



**Figure 1** Schematic representation of the four paradigms for metacommunity theory for two competing species with populations A and B. Arrows connect donor populations with potential colonization sites, shown as large boxes or ovals. Solid arrows indicate higher dispersal than dashed arrows and either unidirectional movement (single-headed arrows) or bidirectional movement (double-headed arrows). The degree to which a species is the competitive dominant in a site is shown by the matching of the smaller box or oval (denoting its habitat type niche) with the site symbol. The four paradigms illustrated are (a) patch-dynamics, (b) species-sorting, (c) mass-effects and (d) neutral. In (a) the patch-dynamics paradigm is shown with conditions that permit coexistence: a competition-colonization trade-off is illustrated with species A being a superior competitor but species B being a superior colonist; the third patch is vacant and could become occupied by either species. In (b) species are separated into spatial niches and dispersal is not sufficient to alter their distribution. In (c) mass effects cause species to be present in both source and sink habitats; the smaller letters and symbols indicate smaller sized populations. In (d) all species are currently present in all patches; species would gradually be lost from the region and would be replaced by speciation.

### The species-sorting paradigm

The second approach builds on theories of community change over environmental gradients (see Whittaker 1962) and considers the effects of local abiotic features on population vital rates and species interactions (Tilman 1982; Leibold 1998; Chase & Leibold 2003). In this perspective, local patches are viewed as heterogeneous in some factors and the outcome of local species interactions depends on aspects of the abiotic environment. If different species can only inhabit exclusive habitat types, the resulting metacommunity can be broken down into two independent ones, but

when individual species can inhabit multiple habitat types, there are a variety of outcomes that reflect how species interact at larger spatial scales. One way to model such dynamics is to extend assembly models (e.g. Law & Morton 1996) to systems with multiple patch types. Like many patch-dynamics models, this approach assumes that there is a separation of time scales between local population dynamics and colonization-extinction dynamics. Populations are assumed to go to their equilibrium behaviour (be it a stable point or a more complex oscillating or complex attractor) in between colonization events and before environmental perturbations that might cause extinctions