Journal Club

The pond-life is telling us something

Have you ever tried to give a simple, convincing explanation about why diversity increases with productivity from the poles to the equator, but that it tends to peak at intermediate productivity levels when you compare different plots within the same landscape? 'It's all a question of scale' is the most likely phrase to explain it (away). That the relationship between species diversity and ecological productivity changes with scale has long been recognized – the key question here is why.

Jonathan Chase and Mathew Leibold have recently explored these ideas in ponds [1], where they studied primary productivity (estimated as the amount of algal biomass accumulation on artificial substrates) and diversity (estimated as the number of species of animals and primary producers caught in sweeping nets). When comparing different ponds in the same area (local scale), they found a hump-shaped relationship between diversity and productivity. Diversity was higher in ponds with intermediate productivity, and lower in ponds with either low or high productivity. They then made comparisons at the regional scale, comparing different watersheds, each containing three individual ponds. This time, the relationship between diversity and productivity was linear and positive. The more productive watersheds were the ones with higher diversity – but how is this so if productive ponds tended to have low diversity? The reason was that, in productive watersheds, each pond had relatively few species, but also shared very few of them, so that the number of species in the entire watershed has high. By contrast, ponds in less productive areas tended to have most species in common. In other words, the higher the productivity, the higher the species dissimilarity is among ponds.

The authors do not provide a clear mechanistic explanation for this, yet Chase and Leibold's article is interesting because it puts a finger on a new, well-defined component in the productivity–diversity equation: spatial heterogeneity. This is important if we consider that two of the largest impacts of humans on diversity are increases in productivity owing to nutrient loading, and habitat modification by either homogenizing landscape mosaics or creating them. The authors offer testable predictions about the joint impacts of these processes on diversity. If cultural eutrophication comes together with landscape homogenization, they say, then diversity should decrease, but if it comes together with increasing heterogeneity, diversity should actually increase. Of course, this does not apply to species that are typical of low-productivity habitats, which seem to be at a perpetual loss in our present and future world. Controversial? Definitely, but this paper offers clear, testable hypotheses that are easily proved right or wrong. That is just how science, and the whole issue of diversity and productivity, should make progress.

1 Chase, J.M. and Leibold, M.A. (2002) Spatial scale dictates the productivity–biodiversity relationship. *Nature* 416, 427–430

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The Digital Arch Model reconsidered

According to the Digital Arch Model (DAM), all limb bones are derived from a single cell condensation process. First, the condensation of one proximal bone is formed (humerus in the arm, and femur in the leg), which subsequently branches to form two bones (ulna and radius in the arm, and tibia and fibula in the leg). The digits then branch off from the condensation of the ulna or fibula. However, two articles [1,2] have now challenged this model.

Wagner and Chiu [1] contest convincingly that not all digits are derived from the single condensation process that produces the ulna or fibula. Cohn *et al.* [2] support this conclusion with further examples, some of which are only incompatible with DAM in its strictest sense, i.e. that all digit condensations are induced by the initial condensation, but are compatible with DAM if a wider meaning is applied, i.e. as based on the model of Oster *et al.*, in which the width of the limb bud determines the condensation process. The development of digits from the tip of the limb bud, independent of proximal limb structures, is an example of this. Other examples mentioned by Cohn *et al.* are incompatible with this wider interpretation of DAM, for instance the development of digits in the absence of the ulna (ulnar agenesis). The results of Cohn *et al.* on the independent development of proximal and distal limb structures are in agreement with the recent rediscovery of the mosaic nature of limb development.

The deserved enthusiasm of the past few decades for the regulative powers of organizing centres in limb development has overshadowed the mosaic pre-pattern that appears to be present in the early limb bud. Many older studies, for instance that by Stephens and McNulty in 1981 and the classic ones by Saunders, indicate the impossibility of DAM as well as the relatively mosaic nature of limb development. However, it is possible to merge old embryological data with new molecular data: for example, Chiang *et al.* [3] conclude that organizer signals, such as *Sonic Hedgehog*, act upon a mosaic pre-pattern that is present in the early limb bud. The research on limb development continues to provide many exciting results, including the insight that DAM appears, alas, to be of limited value in explaining such development.

1 Wagner, G.P. and Chiu, C. (2001) The tetrapod limb: a hypothesis on its origin. *J. Exp. Zool.* 291, 226–240
2 Cohn, M.J. *et al.* (2002) Branching, segmentation and the metapterygial axis: pattern versus process in the vertebrate limb. *BioEssays* 24, 460–465
3 Chiang, C. *et al.* (2001) Manifestation of the limb prepattern: limb development in the absence of sonic Hedgehog function. *Dev. Biol.* 236, 421–435

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