and evolutionary rates hypotheses of broad-scale
449 variation in taxonomic richness.

450 Tolerance ideas often hold that diversity reflects the number of taxa that can
451 tolerate 'the' conditions of an area, typically defined by measured precipitation and
452 temperature or PET. We argue that resource variability may depend on resource
453 input levels (e.g. of water and solar radiation, Fig.1; solar input, temperature and
454 PET are all strongly positively correlated at the macro scale, Currie, 1991). We
455 suggest that tolerance relates to the realised gradient combinations resulting from
456 this variability, as well as to the ambient levels of non-resource factors such as
457 temperature. Different plant species are expected to be favoured by different gradient
458 combinations. Thus, plant diversity should, at least in part, reflect realised resource
459 heterogeneity via mechanisms akin to those of the evolutionary species pool
460 hypothesis (Taylor *et al.*, 1990), which focuses on opportunities for the
461 diversification of suitably adapted species. More work needs to be done on the
462 mechanisms of diversification and coexistence involved. Currie *et al.* (2004) note
463 that "Many major taxa arose principally in the humid tropics (e.g. angiosperms in
464 south-east Asia; Latham & Ricklefs 1993)...". This raises the question of why so
465 many taxa seem to have originated in the humid tropics; resource heterogeneity

466 could have been part of the reason. Currie *et al.* (2004) continue: "...and
467 progressively more adaptations were presumably required to occupy other habitats."
468 Our model contrasts with this explanation, suggesting instead that fewer gradient
469 combinations exist as latitude increases, and therefore that fewer species are likely to
470 be adapted. In other words, arguments about new adaptations are not necessary to
471 explain fewer species outside the tropics via such tolerance ideas, though the two
472 sets of tolerance arguments are not mutually exclusive and could be mutually
473 reinforcing.

474 Similarly, evolutionary rates explanations of diversity patterns typically relate
475 increased speciation (but not extinction) rates to higher temperatures, via faster
476 operation of biological processes such as mutation, physiological processes and
477 shorter generation times (Rohde, 1992; Allen *et al.*, 2002). Complementary to this,
478 our model suggests that speciation rates could be increased where higher resource
479 inputs result in greater resource heterogeneity, because of the increased opportunity
480 for differentiation.

481 Finally, our model may help to clarify the nature of energy's role in
482 influencing plant diversity. Most recent energy theories for plants focus on ambient
483 temperature conditions and their effects on biological activity, as in the evolutionary
484 rates hypothesis (Rohde, 1992) and O'Brien's (1993, 1998) water–energy dynamics
485 model (which focuses on the energetic state of water within living tissue). Hawkins
486 *et al.* (2003) distinguish between trophic and ambient energy versions of energy–
487 richness hypotheses. The trophic version is based on food availability as determined
488 by productivity and thus includes the idea of climatic parameters (water and energy,
489 implicitly including light) being resources. However, the focus is on the total amount
490 of the food resource and not on variety within the resource template. Our model
491 focuses on environmental parameters as resources that can be used up, creating
492 resource heterogeneity. Although temperature is to some extent 'consumed' by
493 plants via transpiration, it is not a resource in the way that light and water are
494 (Austin and Smith, 1989; Huston, 1994). Temperature is an ambient state, and the
495 physiological responses of plants to resource gradients and gradient-forming non-
496 resources such as temperature and pH are fundamentally and predictably different

497 (Austin and Smith, 1989). Our model, then, should be seen as complementary to, not
498 competing with, models that relate levels of biological activity to diversity. It is also
499 complementary to the ideas of Jackson and Overpeck (2000), which focus on
500 variation in non-resource factors (see also Ackerly, 2003).

501

502 **Limitations**

503 The model outlined in this paper was developed to account for the capacity of
504 different environments to support species, although it may also form part of a
505 generative mechanism in the sense that large resource spaces offer more
506 opportunities for radiating lineages than small ones, as well as more opportunities
507 for dispersers. While it is wrong to think of tropical forests as monotonous biomes
508 lacking abiotic heterogeneity (Hill and Hill, 2001), whether diversity models based
509 on proximate abiotic factors, such as ours, can fully account for one-hectare plots of
510 rainforest that support close to 500 species of tree (Valencia *et al.*, 1994) remains to
511 be seen. In such hyperdiverse environments large numbers of species coexist
512 seemingly by subdividing their environment more finely than is typical (examples in
513 Rosenzweig, 1995) or via other biotic mechanisms (review in Wright, 2002).
514 Similarly, our model seems to be of little help in understanding the famous plant
515 diversity of the fynbos in South Africa. Diversity models founded solely on abiotic
516 variables may thus be incapable of providing precise descriptions of diversity
517 patterns, even when complementary and acting together. Nevertheless, the role of
518 environmental variation must be delimited in order that the relative contributions of
519 different factors influencing diversity gradients may be disentangled.

520

521 **CONCLUSION**

522 The difficulty and undesirability of performing manipulative experiments makes it
523 difficult to falsify hypotheses about spatial diversity patterns, especially at coarse
524 scales. Some of the major theories for macro-scale diversity gradients in particular
525 are based on correlations and, in some instances, reasoning from first principles (e.g.
526 O'Brien, 1993, 1998). The mechanisms underlying the correlations, and even the
527 theoretical postulates, are often unclear or untestable. The ideas that we have

528 presented in this paper represent testable hypotheses about mechanisms that might
529 underlie spatial relationships between plant diversity patterns and environmental
530 factors (including climate). We stress the potential roles of light (PAR) and habitat
531 volume, both of which we think have received too little attention in the literature,
532 and focus on variation in consumable resources. If valid, our conceptual model helps
533 to elucidate the productivity–diversity relationship. It may also help to prescribe the
534 place of history and of biotic interactions in the chain of causation that leads to
535 observed spatial diversity patterns.

536

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756

757 BIOSKETCHES

758 Chris Lavers has wide interests in biogeography, ecology and natural history. He is
759 the author of a book exploring the history and biogeography of metabolism in
760 tetrapods.

761

762 Richard Field is a lecturer in geography at the University of Nottingham and is book
763 reviews editor for the *Journal of Biogeography* suite of journals. His research
764 focuses on the forces that structure ecological communities, particularly modelling

765 and prediction of global patterns of plant diversity, island biogeography and
766 community structure in Indonesia, the ecology of invasive tree species in Britain and
767 the ecology of tropical forests in Honduras.

768

769 **FIGURE LEGENDS**

770 Fig.1 Potential combinations of a light gradient and a water gradient both of length
771 ten (arbitrary units). The number of potential combinations increases linearly with
772 increases in one variable with the other held constant (light and water are
773 interchangeable in the graph) and as the square of either variable when both increase
774 in parallel ($L = W$). Zero water and zero light is counted as a potential combination,
775 which is why $PGC = 1$ when $L = 0$ and $W = 0$. Linear: $y = c(x + 1)$, where $c = 1$
776 $+ \text{the gradient length held constant}$; square: $y = (x + 1)^2$.

777

778 Fig.2 (a) Representations of tundra, tropical forest, tropical swamp without trees, and
779 hot desert. (b) Gradients of light and water. Solid arrows: realised combinations of
780 these resources. Dashed arrows: tundra, moderate or high liquid water locally;
781 swamp, low and moderate energy conditions restricted because of short gradient
782 distances; desert, low and moderate energy conditions restricted or absent because of
783 short gradient distances and sparse vegetation. (c) Resource and structural
784 characteristics of the four environments. Note that productivity fails to predict
785 diversity in the tropical swamp, whereas realised gradient combinations and/or
786 gradient distance succeed (see text).

787

788 Fig.3 (a) Simplified schematic of a standard climate/productivity-based hypothesis of
789 plant diversity. (b) Simplified schematic of our conceptual model, for comparison
790 with (a). Productivity and diversity are dissociated to a large extent, and the template
791 for diversity is set by gradient combinations and distances, rather than by biological
792 activity. (c) Fuller schematic of our model. All arrows signify propositions that are
793 either testable or trivially true. Square symbols refer to the expected spatial scale
794 dependence of the effects represented by the adjacent arrows: nested squares =
795 similar effect at all spatial scales; small squares = scale dependent: stronger effect
796 expected at finer scales (usually because relevant variability is primarily at fine to
797 medium grains, so that averaging is likely to reduce variability and therefore the
798 effect at coarse grains); large squares = scale dependent: stronger effect expected at
799 broader scales. Note that in each of (a), (b) and (c) the proposed transitions into
800 plant diversity require evolutionary opportunity: time and space. Space is accounted
801 for in our model via gradient distance and its effects on habitat volume.

802

803 Fig.4 One reason why productivity and diversity are often inversely related in
804 oligotrophic and eutrophic water bodies. Photosynthesising organisms in eutrophic
805 water bodies consume and scatter more light per unit depth than in oligotrophic
806 ones. Oligotrophic water bodies may support more species because they have longer

807 energy gradients, larger total habitat volumes, and larger volumes at any given
808 energy state.

809

810 Fig.5 Idealized representation of expected changes in realized gradient combinations
811 and plant species richness with increasing area sampled, in two environments
812 contrasting in resource input levels. Each graph depicts two environments, one with
813 high resource input (such as tropical rainforest) and one with low resource input
814 (such as tundra). The graphs on the left represent horizontal change only, and show
815 the sampling effect without any influence of habitat volume. The graphs on the right
816 additionally incorporate the effect of habitat volume. For illustration we have
817 assumed constant resource inputs over the whole sample area, and therefore the
818 realized gradient combinations graphs level off once all gradient combinations that
819 can be realized have been realized. Alpha (local) and gamma (landscape to regional)
820 scales are represented by arbitrary sample areas, for illustrative purposes. The
821 dashed lines show the alpha diversity (bottom two graphs) or the number of realized
822 gradient combinations at the alpha scale (top two graphs), which can be thought of
823 as the potential for alpha diversity. The arrows represent turnover: the difference
824 between gamma and alpha gradient combinations (top two graphs) or diversity
825 (bottom two graphs) – commonly referred to as beta diversity.

826

827

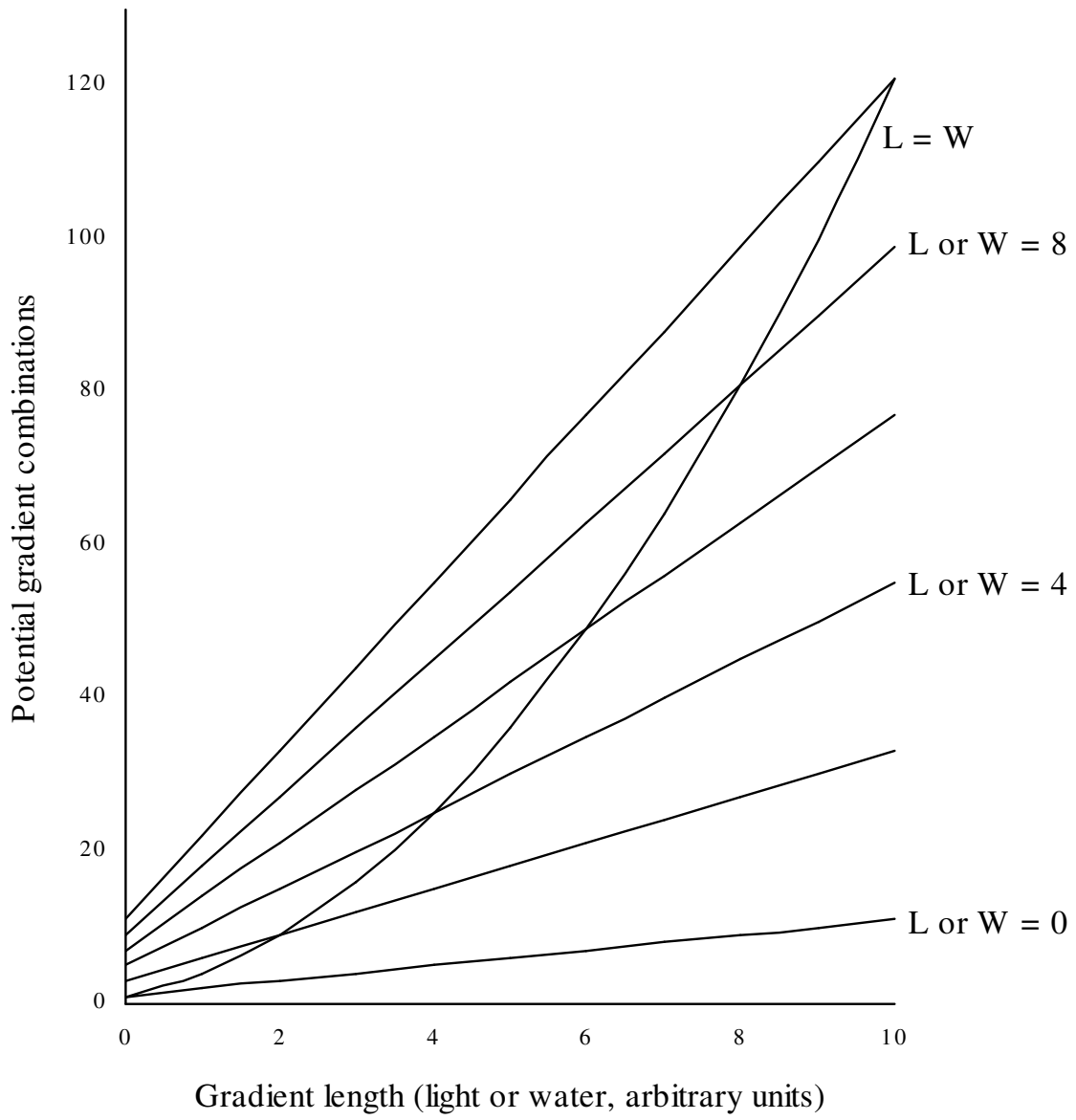
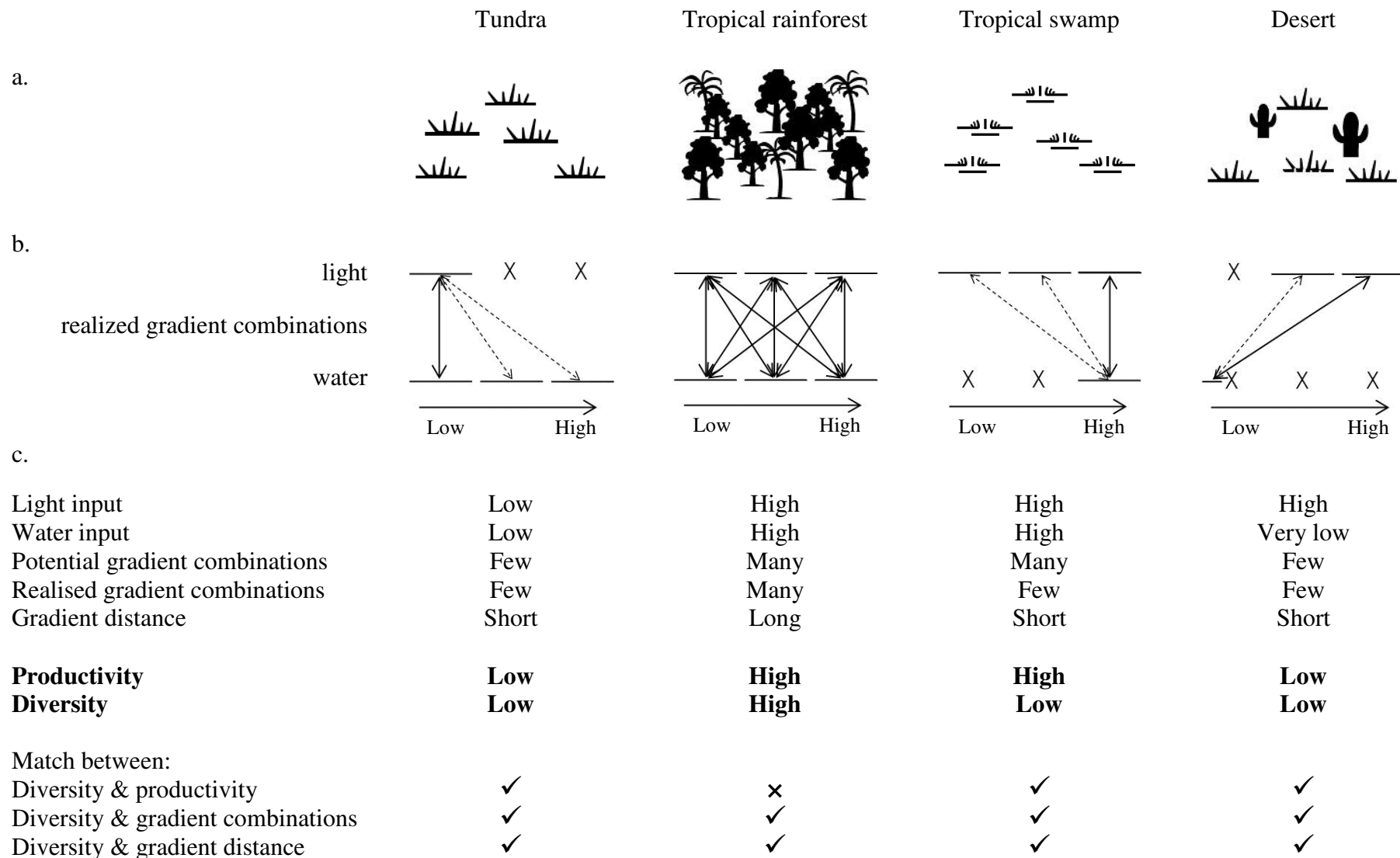
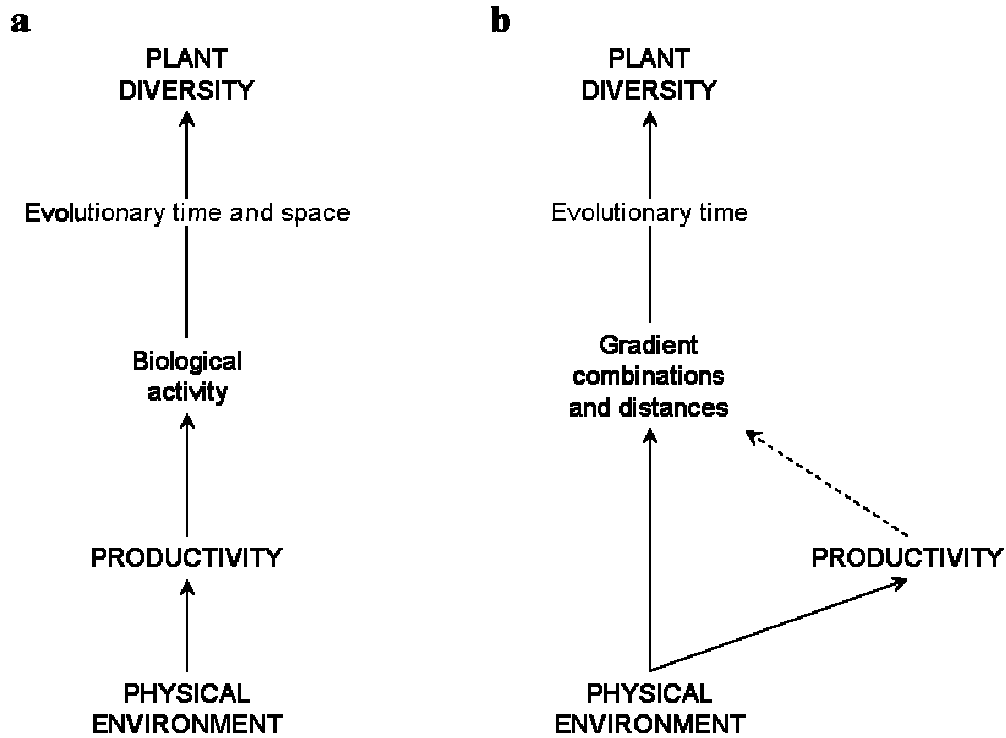


Fig.1

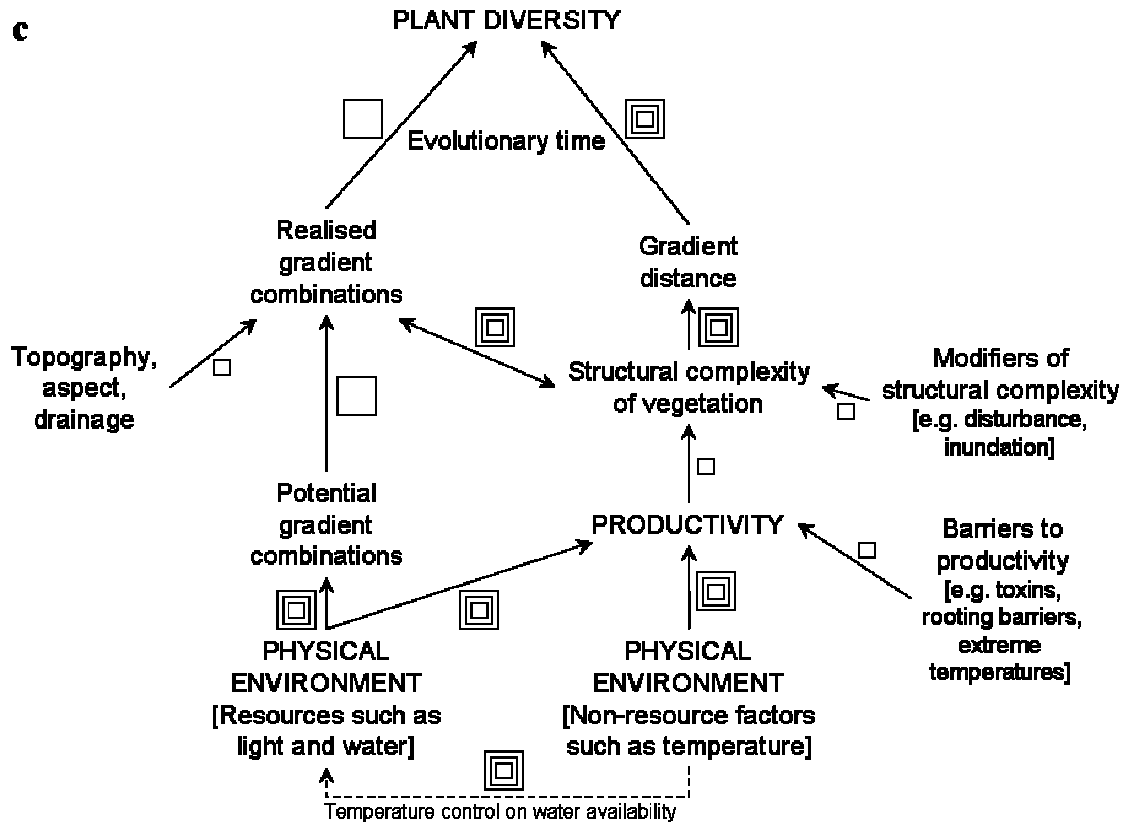


828
829

Fig.2



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833

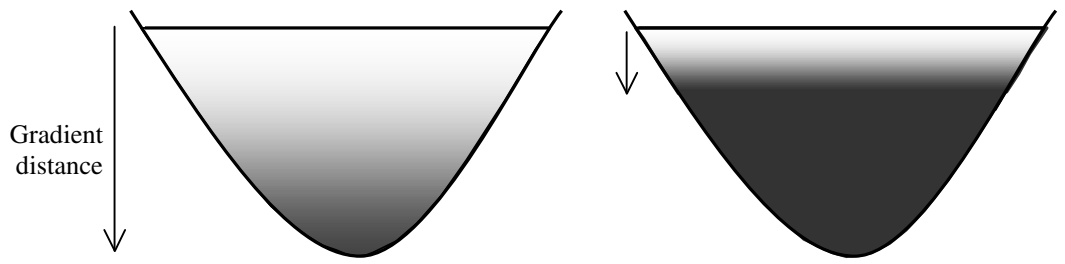


834
835
836

Fig.3

Oligotrophic

Eutrophic



Light input	Various	Various
Water availability	High	High
Gradient distance	Long	Short
Total habitat volume	Large	Small
Volume at each light level	Large	Small
Productivity	Low	High
Diversity	High	Low

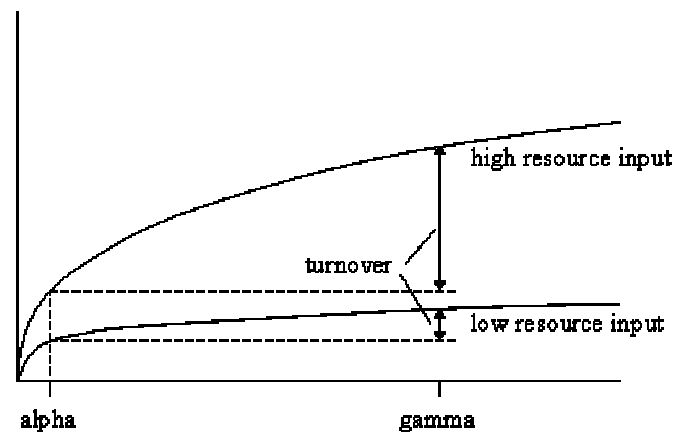
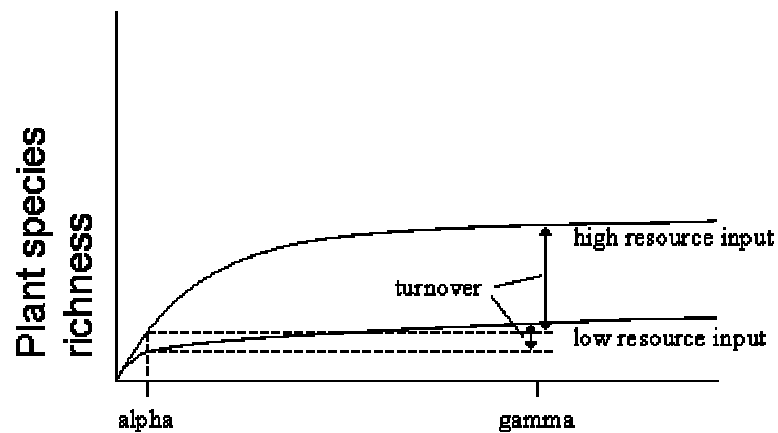
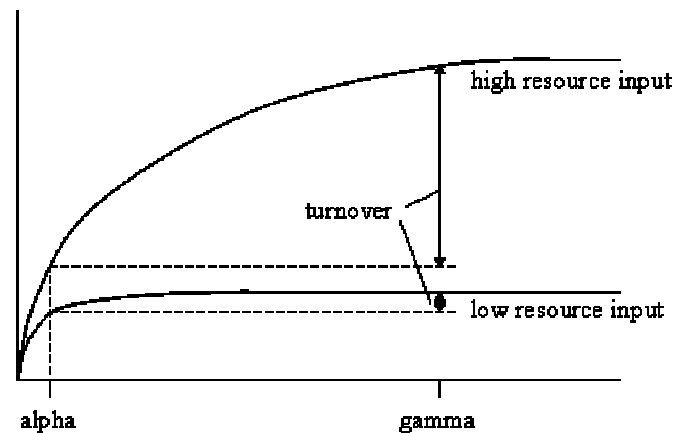
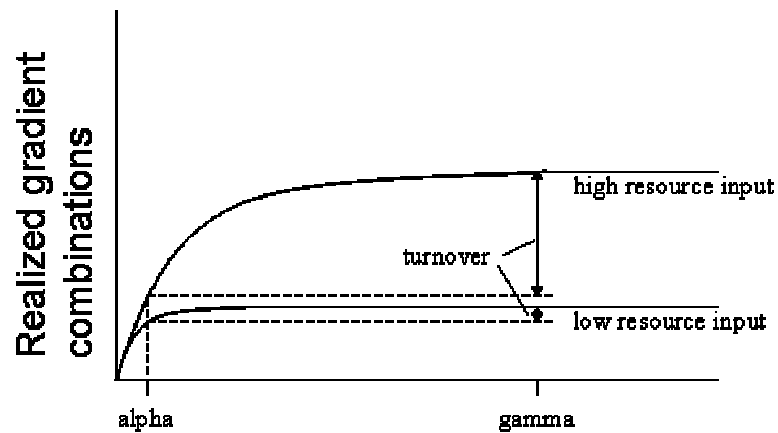
Match between:

Diversity & productivity	×
Diversity & gradient distance	✓
Diversity & total habitat volume	✓
Diversity & volume at each light level	✓

Fig.4

Constant gradient distance:
only horizontal effects

Variable gradient distance:
habitat volume effects
(vertical and horizontal)



Area

Area

837
838
839

Fig.5