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Three evolutionary hypotheses for the hump-shaped productivity–diversity curve

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ABSTRACT

We consider the problem of the hump-shaped relationship between productivity and diversity from an evolutionary perspective, based on the assumption that productivity is positively correlated with population size. Although productivity has little evolutionary meaning, population size is evolutionarily meaningful, leading to three hypotheses: (1) Diversity is higher at intermediate productivities because the maximum difference between speciation rates and extinction rates occurs in such habitats. (2) Diversity is higher at intermediate productivities because, in those areas, most species evolve at the maximal rate. (3) Diversity is higher at intermediate productivities because, in those environments, there are more types of successful adaptations. We recommend tests of the hypotheses based on differing predictions of the origin of evolutionary novelties and the response to mass extinction events.

Keywords: diversity, extinction, hump-shaped curve, population size, productivity, speciation.

INTRODUCTION

A central issue in ecology is what determines diversity and how many species live within and among a set of habitats. Of the many factors thought to influence diversity, the effect of productivity appears straightforward. If more energy goes into a system, the system can hold more individuals and thus a greater number of species (Preston, 1962). However, in several studies (Rosenzweig, 1992; Waide *et al.*, 1999; Mittelbach *et al.*, in press), the relationship between diversity and productivity was shown not to be monotonic, but unimodal, a pattern termed the 'hump-shaped curve' (Fig. 1). A similar trend exists for groups as diverse as zooplankton in Canadian lakes (Patalas, 1990), plants in Israel (Shmida *et al.*, 1986) and North America (Gross *et al.*, 2000), and fossil benthos of the Silurian era (Watkins, 1979; Ziegler *et al.*, 1968). Additional examples can be found in Huston (1994, p. 126) and Rosenzweig (1995, pp. 40–45, 348–351).

So, why does diversity decline at high levels of productivity? Rosenzweig and Abramsky (1993; see also Rosenzweig, 1995) reviewed a number of proposed explanations for this

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Table 1. Previously proposed explanations for the hump-shaped curve (Rosenzweig and Abramsky, 1993)

1. Environmental heterogeneity is greatest at intermediate productivities
2. Dynamical stability decreases at high productivities
3. The ratio of predators to victims increases with productivity
4. Taxa have optimal productivities and are forced out of productivities above and below that optimum by other taxa
5. Interference competition is most intense at intermediate productivities
6. Rich habitats are more recent and not yet at equilibrium
7. Productivity is inversely correlated with disturbance
8. The covariance of population densities drops as productivity rises
9. Intermediate productivity habitats occupy greater geographic area

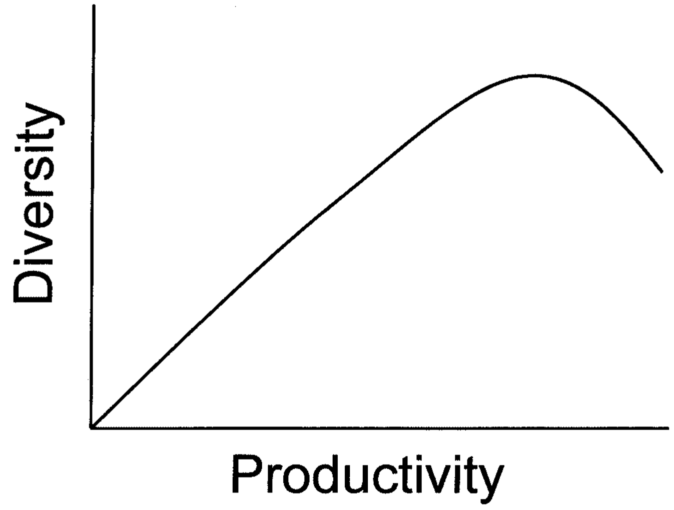

Fig. 1. Many sets of species show a negative quadratic relationship between productivity and diversity with the highest diversity found at intermediate levels of productivity. This relationship is generally known as the hump-shaped productivity–diversity curve.

pattern, but either rejected or cast suspicion on all of them (Table 1). A quick glance at the explanations reveals them to be largely ecological in nature. Abrams (1995) similarly cast doubts on proposed mechanisms for this pattern. However, there are two common features of studies exhibiting the hump-shaped productivity–diversity curve that point to an evolutionary explanation.

First, hump-shaped relationships occur primarily at regional scales. Waide *et al.* (1999) summarize the literature on productivity–diversity relationships. They found that, at between-biome (continental to global) scales, the relationship is predominantly monotonic and positive, especially for plants. At between-community (regional) scales, the relationship is primarily hump-shaped for plants and either hump-shaped or monotonic-positive for animals. At the within-community scale, the relationship varied, often showing no relationship. Second, the groups of organisms that exhibit the pattern are assemblages or guilds of similar species, not entire communities. That is, the pattern is found when looking within groups that are either a phylogenetic unit or a closely interacting set of species. Ricklefs (1989) outlined a number of reasons why evolutionary and historical processes, usually considered too slow-moving to significantly affect diversity, might do so.

AN EVOLUTIONARY PERSPECTIVE

The extant diversity at a site is the product of two factors: (1) the set of species from the regional species pool that can potentially exist at the site, limited by autecological compatibility and distance from a dispersal source; and (2) ecological processes (migration, establishment, competition, predation, mutualism, etc.) that determine which of the potential set become the actual residents. Diversity differences between two sites are, therefore, due either to differences in the set of potential residents (Pärtel *et al.*, 1996; Caley and Schluter, 1997) or to differences in the outcome of ecological processes. The explanations discussed by Rosenzweig and Abramsky (Table 1) rely almost exclusively on ecological processes, with the possible exceptions of explanations 6 and 9, and may, in part, be why they all seem unsatisfactory.

Instead, we consider processes whereby the set of potential residents of a particular region is expanded or reduced. Extinction, either local or complete, will cause a reduction in the set, while both speciation and introductions due to dispersal will cause the set to increase. In addition, micro-evolution may cause a species to become part of a set to which it did not previously belong, or cease to belong to that set. These changes are evolutionary processes, with the exception of introductions. However, on the scale of evolutionary time and regional areas, we can assume that most of the species that could disperse to a particular region have already done so, and so the rate of introductions would be positively correlated with the rate of evolution in adjacent regions. Thus, we can restrict our considerations strictly to evolutionary processes.

We first define our terms so that they have evolutionary meaning. Diversity – measured as the number of species – clearly has evolutionary meaning as the result of the opposing processes of speciation and extinction. Productivity is more difficult to define; it is not clear precisely what the term means in an evolutionary context. This difficulty comes, in part, because productivity is defined differently by different researchers. We solve this difficulty by showing how one measure of productivity can be translated into population size, a term with evolutionary meaning.

We start by recognizing two broad categories of productivity, available energy and utilized energy. Available energy is the amount potentially usable by the organisms at a given trophic level. For example, for herbivores the available energy is the amount fixed in plant tissue per unit area per unit time. Although the best measure would be joules fixed, a reasonable and typical surrogate is grams carbon of plant tissue produced. In contrast, utilized energy is the amount that is then used by those species for growth and reproduction. The utilized energy at one trophic level is the available energy for the next trophic level.

We distinguish between these two measures of productivity – available energy and utilized energy – because only the latter can easily be given evolutionary meaning. Consider an array of ensembles (*sensu* Istock, 1973) that differ in productivity. An ensemble consists of the local representatives of an ecological guild (Fauth *et al.*, 1996). For plants, the ensemble would be members of a single growth form or biome-type (e.g. grasslands, trees in a forest). For animals, an ensemble would be members of a taxonomic group with a shared ecology (e.g. ants, mammalian carnivores). Within an ensemble, an increase in utilized energy will result in an increase in the number of individuals, since growth and reproduction is roughly similar among species in an ensemble. This increase is predicated on the assumption that greater productivity does not simply increase the rate of turnover of individuals at that trophic level. That is, the next trophic level will fail to use all of the new available resources. This positive relationship between productivity and numbers of individuals does not necessarily hold when we cross ensemble boundaries because changes in lifeform (e.g. graminoids to trees) may result in more biomass being confined to fewer individuals. However, within an ensemble, productivity now translates into population size, a term that has evolutionary meaning.

Our distinction between available and utilized energy has not been clearly articulated in the past with regard to issues of diversity. However, this distinction is crucial because different theories about the productivity–diversity relationship are variously based on these two productivity measures. A failure to distinguish these two measures can result in finding or explaining an incorrect relationship. These issues are explored in detail in Waide *et al.* (1999) and Mittelbach *et al.* (in press).

How will population size vary with differences in productivity among ensembles? The absolute minimum population size, which is independent of productivity, is two (or one in species that reproduce asexually), although other factors will raise this minimum. As productivity rises, the total number of individuals in an area will rise. These individuals will be partitioned among the different species of that area such that, on average, mean population size will increase (Fig. 2; Preston, 1962). For our purposes, it does not matter exactly how mean population size rises with productivity, as long as it does so monotonically. Of course, if the mean population size is itself hump-shaped with regard to productivity, this will produce the productivity–diversity hump according to Rosenzweig and Abramsky's eighth explanation.

If we can treat population size as an acceptable evolutionary correlate of productivity, we can look for theories relating diversity and population size. The increase in diversity

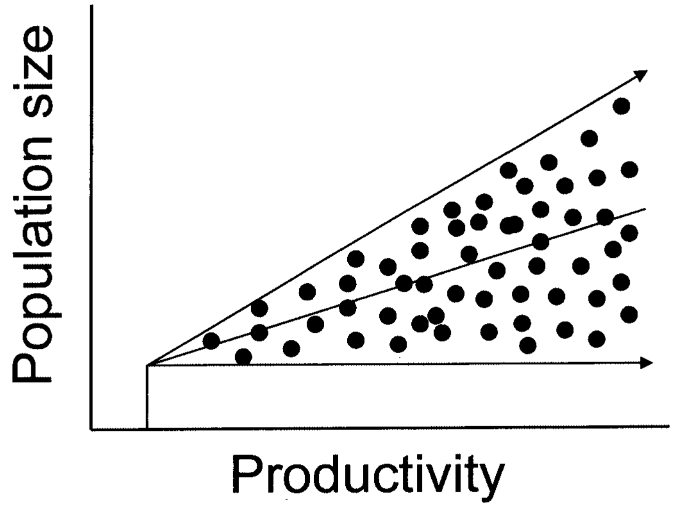

Fig. 2. We assume that mean and maximal population sizes will increase monotonically with productivity. The absolute shape of these curves does not matter.

from low to moderate productivity levels can be explained as the increase in energy used by additional species above the minimal viable population size (Preston, 1962; Wright *et al.*, 1993; Rosenzweig, 1995, pp. 351–353). What needs to be explained is the decreasing phase of the hump-shaped distribution. We present three hypotheses that explain this relationship. We do not claim that any of the hypotheses are correct. Rather, we intend to stimulate interest in the evolutionary consequences of productivity. All three hypotheses are based on theories and assumptions that, although at times controversial, are championed by some.

HYPOTHESIS 1: SPECIATION–EXTINCTION EQUILIBRIUM

Our first hypothesis arises from simple considerations of speciation and extinction processes. Diversity results from the equilibrium between speciation and extinction, two processes possibly affected by population size. The probability of extinction goes to zero at infinite population size. Even at intermediate population sizes, the probability is low. As population size continues to drop, however, we expect the probability to rise fairly quickly. Of course, if population size falls below two (or one), extinction is certain. A plot of extinction rate as a function of population size results in a concave or 'hollow' curve (Fig. 3A). This relationship of population size and extinction rate has received good empirical support (Diamond, 1984; Stanley, 1986; Schoener and Spiller, 1992). Although the above is couched in terms of a single species, it follows that the curve retains the same basic shape over sets of species at each productivity because mean population size of each set will also decrease with decreasing productivity.

For speciation, we might expect a similar concave curve (Fig. 3A). For example, speciation rates and extinction rates are correlated and related to mean population size in marine bivalves (Stanley, 1986). At least one theory, the allopatric speciation–genetic revolution model (Mayr, 1954), predicts that very large populations or metapopulations have a stable genetic structure and a cohesive gene pool. Two factors, isolation and small population size, break down these unifying factors to the point where a population can start evolving into a new species. Under this theory, very small population sizes are proposed as the conditions best suited for undergoing speciation. We know that the speciation rate must be greater than the extinction rate at some population size, or there would be no life on the

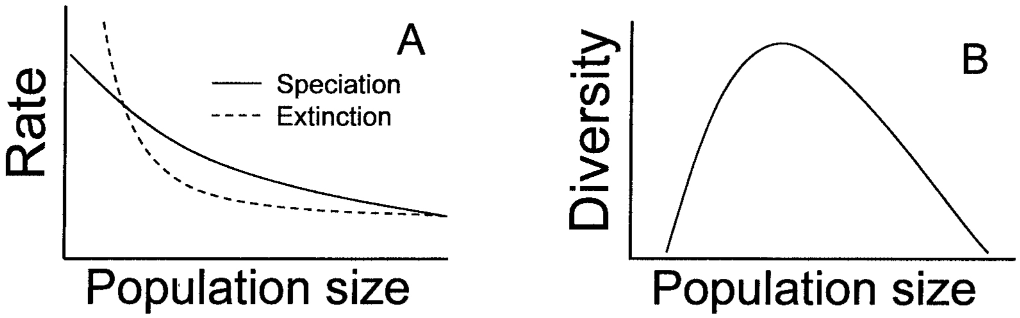

Fig. 3. (A) The hypothesized relationships between population size and either speciation rate or extinction rate based on the theories of Mayr (1954). (B) The equilibrium species diversity in relation to population size. If population size is related to productivity as postulated in Fig. 2, then the hump-shaped productivity–diversity curve results.

planet. That is, the speciation rate curve is shallower (less concave) than the extinction rate curve.

We therefore have three characterizations of how the speciation rate–population size curve compares to that for the extinction rate curve. First, the two correlate positively; the concave extinction rate curve suggests a concave speciation rate curve, although the exact shapes of the curves are not critical for our hypothesis to hold. Second, at very large population sizes, both rates are at or close to zero. Third, at very small population sizes, extinction becomes certain, while the speciation rate remains substantially smaller. We can further deduce that the speciation rate curve must be shallower than the extinction rate curve. The equilibrium diversity will be the difference between the speciation rates and extinction rates. This difference will be greatest at intermediate population sizes (Fig. 3B).

For our hypothesis to explain both the creation of the hump-shaped curve and its maintenance over time, the overall shapes of the extinction and speciation rate curves must remain stable over changing species numbers. We emphasize that only the qualitative shape need remain stable, as we are not trying to make quantitative predictions. The extinction rate at a given productivity will tend to increase as the number of species increases because each species will, perforce, comprise fewer overall populations. However, these changes will simply make the extinction curve less concave rather than change its basic shape.

In contrast, the speciation rate at a given productivity is independent of the number of species. Speciation is a process that occurs within single populations and is thus a function of the number of populations. Changing the number of species does not necessarily change the number of populations. For example, if a species consisted of two populations and evolution proceeded so that they became two different species, the two populations would still remain. So, even though the number of species changes at different productivity levels through evolutionary time, the number of populations will remain the same. Thus, the speciation rate curve as a function of productivity will retain its basic shape.

Thus, our first hypothesis for the hump-shaped curve is that: *Diversity is highest at intermediate productivities because the maximal difference between speciation and extinction occurs in such habitats.*

HYPOTHESIS 2: THE SHIFTING BALANCE

Our next hypothesis is derived from Sewell Wright's (1931) Shifting Balance theory of evolution. According to Wright's theory, evolution proceeds most rapidly when a species is divided into populations of intermediate size. The shifting balance process affects the rates of both speciation and extinction. The effects on either alone could produce a hump-shaped curve, but these effects are likely to be reinforcing.

Wright's theory is not explicitly a theory of speciation. But, if we make the reasonable assumption that speciation rates are positively correlated with micro-evolutionary rates, we can use it in this context. Specifically, we assume that speciation rates will be greatest at intermediate population sizes. Wright's theory has been extrapolated in this fashion previously (e.g. Lande, 1986).

The rate of micro-evolution will also effect the rate of extinction (or the avoidance of extinction, to be exact). We assume that extinction rates will be lower when micro-evolutionary rates are greater. For all habitats, the set of potential residents is continually being reduced by extinction, but less so in intermediate-productivity areas, where faster evolutionary rates allow species to exist longer. However, our assumption leads to the counterintuitive result that, at high productivities, the extinction rate increases with increasing population size. This problem is not quite as thorny as it might appear.

The mean and variance in population size increase together (Fig. 2) such that all environments have some small populations, whereas large populations are found only in the most productive environments. The shifting balance process requires that the individual demes of the metapopulation are at an intermediate size for a sustained period for the combined processes of drift, selection and migration to act rapidly. In areas of high productivity, if biotic or abiotic conditions change, a species that is evolving slowly will no longer be adapted. If population size then drops rapidly, it may go extinct before evolution re-adapts the population. Our notion is similar to that of the Red Queen Hypothesis (Van Valen, 1973); species must continually evolve to avoid extinction due to continuing changes in their environments. Our notion is broader, however, as it also includes evolution in response to abiotic changes.

Thus, our second hypothesis is that: *Diversity is highest at intermediate productivities because, in those areas, most populations evolve at the maximal rate.*

HYPOTHESIS 3: EVOLUTIONARY TRADE-OFFS

Our third hypothesis is based on the concept of evolutionary trade-offs – that is, that organisms cannot do well everywhere. We have two versions of this hypothesis. The general version does not depend on the population size–diversity relationship postulated above. The specific version does.

General version

Assume that different types of specializations have maximal fitnesses at low and high productivities. Assume also that, at the ends of the productivity gradient, there are only one or a few ways of being well adapted. Strong stabilizing selection constrains evolution in these habitats. On the other hand, in the middle of the productivity gradient there are many ways that adaptations could trade off with each other. A relaxation of selection might allow more types of genetic solutions to an ecological problem. That is, the existence of trade-offs effectively creates more niches at intermediate productivities. Our hypothesis is the opposite of the first hypothesis of Rosenzweig and Abramsky, which assumes that, at intermediate productivities, environmental heterogeneity creates more niches independently of the existence of species. It was this ‘cart-before-the-horse’ problem that led them to reject their first hypothesis.

An example of such a trade-off is found in adaptations of plants to water loss along a gradient of water availability (Dudley, 1996). Plants lose water through their stomates as a necessary consequence of carbon dioxide acquisition for photosynthesis. Water loss can be reduced by several methods, such as having smaller leaves and increasing the amount of carbon gained per atom of water lost (water use efficiency). In the annual species *Cakile edentula*, under dry conditions, these traits were both strongly selected for and highly correlated and so did not trade off. In contrast, under more mesic conditions, selection was weaker and the correlation among the traits decreased (Dudley, 1996). That is, as the environment became less extreme, individuals with different combinations of trait values had equal fitnesses. While this example only spans part of the productivity gradient, it demonstrates the principle of multiple equal strategies in intermediate environments.

Thus, our third hypothesis is that: *Diversity is higher at intermediate productivities because in those environments there are more types of successful adaptations.*

Specific version

The above hypothesis relates to all types of gradients, not just those due to productivity differences. However, a productivity gradient potentially generates its own particular kinds of trade-offs. If population size rises with productivity, then population density probably also rises. As density rises, we predict that competition will play an increasingly important role in community structure. For example, competition increases with increasing aboveground biomass in plant communities (e.g. Gurevitch, 1986; Bonser and Reader, 1995). Abrams (1988) demonstrated that density-dependent interspecific competition can reduce diversity significantly (cf. Abrams, 1995). Competitive dominance is often used to explain the hump-shaped curve when it appears (Tilman, 1982; Andersen, 1992). On the other hand, areas of low productivity are areas of high stress (*sensu* Grime, 1977). Therefore, a trade-off might exist between improved stress resistance (the ability to live and reproduce in a less productive environment) and competitive ability (Grime, 1977).

Thus, we restate our third hypothesis as: *Diversity is highest at intermediate productivities because a trade-off between intense competition at high productivities and high stress at low productivities allows more species to be successful by adapting to an intermediate environment.*

A WORD ABOUT SCALE

We noted at the beginning that the hump-shaped curve appears primarily in surveys done on a regional scale, not for either larger or smaller spatial scales. At continental or global scales, diversity increases monotonically with productivity (e.g. terrestrial plants, Scheiner and Rey-Benayas, 1994; deep sea benthos, Rex *et al.*, 1993; see reviews in Waide *et al.*, 1999; Mittelbach *et al.*, in press). At local scales, no consistent relationship is found (Grassle and Maciolek, 1992; Bethke and Nudds, 1993; Waide *et al.*, 1999; Gross *et al.*, 2000; Mittelbach *et al.*, in press). This scale dependence is expected if the productivity–diversity relationship is determined, in part, by evolutionary processes. At a local scale, ecological sorting processes and history play a large role and no universal evolutionary process or relationship exists. The monotonic relationship at the largest scale arises as a function of the summation of patterns across regions (Rosenzweig and Abramsky, 1993). A hump-shaped global curve would occur only if each regional curve happens to peak at approximately the same point on the productivity gradient, a highly unlikely event.

What can we infer from the observation that the global relationship is monotonically increasing? One way to get this global relationship is for the height of the productivity–diversity curve to rise with regional productivity (Fig. 4A). This rising relationship is seen for terrestrial plants globally (Fig. 4B). We can infer that the processes determining the hump-shaped curve are consistently affected by the overall productivity of the region. For example, if, for the speciation–extinction equilibrium, the speciation curve became progressively shallower with increasing regional productivity (Fig. 3), then the peak of the curve would shift to the right towards greater productivity. Across regions, then, diversity would increase monotonically with increasing overall regional productivity. If the effect on the diversity-determining process was not consistent, no global pattern would be found.

Of our three hypotheses, the shifting balance hypothesis is the only one that is inconsistent with the global gradient. It predicts that the hump-shaped curve will be the same across regions because it depends on absolute population size for its effects. As noted above, the speciation–extinction equilibrium can be made consistent with the global gradient if we are willing to make additional assumptions about changes in the speciation curve with productivity. The specific version of the evolutionary trade-off hypothesis is neutral with respect to the current data. It predicts that the peak of the curves will shift leftward with increasing regional productivity. This shift occurs because the effects of stress at the lowest productivities will be reduced as total regional productivity rises. However, this leftward shift of the peak could occur while the range of the entire curve was increasing. Of course, all of the above arguments depend on the assumption that the global gradient is a simple sum of the regional curves. If global patterns are determined by different processes, then none of our hypotheses make predictions at the global scale.

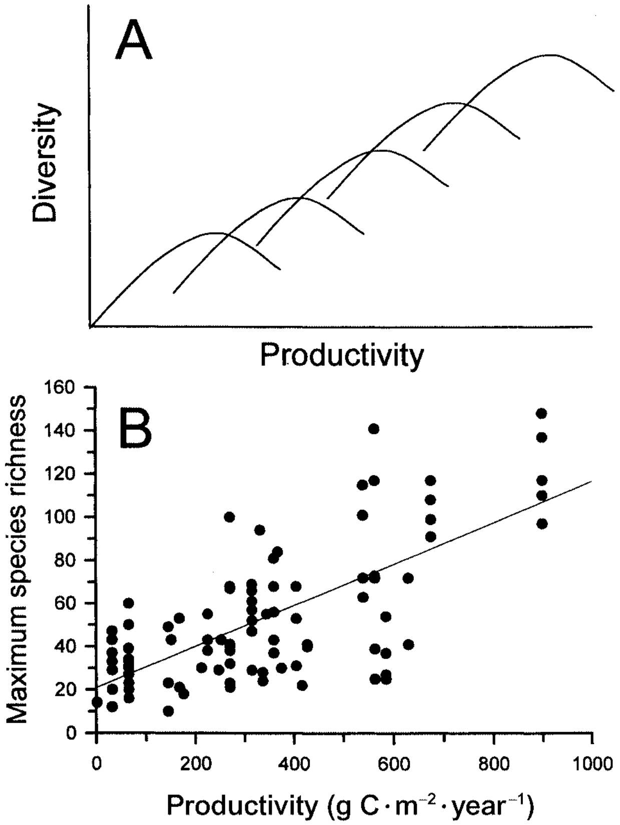

Fig. 4. How a hump-shaped regional productivity–diversity curve can produce a monotonically increasing relationship on a global scale. (A) We hypothesize that the absolute height of each regional curve rises with overall regional productivity. Thus, maximal diversity is positively correlated with regional productivity. (B) Data from a global survey of terrestrial plant landscapes (Scheiner and Rey-Benayas, 1994). Maximal diversity – the number of species in the richest site in each landscape – increases with mean landscape productivity as above.

RELATIONSHIPS AMONG THE HYPOTHESES

The proposed hypotheses are not mutually exclusive. In this section, we deal with incompatibilities among the hypotheses based on their assumptions. In the next section, we deal with differences in predictions. With regard to extinction rates, all three hypotheses either make similar assumptions or are silent and compatible with the specifics of the other hypotheses. In particular, Hypothesis 3 makes no particular assumptions with respect to the shapes of the extinction curves. Although Hypotheses 1 and 2 assume slightly different shapes, the details are not critical to either one. The extinction curve assumed by each hypothesis could be used as part of the other.

The situation with regard to speciation rates is more complex. Hypothesis 1 assumes that speciation rates are maximal at low population sizes, while Hypothesis 2 assumes that they are maximal at intermediate population sizes. Hypothesis 3 makes no assumptions about speciation rates.

TESTS OF OUR HYPOTHESES

All three hypotheses are based on the assumption that mean population size is positively correlated with productivity. We have presented reasons why we believe this assumption to be robust, but it is possible that the problem is more complex than we know. The first test of our hypotheses would be an examination of the relationship between population size and productivity. Among the assumptions of the individual hypotheses, the trade-off between competitive ability and stress reduction is the most controversial (Grime, 1977; Tilman, 1982). The efficacy of Wright's Shifting Balance theory has been debated recently (Crow *et al.*, 1990; Barton, 1992; Moore and Tonsor, 1994; Gavrilets, 1996; Orr and Orr, 1996; Wade and Goodnight, 1998; Coyne *et al.*, 2000; Goodnight and Wade, 2000). It is unclear whether a micro-evolutionary model can validly be substituted for a macro-evolutionary model, although the two are theoretically related. Finally, the speciation–extinction equilibrium hypothesis is based on assuming particular relationships between the speciation rate curve and the extinction rate curve. Thus, our theories are falsifiable by testing these assumptions.

The hypotheses can also be compared and tested based on different predictions regarding the evolutionary history of lineages. Two types of patterns can be examined: the pattern of shifts that lineages make if they evolve across productivity regimes, and the longevity of lineages within each productivity regime. With regard to the pattern of productivity shifts within lineages, the speciation–extinction equilibrium hypothesis predicts that the shift will be from low productivity regimes upward along the productivity gradient, while the shifting balance hypothesis predicts that they will be from the centre to both ends. The evolutionary trade-off hypothesis makes no prediction. Current data do not seem to favour either hypothesis. Benthic lineages spread from nearshore to continental shelf to continental slope habitats, which correspond with high, intermediate and low productivity regimes, respectively (Jablonski and Bottjer, 1990). For vascular plants during the Pennsylvanian and Permian eras, evolutionary novelties and new classes and orders appeared primarily in upland dry regions and spread to lowland wet regions (DiMichele and Aronson, 1992), although whether these upward shifts along the productivity gradient support the shifting balance or speciation–extinction equilibrium hypothesis is unclear. Jablonski (1993) has proposed that the tropics – the upper end of the productivity gradient – are a source of evolutionary novelties.

With regard to the longevity of lineages within each productivity regime, recent studies have indicated that lineages remain largely constant through time for both morphological (Stanley, 1982, 1985; Cheetham, 1986; Stanley and Yang, 1987) and ecological (Jablonski, 1987) characters. All three hypotheses utilize the same (or similar) extinction curve, but the shifting balance hypothesis includes differences in micro-evolutionary rates, which predict that lineages in intermediate productivity regimes will be the longest-lived. The speciation–extinction equilibrium hypothesis predicts that longevity will be greatest at high productivities, where the rate of extinction is lowest. The evolutionary trade-off hypothesis makes no prediction. We are aware of no data that address these predictions directly.

Two of the hypotheses assume different relationships between productivity and the rate of speciation; the evolutionary trade-off hypothesis is once again the one that doesn't. The hypotheses may be tested by examining this relationship. However, speciation rates are difficult to measure. Normally, when examining neontological data, only the net difference between speciation and extinction – extant diversity – can be measured. A potential solution is offered by examining the palaeontological record. Constraining the record's usefulness, however, is the close correlation of rates of extinction and speciation (Stanley, 1979, 1990). It may be possible, however, to observe the speciation rate curve, independent of the effects of extinction, following a mass extinction event. Following such an event, extinction rates may be very low because of the lack of interspecific competition. Then the pattern of diversification would reflect the speciation curve.

Following a mass extinction event, the speciation–extinction equilibrium hypothesis predicts that diversity will increase first in low productivity regimes, where speciation is the highest. The shifting balance and evolutionary trade-off hypotheses both predict that diversity will increase initially in intermediate productivity regimes. We are not aware of any studies of speciation rates in different productivity regimes following mass extinctions.

The general version of the evolutionary trade-off hypothesis predicts that a hump-shaped diversity relationship will be found for many types of gradients, not just those associated with productivity. An additional test of this hypothesis is to look for such relationships. The difficulty is to find gradients at a regional scale that are not also productivity gradients. For example, for plants, most large-scale environmental gradients (e.g. temperature, rainfall, length of growing season) affect productivity in some way. A suitable gradient might be temperature for endotherms (birds and mammals), as temperature has less of a direct effect on their life-history traits than ectotherms.

The three hypotheses are not mutually exclusive. For example, a combination of Hypotheses 2 and 3 might explain the relationship within productivity regimes and between productivity regimes, respectively. Several of our proposed processes may be necessary for a complete account of both the hump-shaped productivity–diversity curve and evolutionary patterns. We urge further examination of the palaeontological record to test our predictions.

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