



INVITED VIEWS IN BASIC AND APPLIED ECOLOGY

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 frustrierender) Teil der Ökologie ist.

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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

have the same range of feeding opportunities. If species utilise different food resources then clearly their niches would not overlap extensively and they will tend to limit themselves more than they limit others. In contrast, most plants rely on a few non-interchangeable inorganic soil resources, plus sunlight, water and carbon dioxide, so the scope for partitioning resources seems limited in the extreme (Tilman 1982). However, despite the apparent difficulties, some enterprising studies have revealed that plants sometimes use different forms of nitrogen (McKane et al. 2002), root at different depths (Berendse 1982) and partition the growing season into early- and late-season specialists (Hooper & Vitousek 1998). This kind of resource specialisation should have the desired effect of concentrating competition within species, and hence creating the all-important frequency dependence that regulates populations and maintains diversity.

Direct evidence for plant niches?

One of the most important sources of evidence for plant niches has come from a relatively new area of ecology: biodiversity experiments. In these experiments, the number of plant species is experimentally manipulated in order to assess the effect of diversity on various ecosystem outputs, such as productivity (Hooper & Vitousek 1997; Hector et al. 1999; Tilman, Reich, & Knops 2006). Most experiments find that average biomass increases with the number of species, but originally ecologists considered that this could be due to two different processes (Huston 1997; Loreau 1998). First, if high-yielding species tend to be competitively dominant, then as diversity increases the chance of including a high-yielding species also increases (sometimes called the sampling effect). Second, higher diversity increases the opportunities for niche differentiation, hence more diverse mixtures might utilise the available resources more completely. As a way to solve this controversy, a new method, the additive partition, was developed by Loreau and Hector (2001). The additive partition separates the contribution of selection effects – where high-yielding monoculture species dominate mixtures – from complementarity effects – where the gains of some species in mixture do not appear to be entirely bought at the expense of others. Such complementarity effects are generally thought to arise when species do not use identical resources, hence the gains of one species do not come at the expected cost to its competitor. Hence the demonstration of widespread complementarity effects (Cardinale et al. 2011) seems to support the idea that plants do indeed have different resource niches, and further that this niche differentiation occurs at small spatial scales (most biodiversity experiments use plots that are just a few square metres, and often less). But, can we accept the presence of complementarity effects as evidence for resource-use complementarity among plant species?

We highlighted the problem with this interpretation in a recent paper (Turnbull, Levine, Loreau, & Hector 2013). We used a simple model of belowground resource competition

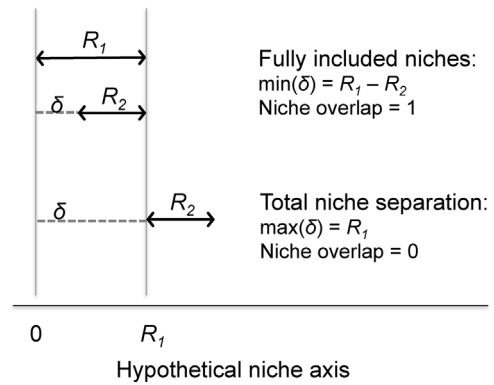


Fig. 1. Schematic of niche overlap. The displacement (δ) of species 2 from species 1 along the hypothetical resource axis varies from a minimum of $R_1 - R_2$ (fully included) to a maximum of R_1 (completely non-overlapping).

in which each species grows in monoculture according to a logistic equation with a resource uptake rate, θ , and a final biomass, R , which reflects the size of the total resource pool the species can access. If plants differ in the size of these resource pools, then complementarity effects arise even when the second species only has access to a resource pool that is completely nested within the first; i.e. when niches are included. Included niches are rather at odds with the term complementarity, as this usually means that each species can access something that the other cannot. Thus the widespread presence of positive complementarity effects in biodiversity-function experiments could simply reflect the fact that species have access to nested subsets of a single large resource pool. Such nested niches, despite giving complementarity effects in the short-term, do not allow stable coexistence, and hence do not support diversity in the long term. Hence the existence of positive complementarity effects is not conclusive evidence that plants utilise resources in complementary ways.

Expanding the model

So is it possible to provide more direct evidence that plants use resources in complementary ways? First, consider a pair of species competing for a belowground limiting resource, R . The precise nature of the resource is unknown, but imagine that the setting is simplified; hence there are no other trophic levels or negative soil feedbacks to complicate the picture. As for the previous model, R_i defines the size of the resource pool that the i th species can access. Now consider that the resource pool accessible to each species is only some subset of the total, and that it has some spatial location along the hypothetical resource axis. This might represent the depths over which species can extract resources, or it might be something less tangible: competition for belowground resources is poorly understood, so it is possible that plants perceive differences in the availability of belowground resources that are still unclear to us. For the two-species case, only a single

axis is required (although adding a third species might entail an additional axis and so on). We denote the species with the larger resource pool, species 1, and arbitrarily locate its resource pool between 0 and R_1 . If we assume that $R_2 \leq R_1$ then the location of R_2 relative to R_1 can be specified by a single parameter, the displacement, δ , that varies from a minimum value signifying fully included niches, to a maximum value signifying entirely non-overlapping niches (Fig. 1). We can then define the degree of niche overlap (o) as $1 - \delta$ and represent it on a scale between 0 and 1.

Competition between the two species occurs only for the shared resource pool (R_{shared}) defined as the region along the resource axis where R_1 and R_2 overlap:

$$R_{\text{shared}} = R_1 - \delta \quad (1)$$

We assume that each unit of resource removed by either species is converted with the same efficiency into biomass; hence the creation of a new unit of biomass of either species removes the same amount of resources overall. However, to create a new unit of biomass of either species, we further assume that resources are drawn equally from all parts of the resource pool available to that species; hence a new unit of biomass of species 1 will come partly from the shared pool and partly from the resource pool that only species 1 can access. The effect of adding a new unit of biomass of species 1 on species 2 is therefore simply the ratio of the size of the shared pool (R_{shared}) to the size of the total resource pool available to species 1. Hence $\alpha_{ij} = R_{\text{shared}}/R_j$. Notice that, if $R_1 \neq R_2$ then $\alpha_{12} \neq \alpha_{21}$. The intraspecific competition coefficients (α_{ii}) are always 1, because by definition, these resources can only come from the resource pool available to species i . To simulate biomass in a mixture of species i and j we use a discrete-time logistic formulation which gives a daily growth increment ($I_{i,t}$) for each species of

$$I_{i,t} = \begin{cases} \theta_i M_{i,t-1} \left[\frac{R_i - (\alpha_{ii} M_{i,t-1} + \alpha_{ij} M_{j,t-1})}{R_i} \right] & \text{if } I_{i,t} \geq 1 \\ 0 & \text{if } I_{i,t} < 0 \end{cases} \quad (2)$$

where θ_i is the resource uptake rate of species i . The model is iterated daily during the growing season to predict the end-of-season biomass of both species from any initial condition.

This model is of course very similar – although not identical – to the classical Lotka–Volterra model of competition, but it makes a different assumption about the way resources are supplied and taken up. The classical Lotka–Volterra competition model is couched in terms of individuals and assumes that the population grows to equilibrium through a process of births and deaths with high levels of individual turnover. However, many herbaceous plants grow in highly seasonal environments, where their biomass is severely reduced at the end of the growing season by cutting or burning, and a high fraction of the resources taken up during the growing season are lost. In the spring, resources are available again, and individuals grow once more. But this process mostly involves the growth of individuals; turnover is normally

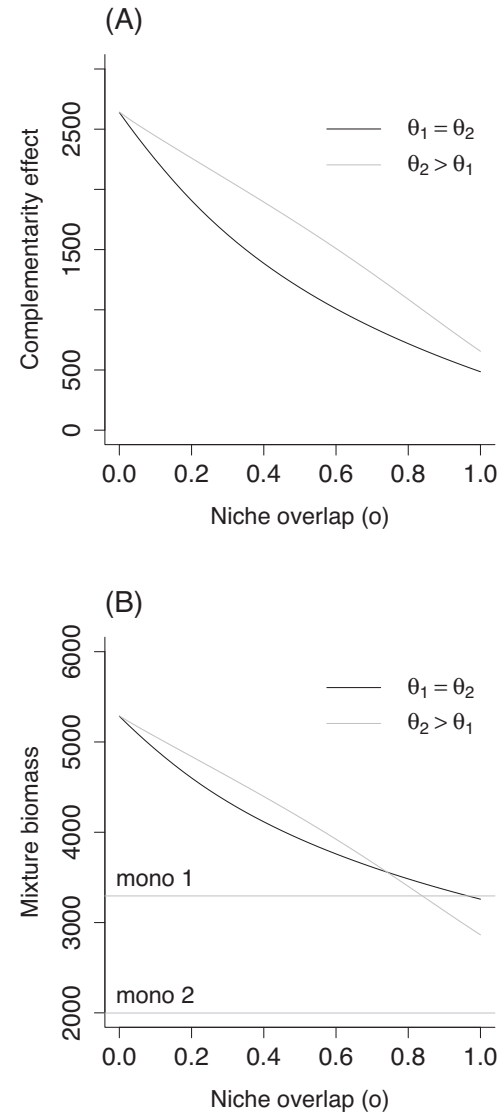


Fig. 2. The effect of increasing the niche overlap on the complementarity effect (A) and the combined biomass of the mixture (B). The species differ in the size of the resource pools they can access ($R_1 > R_2$) but either have the same resource uptake rates ($\theta_1 = \theta_2$; black) or there is a trade-off between the resource uptake rates and the size of the resource pool that species can access ($\theta_2 > \theta_1$; grey). In the second case, transgressive overyielding does not occur until the degree of niche overlap drops below some critical value (in this case ~ 0.8). The absence of transgressive overyielding does not therefore necessarily signify a lack of resource-use complementarity.

low and confined to the beginning and end of the growing season when new seedlings appear. During the growing season, it seems reasonable to assume that resources taken up by either species cannot be lost again (even when individuals die, it's unlikely that they could decompose quickly enough to provide resources to their competitors); hence when $R_1 \neq R_2$, negative growth increments are not allowed. This change in a key assumption means that the coexistence criteria of the Lotka–Volterra model of population dynamics

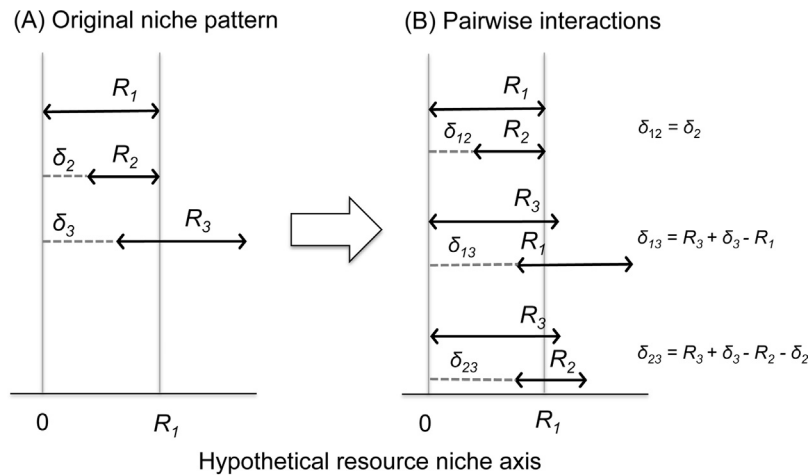


Fig. 3. Schematic of niche overlap among three species along a single hypothetical axis (A). Because we never know how many axes are required to represent the hypothetical niches of multiple species, it is easiest to first estimate the overlap between all pairs of species separately (B). A maximum likelihood estimation of the displacements on a single axis might then reveal that it makes similar predictions to the pairwise estimations, and of course requires fewer parameters.

cannot be applied. The long-term outcome of competition (not shown here) would require using the respective biomass of each species at the end of the growing season to reseed the next generation: an approach we used in a previous paper to show that a trade-off between the uptake rate, θ , and the total resources accessed, R , can allow coexistence of species with nested niches (Turnbull et al., 2013).

By simulating growth of a 2-species mixture with $R_2 \leq R_1$ over a range of values of δ , we see that as the degree of niche overlap increases, the complementarity effect and the biomass of the mixture both decline (Fig. 2). As previously demonstrated, the complementarity effect is positive, even when the niche overlap = 1 (i.e. niches are fully included; Fig. 2A). However, although we might always expect to see transgressive overyielding (where the mixture outperforms the best monoculture) for all values of niche overlap < 1, this is not the case if the species that can access more resources in total (higher value of R) has a lower resource uptake rate (lower value of θ ; Fig. 2B). In this case interspecific competition for the shared resource pool can reduce the growth of the higher yielding species to such a degree that the biomass of the mixture is lower than the biomass of the highest yielding species in monoculture. Thus transgressive overyielding – often regarded as the gold standard for niche complementarity – need not be observed, even when species have complementary resource-use niches. This brief analysis therefore confirms that neither the complementarity effect nor transgressive overyielding provide unambiguous tests of resource-use complementarity.

Estimating niche overlap

Here I consider how we might estimate the degree of resource niche overlap in a real ecological experiment. This

would be most appropriate for a simplified setting in which other confounding niche axes are less likely to operate. I illustrate the method by simulating monocultures and 2-species mixtures from a theoretical three-species community whose patterns of resource niche overlap can be represented on a single hypothetical axis. The niche of species 2 is included within the niche of species 1, but the niche of species 3 is offset, indicating some degree of niche complementarity with species 1 and 2 (Fig. 3A). In addition, the three species have different resource uptake rates (θ_i) and they differ in the size of the resource pool they can access (R_i ; Fig. 3A). These parameters can be estimated by growing each species in monoculture and fitting an appropriate non-linear regression equation to the resulting biomass data through time – in this case the three-parameter logistic (not shown; but see Paine et al. 2012 for details).

We can then use these parameter values to estimate the degree of resource niche overlap between all pairs of species in mixture by assuming that resource uptake rates (θ_i) and the size of the potential resource pool (R_i) do not change between monocultures and mixtures. We treat each pair of species separately because in reality we do not know whether the niches of more than two species can be adequately represented on a single hypothetical axis, but each pairwise interaction can always be represented in this way (see Fig. 3B). Thus for each pair of species, we estimate the degree of niche overlap by first fixing the niche of the species with the larger resource pool (higher R_i) between zero and R_i on the hypothetical resource axis. We then locate the niche of the competitor species along this axis by estimating its displacement from zero (δ ; Fig. 3B). For any value of this displacement, we can then calculate: (1) the size of the shared resource pool (R_{shared} ; Eq. (1)); (2) the interspecific competition coefficients; and (3) the predicted mass of species 1 and 2 in mixture (Eq. (2)). Comparison of these predictions

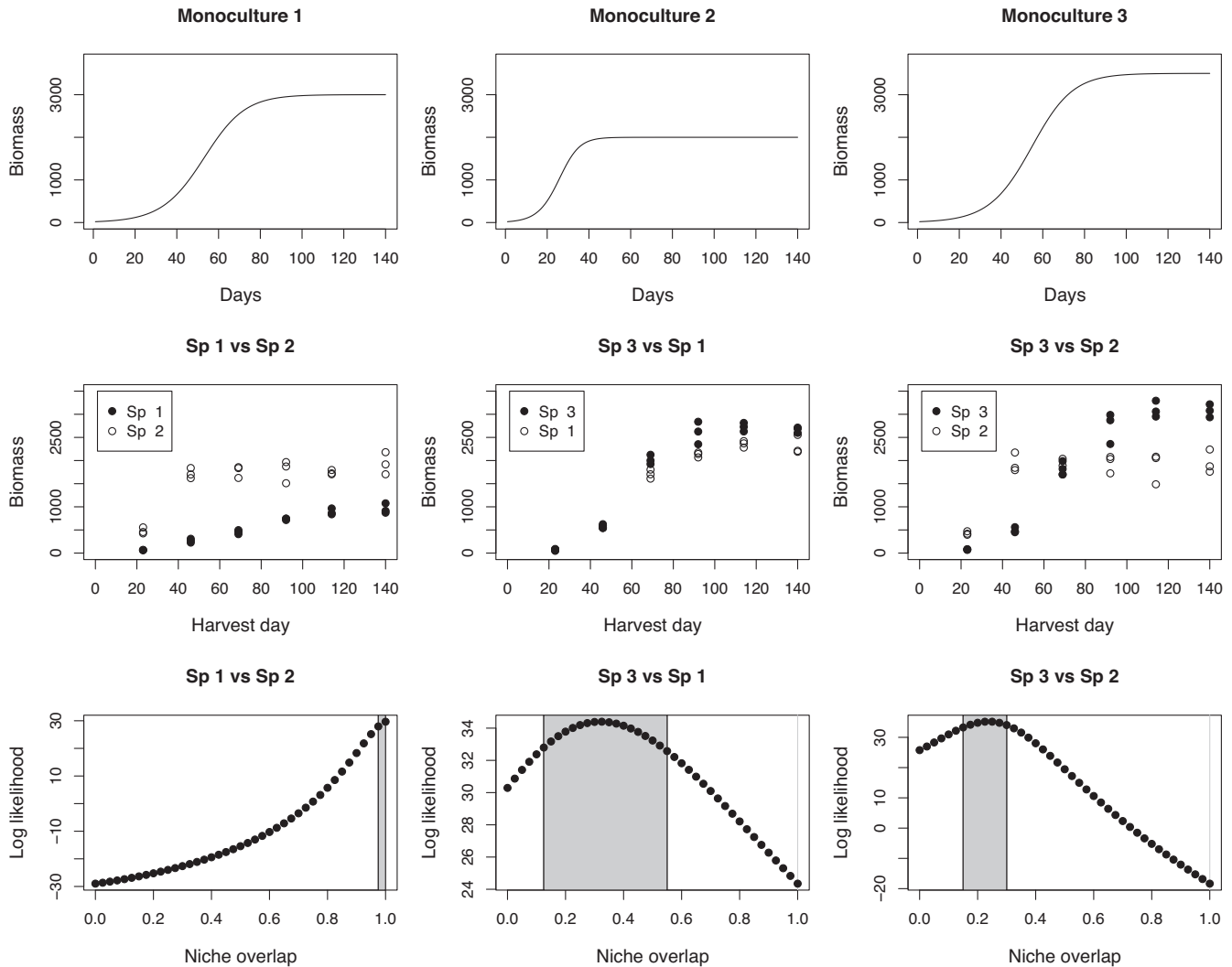


Fig. 4. Hypothetical results of competition between pairs of species from the three-species community illustrated in Fig. 3. *Top row:* monoculture growth curves. *Middle row:* samples from the three pairwise mixtures, drawn from a normal distribution with mean equal to the predicted value and standard deviation equal to one-tenth of the mean. *Bottom row:* Results of a model-fitting exercise where the niche overlap is systematically shifted between 0 and 1, and the likelihood of the data recalculated. Models within 1.92 likelihood units of the maximum likelihood are considered equivalent and shaded in grey.

to the observed biomass of species in mixture enables us to determine the most likely value of the displacement, δ . This procedure is then repeated for each pair of species.

I first simulated monocultures and the three two-species mixtures using parameters corresponding to those depicted in Fig. 3A ($R_1 = 3000$; $R_2 = 2000$; $R_3 = 3500$; $\theta_1 = 0.1$; $\theta_2 = 0.2$, $\theta_3 = 0.1$; $\delta_2 = 1000$; $\delta_3 = 2000$) to reconstruct the pairwise interactions. The monoculture growth curves for each species are shown in Fig. 4 (top row). I used a growing season of 140 days and an initial mass for each species in mixture of 10. For the mixtures, I added measurement error to all values by drawing observations from a normal distribution with mean equal to the predicted value and standard deviation equal to one-tenth of this value. For each mixture, I drew three observations at each of six regularly spaced time intervals over the growing season (Fig. 4; middle row). To estimate the niche

overlap I looped over 40 different values of the niche displacement, δ_i , between the minimum and the maximum value, for each pair of species. For each value of the niche displacement, the predicted values are used as the explanatory variable in a linear model, where the observed data are the response. In each case we can obtain goodness-of-fit criteria, such as the r^2 or the likelihood, which can then be plotted against the niche overlap (Fig. 4; bottom row). The method recovers the degree of niche overlap between the three pairs: revealing that the niche of species 2 is included within species 1, but that the remaining two pairs have a high degree of niche complementarity. How well the method would work in reality would depend on the quality of the data obtained, for example, the number of harvests and the number of replicates, and of course the degree to which the model assumptions are met.

Advantages of this approach

The method outlined here potentially allows direct estimates of resource niche overlap among plant species using simple growth experiments, which the current best methods are unable to do. The method also does not require precise knowledge of the limiting resources, or their direct manipulation. The method also provides separate estimates of likely fitness differences, in the form of resource uptake rates and resource pool sizes, which are inferred from biomass data collected in monoculture. These traits are not confounded with the degree of resource niche overlap, but are also important in determining whether or not species are likely to coexist. While the underlying model is clearly phenomenological, once parameterised it may allow insight into mechanism. For example, difference in uptake rates, resource pool sizes and the degree of resource niche overlap can all potentially be separately related to species traits or the degree of genetic similarity.

Although further development of the method may require maximum likelihood techniques, I believe the basic method could be implemented with conventional statistics. The method only really requires the fitting of non-linear growth curves, which is not difficult (see for example, Paine et al. 2012) coupled with a basic programme to compute and adjust the size of the displacement values, implement competition over the growing season using Eq. (2), and compare predicted to observed values. The method also allows differences in germination times and germination success to be easily incorporated and their impact to be evaluated, which is otherwise difficult within a conventional framework. Although I have only provided a sketch here of how the method might be implemented, this could be further refined. Methodological details that require further attention include: (1) whether and how to propagate error in the estimation of uptake rates and resource pool sizes when estimating niche overlap; (2) whether and how to estimate a one-dimensional niche axis with each species represented by a single displacement value to be compared to predictions from a pairwise analysis.

Conclusions

The nature of niches is as fundamental to ecology as dark matter is to physics, and our current understanding is similarly obscure. However, while physicists have been eager to set up massive arrays of ‘dark detectors’, ecologists have instead become embroiled in endless debates about whether or not niches even exist. While Stephen Hubbell’s formal neutral theory stands as a great intellectual achievement, it is perhaps a good time to move on. Niches are a frustrating but central part of ecology and we need to continue to refine our efforts to quantify and understand them. The method outlined here is clearly only one way of doing this, and continues a phenomenological tradition stretching back

to Lotka–Volterra. Others argue – quite legitimately – that better mechanistic understanding is the only way forward. Whatever the precise choice of methodology, let us hope that ecologists can give up arguing about their existence and concentrate on shedding more light on the dark matter of niches. Then, perhaps, we can finally leave our physics envy behind.

Acknowledgements

I thank the editor and two reviewers who supported the idea to write a rather unconventional article. The other two reviews made it clear that not everyone will enjoy it. The topic of niches is enormous, and the point of this article was not to provide an exhaustive treatment. However, clearly it draws heavily on many works and discussions that I could not include. In particular I would like to thank: Andy Hector, Jonathan Levine, Drew Purves, Forest Isbell, Deborah Vogt and Caroline Farrior for helping me to develop this article and the method described here. However, they should not be held responsible for any problems or inaccuracies.

References

- Adams, D. (1979). *The Hitchhiker’s guide to the galaxy*. Pan Books.
- Adler, P. B., HilleRisLambers, J., & Levine, J. M. (2007). A niche for neutrality. *Ecology Letters*, 10, 95–104.
- Berendse, F. (1982). Competition between plant populations with different rooting depths III. Field experiments. *Oecologia*, 53, 50–55.
- Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., et al. (2011). The functional role of producer diversity in ecosystems. *American Journal of Botany*, 98, 572–592.
- Chesson, P. (1991). A need for niches. *Trends in Ecology & Evolution*, 6, 26–28.
- Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, 31, 343–366.
- Comita, L. S., Muller-Landau, H. C., Aguilar, S., & Hubbell, S. P. (2010). Asymmetric density dependence shapes species abundances in a tropical tree community. *Science*, 329, 330–332.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M. C., Diemer, M., Dimitrakopoulos, P. G., et al. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Hooper, D. U., & Vitousek, P. M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302–1305.
- Hooper, D. U., & Vitousek, P. M. (1998). Effects of plant composition and diversity on nutrient cycling. *Ecological Monographs*, 68, 121–149.

- Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton: Princeton University Press.
- Huston, M. A. (1997). Hidden treatments in ecological experiments: Re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449–460.
- Hutchinson, G. E. (1957). Population studies – animal ecology and demography – concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, 22, 415–427.
- Levine, J. M., & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity. *Nature*, 461, 254–257.
- Loreau, M. (1998). Separating sampling and other effects in biodiversity experiments. *Oikos*, 82, 600–602.
- Loreau, M., & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72–76.
- McKane, R. B., Johnson, L. C., Shaver, G. R., Nadelhoffer, K. J., Rastetter, E. B., Fry, B., et al. (2002). Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415, 68–71.
- Paine, C. E. T., Marthews, T. R., Vogt, D. R., Purves, D. W., Rees, M., Hector, A., et al. (2012). How to fit nonlinear plant growth models and calculate growth rates: an update for ecologists. *Methods in Ecology and Evolution*, 3, 245–256.
- Purves, D. W., & Turnbull, L. A. (2010). Different but equal: The implausible assumption at the heart of neutral theory. *Journal of Animal Ecology*, 79, 1215–1225.
- Tilman, D. (1982). *Resource competition and community structure*. (Mpb-17). Princeton University Press.
- Tilman, D., Reich, P. B., & Knops, J. M. H. (2006). Biodiversity and ecosystem stability in a decade-long grassland experiment. *Nature*, 441, 629–632.
- Turnbull, L. A., Levine, J. M., Loreau, M., & Hector, A. (2013). Coexistence, niches and biodiversity effects on ecosystem functioning. *Ecology Letters*, 16, 116–127.
- Volkov, I., Banavar, J. R., Hubbell, S. P., & Maritan, A. (2009). Inferring species interactions in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 13854–13859.

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