LETTER

Sexual selection enables long–term coexistence despite ecological equivalence

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Empirical data indicate that sexual preferences are critical for maintaining species boundaries[1–4], yet theoretical work has suggested that, on their own, they can have only a minimal role in maintaining biodiversity[5–9]. This is because long-term coexistence within overlapping ranges is thought to be unlikely in the absence of ecological differentiation[9]. Here we challenge this widely held view by generalizing a standard model of sexual selection to include two ubiquitous features of populations with sexual selection: spatial variation in local carrying capacity, and mate-search costs in females. We show that, when these two features are combined, sexual preferences can single-handedly maintain coexistence, even when spatial variation in local carrying capacity is so slight that it might go unnoticed empirically. This theoretical study demonstrates that sexual selection alone can promote the long-term coexistence of ecologically equivalent species with overlapping ranges, and it thus provides a novel explanation for the maintenance of species diversity.

A central objective of evolutionary ecology is to understand the mechanisms that allow species to coexist. One such mechanism is ecological differentiation. By occupying different niches, species in overlapping ranges are able to reduce direct competition[10]. While there are numerous examples of closely related species occupying different ecological niches, many recently diverged and coexisting taxa are known to differ most markedly in their secondary sexual characters, showing few, if any, ecological differences[1–4]. It therefore seems that sexual selection is an important mechanism for maintaining coexistence. Indeed, models of sexual selection have shown that populations of choosy females and their preferred males can arise and, under various conditions, form reproductively isolated mating groups[11–15]. However, because sexual selection does not lead to ecological differentiation, species differing only in their mating preferences compete for the same ecological niche. This has traditionally led to the conclusion that, if their ranges overlap, one of these species will eventually displace the other[5–9].

Coexistence is facilitated by mechanisms that reduce range overlap between species. Sexual selection provides one such mechanism. Any process that creates spatial variation in female preferences indirectly also creates selection on male display traits, locally favouring those males that are most preferred by the local females. As a consequence, spatially segregated mating domains, characterized by the co-occurrence of matching display and preference traits, can emerge from populations with an initially random spatial distribution. Once segregated, interactions between different mating types are limited to individuals at the peripheries of these domains. In finite populations, however, the mating domains may shrink or grow, and the interface between them may drift randomly in space. Such fluctuations eventually lead to one mating domain replacing all others (Fig. 1a, c). In a pioneering study[16], it was argued that lower dispersal in males with better mating prospects facilitates spatial segregation and maintains coexistence. In finite populations, however, such mating-dependent dispersal fails to stabilize long-term coexistence (Supplementary Fig. 3). Given these difficulties

associated with sexual selection, a recent review concluded that sexually divergent, but ecologically equivalent, species cannot coexist for significant lengths of time[9].

Here we report model results that suggest the contrary and demonstrate that sexual selection can promote long-term coexistence, even without any ecological differentiation. Building on a standard model of sexual selection[14], we develop an individual-based model to examine the long-term fate of species differing only in their secondary sexual characters in an ecologically neutral context with finite population sizes (details are given in Supplementary Information). Except where noted, we assume a simple genetic structure with two unlinked haploid
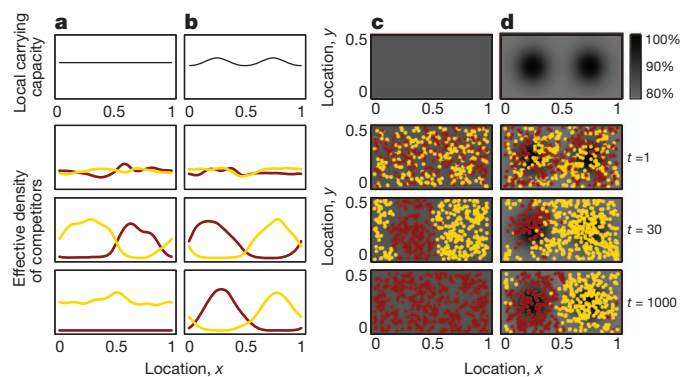

Figure 1 | Sexual selection enables long-term coexistence of ecologically equivalent species. We consider a population distributed across a continuous habitat in one dimension (**a**, **b**) or two dimensions (**c**, **d**) with a local carrying capacity that is either spatially uniform (top panels in **a** and **c**) or that has two peaks (top panels in **b** and **d**). Each peak is of Gaussian shape with standard deviation σ_k. The level v of spatial variation may be altered by changing the height of these peaks relative to the troughs between them. A value of $v = 0.25$, as in **b** and **d**, means that local carrying capacity at the peaks is elevated by 25%. The three lower rows show model runs through time. In each generation, individuals survive after a round of local competition and reproduce after a round of local mating, followed by offspring movement and the death of all parents. Competition between individuals decreases with their distance according to a Gaussian function with standard deviation σ_s. Coloured curves in **a** and **b** show the effective local density of competitors of each type (weighted by their competitive effect; Supplementary Information, equation (4)), and dots in **c** and **d** show surviving adults. Individuals are coloured according to their display locus genotype (similar patterns are observed at the preference locus; Supplementary Fig. 2). Females are α times more likely to mate with a preferred male, when encountered. Males are encountered with a probability that decreases with the distance between them and the female according to a Gaussian function with standard deviation σ_f. Female fecundity declines with the strength of mate-search costs m. Movement distances are drawn from a Gaussian function with standard deviation σ_m, centred at 0, with wrap-around boundaries. The total carrying capacity is $K = 500$, supporting the survival of approximately half of the $N = 1,000$ offspring produced each generation; other parameters: $\sigma_k = 0.1$, $\sigma_s = 0.05$, $\alpha = 5$, $\sigma_f = 0.05$, $\sigma_m = 0.05$, and $m/K = 1$ (roughly halving fecundity, Supplementary Fig. 1).

[1]Department of Zoology, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, Canada, V6T 1Z4. [2]Evolution and Ecology Program, International Institute for Applied Systems Analysis, A-2361 Laxenburg, Austria. †Present address: Department of Environmental Science, Policy, and Management, University of California, Berkeley, 130 Mulford Hall, Berkeley, California 94720, USA.

loci: the first locus (with alleles Q and q) governs a display trait that is expressed only in males, and the second (with alleles P and p) governs a preference trait that is expressed only in females (below we allow for more than two alleles; quantitative mating traits are investigated in the Supplementary Information). Because we are interested in coexistence rather than speciation, we assume that the genetic variation at both loci is already present, for example as a result of recent migration from allopatric ranges. All else being equal, females bearing a P (p) allele prefer[14–16] to mate with males carrying a Q (q) allele by a factor α, and a female's preference for a given male attenuates with increasing distance between them. Similarly, competition decreases as the spatial distance between individuals increases. Competition is assumed to reduce an individual's probability of surviving until reproductive maturity (similar results are obtained if competition reduces fecundity; Supplementary Fig. 4). Other than potentially carrying mismatched preference and trait alleles, hybrids suffer no intrinsic fitness costs.

Mating domains can be lost either through movement of the interface between them or when individuals of one mating type colonize the domain of another mating type. In particular, because selection at the preference locus disappears when th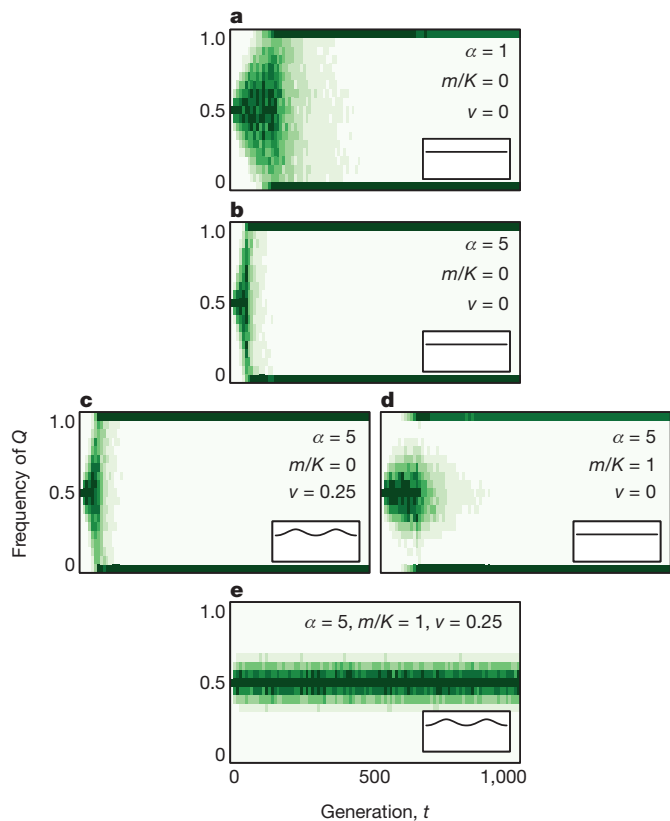ere is no variation at the display locus, foreign preference alleles may drift into regions with low variation in male display alleles, eventually causing displacement. Loss of mating domains can, however, be prevented by including two features ubiquitous in populations experiencing sexual selection: spatial variation in local carrying capacity and mate-search costs in females. Spatial variation in carrying capacity is present in most, if not all, biological systems (see Fig. 1 and Supplementary Information for model details). Mate-search costs occur if a female spends time and energy looking for a suitable mate and rejecting non-preferred males, thereby reducing her ability to invest in offspring. To account for such costs we assume that the fecundity of a particular female increases from 0 to a maximum level with the local density of available males, weighted according to her preference (Supplementary Information).

Our model confirms the long-standing view that sexual selection in homogeneous spatial models, without mate-search costs, does not facilitate coexistence and can, in fact, hasten the loss of diversity (compare Fig. 2a with Fig. 2b). Spatial variation in local carrying capacity, on its own, also has little, if any, effect in stabilizing populations (compare Fig. 2b with Fig. 2c). Sexual selection with mate-search costs slightly prolongs coexistence in a spatially uniform environment by helping to prevent mixing of the mating domains, but this effect is weak (compare Fig. 2b with Fig. 2d). However, in an environment with spatial variation in local carrying capacity, sexual selection with mate-search costs dramatically increases coexistence times (compare Fig. 2b with Fig. 2e and also Fig. 1a, c with Fig. 1b, d). In this case, mate-search costs curb the neutral drift of preference alleles, thus preventing the dilution of mating domains, and areas of high local carrying capacity provide spatial 'anchors', stabilizing the location and size of these domains (Fig. 1b, d).

Although neither spatial variation in local carrying capacity nor mate-search costs suffice on their own to stabilize populations, surprisingly little of both can be enough to ensure the long-term persistence of divergent mating types (Fig. 3). When mate-search costs in females are high, long-term coexistence can be maintained with less than 20% spatial variation in local carrying capacity. When mate-search costs are low, 50% spatial variation in local carrying capacity is sufficient to stabilize mating domains. Throughout this study, we have kept population sizes relatively small, to exacerbate the challenge of coexistence
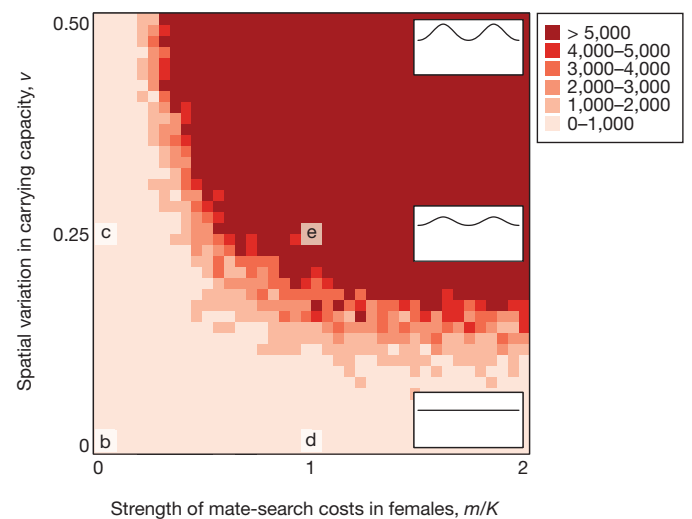

Figure 2 | Loss and maintenance of coexistence. Panels show distributions of allele frequencies at the display locus through time across 1,000 model runs in a two-dimensional landscape; coexistence occurs only while these frequencies remain intermediate. Inset panels depict the spatial variation in local carrying capacity as viewed along transects at $y = 0.25$. **a**, Homogeneous environment with no sexual selection ($\alpha = 1$). **b**, As in **a**, except that females are choosy ($\alpha = 5$). **c**, As in **b**, except with variation in local carrying capacity ($v = 0.25$). **d**, As in **b**, except with mate-search costs in females ($m/K = 1$). **e**, As in **b**, except with spatial variation in local carrying capacity ($v = 0.25$) and mate-search costs in females ($m/K = 1$); only when both features are combined is long-term coexistence observed. To focus on the maintenance of coexistence, we begin with two equally sized and spatially segregated populations of PQ and pq genotypes (all individuals on the left half of the arena initially have the PQ genotype, whereas all individuals on the right initially have the pq genotype). This mimics a situation in which types that previously arose in allopatry come back into contact, revealing the conditions under which they can persist in sympatry. All other parameters are as in Fig. 1.

Figure 3 | Conditions for long-term coexistence. Shading indicates the number of generations that polymorphism at the display locus persists when females are choosy ($\alpha = 5$) in a two-dimensional landscape (darker = longer). Each cell represents the mean time to loss of polymorphism for 10 replicate model runs. Letters indicate parameter combinations used to generate the corresponding panels in Fig. 2. Inset panels illustrate the extent of spatial variation in local carrying capacity for the three parameter values shown along the vertical axis. Model runs are initialized as in Fig. 2. All other parameters are as in Fig. 1.

in finite populations. When population sizes are larger, we find that as little as 10% variation in local carrying capacity suffices to stabilize mating domains (Supplementary Fig. 5d). Levels of variation in this range may be difficult to detect in nature, especially if they are to be inferred from observing the stochastic spatial distribution of individuals.

The stabilizing effect of spatial variation in local carrying capacity and mate-search costs readily extends to more realistic and natural landscapes (Fig. 4) and also to three or more genotypes (Fig. 4c–d). As long as spatial variation in local carrying capacity does not become so insignificant that it hardly affects the landscape, or so asymmetric that a single local population dominates, different mating domains can be maintained in mosaic sympatry[17,18] (Supplementary Fig. 7). Our findings are also robust to changes in female-preference strength, mate-search distance, movement distance and competition distance (Supplementary Figs 5a and 6), to changes in the relative importance of ecological competition versus sexual selection (Supplementary Fig. 5b, c), to changes in the genetic architecture of the display and preference traits (Supplementary Fig. 8), and to the inclusion of selective differences between male display traits (Supplementary Fig. 9). Generally, long-term coexistence occurs if female preferences are sufficiently strong to prevent extensive interbreeding, and if individuals move and interact on a spatial scale such that they are affected by spatial variation in local carrying capacity. This phenomenon can be interpreted more generally: whenever positive frequency dependence creates multiple stable states, global coexistence of these states becomes possible in a spatially structured env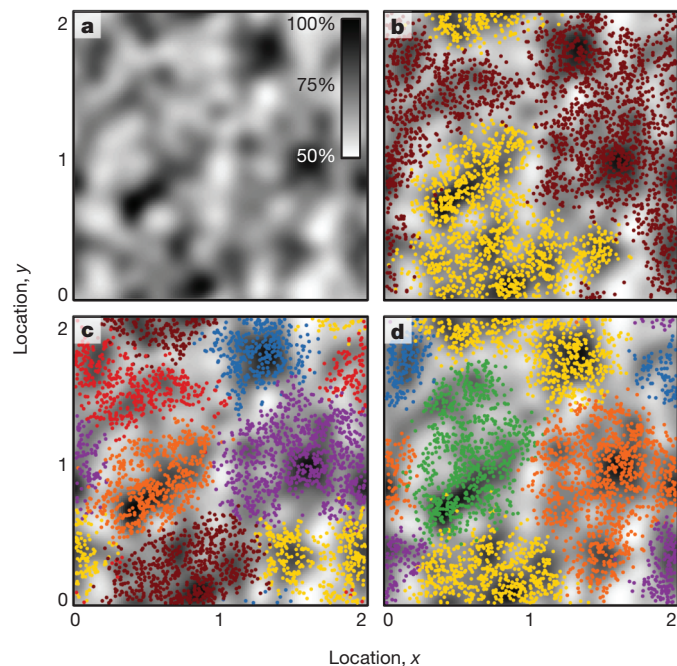ironment if this structure allows the domains in which those states are realized to become anchored in space. In this vein, our results in Fig. 4 extend a previous finding from theoretical work on hybrid zones, predicting that the spatial interface between species moves in space until settling in a region of low population density[19,20]. Similarly, previous theoretical work[21] using habitat boundaries for anchoring mating domains has shown that ecologically equivalent types can coexist when fecundity decreases, or mortality or mobility increase, in the company of heterospecifics.

Because both spatial variation in local carrying capacity and costs associated with mate search are ubiquitous in nature, our model may provide an explanation for the coexistence of many species whose reproductive barriers primarily involve mating preferences. For example, local habitat availability and quality vary around the shoreline of Lake Victoria[22]. The mechanism reported here could help explain how ecologically similar cichlid species can coexist in such vast diversity. That sexual differences have been a primary force maintaining cichlid species' boundaries is supported by the increasing frequency of hybridization that is occurring as a consequence of high turbidity levels, which reduce a female's ability to discern male phenotypes[22]. Similar explanations could plausibly be applied to other species that seem to be largely maintained by sexual selection (for example, species of fruitflies[23], weakly electric fish[24], frogs[25], crickets[3] and grasshoppers[26]). To test this hypothesis, one could analyse spatial associations between mating domains and local carrying capacity: Fig. 4 suggests that boundaries of mating domains often align with troughs of low local carrying capacity.

Our work demonstrates that, with variation in local carrying capacity over space and costs to females that encounter few preferred mates, sexual selection can maintain species that are not ecologically differentiated. This is in stark contrast to the widespread opinion that sexual selection, on its own, is unable to maintain ecologically equivalent species that overlap in space. Throughout this study, we have deliberately avoided making any claims about the emergence of diversity or speciation, choosing instead to focus on the coexistence of mating types. Further theoretical work is therefore needed to determine which conditions are most conducive to the initial appearance of multiple mating types, and further empirical work is needed to show how the mechanism presented here helps to explain natural patterns of coexistence and diversity.

METHODS SUMMARY

We develop an individual-based model of sexual selection[14] in a spatially explicit ecological framework. Individuals are distributed across a continuous habitat in one or two dimensions with wrap-around boundaries. All individuals compete for resources, whose density at any location is given by a local carrying capacity. Except where noted, the local carrying capacity exhibits two peaks, each of the same Gaussian shape. Competition reduces an individual's resource share, and thereby its survival probability, with the competitive impact of other individuals decreasing with distance according to a Gaussian function. Surviving females encounter surviving males with a probability decreasing with distance according to a Gaussian function, and females choose mates on the basis of their preferences for the males' displays. After mating, females produce offspring in proportion to their fecundities, which are lower for females who experienced higher mate-search costs. After producing offspring, the parents die and the offspring move a distance drawn from a Gaussian function in a direction chosen at random. Although the female preference trait and the male display trait are genetically based (each being determined by a diallelic locus, except where noted), there are no genetic differences in ecological function or competitive ability between individuals, which are therefore all ecologically equivalent. See Supplementary Information for complete model details and for information about alternative models explored to examine the robustness of our results.

Figure 4 | Mosaic sympatry. Four representative model runs in a patchy two-dimensional landscape with random variation in local carrying capacity. **a**, Underlying spatial variation in local carrying capacity. **b–d**, Results from independent model runs after 10,000 generations overlaid on the local carrying capacity; **b** is initialized with two types, whereas **c** and **d** are initialized with ten display alleles and ten corresponding preference alleles, all at equal frequencies and distributed randomly across the arena (Supplementary Information). Some of these alleles are then lost during the colonization phase. As in Fig. 1, individuals are coloured according to their genotype at the display locus. The spatial arena is eight times larger than in Fig. 1 and the total carrying capacity is $K = 4,000$, supporting the survival of approximately half of the $N = 8,000$ offspring produced each generation. All other parameters are as in Fig. 1 (except v, which is defined specifically for bimodal landscapes); for comparison, the coefficient of variation in local carrying capacity is 0.125 here and 0.066 in Fig. 1d.

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Author Contributions U.D. and L.K.M. conceived this project. L.K.M., R.M., S.P.O. and U.D. discussed and designed the model. L.K.M. implemented the model with input from R.M., analysed the results together with R.M., S.P.O. and U.D. and prepared the manuscript. L.K.M., R.M., S.P.O. and U.D. jointly edited the manuscript.