RESEARCH NEWS

Core–satellite hypothesis and the distribution of species: Why are species not found everywhere?

K. N. Ganeshaiah

How much we all wished that there was some matter left behind between the earth and the moon so as to form a bridge for us to take a moon-walk!! But we are told that the rules of gravity would not allow such bridges in our solar system and that such matter, if any, would have condensed into either the core-planets or into their satellites with nothing left behind between them. Unless one grapples with the meaning of gravity and the associated physical laws, it is rather difficult to comprehend how such loose matter could condense either into core planets or to satellites. An equally intriguing explanation termed 'core–satellite' hypothesis has been put forth[1–4] by the ecologists to account for a peculiar behaviour of the species while occupying their habitats.

Law of frequencies

Consider a habitat wherein a number of quadrats are laid and the occurrence of all the species in them recorded. Let us say we are interested in knowing how many species occur in only 20% of the quadrats (A), in 20 to 40% (B), in 40 to 60% (C), in 60 to 80% (D) and in 80 to 100% of the quadrats. As early as 1918 Raunkiaer[5] observed that generally the frequency distribution of species with these categories would be bimodal such that $A > B > C \gtreqless D < E$. This is because every habitat shall have a set of dominant or the *core* species and a set of rare or *satellite* species; while the most abundant or the core species of the habitat occur in most of the quadrats (E), the rare species occur in a very small proportion of the quadrats (A). Accordingly, the frequency of species with varying levels of the occupancy of the quadrats can be expected to follow a bimodal distribution (Figure 1). Based on this explanation, Raunkiaer proposed 'Law of Frequencies'.

This explanation[6] and thence the law proposed however, has been highly criticized[7,8] because the shapes and the modes of the distribution curve are highly susceptible to several factors such as the number of quadrats sampled. Nevertheless, the law has resisted 'multiple executions' and Hanski and his colleagues[1–4] have recently shown that such bimodality of species could occur even for a single species in its habitats!! Their argument, called core–satellite hypothesis, implies *that species exhibit a dichotomy in occupying their habitats due to the stochastic processes of colonization and extinction.*

Why are some habitats not occupied?

Animal ecologists have frequently noticed that in some areas, habitats suitable for a given species are not always occupied and, in fact, occasionally most of the patches are found to lie vacant despite their suitability for the species as if the species has become locally threatened. In contrast to this, in certain other areas, the same species might be widely and abundantly distributed in its suitable habitats. Are there any phenomena that are basic to the behaviour of the populations driving such non-occupancy in some areas and otherwise in others? Or do these observations merely reflect the shrinkage of the habitats in some unidentified dimensions? Such questions are the focal issues among the community ecologists because the biological processes underlying these observations could be central to identify the factors driving the extinction of species. Recent work, both theoretical and empirical[1–4,8,9], has shown that the unpredictability in the occupancy of the habitats could, in fact, be a normal behaviour of the structured populations.

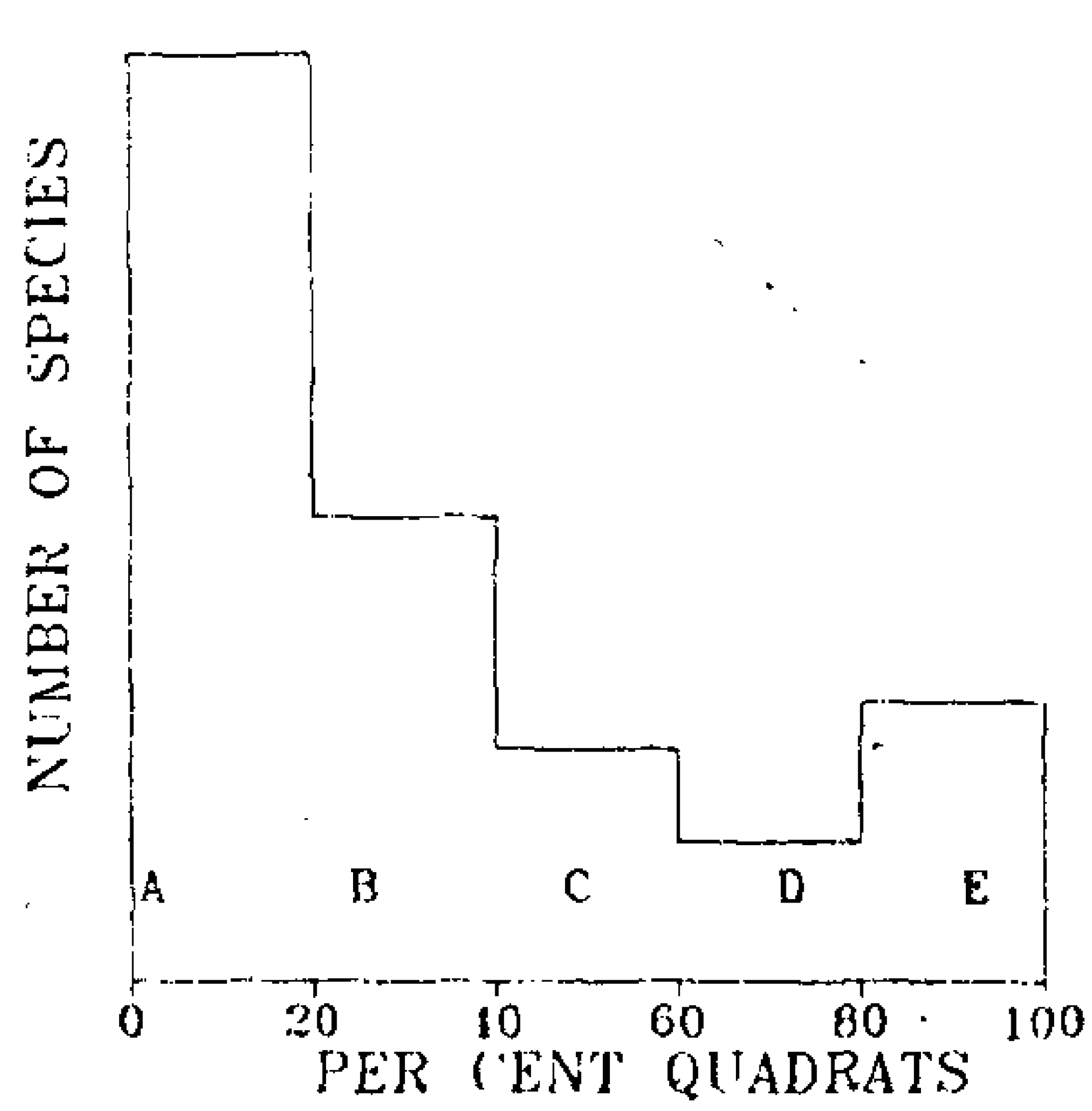

Figure 1. Bimodal distribution of the species that occupy different proportion of the quadrats in a habitat (hypothetical data). The species of the category A are rare in the habitat and hence occur only in a small proportion of the quadrats sampled while those of E category are dominant (and also abundant) in the habitat and hence occur in almost all the quadrats. Hanski *et al.*[1] argue that such bimodal distribution would also occur for individual species in meta-populations such that the populations of the species are either in most or in few habitat patches (see text).

Let us imagine a village with 100 dogs of which a proportion p is infested with ticks. Since all the 100 dogs are likely to physically interact among themselves, it is easy to imagine that the ticks from the infested dogs would move on to the healthy, tick-free dogs and colonize them. Clearly, the rate at which the healthy dogs get colonized increases with p because the more the dogs harbouring ticks, the more likely that the healthy dogs come in contact with them and receive the ticks. This further increases p and such process in which colonization brings about further colonization, pushes the system towards an equilibrium state where all the dogs are infested with the ticks ($p \approx 1$).

However, at the same time, it is also likely that ticks might become extinct on some of the dogs probably due to parasites or pathogens of the ticks or due to any such pressures. Qualitatively speaking, if the rate of extinction of ticks on the colonized dogs exceeds the rate at which the new dogs get colonized, increasingly *more dogs become tick free; in the long run*, most or all dogs would be free from the ticks such that $p \approx 0$. On the other hand, if the rate of colonization greatly exceeds that of extinction, the system moves to $p \approx 1$ where most or all the dogs harbour ticks. Thus depending upon the levels of extinction, the system would be either at $p \approx 0$ or at $p \approx 1$.

Further, Hanski[4] observed that under such situations, as more and more dogs get colonized (occupied), the probability that extinction occurs on any one infested dog decreases. In other words, the probability of local extinction decreases with the spread of the ticks. This facilitates spread of the ticks in almost an irreversible way such that at any given time the dog population would be generally completely infested ($p \approx 1$); if the colonization has not begun at all in a population then $p \approx 0$.

Now let us consider 100 such villages or 'meta-populations' of dogs that are spatially isolated such that the dogs of one village are not likely to pass on or receive ticks from those of the other villages. Dogs in each of these villages are subjected to the phenomenon as above and hence each of these can be expected to be in one of the two states of the *trivial equilibrium. While in some villages* all or most dogs are infested, in others none or a very few are; resulting in bimodal distribution of the villages with varying levels of tick-infested dogs. In the villages where most dogs are tick-free, it does not mean that the dogs are not suitable habitats for ticks; rather it just happens that in these villages the local rate of extinction of ticks is high enough to overtake the rate of colonization. Thus, the non-occupancy of the habitats (and hence local extinction) is merely a consequence of the way in which the colonization and extinction interact stochastically in the structured populations of the dogs.

Another prediction can also be derived from the foregoing. As stated earlier, the probability that a given empty patch gets colonized increases with p and the probability that extinction occurs in a colonized patch decreases with p. Thus for relatively high levels of colonization, the system is likely to move to $p \approx 1$, while for low levels of colonization it would be at $p \approx 0$. In other words, when p is plotted against the rates of colonization, it stays at the lower range of the spectrum for low values of colonization and then shows a sudden transition to the higher spectrum for high levels of colonization (Figure 2).

Testing the predictions

Several workers have arrived at these conclusions[1-4,9,10] using rigorous mathematical formulations. But validating them requires collection of data on a massive scale and on the right kind of the systems that would conform to the assumptions underlying these arguments. In a set of

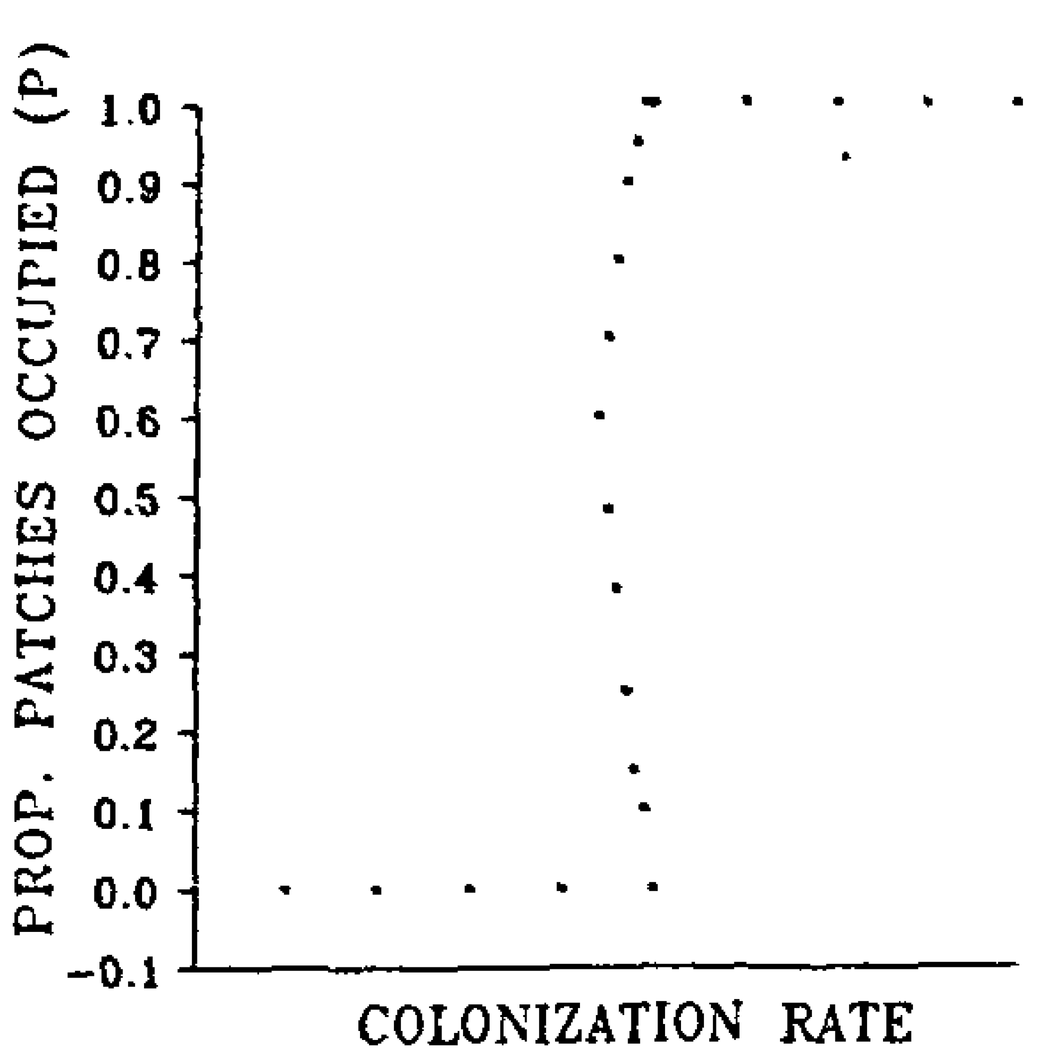

Figure 2. The relation between per cent patches (p) occupied by a species with the colonization rate.

recent papers Hanski and his co-workers[1,3] offer such data for testing their predictions for the behaviour of a single species. Their work involved mapping an area of 3500 km^2 at south west Finland for all the dry meadows containing *Plantago lanceolata* where the larval populations of the butterfly *Melitaea cinxa* could occur; they censused these patches for the occurrence of the groups of larvae of the butterfly. They thus recorded 1530 meadows ranging from 12 m^2 to over seven hectares that could serve as the habitat patches for the butterfly of which only 524 patches were occupied during 1993. They tracked the fate of each meadow through 1994 and observed that while in 256 of these 524 patches the butterfly populations became extinct, 119 fresh habitats were occupied (colonized); as a result, during 1994, only 401 habitats were found occupied.

Because they had completely mapped the area, it was possible to identify about 65 meta-populations or 'villages' that are isolated from each other by at least 1.5 km. Given the distance to which butterflies can fly and, or migrate in a generation (< 1 km), these meta-populations were very isolated and had a very low probability of interacting among themselves for colonization of their habitats. However, unlike in our imaginary example where every 'village' (meta-population) had 100 tick-habitable dogs (habitat patches), these meta-populations had varying number (5 to 95) of habitat patches for butterfly. For each of these meta-populations, they computed the proportion of the patches that were occupied (p) and plotted the frequency of 'villages' with different proportions. The data showed a clear bimodal distribution. Based on the data for the whole area, one in every three (524 out of 1530; 0.34) habitat patches is expected to be occupied with the butterfly larval populations. Thus if the occupied patches are randomly distributed among the meta-populations, one would expect a mode at 0.34; on the contrary, there were two modes, one at the lower end of the spectrum ($p \approx 0$) and the other at higher end ($p \approx 1$), supporting the predictions about the dichotomy in the occupancy of habitats.

The probability that a given habitat patch would receive the butterfly populations from other patches, is a function of the number and size of the populated patches around it, and their distance to it. Accordingly, Hanski *et al.* computed an index of migration for each meta-population based on the available population around each of the habitat in it and this served as an index of rate of colonization (m). They then plotted the p values of a meta-population against the rate of colonization (m) and found that for low levels of colonization, p was constant at almost 0, while for higher rates of colonization (beyond 1.5), p suddenly increases and stabilized at 1. The few meta-populations that occupied the intermediate zone, generally showed a tendency to move to one of the two stable states the next year probably suggesting their transient state. Thus the work by Hanski *et al.* did demonstrate the tendency of the structured populations to be either 'here' ($p \approx 0$) or 'there' ($p \approx 1$) and rarely to be in between; thus species seem not to occur everywhere. The two extreme states seem to act as attractants just as the core planets and the satellites do for their matter.

It has been a common observation that the populations of certain species crash down almost to a situation of threatened state for no immediately obvious reasons. One such observation is the recent widespread and rapid decline of butterflies in northern parts of Europe[11]. Though shrinkage of the available habitat could be offered as an immediate reason, work by Hanski *et al.* suggests that these fluctuations could in fact be a consequence of the normal behaviour of the populations and that it would be rather difficult and risky to make the predictions about the occurrence of the species in fragmented habitats.

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ACKNOWLEDGEMENTS. I thank Dr N. V. Joshi for help in clarifying certain issues during the preparation of the manuscript. This work was partly financed by a CIFOR grant, and McArthur grant to the author and to Prof. Bawa.

K. N. Ganeshaiah is in the Department of Plant Genetics and Breeding, University of Agricultural Sciences, GKVK, Bangalore 560 065, and at Jawaharlal Nehru Centre for Advanced Scientific Research, Bangalore 560 064, India.