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Software Notes

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RangeModel: tools for exploring and assessing geometric constraints on species richness (the mid-domain effect) along transects

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RangeModel is a computer application that offers animated demonstrations of the mechanism behind the mid-domain effect. The program also provides analytical tools for the assessment of geometric constraints in empirical datasets for one-dimensional domains (transects). The mid-domain effect (MDE) is the increasing overlap of species ranges towards the center of a shared, bounded domain due to geometric boundary constraints in relation to the distribution of range sizes, producing a peak or plateau of species richness towards the center of the domain. Domains may be spatial, temporal, or functional. RangeModel is a stand-alone, graphical-interface, freeware application for PC and Mac OS platforms.

Colwell and Hurtt (1994) first showed that the random placement of geographical ranges within a bounded spatial domain (represented by line segments placed at random on the unit line) yield a non-uniform pattern of species richness (line overlap) that under most conditions is characterized by a mid-domain peak in richness. Willig and Lyons (1998) and Colwell and Lees (2000) followed up with analytical models for one dimension, and Jetz and Rahbek (2001) and Bokma et al. (2001) developed two-dimensional models that produce analogous patterns. The mid-domain effect (MDE) is the increasing overlap of species ranges towards the center of a shared, bounded domain due to geometric boundary constraints. The effect is sensitive to the distribution of species' range sizes (the range size frequency distribution, RSFD) in relation to domain size (and shape, for two dimensions) (Dunn et al. 2007), but under most conditions produces a peak or plateau of species richness towards the center of the domain.

Many studies have since treated MDE models as null models, comparing model predictions with empirical patterns of species richness to assess the influence of geometric constraints, in combination with other drivers of species richness (reviewed and debated by Zapata et al. 2003, 2005, Colwell et al. 2004, 2005, Hawkins et al. 2005 and by Dunn et al. 2007; references compiled at <http://purl.oclc.org/RangeModel> – follow the MDE references link).

RangeModel (<http://purl.oclc.org/RangeModel>) is a free, easy-to-use, stand-alone, menu-driven computer application for Windows or Mac OS, dedicated to the study of MDE for one-dimensional domains, including elevational transects (Watkins et al. 2006), latitudinal transects (McCain 2003), distributions along rivercourses (Dunn et al. 2006), microspatial distributions along linear habitats (Tiwari et al. 2005), temporal or phenological distributions (Morales et al. 2004), and distributions along spatially discontinuous environmental gradients or niche axes (Lusk et al. 2006, Carranza et al. in press).

RangeModel serves several purposes. First, by animating the addition of randomly placed ranges on the screen, the program demonstrates graphically the mechanism behind the mid-domain effect and allows visual comparison of the effects of specifying different RSFDs and of stochastic variation among runs (Fig. 1). The user can either input an empirical RSFD and domain size or choose from several theoretical range/midpoint specifications, including bivariate uniform random range/midpoint distribution, uniform RSFD, uniform range midpoints, a one-dimensional equivalent of the spreading dye model of Jetz and Rahbek (2001), a specified constant range size, or a specified range-size minimum and/or maximum. The results are visually displayed in a plot of richness across the domain and in a range-midpoint plot (Fig. 1), and the click of a button shows a Stevens plot (mean range size across the domain, after Stevens 1989). The resulting RSFD and a plot of the distribution of range midpoints can also be displayed. Results from these simulations, like all other results from RangeModel, can be exported to a tab-delimited text file for formal analysis in a spreadsheet or statistical analysis application, if desired.

Second, RangeModel offers powerful tools for modeling and analyzing geometric constraints (MDE) in empirical datasets (Fig. 2). Two distinct models are supported, 1) a continuous model for continuous ranges defined on a

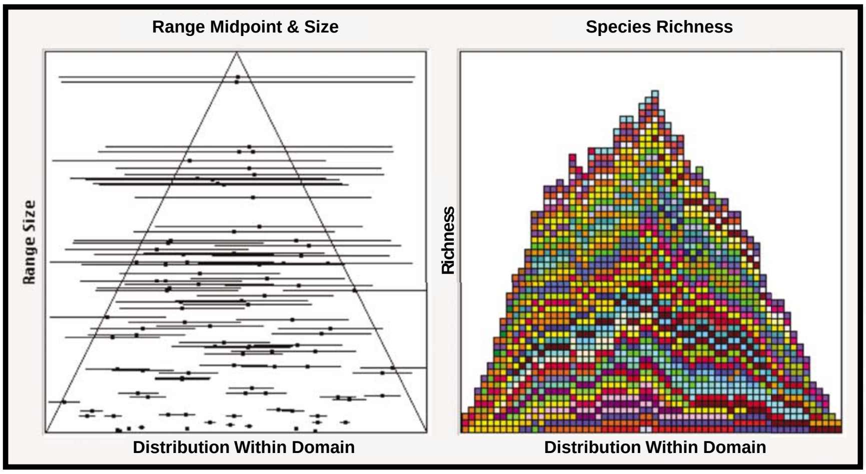

Fig. 1. RangeModel onscreen display of random placement of 100 geographic ranges within a bounded domain (bivariate uniform random range/midpoint distribution). The left panel shows a plot of range size (ordinate) vs range midpoint (abscissa), with ranges shown as line segments. The right panel shows the same information, but with the number of overlapping ranges on the ordinate (richness) vs position along the domain on the abscissa.

continuous domain and 2) a discrete model for ranges based on presence or absence of species at evenly (or approximately evenly) spaced, ordered sampling sites. For discrete data from sampling sites that are substantially uneven in spacing, the continuous model should be used. For both models, the program places each empirical range within the domain at random, without replacement, subject to the constraint that each range fit entirely within the domain (no range truncation).

In the continuous model (Bachman et al. 2004, Romdal et al. 2005), each range is treated as continuous between its endpoints. This approach requires the assumption that a species is present at intermediate sites where it has not actually been recorded – a process called range interpolation, which tends (rightly or wrongly, depending on true distributions between sampling sites) to increase the mid-domain peak of species richness in modeled patterns (Grytnes and Vetaas 2002). In some studies, ranges have

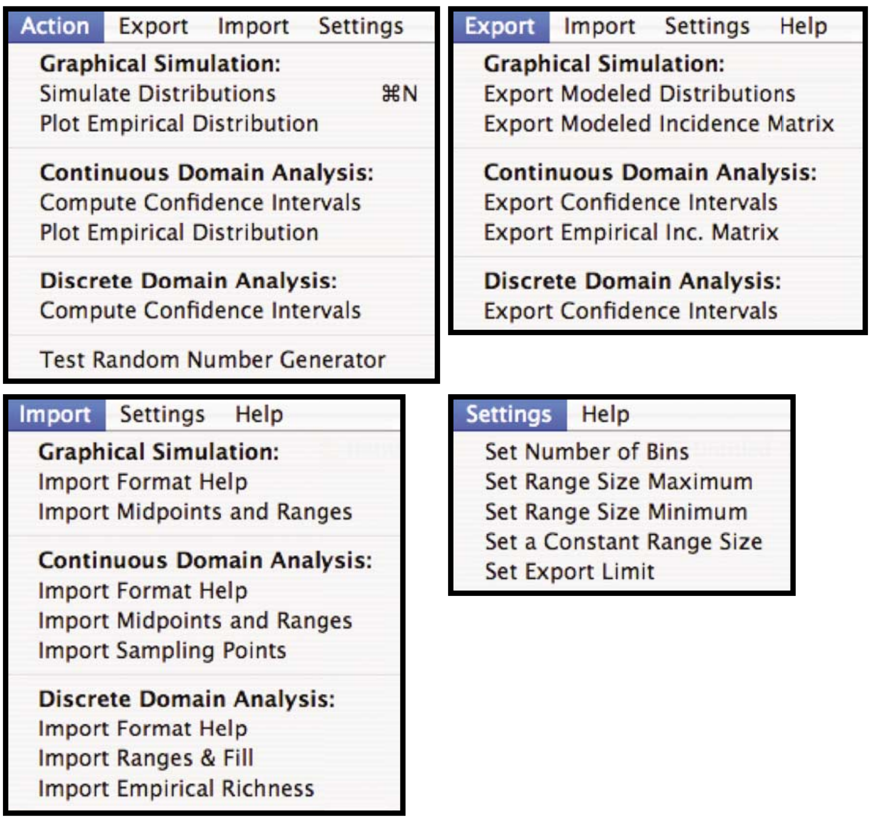

Fig. 2. RangeModel menus showing tools for simulating and analyzing distributions (Action menu), exporting results of simulations and analyses (Export menu), importing data for analysis (Import menu) and setting options (Settings menu).

also been extrapolated, when undersampling was suspected (Cardelús et al. 2006, Watkins et al. 2006, Brehm et al. 2007).

For the discrete model (Dunn et al. 2006), in contrast, the input data for each species include not only range endpoints (extreme occurrences), but also a count of the presences at intermediate sampling sites. Range size in this model is defined for each species as the endpoints (there may be only one, for a species that occurs at only a single site) plus all intermediate sites, whether the species was recorded at all intermediate sites, or not. Range fill is the total number of recorded sites for a species, including range endpoints. If range fill is less than range size, the range is porous, and the program randomly assigns absences to intermediate sites in the randomly placed range to match the fill of the empirical range. In this way, the total number of modeled occurrences exactly equals the total number of observed occurrences for each species, and any possibility of inflation of MDE due to false range interpolation is avoided. On the other hand, if the observed absences are false, MDE will be underestimated.

In addition to predicting the mean pattern of richness over a domain, RangeModel also generates 95% confidence intervals for mean richness across the domain, for any arbitrary number of randomizations of range placement (1000 is suggested), following the approach of McCain (2003) (Fig. 3). Examination of where the empirical richness points lie in relation to the confidence envelope can be instructive by revealing where empirical richness agrees with or departs from MDE-predicted richness along the domain (Brehm et al. 2007).

The program also computes Veech's (2000) statistic, which compares the entire observed distribution of richness across the domain to the expected distribution in a single test, treating MDE as a falsifiable hypothesis. Colwell et al. (2004) argue, instead, for treatment of MDE predicted richness (for example, the mean expected richness output by RangeModel) as a candidate explanatory variable in multivariate analyses or models, on an equal statistical footing with environmental and other variables (including habitat area), under a model selection approach. This treatment, which is strongly supported by theoretical developments showing how MDE interacts with environmental gradients (Rangel and Diniz-Filho 2005), has been successfully implemented in a number of empirical studies that relied on RangeModel (Cardelús et al. 2006, Dunn et al. 2006, Brehm et al. 2007, Sanders et al. 2007) as well as in several two-dimensional studies (Jetz and Rahbek 2001, Storch et al. 2006, Rahbek et al. 2007).

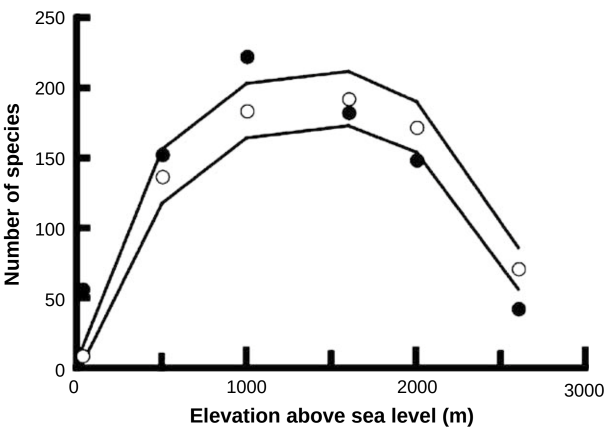

Fig. 3. Observed richness (solid points) and predicted richness (open points, with 95% confidence intervals) for 555 species of epiphytes recorded from the Barva Transect (30–2600 m elevation) in Costa Rica. The predicted richness and its confidence interval were computed by RangeModel by randomizing the placement of observed elevational ranges. (From Cardelús et al. 2006.)

Data input to RangeModel is in the form of simple, tab-delimited text files that can be prepared in a spreadsheet application. RangeModel offers a number of in-context help screens (especially regarding input formats, which depend upon which tools are to be used to analyze the data), plus an online user's guide, available at the RangeModel website (<http://purl.oclc.org/RangeModel>). Email support is available.

To cite RangeModel or acknowledge its use, cite this Software Note as follows, substituting the version of the application that you used for "Ver. 0":

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