

A Need for Niches?

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The idea that different species must have distinct ecologies if they are to coexist has been challenged recently by the claim that some models involving stochastic factors or clumped spatial distributions permit stable coexistence of species that are identical or differ only in competitive ability. However, these models have been misinterpreted; except in rather limited circumstances, they provide further support for the notion that species must be sufficiently ecologically distinct to coexist stably. The possible, limited, exceptions to this rule involve social factors by which individuals of a species discriminate between heterospecifics and conspecifics without there being any true ecological differences between species.

The idea that similar species cannot coexist has been both potent and controversial in ecology¹⁻⁶. Skeptics argue that there is a variety of mechanisms of coexistence that do not rely on ecological differences between species⁷. Mathematical models have been used to support this case⁸⁻¹⁰, which in its most extreme form is the hypothesis that identical species can coexist¹⁰. No one seriously argues that any two species in nature are identical, but if models say that identical species can coexist, we should not expect to find a limit to the similarity of coexisting species².

Models purporting to show coexistence without niche differences have been of two sorts. In the first sort, exemplified by Hubbell's model of tropical forests (see Ref. 8), species are assumed to be identical and coexistence is not indefinite: extinctions occur, but they take a long time. Such models do not confer long-term stability, which is defined here as the tendency for species to recover in the long run after falling to low density. Moreover, a slight variation in the assumption of equality of species, such as differences in average demographic parameters, can upset the conclusions of these models¹¹.

In the second sort of model^{9,10}, there is a stable long-term coexistence: species recover from fluctuations that take them to low density. This involves showing that the invasibility criterion¹² is satisfied, i.e. that a species at low density has an average long-term advantage in per capita

population growth. Moreover, coexistence in this setting can be expected to be robust, for small quantitative changes in the model will not change a low-density advantage to a disadvantage. Here, I discuss two particular models that have been suggested as showing this sort of coexistence. The first is the lottery model for sessile or territorial organisms with fluctuating recruitment rates, in a new formulation due to Fagerstrom (see Ref. 10). The second is a model of aggregated oviposition by competing insect species⁹.

Coexistence satisfying the invasibility criterion has important implications for individual organisms: there is an average advantage to membership of a species at low density, as such species show stronger per capita growth over time. If individuals of one species are indistinguishable from individuals of another, can this criterion possibly be satisfied? The answer seems to be no, for if there is no difference between individuals of different species there can be no advantage to membership in one species over another. As shown below, models purportedly demonstrating long-term stable coexistence of species with identical niches in fact implicitly assume ecological distinctions between individuals of different species that can be considered to be niche differences.

Lottery models for ecologically identical species

The lottery model assumes that space is allocated to juvenile organisms by chance processes, possibly with some bias to one species or another. In unbiased forms of the model, the probability that any juvenile is successful in gaining the space needed for maturity and reproduction is inversely proportional to the density of competing juveniles. The total number of individuals recruiting to the mature stage is limited by the available space, but relative recruitment from different species fluctuates over time due to stochastic fluctuations in relative birth rates and juvenile survival rates. These relative fluctuations in the rates of recruitment are essential for coexistence in the lottery model¹³.

Originally, these fluctuations were assumed to reflect species-specific responses to environmental factors, but Fagerstrom¹⁰ argued that random dispersal between habitats of different quality could generate the necessary asynchronous fluctuations in recruitment rates, without any ecological differences between in-

dividuals of different species. For example, with two habitats and two species, the species that at any time has a higher fraction of its individuals in the better habitat would have the higher recruitment rate. This mechanism would lead to fluctuations in relative recruitment rates, but would it confer an advantage on a species at low density?

Under the assumption that individuals of different species are indistinguishable, the competition that an individual experiences within a habitat depends on the total density of individuals in the habitat, regardless of species. An individual of the rarer species experiences no less competition than an individual of the more abundant species. Since habitat quality is also the same for both species, there can be no species distinction in reproduction within a habitat. Because dispersal of offspring is also identical for both species, individuals of either species in a habitat have identical chances of having offspring that are successfully recruited into the system. Thus, within a given habitat, an individual gains no advantage by belonging to one species or the other, either in the short run or in the long run (i.e. how its offspring and their offspring fare). In particular, viewed within either habitat, and regardless of species composition within a habitat, there is no expectation of more vigorous lines of descent from individuals of the rarer species compared with individuals of the more abundant species.

An individual in the better habitat of course has an advantage over an individual in the poorer habitat. It follows that an advantage to individuals of the rarer species would occur if a given individual of the rarer species had a greater probability of being present in the better habitat than a given individual of the other species. Is this likely to occur? With identical dispersal modes for the two species, the theory of Markov chains¹⁴ shows that any difference between species in the probability that a given individual member will be found in a particular habitat must disappear with time. We conclude, therefore, that the scheme for generating birth-rate fluctuations envisaged by Fagerstrom gives no advantage to a species at low density. It follows that the invasibility criterion is not satisfied, and there is no long-term stable coexistence of identical species in the lottery model.

The argument above is a general one, and applies to models other than the lottery model. It depends primarily on the assumption that individuals of one species are identical in rel-

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evant ecological respects to individuals of other species. It does not depend on just two habitats or two species, random dispersal, or even the nature of population dynamics within a habitat. The important aspect of dispersal is that it is identical for all individuals regardless of species, and satisfies the usual Markov chain model with the mild conditions necessary for convergence to a unique stationary distribution¹⁴. Indeed, dispersal can have the usual leptokurtic distribution often found for plant species¹⁵, so long as all habitats can eventually be reached by descendants of an individual.

Species satisfying these conditions and living in a finite universe will experience the sort of random walk to extinction suggested by Hubbell and Foster⁸. It is possible that this may take a considerable time; nevertheless, it is not the sort of stable coexistence that implies recovery from fluctuations to low density.

Lottery models with ecologically distinct species

In a recent article¹¹, Chesson and Huntly discussed how the rare-species advantage occurs in lottery models and the related broad class of models of communities in fluctuating environments. Such an advantage depends critically on individuals experiencing their most favorable environmental conditions when most other individuals with whom they compete find the environment less favorable. This is only consistently likely when response to the environment is a species-specific trait.

Species-specific responses to the environment can be said to define different niches for different species. Indeed, specific dependence of reproduction and juvenile survival on the temporally variable environment fits well with Grubb's concept of the regeneration niche^{16,17}. However, separate niches defined in this way may not be enough for coexistence. Population growth rates must satisfy additional requirements before coexistence is possible¹¹.

While the lottery model does not show that identical species can coexist, it does imply that some similarities between species favor coexistence. Species obeying the lottery model are more likely to coexist if they have similar properties when averaged over all environmental conditions. Thus, having similar average birth rates, similar average death rates, and similar birth-rate variances (which are also averages), favors coexistence¹⁰. Such similarity precludes any species being significantly

better when all environments are considered¹⁶. However, this is perfectly consistent with the coexistence requirement that each species be favored by some specific environmental conditions under which it performs better than other species. Indeed, this is likely to occur if adaptation to certain environmental conditions trades off against adaptation to other environmental conditions.

The idea that average similarity favors coexistence is not unique to the lottery model. Indeed, it also applies to the deterministic Lotka-Volterra model on which classical ideas of limiting similarity are based. For this model, May¹⁸ showed that species can coexist if they differ only a little in resource use, provided they have similar demographic parameters and can harvest similar average amounts of resource.

Coexistence from clumped egg distributions

Atkinson and Shorrocks⁹ presented a model showing long-term stable coexistence relying on spatially patchy oviposition by the individuals of two competing insect species. While this is not a model of species identical in all respects, it was presumed that appropriately patchy egg distributions do not require any differences in the oviposition behavior of individuals of different species, so long as individuals oviposit in batches. Hence, it has been cited as an example of coexistence without niche differences^{7,19}. Using an argument similar to that above for the lottery model, Green²⁰ showed that long-term stable coexistence could not occur while individuals of different species had identical oviposition behavior. In essence, this situation does not lead to individual females ovipositing in less crowded sites when the species is rare relative to the other species. No advantage of rarity relative to the other species accrues.

Atkinson and Shorrocks⁹ recognized that 'habitat preferences', or species-specific oviposition responses to spatially varying environmental stimuli, could also lead to clumped distributions of eggs. As discussed by Ives²¹, this mechanism of clumping does indeed promote long-term stable coexistence. Such clumping, however, depends on differences between species that might be called 'oviposition niches', and does not represent a fundamentally new mechanism of coexistence.

Coexistence independent of ecological differences?

When discussing identical species, it was assumed above that an individ-

ual's fitness is unaffected by the ratio of conspecifics to heterospecifics among competing individuals. Indeed, this is critical to the arguments (above) that rule out long-term stable coexistence of identical species. Yet individuals might easily distinguish between heterospecifics and conspecifics without there being ecological properties that are unique to a species. Such discrimination by individuals opens up the possibility of long-term stable coexistence without different niches for different species. For example, potentially easier recognition of conspecifics as competitors might lead to greater intraspecific interference than interspecific interference. The species need not exploit different resources or be affected differently by environmental factors for this interference difference to exist, and for it to promote long-term stable coexistence.

Sexual compatibility generally distinguishes heterospecifics and conspecifics. The most likely effect of this sort of distinction, however, is a low-density disadvantage. At low density, individuals might experience problems such as failure of insemination, inbreeding, or insufficient choice among potential sperm donors. This low-density disadvantage would cause a departure from the slow random walk to extinction mentioned above for cases where individuals of different species cannot be distinguished, hastening competitive exclusion.

For a more promising situation, consider the insect oviposition example above. Atkinson and Shorrocks⁹ and Ives²¹ suggest that suitable clumping might result if individuals preferentially oviposit in places that have been visited previously by conspecifics. This could indeed lead to a low-density advantage, and long-term stable species coexistence, under the assumption that intraspecific clump size is lower at lower density. We do not have to argue that species have ecological differences for this to be true. In particular, long-term stable coexistence could occur without separate niches. However, this argument depends on there being a fitness disadvantage to clumping of eggs intraspecifically, making it doubtful that it could persist as a behavior in a population. It seems more likely when such intraspecific aggregation occurs that there is a fitness advantage, and a consequent individual disadvantage at low density as aggregating becomes more difficult.

Social factors such as those discussed here seem to hold the key to species coexistence without separate

niches, but in any case conditions for it are probably restricted. Plausible examples may require consideration of ecological and evolutionary processes on different temporal or spatial scales, so that a trait conferring a fitness disadvantage under some ecological conditions can persist.

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Polar Dinosaurs and Ancient Climates

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Dinosaur skeletons have recently been found well within the contemporary Arctic and Antarctic Circles. These discoveries have surprised palaeontologists who regarded the dinosaurs as warm-adapted animals. New geological evidence suggests that these polar areas were also rather colder than had been thought, and this raises further problems in interpreting dinosaurian palaeobiology: were the dinosaurs fully endothermic and able to survive the darkness and cold of the polar regions, or could they undertake vast annual migrations of 3000–4000 km?

Dinosaurs are usually pictured against a background of damp tropical jungle-like foliage or sandy deserts. Most fossil skeletons of dinosaurs have been found associated with tropical or subtropical floras, and often with various sedimentological indicators of humid or arid conditions. Further, their postulated thermal physiology and naked skin was taken to indicate a preference for the environments favoured by living reptiles. New findings, however, show that dinosaurs lived within the ancient Arctic and Antarctic Circles^{1–8} (Fig. 1), and that these zones may have been covered extensively with ice⁹, although this idea is controversial^{10–12}. Should we now

imagine dinosaurs as thermally insulated warm-blooded animals that ploughed through snowdrifts and scraped the ice off the ground to find food?

The first polar dinosaur remains to be reported were some ornithopod footprints from Spitsbergen¹³, which lay at about 60°N in the Early Cretaceous. Further footprints, skin impressions and bones have been reported over the past 30 years from the mid and Late Cretaceous (114–66 million years ago) of the North Slope of Alaska, as well as from the Northwest Territories and Yukon Territories of Canada. Much of this material was collected by prospecting parties from coal and oil companies, and the specimens have only recently been described^{1–3}.

The North Slope of Alaska today lies at latitude 69°N, but geologists estimate that this area was further north in the Late Cretaceous, at 75–85°N. The climate appears to have been cool temperate in the Late Cretaceous, based on studies of the fossil plants. The flora consisted of deciduous plants which shed their leaves and died back or lay dormant in winter. Cross-sections of the fossil wood also show that growth ceased in winter^{2,12,14}. The Alaskan fossils include a freshwater dermatemyid turtle, a freshwater clam bearing tooth marks of a crocodylian or dinosaur, an ornithopod dinosaur footprint, isolated bones of ceratopsian dinosaurs (an occipital condyle, a horn core, and a partial femur) and hadrosaurs, and

teeth of a tyrannosaur and a troodont^{1–3}. (See Box 1 for a glossary of taxa.)

The southern polar dinosaurs were first recorded in 1906, when Woodward¹⁵ reported a lungfish specimen and a dinosaurian claw from the Early Cretaceous (130–105 million years ago) of Victoria, southeastern Australia. Further isolated fossils were found sporadically after 1906, but recent systematic collecting has yielded an extensive fauna^{4,5}. The area lay as far south as 70–85°S in the Early Cretaceous, and it must have experienced up to three months of effective darkness in the austral winter. The fossil plants and invertebrates, and the geochemistry, indicate a cool humid climate.

So far, the Victorian flora and fauna consists of more than 150 species: deciduous and evergreen trees, bushes and low ground cover, aquatic and terrestrial invertebrates (ostracods, cladocerans, other crustaceans, spiders, insects, earthworms, bryozoans, bivalves), fishes (bony fishes, lungfishes), turtles, lizards, pterosaurs, freshwater(?) plesiosaurs, birds and dinosaurs. A jaw bone of a temnospondyl amphibian has also been found: the last survivor of a group that had died out elsewhere long before the Early Cretaceous. The dominant dinosaurs are three or four genera of small- to medium-sized hypsilophodontid ornithopods, and other less-complete remains indicate the presence of two or three theropods.

A single vertebra of a theropod(?) dinosaur has also been recorded from the latest Cretaceous of North Island, New Zealand⁶, in an area that

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