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Ecology's dark matter: The elusive and enigmatic niche

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Abstract

Ecologists are often frustrated that their universe, populated by strange and wilful creatures, seems fuzzy and unpredictable. Physicists, in contrast, seem to have it much better. But that's because we usually focus on Newtonian physics. In fact, physicists seem happy to live with all kinds of strange beasts, including dark matter, something they have never seen, but which they nevertheless believe makes up most of the matter in the universe. Here I argue that niches are ecology's dark matter. We are embarrassed by them, because we do not quite know what they are, and yet their presence can be universally felt; otherwise, ecological communities, like galaxies without dark matter, would simply collapse. I describe how we could potentially better describe these dark shapes that haunt our science and why this is important. In particular, I present the outline of a method for demonstrating whether or not plant species have complementary resource-use niches; something that has been difficult to show unequivocally. The presence of such resource-use niches would put to rest once and for all the notion of species equivalence and the neutral world that this assumption entails. I conclude that ecologists should take a leaf out of the physicists' book and accept that the continued search for the esoteric niche is a legitimate and central (if frustrating) part of ecology.

Zusammenfassung

Ökologen sind häufig frustriert, weil ihre Welt, bewohnt von merkwürdigen und eigenwilligen Kreaturen, unscharf und unvorhersagbar erscheint. Im Gegensatz dazu scheinen es Physiker viel besser zu haben. Aber das ist so, weil wir uns gewöhnlich mit Newtonscher Physik befassen. Tatsächlich scheinen Physiker zufrieden mit allen möglichen seltsamen Geschöpfen zusammenzuleben, einschließlich der Dunklen Materie, etwas, was sie nie gesehen haben, von dem sie aber dennoch glauben, dass es den Hauptteil der Materie im Universum repräsentiert. Hier vertrete ich die Auffassung, dass Nischen die Dunkle Materie der Ökologie sind. Nischen bringen uns in Verlegenheit, weil wir nicht genau wissen, woraus sie bestehen, und dennoch spüren wir ihr Vorhandensein überall. Andernfalls würden Ökosysteme, ganz wie Galaxien ohne Dunkle Materie, schlichtweg zusammenbrechen. Ich stelle dar, wie wir möglicherweise diese dunklen Formen, die in unserer Wissenschaft umhergeistern, besser

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beschreiben können und weshalb das wichtig ist. Insbesondere stelle ich den Entwurf einer Methode vor, mit der gezeigt werden kann, ob oder ob nicht Pflanzenarten komplementäre Nischen der Ressourcennutzung haben, etwas, das nur mit Schwierigkeiten unzweideutig demonstriert werden kann. Die Existenz solcher Nischen der Ressourcennutzung würde ein für allemal die Auffassung von der Äquivalenz der Arten und die neutrale Welt, die diese Vermutung nach sich zieht, zu den Akten legen. Ich schließe, dass sich die Ökologen die Physiker zum Vorbild nehmen und akzeptieren sollten, dass die fortgesetzte Suche nach der esoterischen Nische ein legitimer und zentraler (wenn auch frustierender) Teil der Ökologie ist.

Keywords: Niches; Neutrality; Niche overlap; Plant community ecology; Resource competition

The niche problem

Physics envy is widespread among ecologists. Most of us secretly long for a Newtonian world with a set of laws that would allow us to make accurate predictions about the natural world and its frustrating inhabitants. But physics too has its problems. Take dark matter. Physicists believe that roughly five-sixths of the universe is made out of this invisible stuff – not because they have seen it or been able to conjure it up in the lab – but because dark matter provides the necessary gravity to spawn galaxies and keep them spinning at their observed rates. The visible matter, it turns out, just does not pack enough punch. In short, physicists believe in dark matter because they have to; their model of the universe simply makes no sense without it.

Similarly, I believe in niches – not because I have seen them – but because without them the ecological universe does not make sense. Niches are necessary because they provide stabilisation, without which ecological communities collapse. Specifically, niches cause species to limit themselves more than they limit others – and from this fundamental principle a diverse world teeming with species can emerge and flourish. The only other possibility is a neutral world in which the differences we observe among species have no real consequences (Hubbell 2001) – an assumption that seems at odds with everything we know about both physics and biology (Purves & Turnbull 2010). Because species limit themselves more than they limit others the observable effect of niches is negative frequency dependence. This means that as a species becomes commoner (more frequent), the individuals belonging to that species experience more competition and this reduces the population growth rate. In contrast, individuals of rare species experience reduced competition, and hence their populations will tend to increase. This intraspecific feedback is the key to ecological diversity, as it prevents any one species from dominating the community at the expense of others; but it can only occur when niches are present, otherwise there is no advantage when rare and no disadvantage when common (Chesson 1991, 2000; Adler, HilleRisLambers, & Levine 2007).

Indirect evidence for niches

Indirect evidence for niches, in the form of strong intraspecific density dependence, is widespread. Even studies of tropical trees (where diversity is highest and all species, relatively speaking, are rare) have demonstrated that intraspecific density dependence regulates population growth (Volkov, Banavar, Hubbell, & Maritan 2009; Comita, Muller-Landau, Aguilar, & Hubbell 2010). Although this is not definitive proof of negative frequency dependence, it's certainly suggestive. More ambitious recent work has even succeeded in manipulating seed inputs to simulate the effect of removing niches from communities. Sure enough, niche removal causes a rapid loss of diversity (Levine & HilleRisLambers 2009), which is exactly what we expect if niches are necessary to maintain diversity.

If niches can be inferred from natural communities, why the continued doubt over their existence? Like dark matter, direct observations of niches are lacking, which makes them inherently unsatisfactory. For example, rather typically for ecology, niche definitions often seem to do little more than reveal the extent of the problem. The most famous niche definition is the *n*-dimensional hypervolume, a term that would not be out of place in The Hitchhiker's Guide to the Galaxy (Adams 1979). Hutchinson (1957) coined this term and illustrated the concept with the example of squirrels. He suggested that the squirrel's niche could be defined as a rectangular box with three axes representing temperature, branch density and food size. If the parameters of a forest lie outside this box, then squirrel populations cannot persist. This description certainly conjures up a charming image, but how do we relate this niche concept to the negative frequency dependence outlined above? And how much success have we had identifying the niche axes in the real world, particularly for plant species?

The problem with plants

In truth, plant ecologists have a much more difficult job than their zoological colleagues because plants just do not