

Bock, C.E. and Riefls, R.E. 1983. Range size and local abundance of some North American songbirds: a positive correlation. *The American Naturalist* 122(2):295-299.

One of the earlier papers to positively associate distribution and abundance. Used data from 17,189 Christmas bird counts in North America from 1962 through 1971. This brief and accessible paper is not widely cited today, but is important from a historical perspective.

Brandle, M. and Brandl, R. 2001. Distribution, abundance and niche breadth of birds: scale matters. *Global Ecology and Biogeography* 10(2):173-177.

Discusses local, regional and continental scale. Tries to predict distribution based on 1) abundance, 2) niche breadth (Brown 1984) and 3) body size. Found no correlation between niche breadth and local abundance or between niche breadth and body size. The only correlation found was between regional distribution and local abundance in Kenya, and concluded that even that may be a sampling artifact (Hanski et al. 1993), although they took distribution and abundance data from different datasets to minimize this effect.

Brown, J.H. 1984. On the relationship between abundance and distribution of species. *The American Naturalist* 124:255–279.

Possibly the seminal paper on distribution abundance relationships. Very accessible and a great place to start with DA research (see also Hanski et al. 1993). Cited in numerous DA papers since 1984. Discusses the general theory of DA: 1) organisms with a higher local density have a greater range, and 2) distributions tend to be bell-shaped. Introduces the “niche breadth” hypothesis that suggests generalist species are able to make use of more habitats and are thus more widely dispersed and more locally dense. Introduces some novel ideas: 1) communities of species are not highly integrated and did not necessarily evolve to interact with each other, 2) “centrifugal speciation” where species on the edge of a distribution may evolve into new species through limited gene exchange with other members of the species. Refutes the hypothesis that species with a more narrow range should be able to take advantage of favorable local conditions and be more prevalent.

Falster, D.S., Murray, B.R., Lepschi, B.J. 2001. Linking abundance, occupancy and spatial structure: an empirical test of a neutral model in an open-forest woody plant community in eastern Australia. *Journal of Biogeography* 28:317-323.

Using Wright’s (1991) null model analysis as a starting point, concludes that aggregation is not the cause of a positive DA relationship. Analyzes the possibilities of over-dispersion and aggregation in woody species. Conducted small-scale study, suggested that species were fully sampled and that rare species were not underrepresented. Rejected the null model hypothesis; even without aggregation, a positive DA relationship would still exist.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M., Lawton, J.H. 2000. Abundance-occupancy relationships. *The Journal of Applied Ecology* 37(supplement 1):39-59.

Discusses declines and extinctions. Extensive literature review on DA relationships in plants, butterflies, fish, birds, mosses, protists, others; find many positive correlations and numerous exceptions. Conducted a common bird count over 24 years, looking at DA occupancy over time; found a wide range of variability in *Phylloscopus collybita* (chiffchaff bird). Looks at intraspecific and interspecific DA relationships and reviews several hypotheses that might explain these relationships. Found that the variation in abundance was better explained at smaller scales than larger scales. Discusses practical applications of DA analysis, including conservation, wildlife management, fisheries and pest management. Probably most useful as a literature review and comprehensive bibliography.

Guo, Q., Brown, J.H. and Valone, T.J. 2000. Abundance and distribution of desert annuals: are spatial and temporal patterns related? *The Journal of Ecology* 88(4):551-560.

Temporal (15 year) look at distribution abundance through summer and winter annual plants. Good review of Brown's (1984) and Hanski's (1982) metapopulation models. Found a positive relationship between local abundance, spatial distribution, and persistence in time, but the results came from a subset of annuals where granivore species (seed-eaters) were excluded from test plots. This might call into question ecological effects, eliminating the interspecific interaction addressed by Holt et al. (2004). One wonders if this temporal effect might have been observable without the exclusion of granivores if the experiment had been carried out with more samples.

Hanski, I. 1982. Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 38:210–221.

This paper introduced one of the early DA hypotheses, the core/satellite hypothesis where a few species appear at many sites (the core) and many species appear at only a few sites (satellite). This hypothesis has been widely discussed in literature, although perhaps less so in more recent literature than Hanski et al.'s (1993) three hypotheses. Hanski wrote that before the present time distribution was primarily the realm of biogeographers while abundance was the realm of ecologists. Reading between the lines, one might infer from Hanski's writing that this paper introduced the concept of DA relationships. There are two important premises in the core-satellite hypothesis: 1) regional population is important, and 2) stochasticity in regional dynamics is important. The reliance on stochasticity was criticized in later literature. Hanski introduces an important metapopulation concept, hypothesizing that emigration happens will before a site reaches carrying capacity. Hanski compares the core-satellite hypothesis to the r-K "species continuum", meaning the core-satellite distributions don't always look just like a distinct bimodal graph but more resemble a continuum.

Hanski, I., Kouki, J. & Halkka, A. 1993. Three explanations of the positive relationship between distribution and abundance of species. *Species diversity in ecological communities: historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 108–116. University of Chicago Press, Chicago, IL.

Probably the other place to start with DA research (see also Brown 1984). A very influential paper, as many later studies addressed the hypotheses introduced here. Provides comprehensive definitions of "distribution" and "abundance" used by later literature in varying contexts. Analyzes data from existing studies on many taxa. Introduces three hypotheses to explain DA relationships: sampling effect, metapopulation dynamics and ecological specialization (aka niche position or habitat availability). Finds evidence to support all three explanations, but finds most evidence for sampling effect and concluded that sampling effect cannot be ruled out as the source of a positive DA correlation. Suggests sampling has less effect at the "geographic" (large) scale and more effect at the smaller scales because many small populations will remain undetected. Metapopulation dynamics predicts distribution and abundance will vary over time due to environmental stochasticity. Suggests difficulties in testing Brown's (1984) niche breadth model to circular reasoning; this is addressed by Heino's (2005) use of two distinct samples. See the back of the book (available through Link+) for a complete bibliography.

Heino, J. 2005. Positive relationship between regional distribution and local abundance in stream insects: a consequence of niche breadth or niche position? *Ecography* 28:345–354.

This study makes excellent follow-on reading to Hanski et al. (1993) as it addresses the niche-based v. metapopulation models. Is it a coincidence that all these authors are Finnish? Heino samples stream insects and explains the importance of two separate datasets: 1) aquatic insects under study, and 2) aquatic insects and environmental variables across a much wider range (in this case Finland). The first dataset provides DA info while the second dataset supplies environmental niche info. This addresses Hanski et al.'s (1993) concerns about a single dataset being used to explain both a DA relationship and environmental niche(s) of (a) species. Discounted sampling effect as a confounding factor, and the reasoning is convincing. If Hanski et al.'s hypotheses are of interest to you, this adds much food for thought. The findings support Brown's (1984) niche breadth hypothesis and Heino also discusses Brown's (1984) range edge/range overlap or the notion that species mix can change depending on where you sample.

Holt, A.R., Warren, P.H., and Gaston, K.J. 2004. The importance of habitat heterogeneity, biotic interactions and dispersal in abundance–occupancy relationships. *Journal of Animal Ecology* 73:841–851.

This is the only lab study in this review of DA relationships and as such is well worth reading. Tested interspecific abundance-occupancy in a lab microcosm of protists and bacteria. Assessed the effects of biotic interactions and found that such interactions exert a strong influence on abundance-occupancy levels. Controlled for: dispersal v. no dispersal, heterogeneous habitat v. homogeneous habitat, biotic interaction v. no biotic interaction. Found no evidence of “rescue effect” discussed in metapopulation dynamics. Offers a very thorough discussion of habitat homogeneity and heterogeneity and the concomitant effects. Does a lab experiment eliminate (or at least significantly reduce) sampling effect discussed by Hanski et al. (1993)?

Johnson, C.N. 1998. Rarity in the tropics: latitudinal gradients in distribution and abundance in Australian mammals. *Journal of Animal Ecology* 67:689-698.

Discusses Rapoport’s Rule, that range size increases with higher latitude. Normalized for latitude and size of study area and concluded that tropical species have small geographic ranges and low abundance. Associated Rapoport Rule with niche breadth (Brown 1984); tropical species don’t experience much weather variance, don’t have to migrate as far and consequently have lesser ranges and abundances. May be of particular interest to biogeographers.

Soininen, J. and Heino, J. 2005. Relationships between local population persistence, local abundance and regional occupancy of species: distribution patterns of diatoms in boreal streams. *Journal of Biogeography* 32:1971-1978.

The only normative study of microorganisms in this review (see Holt et al. 2004 for lab study on microorganisms) and one of the few studies in this review (see also Guo et al. 2000, Gaston et al. 2000) looking at distribution and abundance through time as well as space. Demonstrated a positive correlation between abundance and persistence through time. Supports the core/satellite hypothesis (Hanski 1982) along a continuum as opposed to a bimodal distribution. Not particularly groundbreaking, but definitely of interest to those studying microorganism distribution or DA relationships across a wide range of organism types and sizes.

Thompson, K., Hodgson, J.G. and Gaston, K.J. 1998. Abundance-range size relationships in the herbaceous flora of central England. *The Journal of Ecology* 86(3):439-448.

This study surveyed 792 floral species in England, looking at DA correlations over many habitat types. Found no relation between range and abundance at the landscape level, but did find a relationship within a habitat type. Introduced “specialism” index and positively correlated increasing specialization of a species with reduced range. Weakly correlated increasing specialization with increased local abundance, contrary to the niche breadth (Brown 1984) hypothesis. This was an interesting paper well worth reading, and the specialism index is a useful concept.

Wright, D.H. 1991. Correlations between incidence and abundance are expected by chance. *Journal of Biogeography* 18(4):463-466.

Wright takes a contrarian view and takes to task earlier work (ex. Hanski 1982, Brown 1984) claiming that any correlation between incidence (distribution) and abundance isn’t meaningful and cannot be used to support a biological hypothesis without a comparison to a null model (see lit. review on null models Fall 2005 for a more complete discussion). Uses a Poisson probability distribution model in his analysis. Discusses the biological process of species aggregation (clumping) and suggests that at all empirical levels of aggregation, positive DA correlations are expected. Hanski et al. (1993) dismiss Wright’s Poisson model as ignoring effects of aggregation, but the dismissal suggests Hanski et al. didn’t choose to address the 2nd half of Wright’s paper. A short paper well worth reading if for no other reason than to witness a debate in the literature. Cited by many other authors.