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Thoughts of a travelling ecologist 13.

Numbers, rates, ecology

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Numbers and rates are important in ecology. I almost hear you say: "Ehem, and what's news in this? Have you never seen an insect outbreak and its following collapse?" So the starting statement may seem either pompous but obvious, or sneakily provocative, so that I could lament about the lack of mathematical literacy. My intent is neither. Let me instead start by referring to the Hungarian theoretical ecologist, Pal Juhász-Nagy, and his ideas about the conceptual foundations of ecology.

In his small but thoughtful book (Juhász-Nagy, 1986), he constructs these foundations by using the logical tool "*reductio ad absurdum*" (Polya, 1973). He proposes the following Central Hypothesis of ecology: "Any population in nature can be found anywhere, at any time, at any density". This Central Hypothesis is obviously, trivially false. We have plenty of evidence that living organisms have their finite distribution ranges: you cannot find polar bears on the Antarctic, nor penguins on the (disappearing) ice floats of the Arctic. If that does not convince, and you fancy arguing that "in theory, they could survive there", then think of whales in Lake Victoria, or pineapples growing in the Finnish taiga. The same for time: species have their distinct phenology, which can be rather dramatic. In the dry Kirindi Forest of Madagascar, I have myself witnessed the explosive breeding of the mantellid frog *Aglyptodactylus securifer* (Goodman & Benstead, 2003). Arriving at the end of the dry season, we found a parched forest, with no green leaves anywhere, and a dry riverbed with round boulders. The first two rains created a few mid-sized puddles in the riverbed, and the following day, the riverbed and the surrounding forest reverberated from the force of the frog chorus. There were up to seven species singing (and busily mating), but the most common one was *A. securifer*, with its pale brown back and yellow-golden side bar - they were in their hundreds and thousands. The following morning we found a silent forest. All the frogs were gone. Not silent, but gone into hibernation again. Only the masses of eggs testified of the frenzied reproductive activity of the day before. This is at least one species that seems to be active only on one day of the year. The rest it spends in an inactive stage.

So there is plenty of evidence that JNP's Central Hypothesis is false: species demonstrate dramatic shifts in densities, particular seasonal patterns and distinct geographical distributions. This can be called the Central Fact of ecology. The problem that follows from this Central Fact is by no means trivial, though. This is the two-part Central Problem, leading to the

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two fundamental questions of ecology. The Central Problem is: if the Central Hypothesis is false, then, for a given study object, to what degree and why is it false? The first is what Juhász-Nagy calls the Deviation Question, and answering this in totality, for all species, will lead us to a quantitative description of life on Earth. Which species is present where and when, and how does its density fluctuate in space and time? This is a description of patterns, and doing this is a prerequisite to the attempt to answer the second basic question of ecology, the Causative Question: why do the detected patterns exist?

It is not difficult to see that the Deviation Question can be approached and to a certain degree, also answered by using qualitative or categorical variables: is a species rare or common, present or not, at a given location? However, the really helpful answer is quantitative, including the size of distribution areas, densities, and density changes in space and time. Thus numbers are of core importance in ecology. Ecology is a quantitative science.

Notice also that the Deviation Question can be studied on its own, without invoking its Causative twin. Contrary to this, the Causative Question cannot be studied in the absence of its Deviation twin, and the answer to this latter one is a necessary condition before we can turn to studying the Causative Question.

When attempting to answer the second basic question in ecology, the importance of rates becomes quickly evident as well. Take invasions, for example. The impact of an invasive organism crucially depends not only on the "how far?" question. It is easy to see that the "how fast?", i.e. the rate of spread is an equally important factor to influence the final impact of an invasive organism. In some cases, measuring the rate will trigger questions that will shed light on very surprising facts and relationships.

I would like to illustrate the above with examples from Australian herpetologist and ecologist Rick Shine's new book, devoted to the invasion of the cane toad (*Rhinella marina*) in Australia (Shine, 2018). Cane toads were introduced to Australia as biological control agents against insect pests of sugarcane, in 1935. It was one of the big mistakes in the history of biological control. The toad proved to be a very generalist predator, favoured by disturbance and landscape modifications done by people. For example, even after it started to spread, and people realised the ecological problems it creates, the prediction was that this amphibian, tough as it is, still will not be able to spread much under dry, semi-desert conditions. In spite of this expectation, there seemed to be not much slowing down in the rate of spread when the toads reached the drier areas of Australia. This happened because people transformed the landscape by building dams, creating ponds and drinking pools for their farm and domestic animals, as well as introducing electricity to remote locations where the streetlights attracted arthropods, conveniently concentrating food for toads.

In a most interesting twist, measuring the rate of cane toad spread lead to recognising a new form of evolution. The rate of spread of cane toads in Australia has increased over time – which is an answer to a Deviation Question. This lead to a causative Question: why did this happen? The answer is: the individuals at the invasion front today have longer legs, a more linear direction of movement (but also a reduced reproduction rate and compromised immune system) than their conspecifics in areas invaded long ago. Individuals on the areas far from the invasion front do not have these characteristics. Those at the front have become very efficient dispersers, at some cost to other aspects of their biology. Museum specimens collected from the dispersal front in earlier times also have shorter legs. But how could this speeding-up happen? The answer is (retrospectively) simple. The animals at the front, when it comes to reproduction, meet individuals that have similar characteristics. The fast individuals near the invasion front mate with the fast ones (the slow ones are way behind and thus not available as mating partners), and out of that, gradually faster and faster individuals develop. This spatial sorting (Shine *et al.*, 2011) is now recognised as an effective evolutionary mechanism.

Cane toads also possess glands that produce very strong toxins. Potential predators in South America, in their area of origin, either avoid them or are immune to the toxin. Not so, however, many "toad-naive" Australian predators, especially reptiles. Goannas, big varanid lizards are apex predators in Australia, with a vast range of prey. They eagerly attacked and ate cane toads, but they dined with fatal consequences – they usually did not survive. This lead to a classic meso-predator release phenomenon: the smaller predatory lizards, earlier prey for the goannas and thus having reduced densities, now became more abundant, with reverberating consequences for the communities that now lost their top predator. Some, for example the northern blue-tongued lizard (*Tiliqua scincoides*) have also become victims of their prey. But a closer examination brought forward a strange phenomenon. Blue-tongued lizards living in Brisbane, with a long history of coexistence with the toads, became sick after eating a toad, but did not die. Fine, they may have adapted to the new situation. But the blue-tongued lizards of eastern Australia that never had the exposure to cane toads seem also to be resistant to the toad poison. Why? The answer may lie in a very unexpected corner, also linked to invasion. The succulent plant of Madagascar, *Bryophyllum delagoense*, called "mother of millions", was earlier introduced to Australia as a garden plant. It quickly became invasive (not for nothing has it got its name). Their flowers are also consumed by blue-tongued lizards that have a rather catholic diet. The plant happens to produce a toxin that is chemically very similar to the cane toad toxin. Blue-tongued lizards living in eastern Australia have been long exposed to the toxin, via the mother-of-millions plants, and only the progeny of individuals tolerant of this toxin are alive today. Thus, blue-tongued lizards, through a sheer accident of evolution and invasion history, have become cane toad-toxin resistant as well.

Densities, rates and time: their eternal dance, alone or in combination are that create the fascinating living world around us.

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