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Appendix A from C. L. Parr et al., "Constraint and Competition in Assemblages: A Cross-Continental and Modeling Approach for Ants" (Am. Nat., vol. 165, no. 4, p. 481)

Modeling Ants at Baits

Description of Null and Competitive Model Types Used in the Simulations

Null Models

In these simulations, there were no rules restricting the number of ants at baits; thus, no structuring mechanism is implied. Individuals were assigned to species using all three (even, skewed, and realistic) abundance frequency distributions. In model *Null 1*, for a species to be classified as dominant, it had to meet both the abundance and monopolization dominance descriptors. In *Null 2a* and *Null 3*, a species was classified as a dominant based only on the mean abundance threshold (i.e., a species was classified as dominant if it had a mean abundance score of >3.2, but monopolization was not considered). In *Null 2b*, a species was classified as a dominant based only on the percentage of baits that were monopolized (i.e., a dominant species had to monopolize >22.9% of baits where it occurred, but the mean abundance score was not considered). Ants were assigned to baits using either a random, even bait distribution or a Poisson distribution (see table 1). Model *Null 2a* had an even bait distribution, while *Null 3* had a Poisson bait distribution, and the number of baits occupied was limited to simulate vacant baits observed in the field (i.e., varying bait occupancy).

Competitive Models

Competition was incorporated into the simulation using two rules. First, the number of species that could cooccur at a bait was restricted to four (based on the maximum number of species found at a bait during field baiting in Kruger National Park [KNP]) and second, if the abundance of any species at a bait was >20 (i.e., abundance score of >4), no other species were allowed to co-occur at the bait. All ants from other species at that bait were removed and returned to the pool to be reallocated to species and baits. The model did not allow for insinuators, that is, subordinate species that are able to coexist at baits with high numbers of dominants (see Wilson 1971). In all competitive models, dominance was determined using both mean abundance and monopolization dominance measures.

Patchiness in ant occurrence at baits was introduced into the model in two stages. First, model *Competition 1* limited the number of baits that could be occupied by ants (two to 15 baits depending on the model specification) while keeping the distribution at baits uniform and second, additional patchiness was introduced in model *Competition 2* such that the number of baits that could be occupied was limited (two to 15 baits), and ants were assigned to baits using a Poisson distribution (table 1). Although competition, which can create monopolization at baits, is factored into these models by setting the threshold for the abundance at which species cannot co-occur to >20 individuals (abundance score of 4), highly aggressive species may require only a few individuals to effectively control a bait. Thus, a further model, *Competition 3*, was based on *Competition 2* but simulated the effect of increasing competition by using thresholds of >5 and >10 ants per bait (rather than >20) to limit co-occurrence for the monopolization rule. Decreasing the threshold for abundance of ants necessary for monopolization thus simulates the effect of increasing competitive ability. In addition, in model *Competition 4*, the number of species allowed to coexist at a bait was altered (three and five species per bait rather than four species) to simulate the effect of increased competition via a different route in the model. For both models altering co-occurrence thresholds and species coexistence, simulations were run for both bait distributions, for all abundance frequency distributions, and for 15 baits using starting abundances of 250, 500, and 750.

Sensitivity Analyses

Sensitivity analyses for dominance thresholds were performed for models *Competition 1* and *Competition 2* (for even and Poisson bait distributions, respectively) using all three abundance frequency distributions (even, Poisson, and skewed) and 15 baits. Models were rerun with mean abundance score thresholds of 2.8 and 3.8 and with the monopolization percentage threshold set at 15% and 30%.

Recruitment Model

Because recruitment is a fundamental feature of ant communities (Hölldobler and Wilson 1990), some degree of recruitment needs to be included in the model. Recruitment was initially incorporated into the models via abundance frequency distributions for highly abundant species that recruit well and for species with low abundance that do not recruit well. However, to investigate recruitment of highly abundant species that do not recruit well and species with low abundance that do recruit well, a recruitment model was developed based on *Competition 1* and *Competition 2* (i.e., for both bait distributions). Recruitment (or assignment of ants to baits) was manipulated using a recruitment factor (RF), which was the number of conspecifics attracted to a bait for every individual of a species. The RF values were 1, 5, 10, and 20. Simulations were run for Poisson and skewed abundance frequency distributions and for 15 baits with a starting abundance of 750.

Model Results

Null Models

Random, unrestricted assignment of ants to baits means that monopolization of baits (according to the threshold specified in the model) does not occur (there will either always be at least one other species present at any given bait or abundance will be so low that the threshold of >20 individuals set for monopolization will not be reached). Hence, in models *Null 1* and *Null 2b*, there was no dominance. Thus, when there were no competitive rules, dominance could only be quantified using mean abundance score. Therefore, only models using mean abundance score are considered below.

In the null simulations, because there are no rules limiting dominance levels, the maximum dominance attainable was dependent on the starting abundance (and bait occupancy). At lower abundances, there were insufficient ants (once distributed among species and baits) for any ant species to be classified as dominant based on mean abundance score. When the starting abundance of ants (*a*) was sufficiently large, dominance could be attained, but it was considerably higher than observed in the field. With an even distribution, dominance was achieved only when the starting abundance of ants was very large (when a threshold $a > \sim 2,000$). For model *Null 2a*, when individuals were assigned to species using skewed and realistic distributions, the outcome was high species richness (13–14 species) and a range of dominance values from the minimum to very high (>90). Dominance increased with increasing abundance.

There was much greater variation in species richness with the null simulation that incorporated both types of patchiness (*Null 3*). With an even distribution, the abundance of ants required for dominance was low when bait occupancy was low (e.g., for dominance with five baits occupied, the minimum *a* value required for dominance was approximately 500). However, if all baits were occupied, dominance was possible only with very high abundances (figs. B1A, B2A). While dominance varied, species richness did not and remained at 14 species regardless of abundance of ants or bait occupancy.

For both skewed and realistic abundance frequency distributions, when bait occupancy was held constant, the effect of decreasing a was reduced dominance and lower, more variable species richness (fig. B1B, B1C; fig. B2B, B2C). As bait occupancy increased, dominance also tended to increase (fig. B1B, B1C). In addition, as the abundance of ants declined (fig. B2B, B2C), species richness also declined and was more variable. This effect was most pronounced for a skewed distribution.

Competition 1

As with subsequent models, dominance values of 0 were possible with any frequency distribution. Zero dominance values were a function of a; when a low starting abundance of ants was specified, there were insufficient individuals for the mean abundance score to be >3.2 and for a species' score a bait to be >4 (necessary to meet the monopolization rule). Thus, dominance values >0 did not occur because the dominance

descriptors were not met. For all frequency distributions, the effect of varying the abundance of ants was that dominance tended to increase with increasing abundance (figs. B3, B4; although there was sometimes considerable variation in species richness and dominance values for a given a).

With an even distribution, high species richness and low dominance were one possible outcome (where increasing both the number of baits occupied and abundance of ants elevated dominance and species richness but reduced variability in species richness; figs. B3A, B4A). This outcome was realized because only a very low number of baits (usually one) was monopolized. Another outcome using an even distribution was that with low bait occupancy, dominance and species richness were also low, and as occupancy increased, so did dominance and species richness. Thus, with all 15 baits occupied, dominance was high, and species richness ranged from six to 13 species. For a given bait occupancy, species richness values were always more variable than those for dominance, and the range of species richness values increased with the number of baits. This outcome was achieved because each bait was monopolized by one species, thus reducing species richness. However, with an even distribution, simulations indicating high dominance were unrealistic because the number of ant species was similar to the number of dominant ants and was always relatively high. High richness and dominance were a function of excluding the zeros when analyzing the dominance measures per species. Because species absences are excluded from the analyses when calculating dominance, an even distribution can result in the majority of (or all) species being dominant. This is extremely unlikely under natural circumstances and indeed makes the term dominant meaningless.

In the case of a skewed distribution, dominance was high, and species richness was low (fig. B4*B*, B4*C*), whereas the range of dominance values was much wider for a realistic distribution (fig. B3*B*, B3*C*), and species richness varied from low to 14 species. Species richness also declined with increasing abundance.

Competition 2

Using the *Null* and *Competition 1* models, it is possible to place data points only on the periphery of the unimodal dominance–species richness distribution found with field baiting data. Both patchiness measures (number of baits that are occupied and differential chance of these baits attracting ants) were used in this *Competition 2*. As with previous simulations, as bait occupancy increased (corresponding to decreased patchiness), dominance, and to a lesser degree species richness, increased (most noticeably with an even distribution; figs. B5A, B6A). None of the three abundance frequency distributions resulted in high dominance and low species richness. Intermediate to high dominance combined with low species richness could not be achieved using an even abundance frequency (figs. B5A, B6A). When dominance was low, the full range of species richness values was possible, but as dominance increased, species richness increased, and its variation declined. High dominance and high species richness were found when most or all species were dominant, which is highly unlikely in the field.

Using a skewed distribution, the dominance value did not exceed 80, and it was not possible to have high species richness and relatively low dominance (figs. B5*C*, B6*C*). Using a realistic distribution (figs. B5*B*, B6*B*), values of both dominance and species richness tended to be intermediate, with some simulations giving low dominance and low species richness, while others resulted in high dominance and high species richness. Five percent of these data points had dominance scores of >90 because, on occasion, several species per simulated baiting session met the monopolization descriptors. Increasing the monopolization threshold would reduce the number of baiting sessions with dominance scores of >90. As with *Competition 1*, high dominance required a combination of high ant abundance and high bait occupancy.

Competitions 3 and 4

Changing the number of individuals necessary for monopolization of a bait (figs. B7, B8) had a much greater effect than altering the rule restricting the number of species able to coexist at a bait (figs. B9, B10). The effect of increasing competition (i.e., reducing the number of individuals needed to monopolize a bait) was most pronounced for a realistic abundance frequency distribution using both bait distributions (figs. B7*B*, B8*B*). The result of increasing competition was a decline in species richness (even bait distribution) and reduced dominance (both bait distributions). With a realistic abundance frequency distribution and a Poisson bait distribution, when the number of species coexisting at a bait was increased, the result was increased dominance and species richness (fig. B10*B*).

Sensitivity Analyses

Sensitivity analyses for *Competition 1* in which mean abundance and monopolization thresholds were altered indicated that for all three abundance frequency distributions, the simulations were insensitive to changes in these values (figs. B11, B12). The same was true of *Competition 2* (figs. B13, B14).

Recruitment Model

Adding recruitment into the model made little difference to the overall result; simulations using different recruitment models showed little change from the original model without recruitment, and varying the recruitment factor (RF) also resulted in little effect (figs. B15–B18). For a species with a low abundance that recruits well, adding recruitment into the model made no difference to the end result (figs. B15, B16), and altering RF had very little effect except when there was an even abundance frequency distribution (fig. B15A) and an even bait distribution. Recruitment simulations for a species that is highly abundant but does not recruit well to baits indicated that there was little change from the original model without recruitment, and increasing RF (e.g., to 20) resulted in greater evenness between species, and consequently increased richness, although there was no noticeable alteration in dominance values (figs. B17, B18). Although the recruitment model is simplified, it indicates that recruitment has little impact on the modeling outcomes.

Literature Cited in Online Appendix

Wilson, E. O. 1971. The insect societies. Belknap, Cambridge.