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Community-level birth rate: a missing link between ecology, evolution and diversity

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We propose a conceptual model to explain the variation in species richness in local communities and in build-up of regional species pools over time. The idea is that the opportunity for new species to enter a community (its invasibility) determines the present richness of that community as well as the long-term build-up of a species pool by speciation and migration. We propose that a community's invasibility is determined by the turnover rate of reproductive genets in the community, which we call the 'community-level birth rate'. The faster the turn-over, the more species will accumulate per unit time and per unit community size (number of genets) at a given per-birth rate of immigration and speciation. Spatially discrete communities inhabiting similar environments sum up to metacommunities, whose inhabitant species constitute the regional species pool. We propose that the size of a regional species pool is determined by the aggregate community-level birth rate, the size of the metacommunity through time and age of the metacommunity. Thus, the novel contribution is our proposal of a direct effect of local environment on the build-up rate of species pools. The relative importance of immigrating species and neospecies originating locally will change with the temporal and spatial scale under consideration. We propose that the diversification rate specific to evolutionary lineages and the build-up rate of species pools are two sides of the same coin, and that they are both depending on mean generation time. The proposed model offers a reconciliation of two contrasting paradigms in current community ecology, viz. one focussing on present-time ecological processes and one focussing on historical events governing the size of species pools which in turn determines local richness.

Communities are products of immigration and environmental sorting (Warming 1909, Gleason 1926). Hence, formation of a viable population at a site requires successful dispersal, followed by establishment, survival and reproduction. This means that two factors are constraining local species richness in communities, 1) the number of species that have evolved to fit the ecological constraints and dispersed into the area of the community (regional influence), and 2) the environmental regime and species interactions in the community (local influence). Two competing paradigms in community ecology put very different emphasis on either of these two processes, or even tend to neglect the alternative. These paradigms have been coined "dispersal assembly" and "niche assembly" (Hubbell 2001), but we prefer the more general terms "species pool theory" and "ecological rule theory". In the following, we first briefly present evidence for ecological rule theory and species pool theory (with reference to recent reviews and with focus on plant communities). We then argue that there is a direct, but hitherto little emphasized (Huston 1999), link from local environment and community processes to the size of the regional species pool.

Ecological assembly rules and species pool theory

Explanations for species richness in biotic communities have often been sought amongst properties and processes in the community, e.g. resource availability, disturbance (including grazing) and competition (Huston 1979, Grace 1999). Familiar concepts are the intermediate disturbance hypothesis (Grime 1973a, 1973b, Connell 1978) and the humped-back productivity–diversity relationship (Grime 1973a, 1973b, 1979, Huston 1979, Rosenzweig and Abramsky 1993, Aarssen 2001). According to this view, local richness is limited by abiotic constraints at low

productivity and/or high disturbance on one side of the hump, and by competitive exclusion (niche limitation) in environments combining high productivity and low disturbance on the other. Although lottery models have suggested that coexistence is possible even with strong competitive hierarchies (Skellam 1951, Fagerström 1988, Chesson 2000), at least for organisms with a sessile habit, the effect of competition has been demonstrated repeatedly by inductive studies using null models (Wilson et al. 1996) and by experimentation (Connell 1983), e.g. neighbour removal experiments (Aarssen and Epp 1990, Goldberg and Barton 1992) and microcosm experiments (Keddy et al. 1997, Ejrnæs et al. 2006).

During the last decade, the idea that local richness is largely determined by species availability, i.e. by the regional species pool, has gained wide support. Evidence for the species pool theory comes mainly from correlative studies (e.g. vascular plants: Pärtel et al. 1996, Collins et al. 2002, freshwater fishes: Kelso and Minns 1996, zooplankton: Shurin et al. 2000, corals: Karlson and Cornell 1998, and many other lineages: Cornell 1999, Lawton 1999), which have reproduced positive and significant relationships between local and regional species richness, with different local communities as data points. This pattern has been taken to indicate that the more species are available regionally, which may live in a given environment, the more species should be expected to colonise local sites representing that environment. However, the mechanism behind this correlation has received less attention. Without a proposed mechanism, the direction of a causal relationship underlying the correlation cannot be established. Thus, not surprisingly some researchers have suggested the reverse relationship, i.e. a direct effect of the species-richness of communities in a region on the size of the regional species pool (Wisheu and Keddy 1996, Huston 1999). Another line of evidence for the species pool theory comes from experimental seed addition, which has often led to increased local richness and thus demonstrated plant communities to be unsaturated (Turnbull et al. 2000, Zobel et al. 2000).

The species pool theory focusses on the regional influence on local community richness and explains different sizes of regional species pools as follows: "All else being equal, the larger the local and/or global area of a habitat type and the older its geological age, the greater the past opportunity for speciation, and hence, the greater the number of available species adapted to that particular habitat type" (Taylor et al. 1990). This view has been applied to regional species pools for the same environment in different regions (Ricklefs et al. 1999) and to different environments within the same region (Schamp et al. 2002). It has further been developed to include historical factors, especially migrations (Zobel 1992, 1997).

It is striking that, although the two above mentioned theories are generally seen as competing paradigms, they often predict or successfully explain the very same patterns in species richness, i.e. large species pools coincide with optimal environmental conditions for co-existence and vice versa (Wisheu and Keddy 1996, Huston 1999, Liira and Zobel 2000, Safford et al. 2001).

Community-level birth rate and local species richness

We propose that the rate at which new individuals recruit from sexually produced propagules and reach reproductive maturity is a key property of biological communities. That is what we call the community-level birth rate (new genets per established genet per unit time). We define a community as an ensemble of trophically similar individuals inhabiting an area with a relatively well-defined environment (such as a community of emergent macrophytes in a pond). If the community-level birth rate is low, no new species will establish. If it is high, the community is open to newcomers (it is invasible, Burke and Grime 1996, Davis et al. 2000, 2005), and an increase in local species richness will depend on the per-birth immigration rate (the proportion of the recruits in one time-step belonging to species not present in the community) given a constant community size. For a given community-level birth rate, both time and community size will have positive relationships with community species richness, because the absolute number of births increases with these. What really matters, though, is the total number of reproductive events and for this we need to combine the density of individuals in the community with the space occupied by the community, which means that organism size matters.

Our model accounts for the build-up of community species richness by immigration. In real communities, species may also go extinct due to competitive exclusion, predation/parasitism and stochastic processes. However, we propose that establishing individuals and invading species, which inevitably must have a small initial population size, are much more vulnerable to these processes than are already established resident individuals or species. For individuals, appropriation of new resources is much more costly than defence of resources already captured (Dubois and Giraldeau 2005). Therefore, newcomers in a community, in plant communities seedlings, must rely on resources not captured by established individuals. This makes death at early life-stages much more predictable and resource-dependent, while death of established individuals is more stochastic. We have defined community-level birth rate (CBR) to include life-stages up till reproductive maturity. This implies that CBR is depressed by high juvenile mortality, which is the most important process by which competi-

tively superior species suppress subordinate neighbours, at least in plant communities (due to a strongly asymmetric competition, Weiner 1990, Rajaniemi 2003). In any case, model studies and empirical studies (Yurkonis and Meiners 2004) are needed to establish the relative importance of immigration and extinction to the maintenance of community species richness.

We expect the community-level birth rate to be highly dependent on the local environment, e.g. on levels of productivity (Stevens et al. 2004) and disturbance (Foster et al. 2004), as well as trophic interactions with mutualists (van der Heijden 2004) and herbivores (Edwards and Crawley 1999). However, it is not the level of resources available to the community as a whole that matters, but the continuous supply (for plants, over the whole growing season) of free resources in amounts needed by juveniles in order to establish and reach reproductive maturity (Davis and Pelsor 2001, Foster and Dickson 2004). For example, a plant community with ample resources overall will offer little opportunity for seedling establishment if light and soil nutrients are depleted by established individuals (Fig. 1). This proposed mechanism constitutes a unifying explanation for the often cited between-community decrease in richness towards both low and high abiotic productivity (usually explained with resource deficiency and competitive dominance, respectively).

Community-level birth rate and the build-up of species pools

If we extend the perspective to a larger region, but still focus on a relatively well-defined environment, then a metacommunity may be defined as the sum of individuals in the regional collection of local communities of the same kind (Hubbell 2001), e.g. all individuals of
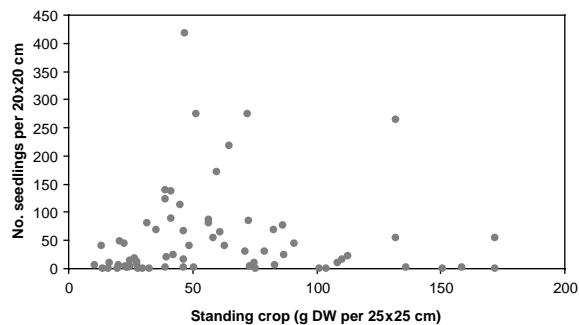

Fig. 1. Number of seedlings per unit area in one growing season in relation to standing crop in Baltic coastal meadows. Although seedling density does not equal community-level birth rate (which includes survival till reproductive maturity), the data indicates that CBR tends to be highest at low-intermediate standing crop. Data courtesy Heli M. Jutila (unpubl.; Jutila 1997, 2003).

emergent macrophytes in all ponds within a biogeographic region. The species richness of single communities will sum up to the regional pool of species, for which the focal environment is suitable (regional species pool).

We propose that the build-up rate of species pools, the metacommunity speciation rate (MSR), is dependent on three factors, the community-level birth rate (CBR; new genets per established genet per unit time) and the per-birth immigration (IR) and speciation (SR) rates, in the following way:

$$MSR = CBR \times (IR + SR)$$

This means that the actual size of a regional species pool depends on CBR, the per-birth immigration/speciation rate, metacommunity size and time, or, in other words, on the total number of births in that metacommunity through time multiplied by the sum of the per-birth immigration and speciation rates. This rationale is similar to Hubbell's (2001) neutral theory of biodiversity, which has the per capita speciation rate, ν, as a fundamental factor, and the constant metacommunity size, J_M, as a precondition. However, the present model is based on deviations from neutrality at both the species level (unequal probability of death and speciation for different individuals in the community) and at the community level (unequal probability of death and speciation in different communities).

The relative importance of immigration rate and speciation rate changes with spatial extend and temporal scale. In-situ speciation has a negligible influence on local species richness, which is almost exclusively controlled by immigration and extinction of species. Conversely at the scale of biogeographic regions, in which most species in the pool have originated somewhere within the region. Within a region, local communities come and go with time and species persist as metapopulations (Harrison 1998).

Assuming a uniform density of individuals allows us to use space as surrogate for metacommunity size, and the actual regional species pool is then determined by the metacommunity speciation rate and by metacommunity continuity in time and space. This partly resembles current species pool theory, which implicitly assumes a positive relationship between geological age of an evolutionary centre (Pärtel 2002, Stephens and Wiens 2003) or an ecosystem (Schamp et al. 2002, 2003) and the size of the resultant species pool. However, this assumption implies that novel species appear at a constant rate, which we find unlikely considering that species pools consist of different evolutionary lineages and are associated with environments differing widely in productivity, disturbance level, and other features affecting mean generation time.

For regional species pools, our model focuses on immigration and origination of species, yet species pools

at the scale of biogeographic provinces are the products of speciation and extinction (Rosenzweig 1995). We propose that speciation, like immigration, depends on the suitability of communities and their local environments for colonisation (invasibility), and therefore is a local process. In contrast, extinction from a regional species pool depends on the simultaneous or sequential local extinction of a species from all populations. It is therefore likely to be caused by regional processes, such as gross climate change combined with barriers to large-scale migration. However, a high CBR is likely to promote recolonization of locally extinct species from the regional pool and thus counteract local extinction.

Community-level speciation and lineage-specific speciation rates

With a constant metacommunity size as a precondition, each birth must be preceded by a death, and thus the number of births in the metacommunity must be inversely related to the longevity of individuals (mean generation time). Although communities often consist of species belonging to different evolutionary lineages, and members of one lineage often inhabit different environments, we propose that low generation time is a feature that unifies metacommunity speciation rate and lineage-specific speciation rates. Thus, low mean generation time in a metacommunity will simultaneously promote the speciation rate in the metacommunity and in the evolutionary lineages to which the species belong. For example, temperate grasslands have low community mean generation time of constituent species, and are mainly inhabited by species belonging to evolutionary lineages with high diversification rates, e.g. Poaceae, Fabaceae and Asteraceae (Magallón and Sanderson 2001, Davies et al. 2004). In contrast, arctic and alpine heaths have high community mean generation time, and are to some extent inhabited by species belonging to evolutionary lineages with more modest diversification rates, e.g. Ericaceae (Magallón and Sanderson 2001, Davies et al. 2004). These are not coincidences, but rather reflect that mean generation time and speciation rate are closely related to the community-level birth rate, which is high in temperate grasslands and low in arctic/alpine heaths.

It is a long-standing trend in evolutionary biology to search for attributes associated with high lineage-dependent diversification rates. Among Angiosperm plants, features relating to both life-form (short life-span: Eriksson 1993, herbaceousness: Dodd et al. 1999), vegetative growth (high growth rate: Midgley and Bond 1991), and reproduction (biotic pollination: Dodd et al. 1999, abiotic seed dispersal: Tiffney and Mazer 1995) have been proposed as factors promoting high diversification rate. Specifically for DNA evolution, short generation time is thought to correlate positively with molecular diversification rate in both animal (Kimura 1984, Weinreich 2001) and plant lineages (Gaut et al. 1997). However, the notion that genetic change in itself influences speciation rate, originally proposed by Mayr (1954), remains much-debated because of inconclusive evidence for its role (Bousquet et al. 1992, Whittle and Johnston 2003) and mechanistic function (Barraclough and Savolainen 2001). In any case, generation time appears to be one of the decisive life-history attributes for speciation rate in evolutionary lineages. However, because communities are mixtures of evolutionary lineages, and members of lineages distributed over different communities, metacommunity speciation rate and lineage-specific speciation rates should be considered separate, yet related, quantities, like a horizontal and a vertical look at the same object.

Local speciation

We propose that evolutionary processes leading to speciation take place in populations inhabiting local environments and embedded in communities (except in the rare case of previously completely unoccupied habitat) and that this condition is independent of the mode of speciation. The community context of sympatric speciation is self-evident, as it implies the entrance of a neospecies into an existing community including the ancestral species. Similarly, allopatric speciation by isolate formation implies, as a first step, the immigration into an existing community of a new species from somewhere else. In the cases of parapatric speciation and allopatric speciation by range break-up, any genetic novelty that contributes to a lasting reproductive isolation must originate in a local community, either as a single mutation or as a local adaptation (Levin 1993), and subsequently spread through the species' range by sexual reproduction. In other words, the first individuals of a neospecies or reproductively isolated genotype have resource demands; they have neighbours, experience stress and disturbances etc. Further population growth or gene flow requires, and is positive related to, the turnover of reproductive genets in the community, i.e. community-level birth rate.

Discussion

Paradigm reconciliation

We have presented a new theoretical framework for local and regional species richness. Our theoretical model shares some features with neutral theory of community assembly (Bell 2001, Hubbell 2001) and species pool

theory (Keddy 1992, Zobel 1997). The presented model acknowledges the regional influence on local richness, through availability of species for colonization, and a local effect on regional richness, because the regional species pool is the union of all local assemblages (Huston 1999, Stephens and Wiens 2003). More importantly, we propose a direct mechanistic effect of local environment, in the past, on the extant size of regional species pools: the local environment experienced by all individuals in the metacommunity has influenced the rate at which new species have originated and established through history.

Ecological assembly rules and species pool influence may be seen as complementary, i.e. that actual local richness is a balance between impoverishment due to local interactions and enrichment from a regional species pool (Ricklefs 1989, Collins et al. 2002). Moreover, it has been suggested that this balance changes with resource levels, with productive habitats being more saturated, i.e. niche-limited, than unproductive habitats (Huston 1999, Pärtel et al. 2000, Foster 2001, Foster et al. 2004). This means that the importance of macroevolutionary and biogeographical processes should be more clearly apparent in communities with less asymmetric competition. In the terms of the presented model, the balance is between impoverishment due to resource deficiency for invaders and enrichment due to immigration (addition from a regional species pool). In addition, our model proposes a direct relationship between local environment (suitability to invaders) and the size of the species pool.

Among the diversity patterns most frequently discussed in the ecological literature are peaks in local richness at intermediate disturbance and productivity. As pointed out by Grime (1979), the initial increase in diversity from low to intermediate productivity is caused by relieved abiotic stress, while the decrease in diversity from intermediate to high productivity is caused by intensified biotic stress, and the height of the modal diversity value is determined by the size of the regional species pool. We propose that community-level birth rate is the main process underlying both the shape of the curve and the height of its mode. At ecological time scales, there is little opportunity for species to invade and establish in communities where high stress (abiotic or biotic) or disturbance levels prevail, with a concomitant low CBR. At the same time, few species adapted to these conditions have evolved and entered the species pool, due to low CBR over evolutionary time scales, and are now available as colonisers of local communities. In addition, the species pool associated with a certain habitat is co-determined by the commonness of that habitat in time and space in the past (Hodgson 1987, Rosenzweig 1995, Schamp et al. 2002, 2003). Together CBR, metacommunity size and continuity in time determine the total number of births in the metacommunity ever, which must be proportional to

the number of species that has originated with the summed per-birth speciation and immigration rates as proportionality factor.

Future challenges

The central prediction of the presented model is that species pools associated with metacommunities with equal spatial and temporal continuity should differ in size according to the community-level birth rate through evolutionary time, and hence, the metacommunity speciation rate (number of speciation events per unit time and community size). In other words, the size of a regional species pool is dependent on both 1) the continuity in space (metacommunity size) and geological time and on 2) the number of speciation events in constituent communities per unit time and community size.

The following two hypotheses could be derived:

1) the birth rate in the community is monotonously positively related to the continuous presence, throughout the growing season, of resources needed for a juvenile plant to reach reproductive maturity. This hypothesis calls for a factorial experimental approach combining levels of productivity and disturbance, including detailed and repeated measurements of resource availability and emergence and survival of seedlings. The model's community size condition must be carefully observed if such experiments should be made in plots of fixed area. This is because the size of individuals in known to vary along gradients in disturbance and productivity (Zobel and Liira 1997, Aarssen and Schamp 2002). In addition to experimentation, evidence from simulation model studies would be helpful too.
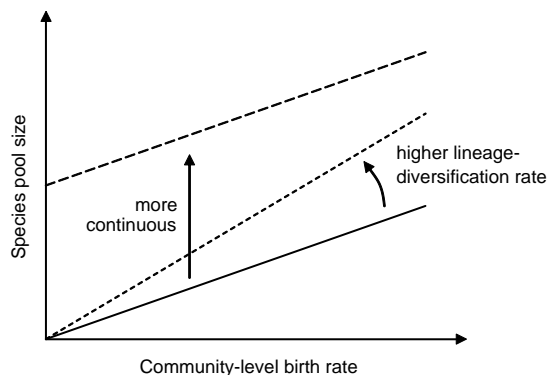

Fig. 2. The expected linear relationship between community-level birth rate and number of species in the metacommunity (size of the regional species pool). Increased spatial and temporal continuity of the metacommunity should result in larger species pools for the same community birth rate (long-broken line), whereas higher mean lineage-specific diversification rate for inhabitant species should increase the slope of the relationship (short-broken line).

2) There is a positive monotonous relationship between community birth rate and size of the species pool given equal speciation rate per birth and equal continuity of the metacommunity in space and time. If metacommunities with constituent species belonging to evolutionary lineages with different diversification rates are compared, we would expect different slopes of this relationship (Fig. 2). Conversely, if metacommunities varying in continuity in space and/or time are compared, we would expect the same slope but different intercepts of the relationship (Fig. 2). This hypothesis should preferably be tested by both correlative studies and simulation studies along synthetic environmental gradients allowing for mutations and hence simulated speciation events (Warren and Topping 2001).

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