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Hybridization can facilitate species invasions, even without enhancing local adaptation

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The founding population in most new species introductions, or at the leading edge of an ongoing invasion, is likely to be small. Severe Allee effects—reductions in individual fitness at low population density—may then result in a failure of the species to colonize, even if the habitat could support a much larger population. Using a simulation model for plant populations that incorporates demography, mating systems, quantitative genetics, and pollinators, we show that Allee effects can potentially be overcome by transient hybridization with a resident species or an earlier colonizer. This mechanism does not require the invocation of adaptive changes usually attributed to invasions following hybridization. We verify our result in a case study of sequential invasions by two plant species where the outcrosser *Cakile maritima* has replaced an earlier, inbreeding, colonizer *Cakile edentula* (Brassicaceae). Observed historical rates of replacement are consistent with model predictions from hybrid-alleviated Allee effects in outcrossers, although other causes cannot be ruled out.

species colonization | mating system | model | *Cakile* | sea-rockets

Colonizing species rarely encounter empty environments and may, as a result, come into contact with close relatives. The most intensively discussed case of related colonizer–resident interactions, although by no means the only example, is the entry of modern humans into regions occupied by Neanderthals (1), eventually replacing them. Colonizing and resident species can interact in various ways, with consequences for their population dynamics. Competition, for example, is likely to impede successful establishment and population growth of newcomers; in contrast, resident species may facilitate new colonizers through hybridization or by shared interactions with organisms from other trophic levels. Although some interactions have been identified and are widely considered to predominate, there may be other interactions whose significance is yet to be explored. These interactions may be important in some or many cases, and a better knowledge of them might alter our interpretations of empirical observations. Here, we will investigate one such potential interaction, arising from hybridization between plant species sharing animal pollinators.

Hybridization can introduce adaptive alleles that contribute to expansion into new habitats (2, 3) and may result in new taxa. Local adaptation, resulting from changes in fitness, is the only positive role for species hybridization considered in the invasion literature; the same is true for admixtures of species genotypes from multiple sources. However, is it possible that there could be other benefits from hybridization, purely demographic ones? Furthermore, are these additional benefits capable of altering invasion dynamics over similar timescales and magnitudes? If so, such interactions would need to be excluded before adaptation can merely be assumed.

Many colonizing populations are susceptible to the demographic challenge of Allee dynamics, either because the initial founding population is small (4, 5) or because rare, long distance dispersers, beyond the present range, will initiate low-density satellite populations (6). Allee effects could slow range expansion or even halt it completely (7). In plants, a small founding population can experience Allee effects because of a scarcity of compatible mates,

low pollinator visitation, or both (8, 9); the term "pollen limitation" is often used as a generic term when the exact mechanism is unclear. In the extreme case of a single arriving adult, population persistence would normally be impossible unless the species is capable of asexual reproduction or self-fertilization ["Baker's Law" (10)]. Here, we propose a positive role for hybridization in species invasions and range expansion, a purely demographic mechanism without the requirement for any new adaptation to result.

If a mate-limited colonizing species is capable of hybridizing with a species already present, the colonizing species could overcome the otherwise insurmountable limitations imposed by Allee effects. Early-generation interspecific crosses (i.e., hybrids) could enable the colonizer genes to establish. Pure colonizer-type individuals can subsequently arise through crossing among hybrid lineages (11) or repeated backcrossing with the colonizer parents. We further hypothesize that this hybridization-rescue effect is more likely to eventuate if the new species and hybrids are more attractive to pollinators or when the hybrids are more compatible (i.e., more likely to produce viable offspring) with the newcomer than with the established species. That is, after sufficient generations of asymmetric breeding (backcrossing to the new colonizer), plants will increasingly come to resemble the original newcomers. The arriving species will essentially have been reconstituted, at least in its nuclear genome, and its population can increase now that it has escaped the critical effects of Allee dynamics. In effect, resident populations of a cross-compatible

Significance

Species colonizations frequently occur in regions already occupied by other species of the same genus, or by other genotypes of the same species. When hybrid genotypes become more invasive than their parents, improved local adaptation is inevitably assumed. Here, we show that there is another way that hybridization could facilitate invasions, by temporarily overcoming pollen limitation when populations are small. We verify this conclusion using two contemporary sequential invaders, a plant analog of the Neanderthal–modern human system. Our findings indicate that it may be misleading to assume that all cases of invasive hybrids result from enhanced phenotypic suitability. Our hypothesis may be even more relevant to animal species because, unlike plants, animals can rarely escape mate limitation by self-fertilization.
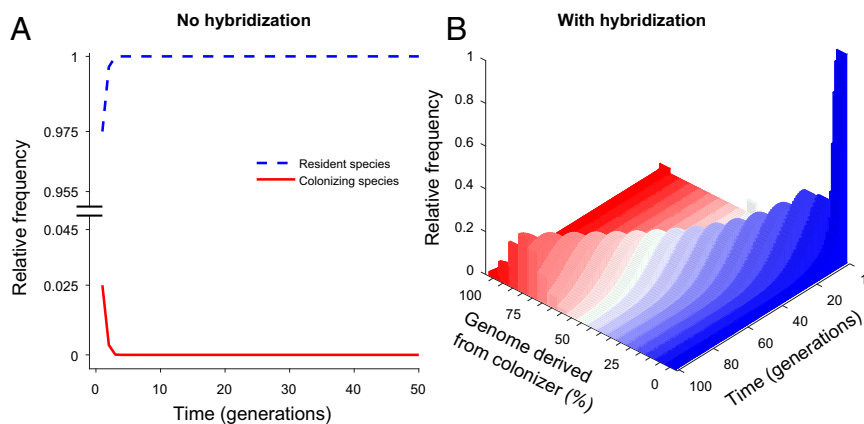
Fig. 1. Dynamics predicted by the generic model when a small number of a colonizing species arrives at a new location currently occupied by a resident species: no hybridization (*A*) and hybridization (*B*). Although in both *A* and *B*, pollinator preference parameter *W* is set to favor more backcrossing to the incoming genotype than to the resident species, the incoming genotype fails to establish when it does not hybridize with the resident species (*A*). However, when there is hybridization (*B*), the population steadily accumulates a higher proportion of individuals similar to the colonizer, whereas the resident genotypes decline in abundance and are finally replaced by the colonizer. Dark red indicates individuals whose genome is indistinguishable from the colonizer, dark blue indicates genomes indistinguishable from the resident species, and gray represents hybrid genotypes comprising 50% of each parental species' genome. See Tables S1 and S2 for lists of parameters and their values.

species, which may otherwise negatively affect the newly colonizing species through competition, become stepping stones through the landscape for a self-incompatible species via hybridization.

We develop a model that confirms that transient hybridization can overcome Allee effects under a wide range of ecological settings in relation to breeding system, pollinator behavior, and life history traits. Moreover, we show in a case study using a simplified version of the model that the parameter values required for the demographic mechanism to be as effective as genetic changes in fitness are fulfilled by the sequential invaders *Cakile edentula* and *Cakile maritima*. Our hypothesis therefore provides a possible explanation for the rapid replacement of *C. edentula* over a large part of its invasive range by *C. maritima* in the west of North America, New Zealand, and Australia (12–15).

Results

Our hypothesis is clearly supported by the model results. In the absence of hybridization, when we introduce a small number of

seeds, the incoming species population declines rapidly to extinction (Fig. 1*A*). The same propagule pressure but with hybridization transforms the population from one dominated by resident species and resident-like genotypes (blue in Fig. 1*B*) to one dominated by colonizer and colonizer-like genotypes (red in Fig. 1*B*). Over time, the colonizer genotype is reconstituted and the resident species is eventually replaced by the new colonizer. Allee population thresholds are always smaller with hybridization than without it, proving that introgression is asymmetric in favor of the colonizer [i.e., when $W_0 > 1$ (Fig. 2*A*) or $\beta > 1$ (Fig. 2*B*)]. Even with no bias in pollinator behavior ($W_0 = 1$) or compatibility ($\beta = 1$), hybridization still reduces the Allee threshold slightly (Fig. 2) because some of the otherwise wasted pollen results in seed production via the resident species, thus contributing positively to the dynamics of colonizer genes.

Consistent with the established theory that selfing provides reproductive assurance (16), the Allee threshold for establishment of colonizing species decreases with its selfing rate for both
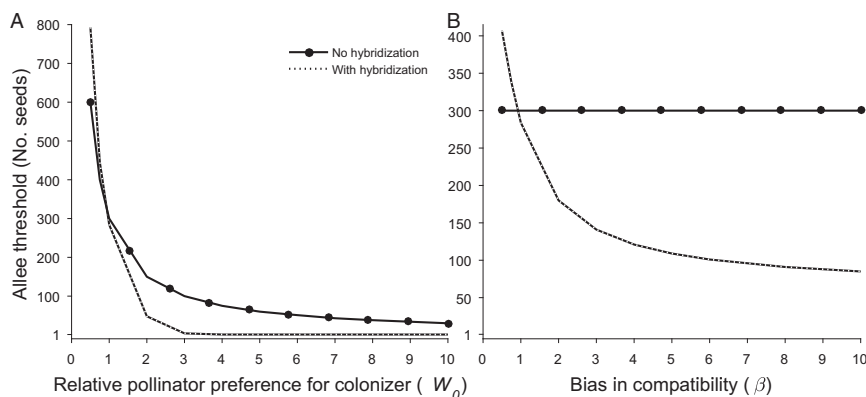
Fig. 2. The critical number of propagules for the establishment of a colonizing species, the predicted Allee threshold, as a function of either pollinator behavior (assuming equal compatibility, $\beta = 1$) (*A*) or reproductive compatibility of hybrids with the parental genotypes (assuming equal pollinator preference, $W_0 = 1$) (*B*). Note that *B* would also indicate the results expected from passive pollination, such as by wind. Compatibility, β, has no effect on the dynamics of either species when they do not hybridize: the Allee threshold is therefore constant for the no-hybridization scenario (solid line in *B*). When $W_0 = 1$ and $\beta = 1$, backcrossing is symmetric, but when β is larger than 1, F1 and later generation hybrids are more compatible with the colonizing-type individuals. In our simulations, the criterion for the Allee threshold was that the population size (seed number) after 100 generations was the same as the initial population size. See Tables S1 and S2 for lists of parameters and their values.
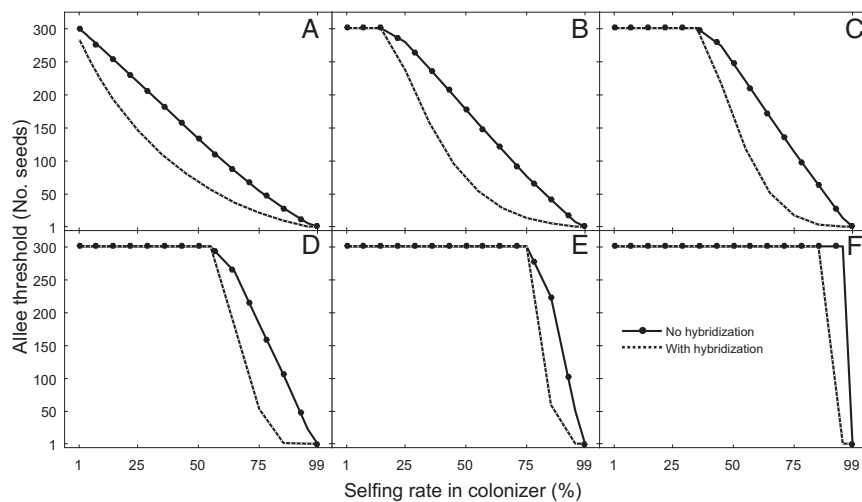
Fig. 3. Predicted Allee thresholds for the establishment of a colonizing species as a function of its self-fertilization rate, assuming that the resident species has a self-fertilization rate of 1% (*A*), 20% (*B*), 40% (*C*), 60% (*D*), 80% (*E*), or 99% (*F*). The minimum number of seeds necessary for the establishment of the colonizer, its Allee threshold, is never larger with hybridization than without. See Tables S1 and S2 for lists of parameters and their values.

hybridization and no-hybridization scenarios. However, Allee thresholds were always smaller for a hybridizing colonizer than the nonhybridizing one over a wider range of simulated breeding systems of both species (Fig. 3). Because the resident species adopts a more autogamous breeding system, Allee thresholds become larger in the colonizing species, but with hybridization, the incoming species could still invade the resident population (Fig. 3).

To test our predictions in a contemporary invasion, we parameterized a simplified version of our model with a single hybrid category (F1 hybrids), using empirical data from *Cakile maritima* [self-compatible (SC) (17)] and *C. edentula* [self-incompatible (SI) (17, 18)]. Why and how the established invader (*C. edentula*) has been replaced by a newly arrived species (*C. maritima*) in three parts of the world has remained a mystery over the 40 y since the replacement was first reported (13). Could hybridization with the prior SC invading plant have increased the probability of subsequent establishment of an SI species? Hybrids between the two species can be produced easily by hand (17). We have also confirmed, using genetic markers, that individuals with intermediate morphology near the leading edge of the *C. maritima* invasion in Tasmania are the results of hybridization (19).

We simulated the dynamics of *C. maritima* with and without hybridization with *C. edentula*. The results indicate that hybridization could facilitate the establishment of a small (otherwise sub-Allee threshold) population of the primarily self-incompatible *C. maritima* (Fig. 4), with a strong correspondence between the timescales for species replacement predicted by the model simulation (Fig. 4*A*) and the frequency of *C. maritima* relative to *C. edentula* in herbarium specimens (Fig. 4*B*) (20). Without hybridization, small initial populations of *C. maritima* were predicted to fail to establish (Fig. 4*C*). A note of caution is required for this comparison: our model simulates the population dynamics within a single location (with no account of subsequent spread), whereas herbarium data give a (very crude) representation of invasion dynamics over a wider geographic scale (21). Our simulation results are, however, also in good agreement with the replacement time-scale observed on Lord Howe Island, where *C. maritima* replaced *C. edentula* in perhaps 20–30 y (14).

Our simulation model and the *Cakile* system provide support for our hypothesis of an overlooked, purely demographic, role for hybridization in both establishment and spread. A robust test of the hypothesis would require deliberate introductions into regions lacking one or other species, which would probably be unethical or unwise. However, in the case of SI and SC *Cakile* species in Australia, there is now clear evidence that interspecific hybridization has occurred during the establishment and expansion of *C. maritima* (19). Genetic and morphological evidence across the current *C. maritima* invasion wave-front in Tasmania
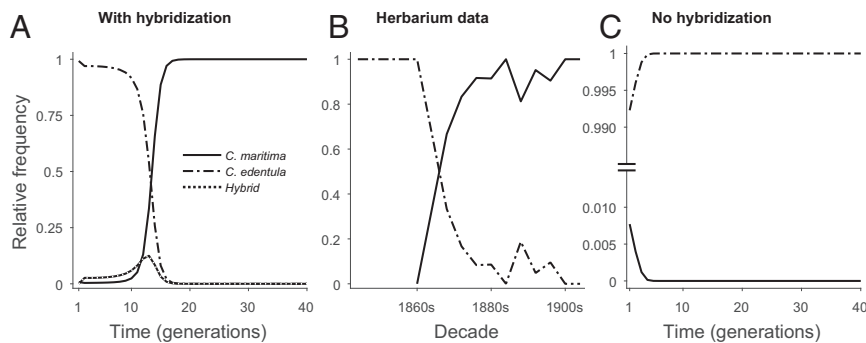

Fig. 4. Population dynamics of *Cakile* predicted by the simplified model (*A* and *C*) and evidence from herbarium samples (*B*). Whereas hybrid presence is predicted to be ephemeral, the predicted dynamics of C. *maritima* and C. *edentula* (*A*) corresponds to the pattern and time scale of change in their representation in herbarium specimens (*B*) collected from Victoria and South Australia. Adapted from ref. 20. *C* shows what would happen without hybridization. Parameters and their values are given in Table S3.

(19) match what would be expected if species replacement by this mechanism had occurred. Specifically, in places where *C. edentula* has a very high relative frequency, hybrids are common and even plants that are morphologically indistinguishable from one parent often have the chloroplast genotypes of the other (19). In regions where *C. edentula* has long since disappeared and there is now little evidence of nuclear introgression, *C. edentula* chloroplasts may still be common in *C. maritima*, indicating extensive past hybridization and reconstitution of parental phenotypes. Although our artificial intercrossing provided no evidence for bias in cross-compatibility of hybrids with the two parental species (Fig. S3), pollinators clearly preferred to visit *C. maritima*-like individuals over *C. edentula* when both were present (*SI Text*, *Simplified Model for* C. maritima *and* C. edentula, *Sources of data for parameterization*). We note that introgression has been proposed before for these species (22) but based on less convincing data and without any mechanism being proposed (19).

If this demographic phenomenon does occur in nature, is it idiosyncratic—a unique combination of species sharing pollinators and invading the same habitat in the same sequence—and of little relevance to ecology and evolution in general, or is it more common? We believe that the latter may be true. First, both hybridization (3) and Allee effects are common in biological invasions (7). Evidence is mounting for the importance of hybridization as one of the processes driving invasions, although so far, the explanations have relied solely upon genetic consequences of hybridization endowing adaptive benefits (refs. 2 and 3 but see ref. 11). Indeed, the risks of extinction and genetic swamping of native species have been raised as dire consequences of hybridization (2). Allee effects or, more specifically, pollen-limited seed production, are expected to be common, because more than 80% of plants rely on pollen transfer for reproduction (23) and ~50% of plant species are obligate outcrossers (24). Pollen limitation, resulting from low availability of both compatible mates and pollinators, seems to be more common in introduced species than their native counterparts (25, 26). First, our model shows that the presence of another species can alleviate such pollen limitation and reduce Allee effects through hybridization with related species. Second, our model shows that the rescue effect of hybridization will be stronger when there is an asymmetry in the direction of introgression (backcrossing): this phenomenon seems to be common in both natural and artificial hybridizations. Pollinators rarely commit to random foraging bouts but rather discriminate among plant types (27); such behavior can result in assortative mating and produce the required asymmetry. Intercrossing success (i.e., the production of viable seeds) is also known to be affected by the direction of crossing (28, 29). The interplay between these pre- and/or postzygotic processes can result in unequal transfer of parental genetic material into the genome of hybrid progeny (28, 29). Whereas the short-term demographic consequence of this asymmetry is facilitation of establishment, the long-term outcome can be species replacement as we see in *Cakile* species.

Materials and Methods

We developed a density-dependent, time-discrete, deterministic model based on the life cycle of an annual plant with no persistent seedbank and occurring in a small, isolated patch of suitable habitat. The model incorporates demography, mating systems, pollinators, and quantitative genetics through the following recurrence difference equation:

$$N_{x(t+1)} = \sum_y M_y \theta_y F_y(M) \left[s_y H(x:y,y) - (1-s_y) \sum_z C(y,z) V_y \phi(M) H(x:y,z) \right],$$

where $N_{x(t+1)}$ is the number of seeds from genotype x in generation $t+1$, and $M_y = N_{y(t)} S_y(N)$ denotes the total number of female adults with genotype y, surviving from $N = \sum_k N_{k(t)}$ total seeds according to a Beverton–Holt type recruitment function, $S(N)$ (Eq. S1). θ_y is the per capita ovule production of female genotype y in the absence of neighboring plants, which decreases

with total adult population size ($M = \sum_k M_{k(t)}$) according to a rectangular hyperbolic function $F_y(M)$ (Eq. S3) because of resource competition and other negative interactions between plants. A fraction s_y of flowers produces seeds through selfing, whereas the $1 - s_y$ nonselfed proportion relies on pollinators for seed production. Not all pollen from other genotypes will result in viable offspring; hence the compatibility of genotype y with genotype z is given by $C(y,z)$ (Fig. S2). The relative frequency of genotype y, adjusted for pollinator preference (Fig. S3), is V_y, whereas the probability of pollination is related to the total adult population size following a Holling type III functional response, $\phi(M)$ (30).

We used the number of chromosomes as a proxy for determining the total number of genotype classes (which is $2n+1$) and the chromosome combination of the two parental species to characterize x (Fig. S4). That is, a pure individual of the incoming species, denoted by $x=0$, has no alien chromosome from the resident species whereas the karyotype of an F1 hybrid embodies an equal number of chromosomes from the two parental species, so it is shown as $x=0.5$. The proportion of ancestry from the incoming species decreases as x approaches 1, whereas that of the resident species increases, with $x=1$ indicating a pure individual of the resident species with no alien chromosome from the incoming species. A diploid individual then undergoes gametogenesis following the principle of independent assortment of chromosomes, assuming no crossing over, where a haploid gamete randomly receives a mixture of chromosomes from the two parental species. By taking the convolution over the gamete types that can be produced by two crossing diploid individuals, we obtained the probability $H(x:y,z)$ of two parents with genotype y and z producing an offspring with genotype x. In essence, our quantitative genetic model is similar to the hypergeometric phenotypic model used previously to study sympatric speciation (31, 32) and risk of extinction by hybridization (33). We mapped genotypic class x to a phenotypic character using a Gaussian model (30) (Fig. S5). We simulated the population dynamics of 19 genotypic classes corresponding to a diploid species with $2n=18$ over 100 generations. This value was chosen to correspond to *Cakile* spp. ($2n=18$) which we consider later. A smaller or larger number of chromosomes will respectively either increase or decrease the speed at which species replacement will occur but without altering the qualitative dynamics. Full details of the model and simulations are provided in *SI Text*, *Generic Model to Simulate the Dynamics of Hybridizing Annual Species*, *Generic model formulation* and *SI Appendix*.

We compared the population dynamics of the newcomer under two scenarios: (*i*) hybridization with an established species; and (*ii*) an established relative present but no hybridization. Fecundity and survival parameters were chosen to be constant and equal for the two species and for all hybrids to ensure no fitness advantage or disadvantage from hybridization. These assumptions can be altered according to the question being investigated. As a measure of establishment success, we estimated "Allee thresholds" as the minimum number of colonizing individuals required to ensure positive population growth for each scenario. A facilitation effect for hybridization would be apparent as a smaller Allee threshold than that observed for the no-hybridization scenario. We investigated the sensitivity of the model predictions over a wide range of parameter values related to initial population size, mating systems of the interacting genotypes, intercrossability, pollinator behavior, and pollination-plant density relationship (Table S2).

To verify the findings of the above theoretical model, a reduced version including only three genotypes, the two parental species, and a single hybrid class (34), was parameterized using empirical data from *Cakile maritima* and *C. edentula* (see Fig. S6 for example simulation). Parameter values related to fecundity were obtained from a common garden experiment. The selfing rates and cross-compatibility of the genotypes were quantified in two artificial crossing experiments (Fig. S1). Pollinator visitation rates were obtained by monitoring a population where the two species had similar relative frequencies. For hybrids, we used the average phenotypic values of the two parental species when no data existed. For all other parameters, we used published data and if no data were available, we ran the model over a wide range of parameter values to ensure consistent outcomes (e.g., Fig. S7). See *SI Text*, *Simplified Model for C. maritima and C. edentula* for detailed descriptions of the estimation of parameters.

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