Spatial structure creates community-level selection for nutrient recycling

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Nutrient cycling is a ubiquitous feature of ecosystems at all scales, allowing productivity to rise beyond the limits set by external nutrient inputs. Nutrient cycling occurs as a side-effect of the metabolism of a diverse set of species that each performs a step in the recycling loop. Recycling loops can be large and involve many steps. At each step the possibility exists for 'side-reactions' in the form of species with metabolisms that consume an intermediate metabolite but do not create the product needed to complete the recycling loop. Also, at least some of the biochemical reactions in any closed recycling loop must be endergonic (energy-consuming) and thus recycling loops may be vulnerable to invasion or parasitism by species that consume intermediates but do not produce costly products needed to close the loop. The possibility of such destabilising side-reactions appears to conflict with the apparent stability and ubiquity of nutrient recycling in nature.

Here we propose that the ecosystem-level autocatalysis provided by nutrient recycling offers a productivity benefit that can be selected at the level of the biological community, provided that certain conditions are met: (1) the benefits of recycling must be localised so that they preferentially accrue to participants, (2) metacommunity structure must be such that multi-species communities can propagate intact. We use an idealised model of a simple microbial ecosystem (Boyle et al, submitted) to show that spatial structure can be sufficient to provide these conditions and allow community-level selection (Williams and Lenton, 2007a, 2008) to stabilise and promote nutrient recycling.

The model is an individual-based evolutionary simulation of a microbial community composed of three species which interact via their metabolic products. The community is distributed across multiple patches arranged in a ring topology to give an approximation to a 1D spatial environment. Each patch is internally well-mixed and connected to its neighbours on either side by a slow rate of diffusive mixing. Three chemical substrates are consumed/produced in the metabolism of the three microbial species. All species are assumed to be identical apart from their pattern of resource utilisation, i.e., no species has any competitive advan-
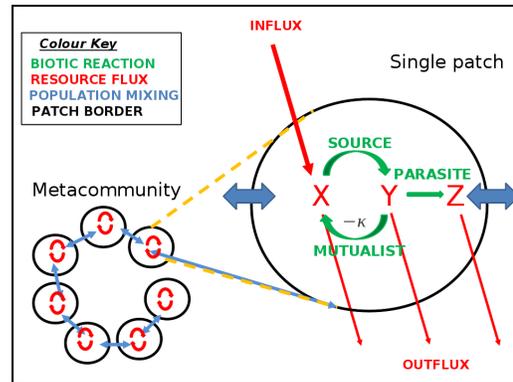

Figure 1: Patches are internally well-mixed and connected (in a ring topology) by a slow rate of diffusive mixing. Each patch is supplied with nutrient substrate X at a uniform rate. The "source" species consumes X and produces a secondary substrate Y. The "mutualist" species consumes Y and regenerates X (incurring growth rate cost κ). The "parasite" species consumes Y and produces substrate Z, which is not consumed by any species.

tage other than from the relative availability of their respective metabolic substrate. The "source" species consumes substrate X and produces substrate Y as a waste product. The "mutualist" species consumes substrate Y and regenerates substrate X as a product. The "parasite" species consumes substrate X and produces substrate Z. Since we assume that the reactions $X \rightarrow Y$ and $Y \rightarrow Z$ are exergonic (energy-releasing), the reaction $Y \rightarrow X$ must therefore be endergonic. Thus the mutualist species incurs an energetic cost which we implement as a growth rate penalty κ. The level of κ at which both mutualists and parasites coexist (i.e. are equal competitors) quantifies the strength of community-level selection for recycling, since coexistence implies balanced selection pressures at the individual level (for parasites) and the community level (for mutualists).

Each patch is supplied with substrate X at a steady rate, while all material substrates are removed from each patch by a slow rate of dilution. Thus in the absence of any microbial
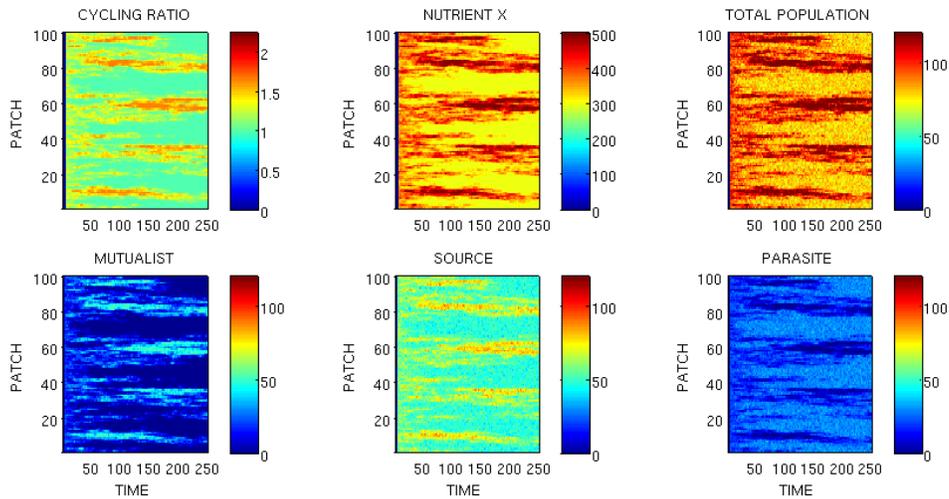
Figure 2: Example of model results showing spatial patterns in a system of 100 patches. Over time (horizontal axes) a heterogeneous distribution of species and resources over space (vertical axes) emerges from the initially homogeneous distribution. Nutrient cycling ratios are positively correlated with high density of mutualists (since this species regenerates resource X) and patch-level productivity, and negatively correlated with parasite density. Global coexistence of mutualists and parasites is stabilised by patch-level fecundity selection for recycling based on between-patch gradients in community productivity, which counteracts the within-patch advantage of the parasite.

populations the system would equilibriate with a fixed concentration of X and zero concentrations of Y and Z. The microbial community is initialised with a uniform distribution of individuals from each species. Microbes can diffuse to neighbouring patches with low probability at each timestep. There is no material mixing. Microbes grow dependent on the availability of their required substrate and reproduce by fission when their biomass reaches a fixed threshold. Microbes can die from starvation when their biomass drops below a critical threshold or stochastically with low probability (serving to represent all other causes of mortality). The system is numerically integrated using Euler's forward method.

Analytic and numerical results show that for any non-zero cost of recycling (i.e. any $\kappa > 0$) parasites always exclude mutualists within a single isolated patch. Yet spatial simulations show sustained coexistence of mutualists and parasites. Mutualist frequencies in local patches are positively correlated with nutrient recycling and patch productivity. The mechanism for global coexistence of mutualists and parasites is patch-level fecundity selection; patches with higher frequencies of mutualists have higher total productivity and hence export more individuals (of all kinds) to neighbouring patches, counteracting the within-patch advantage of parasites. This is confirmed by mutualist extinction and loss of recycling when patch productivity is normalised to remove between-patch productivity gradients. Varying the spatial heterogeneity of the system by varying the between-patch mixing rate shows that recycling rates (and hence global productivity) are positively related to the 'patchiness' of the sys-

tem; low positive mixing rates that maximise spatial heterogeneity also maximise recycling. Removing spatial structure by implementing perfect between-patch mixing recovers the single-patch result of mutualist exclusion and no recycling.

The community-level selection mechanism we propose is not necessary for the formation of nutrient recycling loops in nature, which can be easily formed by aggregation of metabolically diverse species that each gain a selfish benefit from the biochemical transformations they conduct (Williams and Lenton, 2007b). However, the synergistic benefits of recycling permit community-level selection to stabilise and promote recycling, even in cases where participation incurs an individual-level cost. This finding suggests a number of testable predictions: (1) nutrient recycling should be favoured in spatially structured environments such as soils and microbial biofilms, (2) community-level productivity benefits can stabilise costly trophic mutualisms in spatially structured environments, and (3) species with complementary metabolisms should evolve traits that promote their spatial association.

References

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