Understanding local plant extinctions before it's too late: bridging evolutionary genomics with global ecology.

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Content

Summary

Understanding evolutionary genomic and population processes within a species range is key to anticipating the extinction of plant species before it is too late. However, most models of biodiversity risk under global change do not account for the genetic variation and local adaptation of different populations. Population diversity is critical to understanding extinction because different populations may be more or less susceptible to global change and, if lost, would reduce the total diversity within a species. Two new modeling frameworks advance our understanding of extinction from a population and evolutionary angle: Rapid climate change-driven disruptions in population adaptation are predicted from associations between genomes and local climates. Furthermore, losses of population diversity from global land use transformations are estimated by scaling relationships of species' genomic diversity with habitat area. Overall, these global eco-evolutionary methods advance the predictability—and possibly the preventability—of the ongoing extinction of plant species.

Keywords: extinction, genetic diversity, climate change, habitat loss, macrogenetics, genomic offset, biodiversity, environmental niche models, mutations-area relationship, landscape genomics.

I. Introduction

Anthropogenic habitat loss and climate change have increased the extinction rate of plant species by 25-fold (Humphreys *et al.*, 2019). Though much extinction research has focused on the loss of entire species, the process of extinction starts within a species distribution, where local abundance or specific populations are lost in local extinctions. In fact, though only 0.3% of plant species evaluated by the International Union for Conservation of Nature are extinct, 37% (including most "non-threatened" species) suffered such a population decline (IUCN.org). Local extinction has thus affected two orders of magnitude more species than full extinctions, but it has been difficult to account for in biodiversity evaluations, which must integrate eco-evolutionary processes across populations.

Far from being identical, species consist of dynamic ensembles of populations that are constantly mutating and evolving, so ignoring population-level diversity not only underestimates biodiversity loss but could also silently accelerate the extinction of a species across its range. For instance, populations within a species are generally adapted to local environments across their geographic distribution (Bontrager *et al.*, 2021), and this standing genetic variation could fuel future adaptations. Here I review two immediate consequences of population differences for extinction (**Fig. 1**) and highlight novel methods that use population genomic datasets to predict biodiversity change: (i) within-species diversity causes variable evolutionary ***responses*** to climate change through adaptation or maladaptation—so-called genomic offset (GO) methods attempt to characterize local (mal)adaptation and project changes in space and time (**Fig. 2**); (ii) rapid local extinction due to climate- or land–use-changes negatively ***impact*** within-species variation—at a rate recently described by the mutations-area relationship (MAR) (**Fig. 3**). To illustrate these new quantitative frameworks, I use data from the model plant species *Arabidopsis thaliana* while reviewing evidence for other systems. Finally, I conclude with future directions on the potential to integrate new continental-scale population genomic datasets of non-model plant species with global land-use and climate-change databases to track global extinctions at population and evolutionary levels (**Fig. 4**).

II. (Mal)adaptive evolutionary genomic *response* of populations to climate change.

Early modeling of biodiversity responses under global change was built using environmental niche models (ENMs, also called species distribution models or habitat suitability range), which construct species ranges using environmental optima and tolerance limits. ENMs project either expansions of geographic ranges when novel environments for a species' optimal niche become available or contractions in regions where the environment crosses the species' tolerance limits. For instance, an ENM of *A. thaliana* predicts an ~30% future shrinkage in its suitable habitat from its Southern Eurasian range with an upwards latitudinal shift (**Fig. 2A-B**); a commonly predicted pattern of range reduction across the world's floras (Thuiller *et al.*, 2005; Dullinger *et al.*, 2012; Pillet *et al.*, 2022; Jandt *et al.*, 2022). Although these models are convenient, it is populations, not species, that respond to climate change, and ENMs do not capture the biology of populations well (A. Lee-Yaw *et al.*, 2021).

Standing variation within and between populations of a species can dictate rapid evolutionary (mal)adaptation to changing environments (Nosil *et al.*, 2018; Rudman *et al.*, 2022; Czech *et al.*, 2022). Here, (mal)adaptation refers to relative fitness differences among genotypes, which may help explain absolute fitness (total viable offspring) and population decline (Brady *et al.*, 2019). To understand large-scale patterns of (mal)adaptation across species and their geographic ranges, Bontrager et al. (2021) summarized published studies of 130 plant species in which multiple populations were grown in common gardens at different locations within their range. This analysis confirmed the well-known pattern that adaptation decays as populations are transplanted further from their environment of origin and supported two long-theorized hypotheses of species' geographic range evolution (Angert *et al.*, 2020): (i) cold (poleward) range edge populations, which were likely established during post-glacial expansions, show signs of general maladaptation with a ~18% fitness disadvantage across all gardens compared to all other populations; (ii) warm (equatorial) range edge populations had strong local adaptation with a fitness advantage of ~16% compared to all other populations, but only in common gardens in extreme environments. Similarly, large-scale common gardens with *A. thaliana* displayed stark survival differences: 63% of over 500 populations perished in a warm edge common garden, while the fitness of the top lines surpassed 1200% of the population fitness average (Exposito-Alonso *et al.*, 2019) (**Fig. 2C**). These differences make populations dramatically more or less susceptible to maladaptation to future environments. A parallel meta-analysis by Bontrager et al. combined metrics of local adaptation with climate anomalies occurring in the years that the common gardens were conducted (1970s to the 2010s); if temperature anomalies that year exceeded 2°C, local adaptation was erased (Bontrager *et al.*, 2020), while without anomalies, local adaptation provided an average fitness advantage of 30%. In a world heading to an average 1.8°C warming, we should thus expect pervasive population maladaptations. Harnessing such knowledge will be crucial for accurate biodiversity loss projections (Urban *et al.*, 2022).

Although common gardens provide robust evidence of local adaptation, they are time-consuming and impractical for some species, such as long-lived trees or non-native plants. Landscape genomic approaches have thus emerged as scalable tools to study local adaptation, where evidence of past evolutionary adaptation can come from overly high genomic divergence among populations collected in different climates (genome-environment association [GEA], see reviews (Lasky *et al.*, 2022)). However, it is unclear how to include this genomic evidence of past local adaptation in forecasts of species responses to global change. To fill this gap, a new family of environmental niche models called "genomic offset" (GO, also called Genome-Wide Environment Selection, Risk Of Non-Adaptiveness, or hybrid SDMs, reviewed elsewhere (Capblancq *et al.*, 2020)) aim to quantitatively project how rapid climate shifts disrupt genome-environment relationships, potentially putting populations with more vulnerable genetic makeups at higher risk of local extinction.

To anticipate which populations may become maladapted and are thus of conservation concern, GO projections for several species have been calculated for the mid-21st century (Waldvogel *et al.*, 2020; Capblancq *et al.*, 2020). However, these methods still require validation (Fitzpatrick *et al.*, 2018; Hoffmann *et al.*, 2021; Rellstab *et al.*, 2021), including studies of how well relative (mal)adaptation predicts populations' absolute fitness and mortality risk. This is being addressed by combining common gardens with genomics-informed niche modeling. For instance, Exposito-Alonso et al. (2019) investigated the genetic basis of local adaptation using A. thaliana, a primary model species for genomics with 1,135 publicly available whole-genome sequences (1001 Genomes Consortium, 2016), using genome-wide associations with fitness of 500 populations grown in climatically contrasting common gardens. Here, the genetic basis of fitness was significantly predictable only from genome-environment associations using the climate of origin of the 500 populations as proxy of local adaptation. This was then used to make common-garden-calibrated GO projections of (mal)adaptation. To illustrate the signal of potential future maladaptation in *A. thaliana*, for this review I conducted a simplified GO projection using an ENM to geographically map only populations containing genotypes with at least one of the significant alleles identified to increase survival in warm edge common gardens and compared this with the species-wide map (**Fig. 2C**). This showed that locally adapted genotypes are enriched in the range edges of the species (**Fig. 2C**) (Exposito-Alonso *et al.*, 2018). Projecting their niche using 2050 climate data from IPCC shows that these more resilient genotypes have an increased projected distribution towards the central latitudes of the species (**Fig. 2D**) (Exposito-Alonso *et al.*, 2019). The GO metric may be interpreted as current populations needing natural or assisted migration of adaptive genotypes to maintain the same level of fitness and local adaptation in the future (~75% of cells in map, **Fig. 2D**) (Gougherty *et al.*, 2021).

New datasets of plant species are supporting GO predictions. For instance, 10 common gardens of *Panicum virgatum* across North America showed that 30% of genomic regions explaining fitness variation were also discovered from simple genome-environment associations (Lovell *et al.*, 2021). The same was true for ~60% of loci related to phenotypes such as cold injury in long-term *Pinus contorta* trials in Canada (Mahony *et al.*, 2020). GO of *Pennisetum glaucum* land races in Niger correlated 40% with sied yield (Rhoné *et al.*, 2020), and in the tree *Populus balsamifera,* GO explained 60% of the tree height growth in US and Canada (Fitzpatrick *et al.*, 2021). While these results are encouraging, it remains uncertain whether relative (mal)adaptation projections from GO will improve predictions of the vulnerability of populations to extinction. For instance, because GO does not include population dynamics and evolutionary forces acting in time or because maladaptation is vastly more complex than just the lack of local adaptation, including processes happening in small populations such as like inbreeding (Brady *et al.*, 2019). Regardless, GO is a first to integrate evolutionary genomics and within-species variation into large-scale spatial biodiversity projections of species extinction risk.

III. *Impact* of global habitat changes on within-species genetic diversity.

Global change has not only put evolutionary pressure on maladapted populations, but it has already *impacted* species by reducing populations and geographic ranges, often due to direct habitat extirpation. This erodes the genetic diversity of such species, which further reduces the possibility of rescuing maladapted populations from neighboring populations with adaptive genotypes. Alarmingly, there is plenty of evidence of the widespread decline in and loss of populations (Ceballos *et al.*, 2020). Land-use-based habitat suitability modeling of 19,400 species (virtually all amphibians, birds, and animals; no plants) shows that 21st century land transformations alone may already cause geographic range losses of 6.2–10.7% per decade (Powers & Jetz, 2019).

The new field of “macrogenetics” studies how this dramatic reduction of habitat and populations has already caused within-species genetic diversity loss (Leigh *et al.*, 2021). In contrast to studies predicting (mal)adaptation, macrogenetic and conservation genetics studies typically assume that monitoring genome-wide or neutral genetic diversity is the safest and often the only option to account for future evolution in conservation (Kardos *et al.*, 2021). Surprisingly, results from early macrogenetics studies have been mixed: a study using nuclear microsatellites that sampled populations of 91 animal species in at least two time points found a 6% reduction in within-population diversity (Leigh *et al.*, 2019); a study of conserved mitochondrial marker genes across 17,082 animal species did *not* find decreased diversity with increasing land-use change (Millette *et al.*, 2020); another study on two marker genes for 4,500 mammals predicts that ongoing and future land-use transformations to mid-21st century overlap with currently high genetically diverse regions and thus large losses are expected (Theodoridis *et al.*, 2021).

These early macrogenetic studies provide a new angle for studying within-species extinction and highlight the need for standardized genetic diversity targets in conservation metrics, including new genetic essential biodiversity variables (Hoban *et al.*, 2020), which must be computed for entire ecosystems and not only for endangered species. However, macrogenetics also suffer from several limitations (Leigh *et al.*, 2021), including (i) the use of a single or several genetic markers rather than whole-genome variation, where genetic markers can be less sensitive to global change impacts; (ii) no theoretical framework for how habitat alterations relate to population structure and local adaptation; and (iii) "shifting baseline" syndrome, referring to loss underestimations from studying ecosystems that have already degraded.

Exposito-Alonso et al. (2022) developed a macrogenetics theory that predicts the percentage of genome-wide diversity loss (as allelic richness or mutations) for a given percentage of habitat area loss within a species' geographic range. Analogous to the well-known species-area relationship, the number of alleles also follows a power scaling law function coined the "mutations-area relationship" (MAR) with one parameter, z_{MAR}. This parameter quantifies the level of geographic mixing of genetic diversity, a balance of drift, migration, and local adaptation and differentiation. Here, species with complete population divergence and local adaptation, thus little mixing of genetic diversity, is represented by $z_{MAR}=1$, while a species with little differentiation or a high mixing of genetic diversity is represented by $z_{MAR}\sim 0$. Intuitively, species with strong local adaptation and genetic differentiation (high z_{MAR}) will lose a greater fraction of genetic diversity when a fraction of their geographic range is lost. Fitting MAR to *A. thaliana*'s 1001 Genomes sampled across Eurasia shows this species' substantial spatial structure ($z_{MAR}=0.3$). Simulating the loss of habitats in *A. thaliana* by progressively removing populations from the warm to the cold edge (**Fig. 3A**) and quantifying the loss of genetic diversity shows that the MAR is a good predictor of the impact of habitat range loss on within-species diversity (**Fig. 3B**). Because MAR accounts for spatial local adaptation and differentiation processes, its predictions are more accurate than the naive application of classic genetic theory of population bottlenecks (**Fig. 3B**, gray line). Nevertheless, MAR predictions should be regarded as the minimum loss from an immediate habitat loss, as it does not include (mal)adaptation nor genetic drift, which could produce further genetic diversity losses in the long term, but incorporating these dynamics in MAR will require further modeling.

Using the MAR framework on one of the first macrogenetic studies that included plants (De Kort *et al.*, 2021), Exposito-Alonso et al. (2022) studied within-species trends of genetic diversity by combining over 10,000 individuals with genome-wide variation data for 11 plant and 9 animal species (**Fig. 4C**). Expectedly, the degree of population structure and prior anthropogenic impacts affected genetic diversity loss dynamics. For instance, the perennial American grass *Panicum hallii* has a strong genetic structure ($z_{MAR}=0.8$) (Palacio-Mejía *et al.*, 2021), and while not categorized as threatened, its exposure to recent transformations in the lower Great Plains of the US and Northern Mexico could have already caused substantial losses. The tree *Eucalyptus melliodora* in Australia shows an intermediate genetic structure ($z_{MAR}=0.4$) (Supple *et al.*, 2018), and its category of "vulnerable" under the Red List criteria A2c indicates it has lost at least 30% of its habitat; or the equivalent of 13% genetic diversity loss according to the MAR. The critically endangered *Pinus torreyana,* with only 4,500 mature individuals left near Los Angeles, US, has very low genetic diversity, and consequently structure ($z_{MAR}\sim 0$), reflecting either historically small population sizes or recent dramatic losses (Di Santo *et al.*, 2022).

The importance of sustaining within-species genetic diversity is now recognized in preliminary post-2020 United Nations' Sustainability Goals, which aim to "protect 90% of genetic diversity within all species" (CBD, 2021). However, evaluating these targets using empirical data appears technically challenging and costly (Thurfjell *et al.*, 2022). While a rough approximation, we can leverage the MAR to scale our understanding of population genetics to at least make high-uncertainty global average projections by incorporating global land-use changes. For instance, since the 1850s, 45% of global terrestrial ecosystems have been transformed, as per the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) (see **Fig. 4A** primary forest loss from the LUH2 database [(Hurtt *et al.*, 2020)). Assuming an average MAR with broad confidence intervals, the average species may thus have lost ~16% of within-species genetic diversity (**Fig. 4D**). Note that although genomic diversity is not tracked over time, MAR allows for "shifting back the baseline" and inferring past genetic losses from known habitat changes (this could complement DNA sequencing of historical specimens from herbaria, see review (Lang *et al.*, 2018)). Moving forward, land use and climate feedbacks need to be combined to create fine-grained maps of within-species genetic diversity loss across the world. In addition, theoretical MAR developments are required to incorporate feedbacks from local (mal)adaptation, which could accelerate the within-species diversity loss and extinction risk (**Fig. 4D, Fig. 2-3**).

IV. Open questions and conclusions

Plant species extinctions are rising under global change, but it is populations that are impacted and need to respond. Recent genomic technologies have provided invaluable insights into the local adaptation of populations, with rich spatial coverage at continental scales, and have enabled the integration of evolutionary processes into global biodiversity modeling. Genomics-informed environmental niche modeling within species, such as GO, now allows predictions of plant population (mal)adaptation responses to climate change via local adaptation disruptions, and the MAR can better track how many genetically unique populations may be lost due to habitat changes at global scales. Model plant species, where genetic variation can be directly associated with fitness in common garden experiments, will be critical to understanding the quantitative feedback between loss of genetic diversity and (mal)adaptation. With continued habitat destruction and accelerating climate change, these frameworks have the potential to create projections and hypotheses on the silent extinction of within-species diversity and erosion of evolutionary potential.

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References

1001 Genomes Consortium. **2016**. 1,135 Genomes Reveal the Global Pattern of Polymorphism in Arabidopsis thaliana. *Cell* **166**: 481–491.

A. Lee-Yaw J, L. McCune J, Pironon S, N. Sheth S. **2021**. Species distribution models rarely predict the biology of real populations. *Ecography*.

Angert AL, Bontrager MG, Ågren J. **2020**. What do we really know about adaptation at range edges? *Annual review of ecology, evolution, and systematics* **51**: 341–361.

Bontrager M, Muir CD, Mahony C, Gamble DE, Germain RM, Hargreaves AL, Kleynhans EJ, Thompson KA, Angert AL. **2020**. Climate warming weakens local adaptation. *bioRxiv*: 2020.11.01.364349.

Bontrager M, Usui T, Lee-Yaw JA, Anstett DN, Branch HA, Hargreaves AL, Muir CD, Angert AL. **2021**. Adaptation across geographic ranges is consistent with strong selection in marginal climates and legacies of range expansion. *Evolution; international journal of organic evolution* **75**: 1316–1333.

Brady SP, Bolnick DI, Barrett RDH, Chapman L, Crispo E, Derry AM, Eckert CG, Fraser DJ, Fussmann GF, Gonzalez A, ***et al.*** **2019**. Understanding Maladaptation by Uniting Ecological and Evolutionary Perspectives. *The American naturalist* **194**: 495–515.

Capblancq T, Fitzpatrick MC, Bay RA, Exposito-Alonso M, Keller SR. **2020**. Genomic Prediction of (Mal)Adaptation Across Current and Future Climatic Landscapes. *Annual review of ecology, evolution, and systematics* **51**: 245–269.

CBD. **2021**. First Draft of The Post-2020 Global Biodiversity Framework.

Ceballos G, Ehrlich PR, Raven PH. **2020**. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proceedings of the National Academy of Sciences of the United States of America*.

Czech L, Peng Y, Spence JP, Lang PLM, Bellagio T, Hildebrandt J, Fritschi K, Schwab R, Rowan BA, GrENE-net consortium, ***et al.*** **2022**. Monitoring rapid evolution of plant populations at scale with Pool-Sequencing. *bioRxiv*: 2022.02.02.477408.

De Kort H, Prunier JG, Ducatez S, Honnay O, Baguette M, Stevens VM, Blanchet S. **2021**. Life history, climate and biogeography interactively affect worldwide genetic diversity of plant and animal populations. *Nature communications* **12**: 516.

Di Santo LN, Hoban S, Parchman TL, Wright JW, Hamilton JA. **2022**. Reduced representation sequencing to understand the evolutionary history of Torrey pine (Pinus torreyana parry) with implications for rare species conservation. *Mol. Ecol.*: 2021.07.02.450939.

Dullinger S, Gattringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A, Willner W, Plutzar C, Leitner M, Mang T, ***et al.*** **2012**. Extinction debt of high-mountain plants under twenty-first-century climate change. *Nature climate change* **2**: 619–622.

Exposito-Alonso M, 500 Genomes Field Experiment Team, Burbano HA, Bossdorf O, Nielsen R, Weigel D. **2019**. Natural selection on the Arabidopsis thaliana genome in present and future climates. *Nature* **573**: 126–129.

Exposito-Alonso M, Booker TR, Czech L, Gillespie L, Hateley S, Kyriazis CC, Lang PLM, Leventhal L, Nogues-Bravo D, Pagowski V, ***et al.*** **2022**. Genetic diversity loss in the Anthropocene. *Science* **377**: 1431–1435.

Exposito-Alonso M, Vasseur F, Ding W, Wang G, Burbano HA, Weigel D. **2018**. Genomic basis and evolutionary potential for extreme drought adaptation in Arabidopsis thaliana. *Nature ecology & evolution* **2**: 352–358.

Fitzpatrick MC, Chhatre VE, Soolanayakanahally RY, Keller SR. **2021**. Experimental support for genomic prediction of climate maladaptation using the machine learning approach Gradient Forests. *Molecular ecology* *resources*.

Fitzpatrick MC, Keller SR, Lotterhos KE. **2018**. Comment on ‘Genomic signals of selection predict climate-driven population declines in a migratory bird’. *Science* **361**: eaat7279.

Gougherty AV, Keller SR, Fitzpatrick MC. **2021**. Maladaptation, migration and extirpation fuel climate change risk in a forest tree species. *Nature climate change*.

Hoban S, Bruford M, D’Urban Jackson J, Lopes-Fernandes M, Heuertz M, Hohenlohe PA, Paz-Vinas I, Sjögren-Gulve P, Segelbacher G, Vernesi C, *et al.* **2020**. Genetic diversity targets and indicators in the CBD post-2020 Global Biodiversity Framework must be improved. *Biological conservation* **248**: 108654.

Hoffmann AA, Weeks AR, Sgrò CM. **2021**. Opportunities and challenges in assessing climate change vulnerability through genomics. *Cell* **184**: 1420–1425.

Humphreys AM, Govaerts R, Ficinski SZ, Nic Lughadha E, Vorontsova MS. **2019**. Global dataset shows geography and life form predict modern plant extinction and rediscovery. *Nature Ecology & Evolution*.

Hurtt GC, Chini L, Sahajpal R, Frolking S, Bodirsky BL, Calvin K, Doelman JC, Fisk J, Fujimori S, Goldewijk KK, *et al.* **2020**. Harmonization of global land-use change and management for the period 850–2100 (LUH2) for CMIP6.

Jandt U, Bruelheide H, Jansen F, Bonn A, Grescho V, Klenke RA, Sabatini FM, Bernhardt-Römermann M, Blüml V, Dengler J, *et al.* **2022**. More losses than gains during one century of plant biodiversity change in Germany. *Nature*.

Kardos M, Armstrong EE, Fitzpatrick SW, Hauser S, Hedrick PW, Miller JM, Tallmon DA, Funk WC. **2021**. The crucial role of genome-wide genetic variation in conservation. *Proceedings of the National Academy of Sciences of the United States of America* **118**.

Lang PLM, Willems FM, Scheepens JF, Burbano HA, Bossdorf O. **2018**. Using herbaria to study global environmental change. *The New phytologist*.

Lasky JR, Josephs EB, Morris GP. **2022**. Genotype-environment associations to reveal the molecular basis of environmental adaptation. *The Plant cell*.

Leigh DM, Hendry AP, Vázquez-Domínguez E, Friesen VL. **2019**. Estimated six per cent loss of genetic variation in wild populations since the industrial revolution. *Evolutionary applications* **12**: 1505–1512.

Leigh DM, van Rees CB, Millette KL, Breed MF, Schmidt C, Bertola LD, Hand BK, Hunter ME, Jensen EL, Kershaw F, *et al.* **2021**. Opportunities and challenges of macrogenetic studies. *Nature reviews. Genetics* **22**: 791–807.

Lovell JT, MacQueen AH, Mamidi S, Bonnette J, Jenkins J, Napier JD, Sreedasyam A, Healey A, Session A, Shu S, *et al.* **2021**. Genomic mechanisms of climate adaptation in polyploid bioenergy switchgrass. *Nature*.

Mahony CR, MacLachlan IR, Lind BM, Yoder JB, Wang T, Aitken SN. **2020**. Evaluating genomic data for management of local adaptation in a changing climate: A lodgepole pine case study. *Evolutionary applications* **13**: 116–131.

Millette KL, Fugère V, Debyser C, Greiner A, Chain FJJ, Gonzalez A. **2020**. No consistent effects of humans on animal genetic diversity worldwide. *Ecology letters* **23**: 55–67.

Nosil P, Villoutreix R, de Carvalho CF, Farkas TE, Soria-Carrasco V, Feder JL, Crespi BJ, Gompert Z. **2018**. Natural selection and the predictability of evolution in Timema stick insects. *Science* **359**: 765–770.

Palacio-Mejía JD, Grabowski PP, Ortiz EM, Silva-Arias GA, Haque T, Des Marais DL, Bonnette J, Lowry DB, Juenger TE. **2021**. Geographic patterns of genomic diversity and structure in the C4 grass Panicum hallii across its natural distribution. *AoB plants* **13**: lab002.

Pillet M, Goettsch B, Merow C, Maitner B, Feng X, Roehrdanz PR, Enquist BJ. **2022**. Elevated extinction risk of cacti under climate change. *Nature plants* **8**: 366–372.

Powers RP, Jetz W. **2019**. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature climate change* **9**: 323–329.

Rellstab C, Dauphin B, Exposito-Alonso M. **2021**. Prospects and limitations of genomic offset in conservation management. *Evolutionary applications* **14**: 1202–1212.

Rhoné B, Defrance D, Berthouly-Salazar C, Mariac C, Cubry P, Couderc M, Dequincey A, Assoumanne A, Kane NA, Sultan B, *et al.* 2020. Pearl millet genomic vulnerability to climate change in West Africa highlights the need for regional collaboration. *Nature communications* **11**: 5274.

Rudman SM, Greenblum SI, Rajpurohit S, Betancourt NJ, Hanna J, Tilk S, Yokoyama T, Petrov DA, Schmidt P. **2022**. Direct observation of adaptive tracking on ecological time scales in *Drosophila*. *Science* **375**: eabj7484.

Supple MA, Bragg JG, Broadhurst LM, Nicotra AB, Byrne M, Andrew RL, Widdup A, Aitken NC, Borevitz JO. **2018**. Landscape genomic prediction for restoration of a Eucalyptus foundation species under climate change. *eLife* **7**.

Theodoridis S, Rahbek C, Nogues−Bravo D. **2021**. Exposure of mammal genetic diversity to mid−21st century global change. *Ecography*.

Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC. **2005**. Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America* **102**: 8245–8250.

Thurfjell H, Laikre L, Ekblom R, Hoban S, Sjögren-Gulve P. **2022**. Practical application of indicators for genetic diversity in CBD post-2020 Global Biodiversity Framework implementation. *bioRxiv*: 2022.02.18.481087.

Urban MC, Travis JMJ, Zurell D, Thompson PL, Synes NW, Scarpa A, Peres-Neto PR, Malchow A-K, James PMA, Gravel D, *et al.* 2022. Coding for Life: Designing a Platform for Projecting and Protecting Global Biodiversity. *Bioscience*.

Waldvogel A-M, Feldmeyer B, Rolshausen G, Exposito-Alonso M, Rellstab C, Kofler R, Mock T, Schmid K, Schmitt I, Bataillon T, *et al.* 2020. Evolutionary genomics can improve prediction of species' responses to climate change. *Evolution letters* **4**: 4–18.

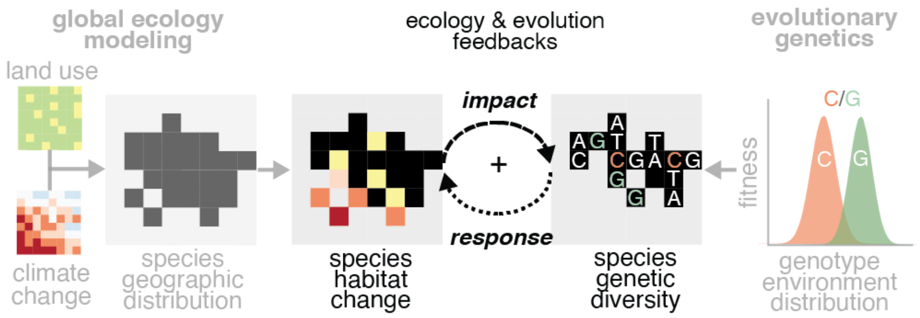

Fig. 1 | The eco-evolutionary bridges of species local extinctions in the Anthropocene. *Global ecology modeling attempts to understand anthropogenic impacts on ecosystems and species extinction without accounting for evolution (left). Evolutionary genetics models explain how different genotypes (e.g. with a C/G single nucleotide polymorphism) may be better fit to different environments (right). Bridging these two fields, new connections and feedback between ecology and evolutionary models can help explain extinction within a species in the face of global change (center).*

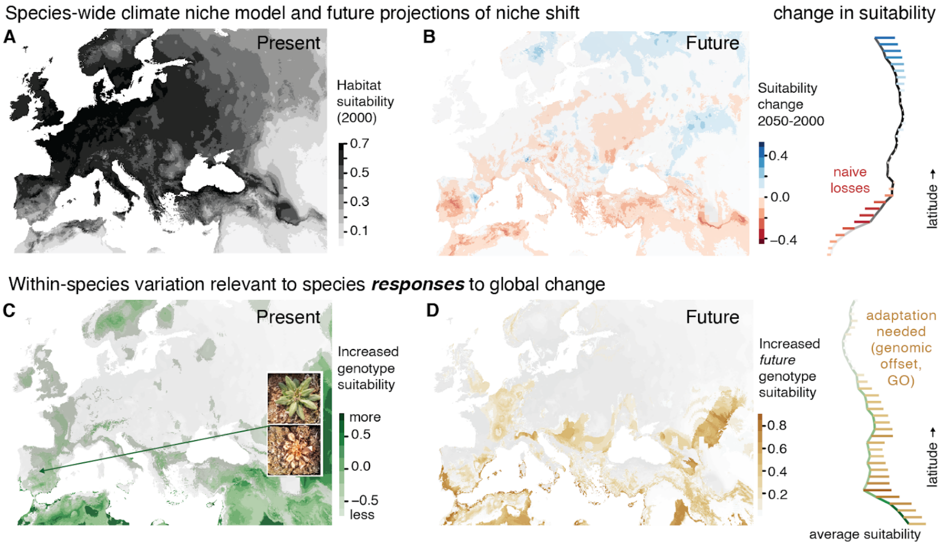

Fig. 2 | Integrating (mal)adaptive evolutionary genomic responses to climate change in species-focused niche models

*(**A**) Example Environmental Niche Model (ENM) of* Arabidopsis thaliana *using MaxEnt algorithm and bioclimate variables from WorldClim.org. (**B**) ENM projection into future 2050 climates, "business-as-usual" socio-economic pathway (SPP5), and high CO_2 representative concentration pathway (8.5) using Max Planck Institute's Global Circulation Model predictions (CMIP5-MPI). (**C**) To showcase the deviation in the geographic distribution of the high-survival genotypes, an ENM was fitted as in (A) to predict habitat suitability only of populations with at least one top allele associated with high survival in a genome-wide association in a common garden in Madrid, Spain (location marked with green arrow) (Exposito-Alonso et al. 2019). Green indicates regions with increased habitat suitability of these locally adapted genotypes compared to the species-wide ENM in (A). (**D**) To conceptually showcase genomic offset (GO) projections, the genomics-informed ENM of locally adapted genotypes was projected to 2050. Brown color indicates regions projected to have higher suitability of the locally adapted genotypes than at present, indicating populations in these locations may need these genotypes to maintain the same level of local adaptation. (Source of* A. thaliana *ENM and code: github.com/moisesexpositoalonso/arabidopsisrange).*

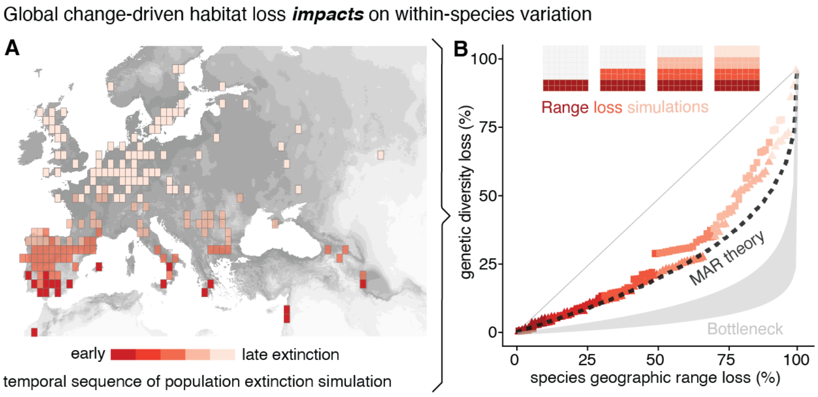

Fig. 3 | Using the mutations-area relationship (MAR) to quantify the loss of genomic diversity with population extirpation

(A) *A simulation of removal of* A. thaliana *populations in silico from south to north and (****B****) the consequence of loss of area on species-wide genomic diversity in the same simulation. The theoretical MAR (dashed lines) is predictive of the genetic diversity loss dynamics compared to classic population genetic expectations of individual bottleneck reductions.*

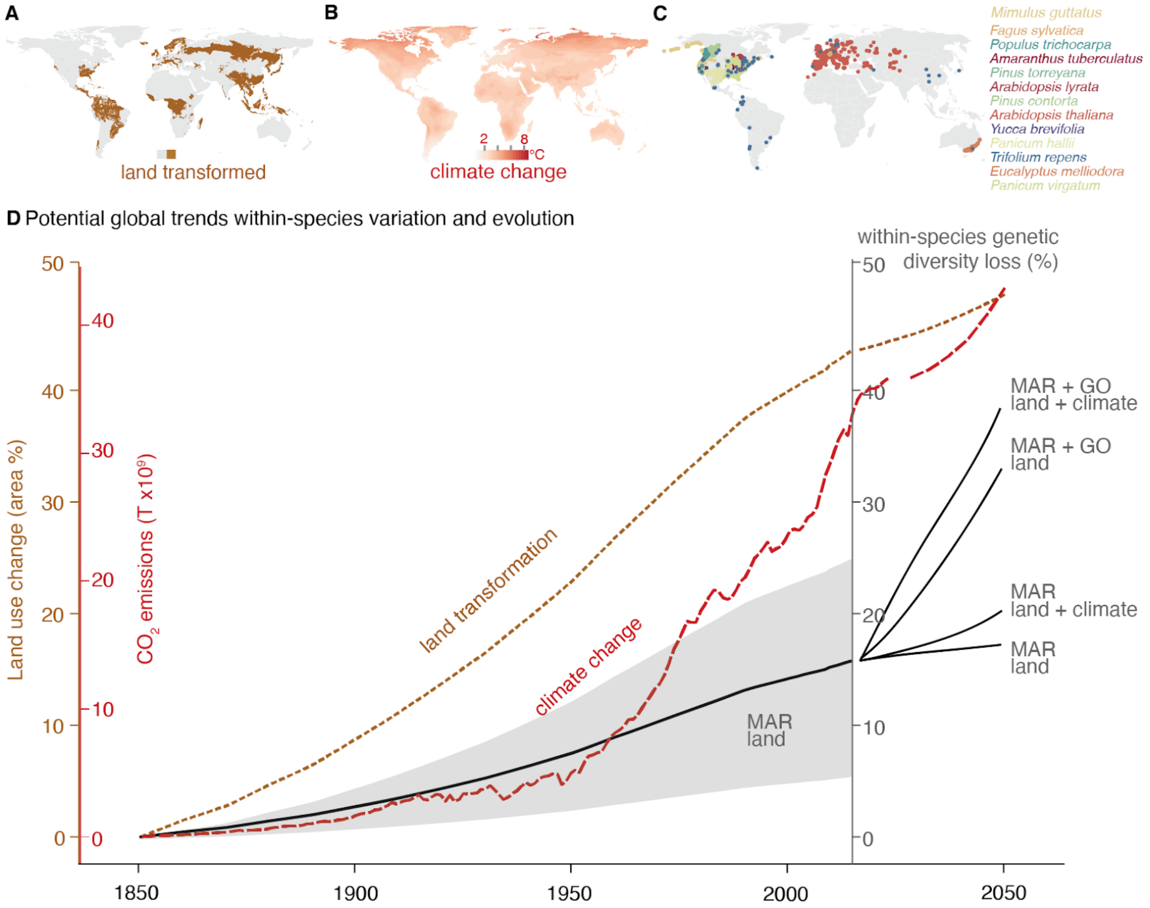

Fig. 4 | Datasets of global land use, climate change, and plant population genomics and new frameworks to understand the within-species erosion of genetic variation and evolutionary potential leading to extinctions

*(**A**) Primary forest transformation since 1850 from the Land Use Harmonization (LUH2). (**B**) Future changes in average annual temperature from IPCC (CMIP5, retrieved from worldclim.org). (**C**) Plant population genomic datasets from 13 plant species (11 analyzed in Exposito-Alonso et al. 2022). (**D**) Temporal trends of land use (LUH2) and CO$_2$ emissions (CO$_2$, icos-cp.eu) since 1850 and their predictions to 2050 under a business-as-usual socio-economic scenario (SSP1-5, RCP8.5). Overlaid, a MAR-based projection on how within-species variation may have been eroded and future hypothetical projections under various future environmental change scenarios and eco-evolutionary feedbacks of (mal)adaptation and extinction.*