

The Ghost of Competition Present

T. E. Miller,^{*} C. P. terHorst, and J. H. Burns

Department of Biological Science, Florida State University, Tallahassee, Florida 32306

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ABSTRACT: Communities have been viewed as the end product of an assembly process that results in increasing stability through time as progressively better competitors eventually dominate the other species that can emigrate from a regional pool. Previous work has explained species assemblages based on the traits of the successful species. We suggest that the traits of unsuccessful species in the regional pool may also be important for understanding which species are successful in communities. We constructed a simulation model to study what distinguishes stable, uninvadable assemblages from other possible assemblages from a regional pool of species. Our model demonstrates that both the interactions among the successful species and the interactions between these species and unsuccessful species attempting to invade the community contribute significantly to determining success in the final stable community. Understanding the structure of natural communities may require some knowledge of the unobserved “ghost” species that fail to establish in that same community yet still have significant effects on structure.

Keywords: community, invasion, migration, assembly, stability, catalytic species.

Introduction

Coexistence and diversity are among the oldest subjects in ecology, and a substantial body of theory is available from which to draw inference. Early studies (e.g., Hutchinson 1959; May and MacArthur 1972) predicted that species with low resource overlap (niche partitioning) were more likely to coexist. Low resource overlap was thought to result in low competitive interactions and higher growth rates, allowing species to grow quickly, monopolize resources, and exclude those species with lower growth rates (Chase and Leibold 2003). Niche partitioning therefore predicts weak competition among the successful species in a stable community (Kokkoris et al. 1999).

However, strong competition between successful species and potential invaders is thought to prevent invasion of communities and facilitate stability. Post and Pimm's (1983) influential study assembled model communities through migration of species into an “open” habitat (see

also Drake 1990*b*). This process of sequential invasion suggested that a community becomes less invadable as resources become more limiting, which selects for more competitive species. Law and Morton (1996) extended this approach and used the boundary where densities of all species remain positive and finite to quantify stability in different species assemblages. They concluded that the invasibility of communities goes through three distinct stages: invasion resistance first declines, then remains fairly constant for a long period of species sorting, and then increases quickly as the final stable community is achieved.

Case (1990, 1991) created communities of consumer species whose dynamics were described by simple Lotka-Volterra dynamics based on randomly determined species interaction matrices. Stable communities were created either by rejection of unstable species combinations or by manipulation of the carrying capacities of the species in the starting community. These communities were then “invaded” by species whose traits (interaction coefficients and carrying capacities) were drawn from the same distribution as those of the resident species. Case was able to demonstrate that invasion probability decreases with both the number of resident species and their mean interaction strength.

These studies and others demonstrate that two factors must be considered in determining why any particular group of species occurs in a given habitat. First, successful competitors may be those that interact less with each other, possibly through some form of niche partitioning. Second, successful species may have strong negative effects on later invaders, preserving stability. We suggest that a third factor must be considered: the traits of the species that continually attempt, but fail, to invade a community. If some successful species are included in part because they keep out particular invaders, then the traits of those unsuccessful invaders must be considered if we are to understand which species are successful. Case (1995) first noted this phenomenon as “surprising behavior from a familiar model.” We call the effects of unsuccessful species on the final stable community the “ghost of competition present” and suggest that such “ghosts” may have important implications for understanding natural communities.

^{*} Corresponding author; e-mail: miller@bio.fsu.edu.

We constructed a simple model to investigate how unsuccessful invading species influence which species are successful in communities. The intent of the model was to illustrate the potential importance of “ghost species” and not to mimic any specific natural community. We defined ghost species as those that had significant effects on community assembly but were themselves unsuccessful in the stable community. As in previous studies (especially Case 1990, 1991), a pool of species was allowed to invade an empty habitat, and assembly was followed until a stable and invasion-resistant community resulted. We then asked what traits distinguished the successful suite of species from other potential colonizers, that is, whether we could predict which species from the original species pool would form a stable, persistent assemblage. In particular, we quantified the importance of interactions between successful and unsuccessful species in determining which species make up the final community.

Modeling Methods

We used a computer simulation to construct pools of N competing species and allowed these species to migrate at a low rate into originally empty habitats. Such open dynamics are thought to be common in natural communities (Leibold and Miller 2004). Once in a habitat, each species could either grow in number or decline to extinction as a result of interactions with other species as determined by simple Lotka-Volterra competition equations. Species driven to extinction could reinvade at any later time with the original migration probability. This assembly process generally produced a stable, uninvasible group of two to four species after 50–150 generations. A community was judged to be stable if a suite of species persisted for 250 generations without further successful invasions (e.g., fig. 1).

Similar models have been shown generally to produce a single stable assemblage, regardless of assembly order (Case 1990, 1991), but alternate stable states were possible in our model. Alternate states have been the subject of both theoretical (May 1977; Post and Pimm 1983; Drake 1990a; Law and Morton 1993, 1996) and empirical (e.g., Drake 1991; Petraitis and Dudgeon 1999) studies and are not further discussed here. A small but significant proportion of runs (<6%) also resulted in semistable assemblages that were persistent until invaded by particular suites of invaders that disrupted the community but that did not form stable assemblages themselves. Although such invaders might be considered ghost species, we were interested in stable assemblages, and such runs were eliminated from the analyses below.

Our model is very similar to those used in many other theoretical studies (e.g., Taylor 1988; Case 1990, 1991; Law

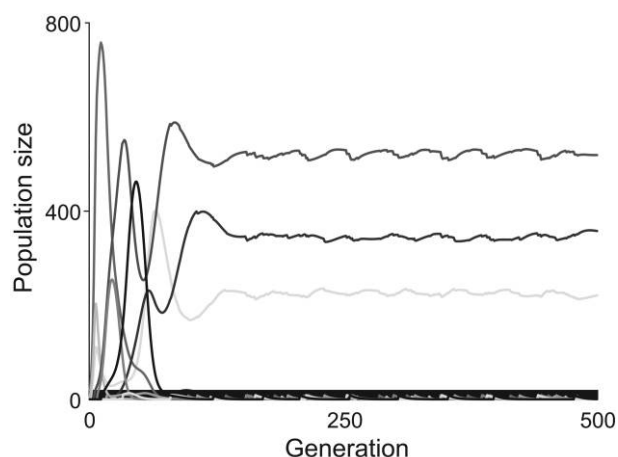


Figure 1: Example of one run of the assembly model, showing the population sizes of 10 species over 500 generations. Note increasing invasion resistance in the first 50 generations, followed by the continued attempts at invasion by unsuccessful species.

and Morton 1996): the basic growth equations are a discrete approximation to continuous Lotka-Volterra dynamics, and migration is stochastic at some fixed probability. Growth rates of individual species are given by

$$N_{t+1} = N_t \left(1 + r_i \frac{\sum \alpha_{ij} N_{jt}}{K_i} \right).$$

A species is declared extinct when its population drops below 0.1 individuals. The unique features of our model are that the pool of species remains constant and relatively small (maximum of 10) and that species can continue to reinvade after they are competitively excluded. Most previous models either create novel species for invasion (Case 1990, 1991) or the size of the pool of invasive species is either large or not stated (e.g., Post and Pimm 1983).

For each 10-species pool of potential colonists, values for interaction coefficients describing the effect of species j on species i (α_{ij}) were randomly drawn from a uniform distribution with a mean and range of 1.0. Varying the mean interaction strength confirmed the result of Case (1990, 1991) that increasing interaction strength decreases the likelihood of invasion. For convenience, the carrying capacities ($K_i = 1,000$) and intrinsic growth rates ($r_i = 1.0$) of all species were equal. The probability that a species would migrate into the community was 0.05 per generation for different trials; initial colonist population size was five individuals. Versions of the model varying the migration probability, K_i , and r_i and using different distributions for α_{ij} yielded similar results and are not presented here.

The goal of the analyses was to determine what distin-

guished stable, uninvadable assemblages from other possible assemblages. A 10-species pool of possible immigrants can produce 375 different one-, two-, three-, or four-species combinations, and of these, typically 50–90 are stable (have no positive eigenvalues; May 1973). Yet only a small number (usually one) of these possible combinations of species are produced by the immigration, interaction, extinction, and reinvasion process (e.g., Law and Morton 1996). For each run of the model, we partitioned the interaction coefficients from the pool of potential species into groups defined by species' membership (or lack of it) in the final stable community—a group of successful invaders (S) and a group of unsuccessful ones (U). To test the hypothesis that successful competitors are those that interact less with other successful species, we determined the mean interaction coefficients among successful species (SS). To determine whether the successful competitors had strong effects on the unsuccessful species, we also determined the mean interaction coefficients describing the effects of successful on unsuccessful species (SU) and of unsuccessful on successful species (US). The remaining coefficients described the effects of unsuccessful species on other unsuccessful species (UU). We generated 200 unique random stable communities and determined the four mean coefficients for each community. We compared the mean coefficients to the null expectation of 1.0 by determining the 95% confidence intervals of the overall means.

Pairwise associations between the values for SS, SU, US, and UU were determined as Pearson product-moment correlations. Reduced major axis regression (Bohonak and van der Linde 2004) was used to describe any significant relationships between effects for communities of different sizes (two, three, and four species).

Our simulations suggested that ghost species may commonly occur. To determine the mechanism by which ghost species might influence community structure, we conducted a second set of simulations. An additional 100 stable communities were generated, using a pool of 10 species whose interaction coefficients were determined randomly as above. We then reassembled each community after removing each of the unsuccessful species one at a time. If the removal of one unsuccessful species resulted in a new stable community, then that species was deemed to be a ghost species. We determined the percent of the stable communities that were found to be affected by ghost species, as well as the average competitive effect of (a) ghost species on previously successful species that were displaced from the original community ("displaced species"), (b) ghost species on newly successful species that were unsuccessful with the ghost present ("newly successful species"), and (c) newly successful species on displaced species.

Results

Most runs of the program produced similar patterns of community development. Species immigrated to the community and increased rapidly in abundance in the first few generations before competitive interactions among species slowed their growth (fig. 1). Generally, a period of significant transitions preceded development of a stable community of two to four species within 50–100 generations. This final community was usually resistant to any establishment by the constantly reimmigrating species from the pool of possible immigrants. This pattern of invasion, species transitions, and final invasion-resistant stability is consistent with similar models (e.g., Case 1990, 1991; Law and Morton 1996).

As expected, the mean interaction coefficients among successful species (SS) were always less than 1, consistent with niche partitioning; the mean value was 0.79 (fig. 2). Conversely, the mean SU effect was 1.07, significantly greater than 1, demonstrating that there are significant interactions between the successful and unsuccessful species. The mean US effect was 0.98, also significantly different from 1. Finally, the UU effects were not significantly different from the random expectation of 1.0 (fig. 2).

The SS and SU effects were significantly correlated, but only if the size of the stable community was taken into account (fig. 3A). For communities of two, three, or four

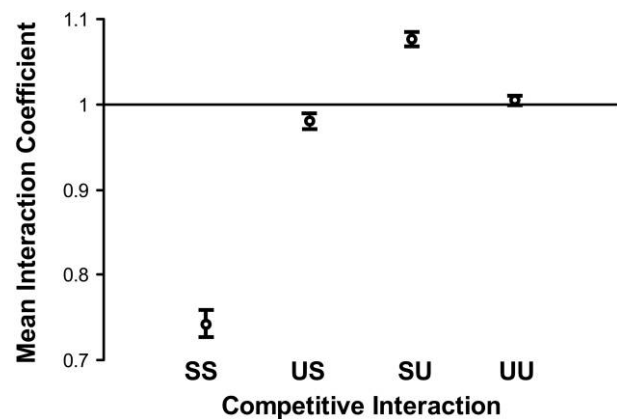


Figure 2: Mean interaction coefficients from different suites of species from the species pool, with 95% confidence intervals of the estimated mean. All initial coefficients were randomly drawn from a distribution with a mean and range of 1.0. The interaction coefficients can be broken down into effects of the successful species in the resulting community on the other successful species (SS), those of successful on unsuccessful species (SU), those of unsuccessful on successful species (US), and those of unsuccessful species on one another (UU). The simulation model was run 200 times, determining the mean SS, SU, US, and UU values each time. The estimated overall mean SS, SU, and US are significantly different from 1.0, while UU is not.

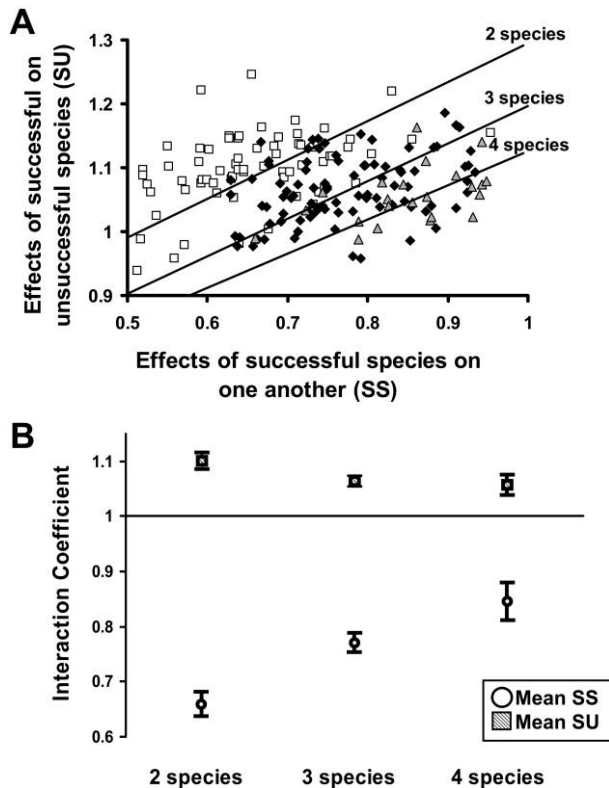


Figure 3: A, Association between SS and SU for stable communities of different levels of species richness. Values greater than 1 indicate relatively strong effects. Within each community size, SU and SS are significantly correlated (two species: $r = 0.43$, $P < .001$, $n = 73$; three species: $r = 0.39$, $P < .001$, $n = 99$; four species: $r = 0.45$, $P < .02$, $n = 24$). B, Mean SS and SU effects ($\pm 95\%$ confidence limits of the estimated mean) are shown for three levels of richness. SS effects increase and SU effects decrease with species richness.

species, SS increased significantly with SU. All other pairwise correlations between mean interaction types (SS, SU, US, and UU) were not significant. Mean values of SS increased significantly with species richness, while values of SU decreased significantly (fig. 3B).

Our second set of simulations was designed to test for the prevalence of ghost species more directly by allowing communities to assemble with each unsuccessful species removed one at a time. The simulations confirm the existence of ghost species, as 49% of communities contained at least one ghost species. Of those communities that contained a ghost species, 61% contained a single ghost species, 20% contained two ghosts, 10% contained three ghosts, and 8% contained four ghosts. The competitive effect of ghost species on those species displaced by ghosts was 0.88 and significantly less than 1 (fig. 4). However, ghost species had competitive effects of 1.15 (significantly greater than 1; fig. 4) on the species that establish when

ghost species are removed. Similarly, these newly successful species had competitive effects of 1.07 (significantly greater than 1; fig. 4) on those species displaced when ghosts were removed.

Discussion

When asked to explain the persistence of a suite of competing species in a particular community, many ecologists would probably begin by looking for patterns of resource-use partitioning among the constituent species. That is, they would begin with two assumptions: competing species must differ to coexist, and ecologists need only consider interactions among the species currently present. The first assumption has recently been challenged by neutral theory (Bell 2000; Hubbell 2001; Chave 2004). Here we challenge the second assumption as well. Our model demonstrates that interactions between the species currently in the community and the unobserved ghost species in the larger species pool may determine which species are successful in the final stable community.

The presence of ghost species should be of some concern for those attempting to understand current community patterns solely on the basis of extant species abundances (Case 1995). Ghost species were present in approximately half of our simulated communities, suggesting that the effects of unobserved species may be common in natural communities. Preliminary data from further model runs suggest that removing two unsuccessful species simultaneously can also result in similar ghost effects on the community. The two-ghost combinations occur in an additional 25% of our theoretical communities (C. P. terHorst and T. E. Miller, unpublished data), so that most of our model communities appear to be affected by ghost species.

Our model demonstrates that three conditions are required for a species to persist successfully in a stable community, yet only the first condition is generally appreciated by ecologists. A successful species must have weak interactions with other successful species (show low SS consistent with niche partitioning), interact strongly with potentially invading species (show high SU), but be influenced less by competition with those potential invaders (show low US). The last two criteria require consideration of the traits of those species not present in the final community, and these ghost species therefore can play a crucial role in determining community structure.

Although a successful species must meet the three criteria above, the necessity to meet one criterion may be alleviated by strength in another criterion. The significant relationship between SS and SU (fig. 3A) suggests that a species with very weak interactions with other successful species (very low SS) need only have moderately strong negative effects on potential invaders (moderately high

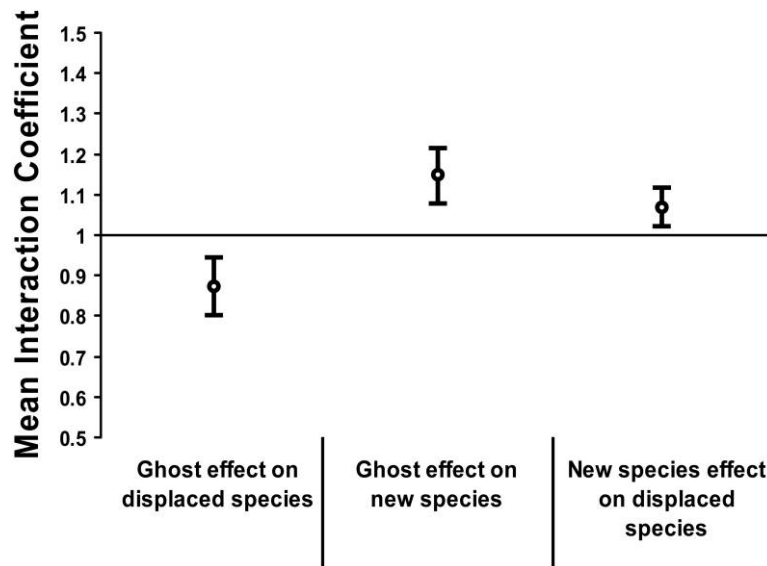


Figure 4: Mean interaction coefficients (with 95% confidence intervals of the estimated mean) of different suites of species: the effect of ghost species on species that are displaced when the ghost is removed, the effect of ghost species on species that are successful only when the ghost is not present, and the effect of previously unsuccessful species on displaced species.

SU). Successful species must be very good at either coexisting with other species or increasing invasion resistance of the community or at some intermediate combination of those two traits. This is not a trade-off in the strict sense, as having a low SS does not prevent a species from having a high SU.

The positive relationship between SS and SU (fig. 3A) can be predicted from first principles. In general, for any suite of species to coexist, we would expect their per capita effects on one another (SS) to be relatively small, which allows the successful species to have positive abundances (N_i) at equilibrium. For these same species to resist invasion, the product of SU and their abundances (i.e., $\alpha_{ji}N_i$ or $\Sigma\alpha_{ji}N_i$) is likely to be high. If successful species have larger effects on one another (SS), then they will also have lower equilibrium abundances, which in turn will require higher per capita effects (SU) to exclude potentially invading species.

Note that, when community size is not considered, SS and SU are not significantly correlated ($r = 0.11$, $P = .12$; fig. 3A). As community size increases, values of SS increase (fig. 3B), probably as a result of niche packing. That is, the greater the number of species, the greater the relative per capita strength of competition for shared resources. Values of SU decrease with increasing community size (fig. 3B), probably because the burden of preventing invasion by other species is shared by a greater number of species.

The strength of ghost species' interactions with other

species reveals the mechanism by which these species affect community composition. Ghost species have lower than average competitive effects on successful species (fig. 4). Further, those unsuccessful species that have the largest potential effects on successful species (high US) are the most suppressed by competition with ghost species. So ghost species appear to operate through simple indirect effects. When ghost species are removed from the community, species that would previously be suppressed by the ghost become successful and alter the structure of the community by displacing previously successful species. The overall ghost effect might occur as the result of diffuse direct and indirect effects among additional species in the community, but the observed strong patterns (fig. 4) suggest that the community changes occur as a result of indirect effects mediated through relatively few species. Experiments (e.g., Vandermeer 1969; Lawler 1993; Wootton 1993; Miller 1994; Menge 1995) support the prediction that indirect interactions have large effects on community structure (e.g., Caswell 1978; Miller and Kerfoot 1987; Strauss 1991; Wootton 1994), but indirect effects are rarely attributed to species that are only present in the regional pool but not successful in the local community, such as the ghost species described here (but see Case 1995; Warren et al. 2003).

Previous studies have noted that community composition can depend on factors other than the properties of the component species (e.g., invasion history: Law and Morton 1996). In theoretical models of community as-

sembly, both Pimm (1991) and Law and Morton (1996) noted the existence of “Humpty Dumpty” communities that could not be reassembled from the species in the stable community. They suggested that some species might serve as catalysts that alter assembly pathways but do not persist in the final assemblage of species. In that sense, these species appear similar to our ghost species.

Prior studies have generally not considered species that continually attempt to invade from the larger regional pool. In a metacommunity context, species often exist in some local communities but not others due to patch heterogeneity, so migration without successful recruitment may be common (Leibold and Miller 2004). Ives et al. (1999) found that competition can increase population variability, which will increase instability and affect community structure and the role of migration. Case (1990, 1991) noted the potential conflict between theories about stability and invasibility. The stability criterion of Lotka-Volterra systems can be found in most elementary ecology texts: in its simplest form, species must restrict their own abundance more than their competitors do (cf. May 1973). By this criterion, low interaction coefficients among successful species will be favored because they are more likely to produce stable assemblages. However, assemblages will be more likely to be resistant to invasion if their mean interaction coefficients are high (Case 1990, 1991), such that they prevent new species from invading. Low interaction coefficients with co-occurring species are therefore expected to be associated with stability of the current species, whereas high interaction coefficients with migrant species are related to resistance of the current species to invasion by other species. Case (1995) later extended this approach to illustrate that a positive population growth rate when a species is rare does not ensure that an invading species will be represented in the final, postinvasion community. Although both our model and those of Case are certainly simplistic, the qualitative patterns they exhibit may be robust and relevant for our understanding of natural communities.

Empirical evidence for effects of nonresident species on community composition is rare because of the nature of the effect itself—previous studies have seldom looked for the effects of species that are not present. One experiment that may serve as a model for testing for ghost effects is Warren et al.’s (2003) study of community assembly in protist systems. The authors first created all possible combinations of six different protozoan species, finding eight persistent, apparently stable, communities out of the 63 possible combinations. They then studied the potential invasion of each of these stable assemblages by individuals of the remaining species. They found several instances where the potential invasive species failed to establish but did change the constitution of the stable assemblage; these

“catalytic species” appear to provide evidence for what we are calling ghost species. Testing for ghost effects need not be limited to microcosm experiments, however. Ghost effects can be tested in any system where the regional species pool can be manipulated, either by limiting immigration by species from the regional species pool or by increasing immigration by regional species with traits that match those of ghost species (small effects on successful species but large effects on other unsuccessful species).

Empirical ecologists should consider the effects of species in the regional pool of possible migrants, rather than just the effects of species that successfully recruit into a community. Different local communities that may appear as alternate stable states may only appear as such because a ghost species continually invades one community and not the other. However, it may be difficult to identify ghost species without using something similar to Warren et al.’s (2003) direct experimental approach. Observationally, ecologists may be able to predict potential ghost species with a significant knowledge of both the local successful species and the larger regional pool of unsuccessful migrant species. In our model, ghost species usually act through indirect pathways (fig. 4), which suggests that ghost species are unsuccessful species that markedly suppress other unsuccessful species, which prevents this second species from suppressing a species that is ultimately successful in the local community. Such chains of strong, possibly asymmetric, interactions are likely to be found among suites of species with high resource overlap, for example, species with similar niches.

We realize that we are being somewhat heretical in suggesting that community ecologists may have ignored a large set of important interactions when attempting to explain natural patterns of diversity among competitors. However, we feel that ghost effects should be common in natural communities that assembled from, and persist with, continuous invasion from a larger species pool. Most natural communities (and “metacommunities”; Leibold and Miller 2004) probably meet these criteria: familiar examples include gap and disturbance communities (e.g., Platt and Weis 1977; Paine and Levin 1981), interconnected pond systems (e.g., Cottenie and De Meester 2005), and a variety of natural microcosms (Srivastava et al. 2004). The theory also has implications for conservation; for example, restoration ecology is faced with the problem of predicting what species will create stable communities in restored habitats. If our hypothesis is correct, and ghost species not present in the current community influence community composition, ecologists cannot understand and predict community composition without considering the complex potential influences of the often unseen species pool.

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