

Box 15.1 Assortative mating and spatial coexistence

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Coexistence in ecological communities is limited by the diversity of underlying resources and by the similarity of the species involved (Gause 1934; Hardin 1960; Hutchinson 1961; MacArthur and Levins 1967; MacArthur 1970; Armstrong and McGehee 1980; Yodzis 1989; Grover 1997). Such constraints restrict the *number* and *similarity* of incipient species that originate from adaptive radiation. Temporal fluctuations (e.g., Huisman and Weissing 1999; see also Lundberg *et al.* 1999 and references therein) and spatial structure (e.g., Pacala and Tilman 1994; Law and Dieckmann 2000) have been shown to allow a greater number of species to coexist.

Here we illustrate that spatial structure, in conjunction with mate recognition and local assortative mating, can also overcome limiting similarity; this allows ecologically equivalent species to coexist, albeit in spatial segregation. For this book and chapter there are two important implications:

- Speciation by sexual selection without ecological differentiation of the resultant species can lead to their long-term coexistence in segregated ranges. Flocks of ecological sister species are thus not necessarily ephemeral.
- When the spatial segregation of populations is promoted by processes associated with assortative mating, phase-1 and phase-2 species pairs, as described in Section 15.2, may already display distribution patterns that could be mistaken as evidence for their allopatric origin (Section 7.3).

To underpin these claims, we introduce a simple reaction–diffusion model to describe the dynamics of two ecological sister species along a one-dimensional spatial coordinate z (varying between 0 and 1, with reflective boundary conditions). Density regulation is of logistic type and acts on mortality, with carrying capacity density $K(z) = 1$. Birth rates are $b_1(z)$, $b_2(z)$; death rates at carrying capacity are $d_1(z)$, $d_2(z)$; and the coefficients of diffusive movement are $m_1(z)$, $m_2(z)$. The dynamics of local densities $n_1(z)$ and $n_2(z)$ are then described by

$$\frac{\partial}{\partial t} n_i(z) = b_i(z)n_i(z) - d_i(z) \frac{n_1(z) + n_2(z)}{K(z)} n_i(z) + \frac{\partial}{\partial z} \left[m_i(z) \frac{\partial}{\partial z} n_i(z) \right], \quad (a)$$

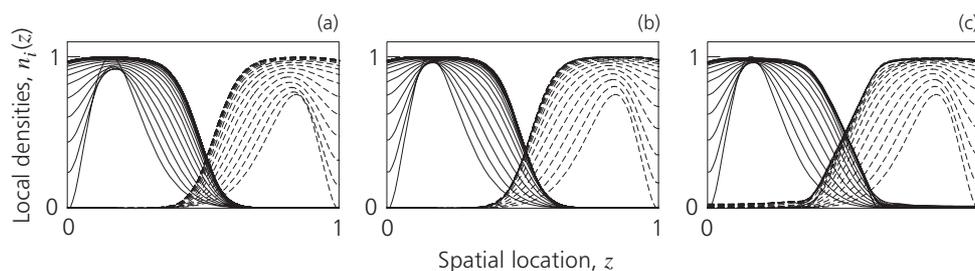
for $i = 1, 2$. The last term on the right-hand side is the standard expression for describing diffusion with spatially varying coefficients (Okubo 1980). No environmental heterogeneity is considered. In particular, we do not allow for the two species being differentially adapted to specific locations of their habitat (Lande 1982; Payne and Krakauer 1997), since this would render them ecologically nonequivalent. Importantly, the two sister species are assumed to be isolated reproductively by mating fully assortatively.

Assortative mating usually depends on differential behavior towards conspecifics and heterospecifics. To highlight the resultant effects, we consider four instances of this model:

continued

Box 15.1 *continued*

- *No coexistence with density-independent vital rates.* When all vital rates are independent of local densities, varying the relative abundance of the two sister species has no effect. The demographic and environmental stochasticity (not considered in the deterministic model above) results in one of them being ousted.
- *Coexistence with fecundity depending on the density of conspecifics.* If no suitable mates are locally available, the fecundity of a sexual species is bound to decrease, which causes an Allee effect. This stabilizes spatial segregation and coexistence, as shown in panel (a) below, in which continuous curves depict $n_1(z)$ and dashed curves $n_2(z)$ at different moments in time. Parameters: $d_i = 1$, $m_i = 0.001$, and $b_i(z) = \sqrt{n_i(z)}$.
- *Coexistence with mortality depending on the density of heterospecifics.* If interspecific interference is particularly vigorous (e.g., through territorial fighting), a high density of heterospecifics can induce extra mortality. With suitable initial conditions, this mechanism leads to spatial segregation and stable coexistence, as illustrated in panel (b) below. Notice that the dynamics of the two ecological sister species in isolation remain identical, and that the differential interference behavior considered here occurs only in response to differentiated mating phenotypes, retaining the species' ecological equivalence. Parameters: $b_i = 1$, $m_i = 0.001$, and $d_i(z) = 1 + n_{\tilde{i}}(z)$ with $\tilde{1} = 2, \tilde{2} = 1$.
- *Coexistence with mobility depending on the density of heterospecifics.* If a high density of heterospecifics induces increased mobility (a simple strategy for returning to the conspecific range and thus for finding mates), the heterospecific range is escaped rapidly. Panel (c) below shows the resultant pattern of segregated coexistence. Parameters: $b_i = 1$, $d_i = 1$, and $m_i(z) = 0.001 + 0.01/\{1 + \exp(50[0.9 - n_{\tilde{i}}(z)])\}$.



In nature, the three coexistence-enabling mechanisms described above are expected often to act simultaneously. For illustrative purposes, we have assumed reproductive isolation between the ecological sister species. More intriguing questions arise as to how the underlying assortativeness occurs evolutionarily and how the spatial dynamics of incipient species behave under intermediate degrees of assortativeness. These issues are touched on in Chapter 7, but in general still await systematic analysis.