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Chaos and scale

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In a recent issue of *TREE*, Ruxton¹ points out Csilling *et al.*'s results² concerning the dynamic of a theoretical metapopulation. They observed that a set of linked chaotic populations exhibits neither chaotic temporal variations nor spatial structuring. In other studies, the opposite result was observed³⁻⁶. Ruxton argued that this contrast could be explained by the fact that the timescales of reproduction and dispersal are decoupled in Csilling *et al.*'s model.

I think the absence of chaos in Csilling et al.'s study could be explained by a particular feature of their model. The modelled metapopulation occupies a landscape composed of a finite number of patches. All local populations have the same chaotic dynamic. Dispersal occurs when the population density exceeds a fixed threshold according to a stepping-stone rule. A fixed fraction of the population emigrates to neighbouring patches. The dispersal process is reiterated until all populations are below the threshold, then reproduction starts again. Since a given population may receive dispersers from other patches, numerous dispersal steps may occur in what Csilling et al. call a 'migration avalanche'. The individuals dispersing out of the landscape are lost, so that all excess individuals are eliminated. Such a dispersal process is an efficient density- dependent regulating mechanism. It should be interpreted as an inhibition of reproduction in local populations as long as at least one population density exceeds the threshold. Such a mechanism does not seem biologically realistic, since it assumes that reproduction in a population is not only directly influenced by its own density but also by densities in the other populations. May and his collaborators^{7,8} pointed out a long time ago that chaos occurs when there is a discrepancy between the timescales of reproduction and its density-dependent inhibition. In Csilling et al.'s model, the local density-dependent mechanisms are outweighed by the dispersal mechanism.

As rightly emphasized by Ruxton, the relative timescales of reproduction and dispersal are critical for the dynamic of a metapopulation when local dynamics are taken into account. Two mechanisms of dispersal can be distinguished as extremes along a continuum – the stepping-stone mechanism whereby the dispersers can reach only the neighbouring patches, and the 'common pool' of dispersers where the distance between patches is unimportant for the

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dispersers. This general scheme is further complicated by habitat selection when habitat quality varies among patches, and by the triggering mechanism of dispersal. The 'common pool' mechanism can have a strong stabilizing influence both on population and metapopulation dynamics even when local dynamics are strongly chaotic^{9,10}. This is achieved providing the dispersal rate is sufficiently low. When dispersal rate increases, it 'homogenizes' the whole system (as seasonality can do¹¹) so that chaos occurs. Stepping-stone dispersal contributes critically to metapopulation persistence^{3,4}; however, its stabilizing influence on global dynamics is yet to be demonstrated under realistic biological assumptions¹². Both dispersal mechanisms could be important for the same species at different spatial or temporal scales.

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