

Studies targeting higher-frequency periodic signals have found statistically similar oscillations in the Phanerozoic rock and fossil records (12, 31) that are comparable to cyclic variations in $\delta^{34}\text{S}$ and $^{87}\text{Sr}/^{86}\text{Sr}$ (9). Although the presence of statistically similar frequency components suggests the presence of an underlying oscillatory mechanism, documenting such similarities in the rock and fossil records does not provide a conclusive test of the rock-record bias or common-cause hypotheses. By quantifying the relative merit of the two hypotheses in light of environmental records that are related to Phanerozoic-scale Earth system evolution, we found compelling evidence to suggest that linkages among shelf redox conditions, biogeochemical cycling, and continental flooding have played a more fundamental role in determining the Phanerozoic history of marine biodiversity (as preserved in the fossil record) than sampling biases and variability in the amount of preserved sedimentary rock. Although our results do not address the specific environmental mechanisms that were important in determining the selectivity and magnitude of individual biological turnover events, they do provide quantitative support for the hypothesis that there has been a long-term coupling between

physical environmental changes and marine biodiversity during the Phanerozoic.

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Supporting Online Material

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Climate Change, Keystone Predation, and Biodiversity Loss

Christopher D. G. Harley

Climate change can affect organisms both directly via physiological stress and indirectly via changing relationships among species. However, we do not fully understand how changing interspecific relationships contribute to community- and ecosystem-level responses to environmental forcing. I used experiments and spatial and temporal comparisons to demonstrate that warming substantially reduces predator-free space on rocky shores. The vertical extent of mussel beds decreased by 51% in 52 years, and reproductive populations of mussels disappeared at several sites. Prey species were able to occupy a hot, extralimital site if predation pressure was experimentally reduced, and local species richness more than doubled as a result. These results suggest that anthropogenic climate change can alter interspecific interactions and produce unexpected changes in species distributions, community structure, and diversity.

Predictions concerning biological responses to climate change are largely based on the environmental tolerances of individual species and the assumption that these species will remain within their bioclimatic envelope as conditions change (1). At coarse scales, these predictions generally match observed changes in distribution and abundance across gradients such as latitude, elevation, and depth (2, 3). However, changing climatic conditions also lead to altered community composition (4) and shifts in the strength and sign of interspecific interactions

(5, 6)—changes that may greatly affect community dynamics and ecosystem function (7). Because species interactions can accelerate, retard, prevent, or even reverse predicted biotic changes based solely on simplistic models, interspecific relationships must be incorporated into the predictive framework of climate change (1, 8). Although distributional shifts forced by interspecific relationships have been demonstrated in the lab (9) and predicted by data-driven models (10), appropriate field tests are largely absent.

Rocky intertidal communities are ideal testbeds for studying the effects of climatic warming because many intertidal organisms already live very close to their thermal tolerance limits (11). Intertidal species' distributional limits are correlated with their upper thermal tolerance (12), and

changes in their distribution and abundance over time are associated with warming temperatures (13–15). However, species distributions are also strongly influenced by interspecific interactions (16), and these interactions are temperature-sensitive (6). Observed ecological patterns will therefore depend on both environmental stress and interspecific interactions (10, 17, 18).

In this study, I examined the roles of temperature and predation on the intertidal community in the Salish Sea, which spans a regional-scale thermal gradient from west to east (Fig. 1 and table S1). The oceanic terminus of the Salish Sea (the western end of the Strait of Juan de Fuca) is exposed to cool maritime weather, frequent fog and cloud cover, and early morning low tides, resulting in minimal intertidal thermal stress. The more eastern portions of the Salish Sea are warmer and sunnier, receive less cooling wave swash and spray, and feature summer low tides near midday. As a result, mid-intertidal rocks and organismal body temperatures become progressively hotter from west to east (Fig. 1) (19, 20).

To determine the ecological consequences of this spatial gradient in thermal stress, I first surveyed vertical zonation patterns of sessile invertebrate species and their principle predator. The upper limits of the mussels *Mytilus californianus* and *M. trossulus* and the barnacles *Semibalanus cariosus* and *Balanus glandula* were all negatively correlated with mid-intertidal rock temperatures (Fig. 2, A to D). In contrast, the upper foraging limit of the predatory sea star *Pisaster ochraceus* was independent of the thermal stress gradient (Fig. 2E). The slope of upper limits ver-

Department of Zoology and Biodiversity Research Centre, University of British Columbia, 6270 University Boulevard, Vancouver, British Columbia, V6T1Z4, Canada. E-mail: harley@zoology.ubc.ca

sus temperature was significantly steeper for prey species than for the predators [analysis of covariance (ANCOVA) using site means, species nested within trophic level; trophic level \times temperature interaction $F = 9.37$, $P = 0.006$] (Fig. 2F).

Because upper distributional limits of predator and prey do not shift in unison, there exists a thermally forced reduction in enemy-free space that could result in the exclusion of some sessile species from thermally stressful sites, as has been shown for an intertidal alga (17). The

reduction and/or disappearance of sessile invertebrates from west to east is related to their vertical proximity to the foraging range of *P. ochraceus*; mid-intertidal mussels (*M. californianus*) do not occur at the two easternmost study sites, and higher-intertidal *M. trossulus* and *S. cariosus* are exceedingly rare and do not typically reach adulthood at the most eastern sites (table S1). To test the importance of predation in a thermally stressful environment, I experimentally excluded *P. ochraceus* from plots in the high-

intertidal barnacle zone on Saddlebag Island, Washington, which was the easternmost and hottest site along the gradient. *M. trossulus* and *S. cariosus*, which were common at cool sites but virtually absent on Saddlebag Island, came to dominate free space in *Pisaster*-exclusion cages (Fig. 3A). Because *M. trossulus* and *S. cariosus* are ecosystem engineers and provide cool, moist microhabitats for a diverse suite of other species, total species richness increased by a factor of 2.5 after the exclusion of *P. ochraceus* (Fig. 3B and tables S4 and S5).

These spatial patterns and experimental results suggest that the upper limits of sessile species are largely controlled by thermal stress, lower limits are determined by predation, and the intertidal (vertical) variation in predation pressure is not sensitive to among-site variation in temperature. This leads to three testable predictions with regard to climate change: (i) Climatic warming through time should result in downshore shifts in the upper limits of sessile invertebrates; (ii) lower limits should remain invariant through time; and (iii) the vertical zones of sessile species should become compressed, potentially resulting in local extinction at some sites. To test these predictions, I compared Salish Sea zonation patterns in acorn barnacles (*Chthamalus dalli* and *B. glandula* combined) and mussels (*M. californianus*) in 2009 to 2010 to a historical data set from 1957 to 1958 (21). Sampling sites were relocated with the aid of the original investigator and, in most cases, the 2009 to 2010 surveys are believed to be within ~ 30 m of the original survey sites (22).

The 52 years separating the two sampling intervals span a period of climatic warming. During the latter half of the 20th century, maximum air temperatures near the eastern and western ends of the Strait of Juan de Fuca increased by

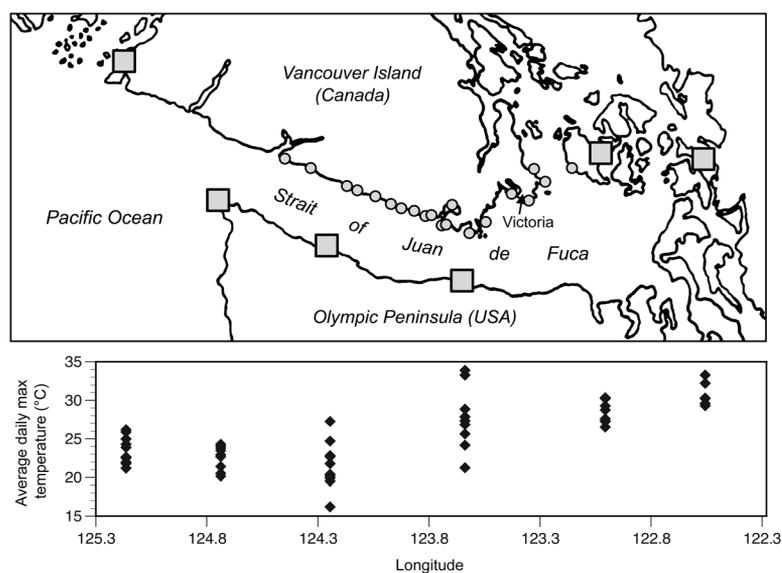


Fig. 1. Study region and thermal gradient. The Salish Sea includes the Strait of Juan de Fuca and the interconnected water bodies to the north and south of the Strait's eastern terminus. The study sites indicated by gray squares were used in the spatial comparison of temperature and zonation. Gray circles represent sites used for the temporal comparison. The graph shows the increase in mid-intertidal rock temperatures from west to east.

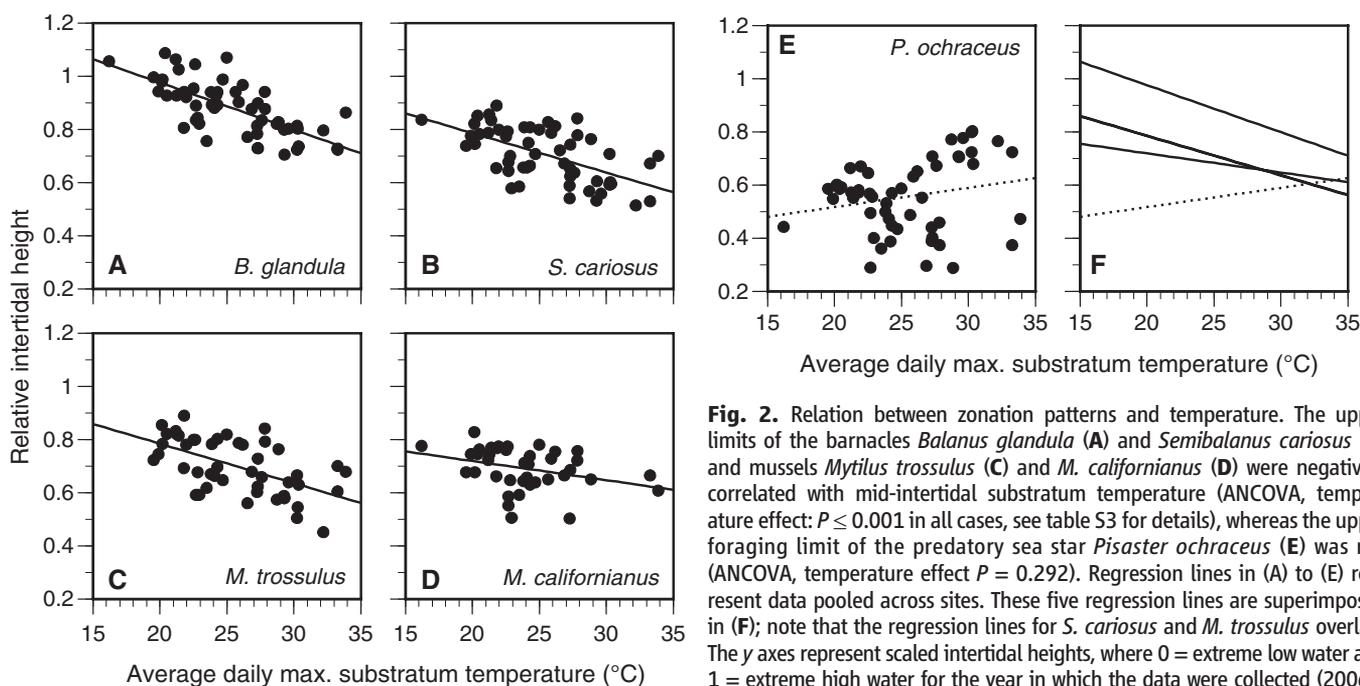
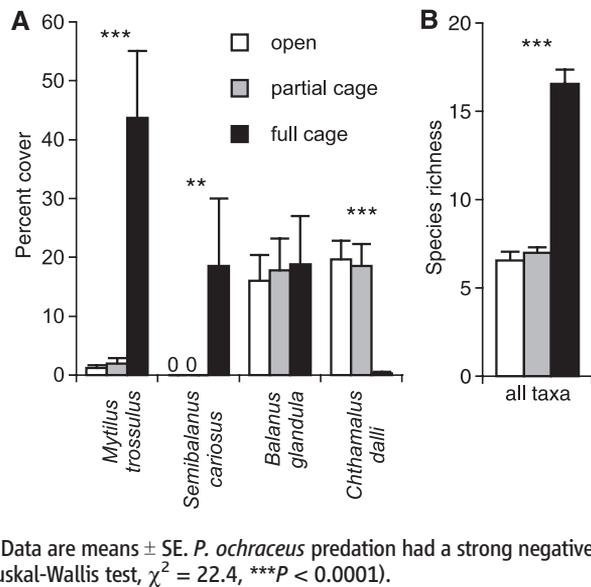


Fig. 2. Relation between zonation patterns and temperature. The upper limits of the barnacles *Balanus glandula* (A) and *Semibalanus cariosus* (B) and mussels *Mytilus trossulus* (C) and *M. californianus* (D) were negatively correlated with mid-intertidal substratum temperature (ANCOVA, temperature effect: $P \leq 0.001$ in all cases, see table S3 for details), whereas the upper foraging limit of the predatory sea star *Pisaster ochraceus* (E) was not (ANCOVA, temperature effect $P = 0.292$). Regression lines in (A) to (E) represent data pooled across sites. These five regression lines are superimposed in (F); note that the regression lines for *S. cariosus* and *M. trossulus* overlap. The y axes represent scaled intertidal heights, where 0 = extreme low water and 1 = extreme high water for the year in which the data were collected (2006).

Fig. 3. Effects of predator removals at a “hot” site (Saddlebag Island). **(A)** *P. ochraceus* exclusion altered sessile invertebrate cover in the stressful high-intertidal barnacle zone. Data are means \pm SE. Treatment differences (nonparametric Kruskal-Wallis tests were used to overcome departures from normality) were significant for *M. trossulus* ($\chi^2 = 18.0$, $***P < 0.0001$), *S. cariosus* ($\chi^2 = 12.3$, $**P = 0.002$), and *C. dalli* ($\chi^2 = 20.8$, $***P < 0.0001$), but not for *B. glandula* ($\chi^2 = 0.74$, $P = 0.69$). The few *M. trossulus* and *S. cariosus* recorded outside of predator exclusion cages were recent recruits that would typically be consumed well before adulthood. **(B)** Species richness (all taxa) in *P. ochraceus* exclusion experiments. Data are means \pm SE. *P. ochraceus* predation had a strong negative effect on overall species richness (Kruskal-Wallis test, $\chi^2 = 22.4$, $***P < 0.0001$).



$\sim 0.2^\circ$ and $\sim 0.13^\circ\text{C}$ per decade, respectively, and mean annual water temperatures along the southern and western Vancouver Island coast have warmed by $\sim 0.08^\circ$ to 0.11°C per decade (14, 23). Average daily maximum air temperatures during the summer, which are particularly relevant to thermal stress experienced in the intertidal zone, have warmed even more rapidly. At Victoria, summer average daily maxima have risen approximately linearly at a rate of 0.654°C per decade since 1950, which corresponds to an increase of 3.40°C over 52 years (Fig. 4A). As predicted, invertebrate upper limits have shifted significantly downward during this period of warming, whereas lower limits did not change (Fig. 4B). As a result, the vertical range of *M. californianus* was reduced by 50.9 ± 10.0 cm (mean \pm SE; one-tailed paired *t* test: $N = 15$ sites, $t = -5.08$, $P < 0.0001$), which corresponds to a 50.6% reduction of the *M. californianus* zone. Associated with this collapse in vertical range were *M. californianus* local extinctions at 13.3% (2 of 15) of the sites resurveyed in 2009 to 2010. Historical data for *M. trossulus* were only available for one site (former vertical range = 49 cm). *M. trossulus* had been completely eliminated from that site by 2010, with the exception of three small juveniles found under a single rock.

Large-scale patterns of intertidal species' distributions in the Salish Sea result from the increased overlap between the foraging range of the dominant predator and the habitable zone of its prey. At cool, wave exposed sites, sessile invertebrates can occupy shore levels well above the foraging range of *P. ochraceus*. At hotter, wave-protected sites, this high shore refuge becomes unavailable as thermal and desiccation stresses restrict sessile invertebrates to lower shore levels (19). In contrast, mobile *P. ochraceus* are capable of avoiding or adjusting to periods of thermal stress (24, 25); thus, it is not surprising that the upper limit of *P. ochraceus* foraging is independent

of the regional-scale stress gradient. As enemy-free space is reduced or eliminated at hotter sites, certain sessile species are excluded from these sites [see (26) for a wave-exposure analog]. A similar phenomenon pertains to climatically forced change through time. Upper limits of sessile species have shifted downward, presumably due to warming, whereas their lower limits have remained stationary, presumably due to constant predation pressure. Just as *M. californianus* is excluded from eastern sites by a lack of predator-free space, it has also suffered local extinctions through time as a result of climatic warming. Because species such as mussels provide critical habitat for an array of mesofaunal species (27), the loss of mussel beds over time has probably resulted in declines in species richness similar to those I have demonstrated experimentally on the stressful shores of Saddlebag Island.

These results are applicable to a variety of systems through both space and time. At local scales, experimental warming increased the vertical (plant-stem scale) overlap of two species of spiders in New England grasslands (28). This increased overlap resulted in the elimination of one spider from the system via intraguild predation and had considerable direct and indirect consequences for both herbivores and primary producers (28). At broader scales, observations and predictions regarding the effects of climate change in strongly zoned systems (such as montane forests or the coastal marine benthos) invoked changing patterns of zonation (8, 29, 30). Indeed, many species are predicted to go, or have already gone, locally extinct as their vertical zones collapse in response to biotic, abiotic, and anthropogenic changes (30, 31). More broadly, these results highlight the importance of incorporating interspecific interactions into predictions regarding ecological responses to climate change. Ecological change can only be accurately anticipated if we are able to understand the ways in which

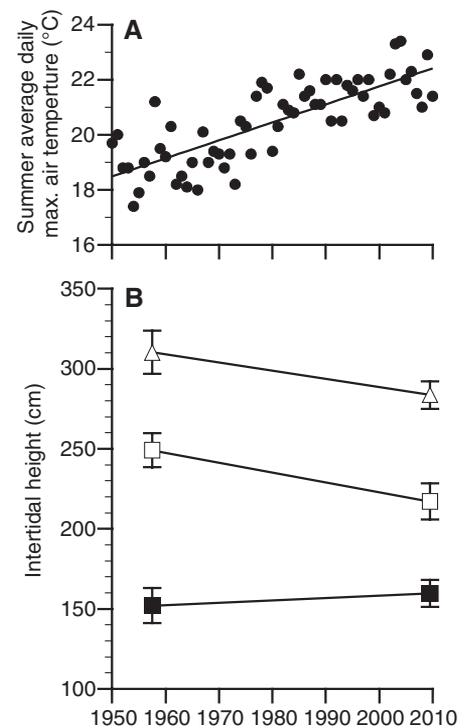


Fig. 4. Changes in temperature and sessile invertebrate zonation through time. **(A)** Long-term trend in average daily maximum air temperature for the summer months (June to August) in Victoria, British Columbia. Data are second-generation homogenized temperatures, which account for non-climatic shifts such as changes in sensors or observing practices, obtained from Environment Canada. The warming trend is highly significant ($F = 98.4$, $P < 0.0001$, $R^2 = 0.625$). **(B)** Upper limits of acorn barnacles (open triangles) and mussels (open squares) were significantly lower in 2009 to 2010 for both taxa (one-tailed paired *t* tests, acorn barnacles: $N = 18$, $t = -3.30$, $P = 0.002$; mussels $N = 13$, $t = -4.23$, $P < 0.001$). Mussel lower limits (black squares) were not significantly different (two-tailed paired *t* tests, mussels $N = 13$, $t = 1.15$, $P = 0.27$; historical lower limits for acorn barnacles were not available for comparison). Data are means \pm SE. The y axis is height above Canadian chart datum, which approximates the lowest astronomical tide.

biotic and abiotic factors interact to determine the distribution and abundance of species in space and time.

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Supporting Online Material

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Experimental Evolution of Reduced Sex Ratio Adjustment Under Local Mate Competition

Emilie Macke,^{1*} Sara Magalhães,^{2*} Fabien Bach,¹ Isabelle Olivieri^{1*}

Theory predicts that local mate competition (LMC) favors the evolution of female-biased sex ratios. Empirical support of this prediction is indirect and comes from comparative studies or from studies showing that individuals can adjust their offspring sex ratio in response to varying LMC intensities. Replicate lines from a population of the spider mite *Tetranychus urticae* were selected under three LMC intensities for up to 54 generations. Within each selection regime, the final sex ratio matched theoretical predictions. Furthermore, the ability of individuals to adjust their offspring sex ratio diminished in females evolving under strict LMC, but not in females evolving under relaxed LMC levels. These results provide direct experimental evidence for the evolutionary process by which LMC modifies sex-allocation strategies and suggest that evolution under strict and constant LMC may lead to a loss of phenotypic plasticity.

Hamilton's theory of local mate competition (LMC) predicts that in structured populations, when mating takes place locally among the offspring of one or few foundress mothers after which mated daughters disperse, mothers are selected to bias their offspring sex ratio toward females (1). As the number of foundresses contributing offspring to local mating groups increases, a more balanced sex ratio is favored and will approach an equal sex ratio, as predicted for panmictic populations (2, 3).

If males can inseminate several females, under LMC, brothers will compete with one another for mating partners. However, under these conditions, no such competition exists for their sisters. This reduces the value of producing sons rather than daughters, resulting in females allocating more resources to the production of

daughters. Biasing the sex ratio toward daughters allows females to maximize the fitness of her sons, by reducing her male offspring's mate competition and increasing their mating opportunities (1, 4, 5). Hamilton's model prediction can also be understood through a multilevel selection argument: Within groups, females maximize their number of grandchildren (hence, their fitness) by producing even (Fisherian) sex ratios, but groups that produce female-biased sex ratios are more productive because more granddaughters are produced. The relative strength of within- and among-group selective forces will depend

on the number of foundresses (N) per group and on the number of groups. As N increases or the number of groups decreases, within-group selection for an even sex ratio becomes stronger, whereas among-group selection for a female-biased sex ratio becomes weaker (5, 6).

Thus, theory makes three main predictions. First, populations evolving under higher LMC should exhibit a greater mean female bias. Second, individual females should adjust their sex ratios in response to different intensities of LMC through phenotypic plasticity (7, 8). Third, controlling the mean sex ratio and its variance is adaptive (9). Hence, individuals should produce precise sex ratios that exhibit lower than binomial variances, in particular under high LMC levels, where precision is expected to be under stronger selection (9, 10).

Support of these theoretical predictions comes predominantly from three empirical approaches. First, comparative studies have shown that in populations or species where the intensity of LMC is likely to be high, the sex ratio is more female-biased than in populations or species with lower levels of LMC [e.g., (11); see also (2, 5)]. Second, at the individual level, females of various species produce a higher proportion of sons as the number of foundresses laying eggs on a patch increases (5, 12). Third, the variance of the number of sons is smaller than the variance under binomial sampling, in particular for species experiencing greater LMC conditions (10).

However, these approaches do not directly test the evolutionary process that leads to the

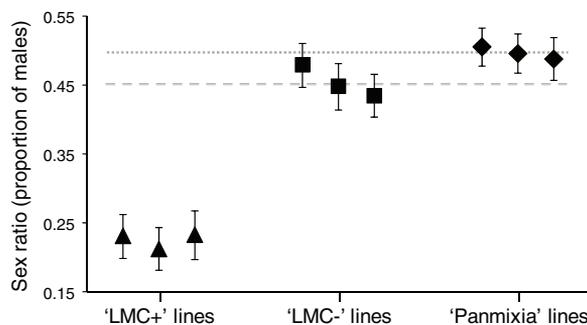


Fig. 1. The proportion of males increases with decreasing intensity of LMC imposed during the selection process. Symbols represent mean sex ratio values (triangle: LMC+ lines; squares: LMC- lines; diamonds: Panmixia lines), error bars the 95% confidence limits, and lines the predicted sex ratios (dashed: for LMC- lines; dotted: for Panmixia lines).

¹Institut des Sciences de l'Évolution, UMR 5554, Université Montpellier 2, Place Eugène Bataillon, F-34095 Montpellier cedex 05, France. ²Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Edifício C2, 3º Piso, Campo Grande, P-1749016 Lisbon, Portugal.

*To whom correspondence should be addressed. E-mail: isabelle.olivieri@univ-montp2.fr (I.O.); smagalhaes@fc.ul.pt (S.M.); emilie.macke@univ-montp2.fr (E.M.)

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Christopher D. G. Harley

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