Human Land Use Impacts on Native Plant Genetic Diversity

by

John Ferris

A thesis submitted to the Department of Biological Sciences, University of Manitoba,

in partial fulfillment of the requirements for the course

BIOL 4100 (Honours Thesis)

for the degree of

Bachelor of Science (Honours)

Abstract

Extensive research has been conducted to determine how urbanization and human land use affect the genetic diversity and population structure of animal populations. Plant populations experience many direct and indirect effects of human activities, such as habitat fragmentation, the introduction of invasive species and herbivores, and declines in pollinators. Despite awareness that urbanization and agriculture are the largest threats to plants globally, very little research has directly assessed this relationship on a broad scale. To examine this, I compiled a list of 2745 terrestrial plant species endemic to North America from the IUCN and then conducted a programmatic search of the Dryad Digital Repository for microsatellite genetic datasets for these species. Upon manual review of these datasets, 15 appropriate datasets with georeferencing were selected for usage in this study. The final database comprised 7535 individuals of 427 populations of 21 species. I estimated gene diversity, rarefied allelic richness, and population-specific FST for each site and used these values as response variables in a series of Bayesian Hierarchical Generalized Linear Mixed Models (GLMMs) to test relationships between population genetic composition and human land use. I treated species as a random effect with random slopes and intercepts. This allowed me to observe species-specific trends in the data. My results indicated that across 21 species, populations in areas with high rates of human land use exhibit greater population differentiation and higher overall genetic diversity. In contrast, areas with high human population density showed overall increases in genetic diversity and decreased population differentiation. My results show clear, albeit weak,

trends, suggesting that the small sample size and lack of diversity in life history traits were limitations.

Table of Contents

List of Tables

List of Figures

Introduction

Genetic diversity determines a population's ability to adapt and survive. It is intrinsically linked to population fitness, as a population's gene set constitutes the raw material for natural selection (Palumbi 2001). Humans now decrease genetic diversity globally and could be considered the primary drivers of evolutionary change (Palumbi 2001). Anthropogenic disturbances such as habitat loss, habitat fragmentation (Schlaepfer et al. 2018; Fahrig 2003), and urbanization (Schmidt et al. 2020, Schmidt and Garroway 2021, Kinnunen et al. 2025, Karachaliou et al. 2025) are strongly associated with shifts in animal genetic diversity. Despite the importance of plants to the ecosystem, most broad-scale syntheses on genetic diversity loss have focused primarily on animals.

Human activities can both directly and indirectly decrease native plant genetic diversity (IUCN 2024; Winfree et al. 2009). Humans directly affect the genetic diversity of wild populations and their differentiation through disturbances such as habitat destruction and fragmentation. Examples of disturbance include habitat loss from urbanization (Schmidt et al. 2020) and farming (IUCN 2024), as well as habitat destruction/disturbance from logging (Ding et al. 2017; Fontúrbel et al. 2024) and mining (IUCN 2024). Through these habitat changes, populations become divided into smaller subpopulations, resulting in population bottlenecks and the loss of alleles due to increased genetic drift and reduced population size. Currently, at least 11% of all vascular plant species are threatened with global extinction, with one of the primary components of this threat being the conversion of their habitats to cropland (Moreira et al. 2023). The IUCN Red List has assessed 47% of vascular plant species as being of least concern, citing urbanization and agriculture as the greatest threats to population persistence (IUCN 2024).

Human activities, therefore, may constitute a significant threat to plant genetic diversity through direct reductions in population size.

The full extent of current anthropogenic habitat fragmentation on plant genetic diversity is likely underestimated. This underestimation is due to extinction debt (Tilman et al. 1994; Gargiulo et al. 2025), in which species are on a trajectory toward extinction because of past environmental changes or habitat loss, even if current conditions, such as population size and recruitment, appear stable or favourable. The "debt" is repaid later, resulting in a seemingly delayed extinction event due to genetic drift over multiple generations, leading to losses of genetic diversity. Therefore, due to extinction debt, species that do not currently appear to be at risk of extinction may already be on the path to extinction, already having lost the genetic diversity required to maintain population viability. Fragmentation combined with contemporary human land use results in a marked decline in genetic diversity (Helm et al. 2009). There are also debates in the literature on this subject; a global meta-analysis (González et al. 2020) suggests that habitat degradation has little effect on heterozygosity and genetic diversity, but a localized study on logging intensity (Fontúrbel et al. 2024) suggests that habitat degradation has a significant impact on heterozygosity, allelic richness, and inbreeding rates in non-woody plant species.

Some angiosperms can undergo "extreme inbreeding", which can delay some of the negative outcomes of habitat degradation and fragmentation. With reductions in population size, the potential for pollination is restricted (Makowski et al. 2024). However, perfect-flowered species (angiosperms that possess fertile parts of both sexes) may be facultative self-pollinators, meaning that they can breed with themselves. The

ability to self-pollinate is more prevalent within annual species, as it allows them to persist in the absence of pollen from another individual. However, overreliance on this mode of reproduction can exacerbate the negative consequences of reduced population size, as it involves extreme inbreeding (Bello-bedoy and Núñez-Farfán 2011). Accumulation of deleterious alleles can occur in self-pollinating populations due to a reduced ability to purge mildly deleterious alleles within inbreeding populations, like the concept of Muller's Ratchet (Freund et al. 2025). Therefore, while aiding population persistence in heavily human-impacted landscapes, increased reliance on this reproductive mode seems to lead to a drastic decrease in genetic diversity (Bello-bedoy and Núñez-Farfán 2011).

While inbreeding via self-pollination has negative consequences for plant genetic diversity, it can facilitate the colonization of new habitats, expand niche breadth, and improve genetic composition (Grossenbacher et al. 2015). Although self-pollinating plants cannot purge mildly deleterious alleles easily, deadly homozygous recessive alleles can sometimes be efficiently expelled from the gene pool, generally increasing the mean fitness of a population in the short term (Grossenbacher et al. 2015; Zeitler et al. 2023). Plants that can self-pollinate can establish themselves more successfully in environments with unpredictable pollinators or even in the complete absence of pollinators. With human-caused global declines in pollinators (Winfree et al. 2009), this ability to self-pollinate is becoming increasingly important. Sister species studies show that plants that can self-pollinate have much larger ranges than their obligate outcrossing counterparts (Grossenbacher et al. 2015). The occurrence of self-pollinators increases with latitude because pollinator availability is less predictable at higher latitudes. This increased

prevalence of self-pollinators poses a problem, as newly widespread self-pollinating populations with extremely low genetic diversity can be at risk of collapse due to sudden shifts in their environment (ex. climate change, urbanization, agriculture) (Stebbins 1957).

Indirect effects on the genetic diversity of plants also occur through human land usage, as increased land usage is linked to pollinator decline (Winfree et al. 2009; Librán-Embid et al. 2021; Gegear et al. 2021), and native herbivore populations being fragmented and declining (Rossetti et al. 2017; Fernández-Murillo et al. 2023). Additionally, humans affect the genetic diversity of native populations by introducing invasive species (Davies 2011; Hejda et al. 2009; Vilà et al. 2011; Van Kleunen et al. 2010), parasites (Miedaner and Garbelotto 2024), and pathogens (Perrin et al. 2023; Zaffarano et al. 2008).

Human disturbance has been a prevailing cause of global pollinator declines (Winfree et al. 2009). Insect pollinators, and other animals such as certain birds and small mammals, are essential mutualistic partners to members of the seed plant taxa, which together comprise the largest clade of plants. Pollinators are adversely affected by human land use, and humans currently use about 50-75% of the world's land (Winfree et al. 2009). Wild plant species can exhibit a phenomenon called pollen limitation of reproduction (Makowski et al. 2024), whereby plants achieve greater reproductive output with greater access to pollinators. This limitation is observed when these plants are experimentally supplemented with pollen, resulting in increased seed set. This finding that plants are reproductively limited by pollinator abundance (Makowski et al. 2024) suggests that increases in human land use could reduce the effective population size of wild plant populations by negatively affecting pollinators.

Herbivory is one of the main threats plants face, and humans have dramatically altered the composition of herbivore communities. Plant-herbivore interactions have long driven co-evolutionary arms races, but if human disturbance directly harms herbivores more than plants, could habitat fragmentation benefit plants? Interestingly, even with reduced native herbivore populations, overall herbivory rates on plants do not decline, as other generalist herbivores expand their populations to fill the niche (Rossetti et al. 2017). A major agricultural practice that drives declines in plant genetic diversity is the introduction of herbivores, such as livestock. Livestock grazing has a profound impact on community composition, as the inclusion of livestock generally drives declines in herbivore and other plant-dependent species diversity in an area (Filazzola et al. 2020).

Similarly, livestock-driven declines in native herbivores and the spread of human-introduced non-native plant species pose a serious competitive threat to native plant species. It has been suggested that the largest group of globally invasive species is European plant species (Van Kleunen et al. 2010), due to long-term selective pressures from human activity, which increases their invasion potential in human-disturbed habitats. Meta-analyses highlight a strong association between certain traits and the ability to invade, including growth rate, shoot allocation, leaf-area allocation, and physiology (Van Kleunen et al. 2010; Vilà et al. 2011). Statistical analyses support the idea that invasive species have higher values for these traits (Van Kleunen et al. 2010). These invading plants reduce species richness, diversity, and evenness, and in some cases, species numbers in an area can decline by up to 90% (Hejda et al. 2009). Thus, as human land use increases, these invasive species are likely to take over habitats, causing declines and potential extinctions of native plant populations.

Human-driven global agricultural expansion has increased the geographic range and prevalence of many plant-hosted parasites and pathogens. Foreign pathogens are spread through crop plants and can locate new potential hosts in new areas as agricultural expansion increases host population sizes, which permits divergence into many new pathogen species (Zaffarano et al. 2008). Plants and their pathogens/parasites are intertwined in a co-evolutionary relationship via reciprocal selection, giving host plants that have undergone reciprocal selection more tolerance to pathogens. When plants are moved out of their original habitat where co-speciation occurred, or when crop plants are introduced into this habitat, pathogens and parasites can switch hosts (Bartoli et al. 2015). Because human cultivars are genetically similar, these pathogens can be transmitted rapidly and widely, resulting in large-scale epidemics that then spread to native plant species, causing major declines in population genetic diversity (Mitchell et al. 2010). While there are many studies into the specifics of parasites and pathogens, the methods of how they spread seem to be surprisingly understudied, considering the pathogens that humans spread cause marked effects on the fitness of native plant species, such as reductions in size and fecundity (van Dijk et al. 2021), as well as overall survival (Springer 2009).

Despite the extensive putative negative effects of humans on plant genetic diversity, some positive effects have been observed. Urban conservation areas such as parks and heterogeneous residential areas with gardens and lawns can greatly enhance biodiversity within cities (Lososová et al. 2011). Domestic gardens and botanical gardens play an important role in conserving native species in endangered areas that would otherwise be lost (Al-Kofahi et al. 2024). Additionally, garden composition is an effective

way to reduce the impacts of habitat loss on pollinator species (Majewska and Altizer 2020), as intrinsic garden features are more important than external landscape features. Urban gardens are therefore an important way to manage both plant and pollinator diversity, even amid the intense fragmentation of cities.

Despite these various effects, very little research has assessed their combined outcomes on a broad scale. The objective of this study is to quantify the broad-scale impacts of human activity on plant genetic diversity by comparing genetic diversity with the extent of human land use. To accomplish this goal, I used publicly available microsatellite data from wild plant populations. I compared them with human population density and the Human Footprint Index (HFI) (Sanderson et al. 2002), which quantifies the extent of human effects in an area on a numerical scale. I hypothesize that plant populations in areas with high rates of human land use will exhibit reduced effective population size and genetic diversity, and higher rates of population differentiation due to habitat degradation. Through this study, I hope to enhance our understanding of how various forms of human activity affect different plant groups and, therefore, enhance our ability to conserve and promote the genetic diversity of these wild plant populations.

Methods and Materials

The current literature reports that most of the effects humans have on the genetic diversity of plant populations occur through land use. For my study, I analyzed the effects of human land use on wild plant populations across North America. First, I compiled a list of endemic diploid tracheophyte species in North America. To obtain the list of species, I retrieved data from the IUCN Red List database (IUCN 2024). Next, I collected

georeferenced microsatellite data published in peer-reviewed research, which I found using a systematic keyword search of Dryad using a custom R script adapted from Schmidt et al. 2020. This was done by searching for the species name (ex, "*Quercus fusiformis*") in addition to the term "microsat*". This ensured that the data collected for this study was gathered in a machine-replicable manner. I then manually curated the results and compiled them into one database. During curation, I also excluded non-terrestrial species, as the measures of human influence I use do not include non-terrestrial biomes. Given that the microsatellite data for this study were collected from other studies with a variety of goals, I expect the likelihood of publication bias, in this case a tendency for researchers to publish positive results, in this study was greatly reduced. Additionally, I assume that the authors and the peer-review process of these studies helped select appropriate neutral markers.

I chose to use microsatellite data because it is a commonly used neutral marker in studies of genetic variation. Evolutionary processes this study is interested in, such as gene flow and drift, are best measured using neutral markers. Typically, microsatellite datasets use data from around 10 loci, but there is only a slight loss in accuracy with further genotyping (Mittell et al. 2015). Variation in microsatellite markers should help us capture recent changes in plant population structure, as these markers exhibit a high mutation rate (Mittell et al. 2015).

Once the combined microsatellite dataset was organized, the locations of each site were researched to determine the level of human impact/activity in 2 ways. First, ASCII grid data from NASA EARTHDATA Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11 (Earth Science Data Systems 2025) was used

to find population density. This can be expressed as density per square km. Therefore, this data allows for analyses over broad spatial scales. For finer-scale information, the Human Footprint Index (HFI) (Wildlife Conservation Society and CIESIN 2005) was used to summarize the human land usage in the area. The HFI summarizes the level of human influence in an area on a scale of 1 to 50. A score of 1 represents little to no human impact, such as an undisturbed rainforest, while a score of 50 represents a heavily industrialized area. Each graded area represents 1 square kilometre and is also scaled by relative human influence within each terrestrial biome (the amount/type of impact in that biome). An advantage of the HFI is that it accounts for different forms of land use, in addition to human population density, such as roads, railways, navigable rivers, and farmland.

Three metrics were estimated to assess population genetic diversity. These were gene diversity, allelic richness, and population-specific F_{ST} (site-specific in this case). Gene diversity is the average probability that 2 randomly sampled alleles at the same locus in a population differ (Nei 1973). Therefore, gene diversity is a good indicator of overall genetic diversity in a population, as it is slowly lost because rare alleles, which are lost most quickly to genetic drift, have little influence on this measure. Gene diversity will be calculated using the *Hs()* function in the *adegenet* package (Jombart et al. 2025).

My second measure, allelic richness, is an estimate of the total number of alleles at a given locus in a population (Goudet and Jombart 2004). This estimate is then corrected for sample size using rarefaction (Goudet and Jombart 2004). For this, I set a minimum sample size of 5 individuals, as in Schmidt and Garroway 2021. Allelic richness can be determined from microsatellite data using the *allelic.richness()* function in the *hierfstat* R

package. The key difference between the two metrics is that allelic richness, unlike gene diversity, quantifies the number of rare alleles. Traditionally, gene diversity was used alongside observed and expected heterozygosity. However, these metrics alone did not provide a full picture of standing variation within a population, which reflects the latent capacity for evolutionary change (also the level of inbreeding risk) of a population (Wagner, 2008). Therefore, measuring genetic diversity using both gene diversity and allelic richness provides a more complete picture of the population.

The third metric is population-specific F_{ST}, which can be interpreted as a statistical representation of the degree of divergence of a population from a reference (or ancestral) population (this can only be determined if there are 2 populations of a species, but since this study is comparative in nature, there should always be at least two sites/populations for each species). Population-specific F_{ST} can be determined using the *betas()* function in the *hierfstat* R package.

Once the microsatellite and location data were combined, the previous 3 metrics were modelled as response variables in Bayesian hierarchical generalized linear mixed-effects models (GLMMs). These 3 models showed a general "response" to urban/rural environments, human population density, and human land use (via HFI). Each model had variable slopes and intercepts, with the expectation that each species would likely differ in its response to urbanization and should be treated as separate yet still contribute to an overarching pattern. Therefore, species were considered as random effects in these models to allow for variation in the direction and strength of the relationship between land usage and genetic composition. The greatest strength of using a hierarchical model such as this is that partial pooling reduces bias in my parameter estimates (McElreath 2020).

Spatial variation due to past events or life-history traits is a factor that needs to be modelled alongside genetic and environmental metrics. Distance-based Moran's eigenvector maps (dbMEMs) are specialized eigenvectors that account for spatial autocorrelation (Dray et al. 2006) and therefore directly capture other contributors to spatial variation in models. Using this method, a distance-based neighbourhood matrix is produced with positive eigenvalues that are directly proportional to Moran's I index of spatial autocorrelation. Moran's I is comparable to Malécot's estimator of spatial autocorrelation in allele frequencies (Epperson 2005; Malécot 1955), which underpins an isolation-by-distance model. Moran's I also captures processes that lead to neutral genetic variation accurately (Epperson 2005; Sokal and Oden 1978). dbMEMs were computed using functions from the adespatial R package (version 0.3-28; Dray et al. 2025), and a forward selection procedure was also used to select dbMEMs important for the variables in my study (gene diversity, allelic richness, and population-specific F_{ST}).

Results

The initial species list from the IUCN comprised 2,745 endemic species in North America, resulting in 470 hits in a programmatic search of the Dryad Digital Repository. Upon manual review, this number was narrowed down to 15 datasets comprising 489 populations of 20 plant species. Gene diversity, allelic richness, and population-specific F_{ST} were calculated for all populations, excluding those with $n < 5$, yielding 427 populations. The values of these raw metrics, calculated by location, are shown in Figure 1. The GLMM model values are shown in Table 1. These results do not meet conventional standards of significance, but still show distinct responses.

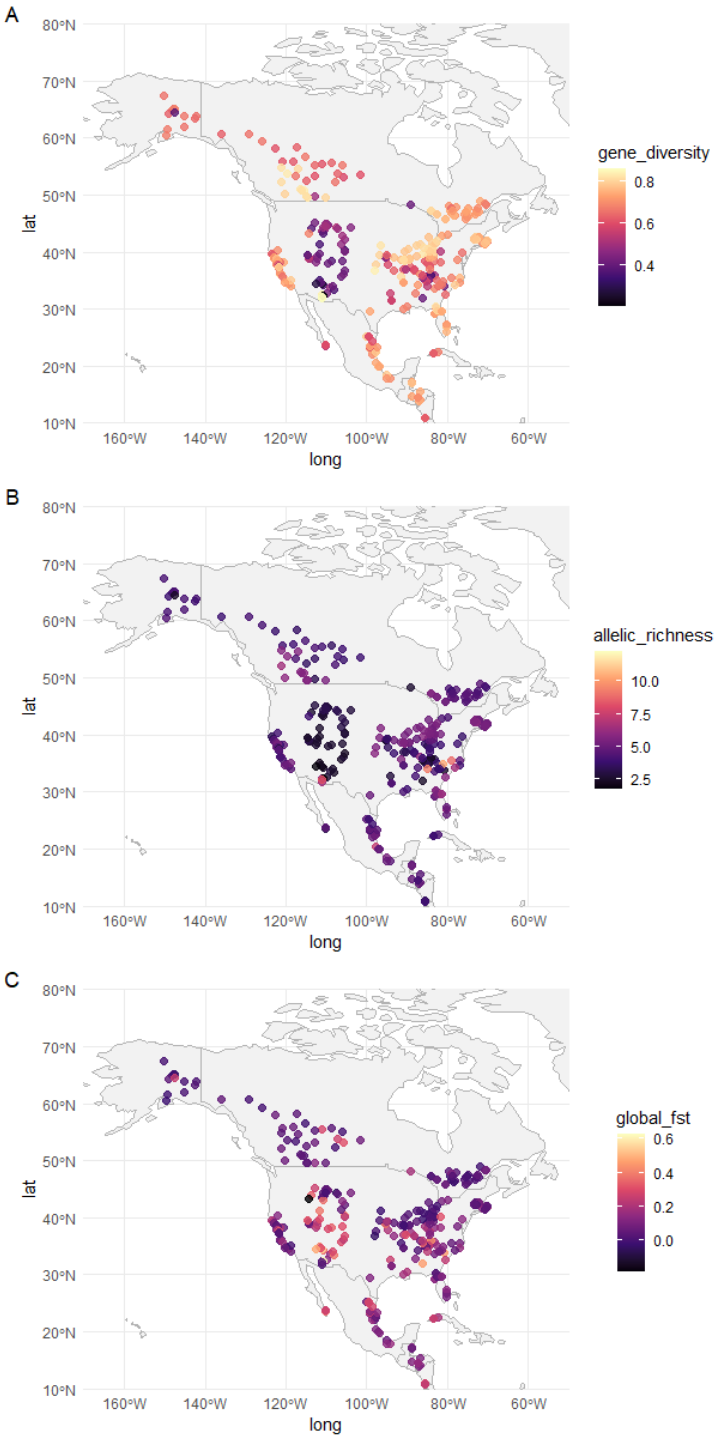

Figure 1) Locations of 427 populations of seed plant populations from 21 species used in this study. Colour gradient corresponds to levels of gene diversity (A), allelic richness (B), and population-specific FST (C) values.

Table 1: Model summaries for GLMMs. Two models were constructed for each response variable, including indices of human disturbance: human population density and the Human Footprint Index (HFI). Mean credible intervals for 95% credible interval (CI), probability of direction (Pd) as a %, and the Bayesian coefficient of variation (R^2) is the variation explained by both fixed and random effects.

	Predictor	Mean (95% CI)	Pd	Bayesian R^2
Gene Diversity	Human Population Density	0.00 (-0.01,0.02)	67.29%	0.671
	Human Footprint Index	0.00 (-0.02, 0.01)	67.14%	0.673
Allelic Richness	Human Population Density	0.04 (-0.14, 0.24)	67.76%	0.364
	Human Footprint Index	-0.04 (-0.32, 0.28)	61.09%	0.372
Population-Specific FST	Human Population Density	-0.01 (-0.14, 0.10)	60.06%	0.421
	Human Footprint Index	0.09 (-0.05, 0.23)	90.60%	0.425

The models of human population density (Figure 2a) have gene diversity slopes clustered around zero, with the lowest at -0.01 and the highest at 0.02. Allelic Richness shows an overall positive association, with a mean of 0.04 within the 95% credible interval. Population-specific F_{ST} shows a negative association, with a mean of -0.01. In summary, human population density, as a predictor, elicits a neutral association with gene diversity, a positive association with allelic richness, and a negative association with population-specific F_{ST}.

The models of the human footprint index (Figure 2b) show overall opposite responses to human population density across all three response variables, with negative allelic richness and gene diversity and positive allelic richness. Gene diversity shows an overall negative response, closely clustered around zero, with a lowest score of -0.01 and a highest score of 0.02. Allelic richness shows an overall negative skew, with the lowest slope value at -0.32 and the highest at 0.28, with values clustered around -0.04. Population-specific F_{ST} shows a quite strong negative association with the human footprint index, with a mean of 0.09, a lowest score of -0.05, and a highest value of 0.23.

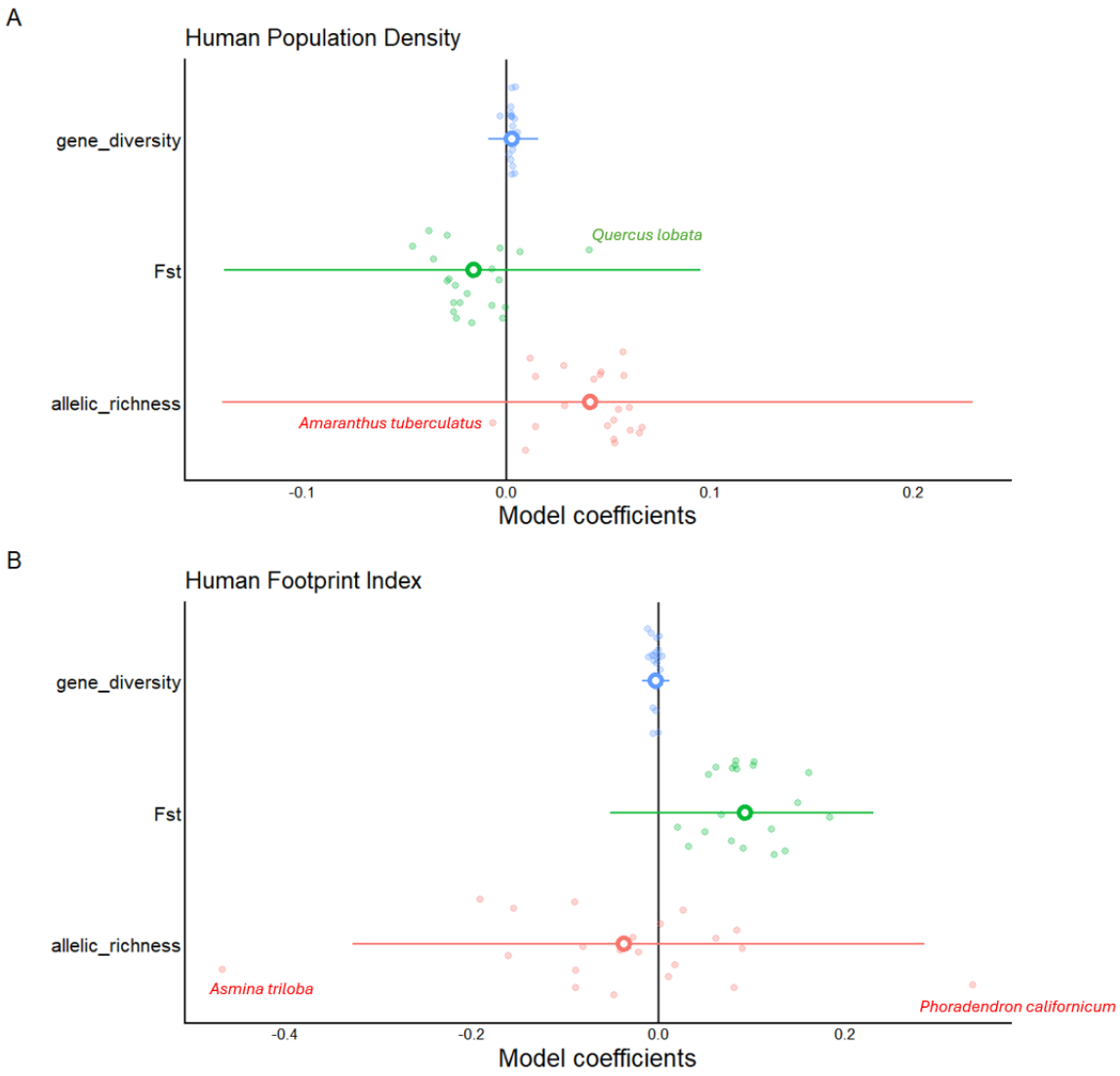

Figure 2) Results of Bayesian hierarchical generalized linear mixed effects model assessing the relationship between human population density and cumulative human land usage (Human Footprint Index), and gene diversity, allelic richness, and site-specific F_{ST} in 427 populations from 21 tracheophyte species. Slopes were allowed to vary with species. Open circles denote mean parameter estimates, while closed circles denote species-specific values. Bold lines represent the 95% credible interval.

Discussion

Albeit weak across all metrics, my results exhibited clear trends. First, the fact that genetic diversity (across all metrics) shows nearly opposite effects to both human population density and human land usage (via HFI) (see Figure 2), with human population density exhibiting an overall positive effect and human land usage exhibiting a negative effect, suggests that populations near cities harbour more alleles. Gene diversity itself shows a highly clustered association around zero in both cases, with all but one species showing a weak positive association with human population density and all but two species showing a weak negative association with human land use. In terms of population-specific F_{ST}, I observe that populations become less differentiated for all but two species in association with human population density. In contrast, the human footprint index increases population differentiation across all species. Thus, in general, my results suggest that human population density is associated with increased genetic diversity and decreased population differentiation. Human land use is associated with decreases in genetic diversity and increases in population differentiation. The results for the human footprint index align with my hypotheses and predictions across all measures, whereas the results for human population density do not. This discrepancy between the effects of human land use and human population density does not align with the relationships reported in previous studies on genetic diversity in animals (Schmidt et al. 2020; Karachaliou et al. 2025), where both factors caused shifts in the same direction.

These aforementioned trends suggest that blending of plant populations may occur near cityscapes, which coincides with previous work done on white clover (Caizergues et

al. 2024), where it was found that populations of white clover in urban areas had a much higher effective population size as compared to rural populations, with the urban populations also exhibiting high rates of gene flow among habitats. While the results of this study do not provide reliable estimates of effective population size, my increased allelic richness in association to higher human population density suggests a similar effect. Further results on effective population size estimates would aid in the explanatory power of my results.

Among notable species-specific trends, Valley Oak (*Quercus lobata*) exhibited extreme deviations from the mean. Valley Oak populations were highly differentiated in areas of high human population density and exhibited low genetic variation, with low allelic richness and gene diversity. Interestingly, these trends for Valley Oak are opposite in their association with HFI: with higher rates of human land use, Valley Oak populations become less differentiated and more genetically diverse. Why would these trends be opposite? One explanation is that populations appear more fragmented at higher human population densities, as planted trees are sourced from nurseries and thus can vary widely across neighbourhoods. This proposed explanation serves as a conjecture for future research, as very few studies have assessed these parameters.

The extreme outliers in the models appeared to be those with very specific interactions with humans. For example, the fruit tree *Asmina triloba* displayed severely reduced allelic richness in areas with a high human footprint, likely owing to an influx of gene flow from artificially selected individuals introduced into wild populations, which is a process that has been documented in other species (Tufto 2010). In contrast, the desert mistletoe *Phoradendron californicum* shows vastly increased genetic diversity in

urbanized areas (see Figure 2), consistent with findings from previous studies (Hood et al. 2025), which found that parasitic mistletoe species excel at opportunistically establishing in urban environments on introduced species, which are much more common in these areas of high human impact. In contrast, the Roughfruit Amaranth (*Amaranthus tuberculatus*) was the only species in our studies to show a negative association of allelic richness with human population density. This is likely due to genetic drift within city populations, as this species is considered a weedy species by many governmental bodies, including the Government of Canada (Weed Seeds Order, 2016).

One potential weakness of this study is that it is limited to woody plants, as 19 of the 21 species assessed were woody trees. Tree species (aka those with strong secondary growth patterns), such as these, tend to have longer lifespans and generation times and thus may show delayed effects towards human population sizes and land use, owing to the recency of human presence and development. Another potential weakness of this study is that we've assessed only 21 species, which limits the sample size for our overall trends. While our species-specific slopes are based on substantial data across populations and individuals, the overall number of species examined in this study is limited, constraining our ability to infer broad-scale patterns. However, this study currently represents all accessible published microsatellite data for North American native plant population. Another source of error that could have biased our results is the lack of major differences between species in relation to pollination syndrome, as most of my species are wind-pollinated species. Differences in seed dispersal mechanism between oak species and conifer species did not seem to drive major differences as well.

Declines in the diversity of wild populations due to human land use have been evaluated in many animal groups (Schmidt et al. 2020, Schmidt and Garroway 2021, Kinnunen et al. 2025, Karachaliou et al. 2025), and now, my results suggest that something complex is occurring within wild plant populations. Evidence from 21 species distributed across North America suggests that populations are generally less differentiated and exhibit higher genetic diversity in areas of high human population density, whereas they show the opposite pattern in areas of high human land use. Future studies should assess the effects of population size, within-city gradients in tree genetic diversity, and conduct another broad-scale synthesis using single-nucleotide polymorphisms (SNPs) to observe trends across a greater number of species and populations.

Appendices

Table S1: An Excel spreadsheet containing information on microsatellite data sources used and population information. Sheet 1 (Data_Sources) gives author's last name, link to the data dryad page (if applicable) and the citation for the original study the data was used in. Sheet 2 (Population_Information) gives the author's last name, the scientific name of the species, the class, the population identifying code, and the latitude and longitude coordinates. Sheet 3 (Initial_Dryad_Results) presents the initial results from the programmatic search, with entries included in the study highlighted in green.

Data_Information.xlsx

Table S2: Posterior draws of the GLMM for the 21 species assessed in this study. Slope means, as well as upper and lower bounds on the 95% credible interval, are stated for each of the 3 response labels (gene diversity, allelic richness, and population-specific F_{ST})

Species	Slope_mean	Lower	Upper	ResponseLabel
Acer_saccharum	-2.05E-03	-0.02771	0.027863	gene_diversity
Amaranthus_tubercula	3.40E-04	-0.01894	0.022101	gene_diversity
Asmina_triloba	-5.90E-03	-0.02412	0.011013	gene_diversity
Cercis_canadensis	-7.84E-03	-0.03539	0.017371	gene_diversity
Fagus_grandifolia	3.03E-04	-0.02043	0.027727	gene_diversity
Phoradendron_califor	3.34E-03	-0.02543	0.040476	gene_diversity
Picea_engelmannii	-5.85E-03	-0.04098	0.032307	gene_diversity
Picea_glauca	-7.08E-03	-0.0443	0.032554	gene_diversity
Pinus_banksiana	-4.51E-03	-0.03262	0.024034	gene_diversity
Pinus_contorta	-1.16E-03	-0.03157	0.031455	gene_diversity
Pinus_strobus	-1.47E-03	-0.03218	0.032954	gene_diversity
Populus_angustifolia	-1.21E-02	-0.0442	0.01229	gene_diversity
Populus_tremuloides	-2.98E-03	-0.02693	0.025513	gene_diversity
Quercus_brandegei	-5.14E-03	-0.03448	0.025981	gene_diversity
Quercus_fusiformis	2.09E-03	-0.02076	0.044349	gene_diversity
Quercus_geminata	-2.05E-03	-0.02659	0.025793	gene_diversity
Quercus_lobata	-1.10E-02	-0.03753	0.007243	gene_diversity
Quercus_minima	-2.47E-03	-0.02623	0.024419	gene_diversity
Quercus_oleoides	-6.37E-05	-0.01948	0.026368	gene_diversity
Quercus_sagraena	-3.11E-03	-0.02773	0.026885	gene_diversity
Quercus_virginiana	8.43E-04	-0.01943	0.02678	gene_diversity
Acer_saccharum	-4.78E-02	-0.71821	0.673166	allelic_richness
Amaranthus_tubercula	-2.77E-02	-0.44769	0.400489	allelic_richness
Asmina_triloba	-4.67E-01	-1.02865	0.002288	allelic_richness
Cercis_canadensis	-1.91E-01	-0.84146	0.401067	allelic_richness
Fagus_grandifolia	8.11E-02	-0.43651	0.726119	allelic_richness
Phoradendron_califor	3.37E-01	-0.38347	1.444275	allelic_richness
Picea_engelmannii	1.11E-02	-0.68934	0.849555	allelic_richness
Picea_glauca	2.23E-03	-0.7604	0.957853	allelic_richness
Pinus_banksiana	-2.17E-02	-0.76328	0.80689	allelic_richness
Pinus_contorta	-8.89E-02	-0.84602	0.62563	allelic_richness
Pinus_strobus	-1.55E-01	-1.00483	0.566967	allelic_richness
Populus_angustifolia	-1.61E-01	-0.69602	0.354566	allelic_richness
Populus_tremuloides	2.58E-02	-0.56122	0.727599	allelic_richness
Quercus_brandegei	-8.15E-02	-0.91325	0.776251	allelic_richness
Quercus_fusiformis	8.39E-02	-0.55735	1.03041	allelic_richness
Quercus_geminata	-4.16E-02	-0.65499	0.640862	allelic_richness
Quercus_lobata	-8.87E-02	-0.5246	0.341571	allelic_richness
Quercus_minima	8.98E-02	-0.45936	0.799751	allelic_richness
Quercus_oleoides	6.11E-02	-0.41057	0.684773	allelic_richness
Quercus_sagraena	-9.04E-02	-0.75064	0.590111	allelic_richness
Quercus_virginiana	1.74E-02	-0.44652	0.602876	allelic_richness
Acer_saccharum	6.14E-02	-0.25419	0.330825	Fst
Amaranthus_tubercula	3.17E-02	-0.20301	0.220678	Fst
Asmina_triloba	1.24E-01	-0.03591	0.296565	Fst
Cercis_canadensis	1.03E-01	-0.13341	0.327344	Fst
Fagus_grandifolia	6.75E-02	-0.18383	0.268142	Fst
Phoradendron_califor	2.05E-02	-0.32024	0.273272	Fst
Picea_engelmannii	7.95E-02	-0.2145	0.344822	Fst
Picea_glauca	1.01E-01	-0.20593	0.373739	Fst
Pinus_banksiana	1.21E-01	-0.19915	0.445982	Fst
Pinus_contorta	7.84E-02	-0.21557	0.346388	Fst
Pinus_strobus	8.20E-02	-0.22097	0.367092	Fst
Populus_angustifolia	1.84E-01	-0.05206	0.490658	Fst
Populus_tremuloides	5.32E-02	-0.26103	0.300514	Fst
Quercus_brandegei	1.50E-01	-0.16723	0.50721	Fst
Quercus_fusiformis	8.38E-02	-0.28526	0.33496	Fst
Quercus_geminata	9.19E-02	-0.16131	0.318736	Fst
Quercus_lobata	1.61E-01	-0.02161	0.408119	Fst
Quercus_minima	9.07E-02	-0.15411	0.31037	Fst
Quercus_oleoides	8.27E-02	-0.1826	0.282753	Fst
Quercus_sagraena	1.36E-01	-0.11344	0.408903	Fst
Quercus_virginiana	4.99E-02	-0.20621	0.234769	Fst

Literature Cited

Al-Kofahi, S.D., Al-Kafawin, A.M., and Al-Gharaibeh, M.M. 2024. Investigating domestic gardens landscape plant diversity, implications for valuable plant species conservation. Environment, Development and Sustainability **26**(8): 21259–21279. doi:10.1007/s10668-023-03528-y.

Bartoli, C., Lamichhane, J.R., Berge, O., Guilbaud, C., Varvaro, L., Balestra, G.M., Vinatzer, B.A., and Morris, C.E. 2015. A framework to gauge the epidemic potential of plant pathogens in environmental reservoirs: the example of kiwifruit canker. Molecular Plant Pathology **16**(2): 137–149. doi:10.1111/mpp.12167.

Bello-bedoy, R., and Núñez-Farfán, J. 2011. The effect of inbreeding on defence against multiple enemies in Datura stramonium. Journal of Evolutionary Biology **24**(3): 518–530. doi:10.1111/j.1420-9101.2010.02185.x.

Caizergues, A.E., Santangelo, J.S., Ness, R.W., Angeoletto, F., Anstett, D.N., Anstett, J., Baena-Diaz, F., Carlen, E.J., Chaves, J.A., Comerford, M.S., Dyson, K., Falahati-Anbaran, M., Fellowes, M.D.E., Hodgins, K.A., Hood, G.R., Iñiguez-Armijos, C., Kooyers, N.J., Lázaro-Lobo, A., Moles, A.T., Munshi-South, J., Paule, J., Porth, I.M., Santiago-Rosario, L.Y., Whitney, K.S., Tack, A.J.M., and Johnson, M.T.J. 2024. Does urbanisation lead to parallel demographic shifts across the world in a cosmopolitan plant? Molecular Ecology **33**(7): e17311. doi:10.1111/mec.17311.

Davies, K.W. 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. Oecologia **167**(2): 481–491. doi:10.1007/s00442-011-1992-2.

Ding, Y., Zang, R., Lu, X., and Huang, J. 2017. The impacts of selective logging and clear-cutting on woody plant diversity after 40years of natural recovery in a tropical montane rain forest, south China. Science of The Total Environment **579**: 1683–1691. doi:10.1016/j.scitotenv.2016.11.185.

Do, C., Waples, R.S., Peel, D., Macbeth, G.M., Tillett, B.J., and Ovenden, J.R. 2014. NeEstimator v2: re-implementation of software for the estimation of contemporary effective population size (Ne) from genetic data. Molecular Ecology Resources **14**(1): 209–214. doi:10.1111/1755-0998.12157.

Dray, S., Bauman, D., Blanchet, G., Borcard, D., Clappe, S., Guenard, G., Jombart, T., Larocque, G., Legendre, P., Madi, N., Wagner, H.H., Siberchicot, A., and SoDA), J.C. (Original author of two functions from package. 2025, April 16. adespatial: Multivariate Multiscale Spatial Analysis. Available from https://cran.r-project.org/web/packages/adespatial/index.html [accessed 2 September 2025].

Dray, S., Legendre, P., and Peres-Neto, P.R. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling **196**(3): 483–493. doi:10.1016/j.ecolmodel.2006.02.015.

Earth Science Data Systems, N. 2025. Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 11 | NASA Earthdata. Earth Science Data Systems, NASA.

Epperson, B.K. 2005. Estimating dispersal from short distance spatial autocorrelation. Heredity **95**(1): 7–15. doi:10.1038/sj.hdy.6800680.

Fahrig, L. 2003. Effects of Habitat Fragmentation on Biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**: 487–515.

Fernández-Murillo, M. del P., Alfaro, F.D., Craven, D., Gutiérrez, J.R., Kelt, D.A., Meserve, P.L., and Troncoso, A.J. 2023. Loss of native herbivores triggers diversity decline of ephemeral plant communities. Journal of Vegetation Science **34**(5): e13210. doi:10.1111/jvs.13210.

Filazzola, A., Brown, C., Dettlaff, M.A., Batbaatar, A., Grenke, J., Bao, T., Peetoom Heida, I., and Cahill Jr, J.F. 2020. The effects of livestock grazing on biodiversity are multi-trophic: a meta-analysis. Ecology Letters **23**(8): 1298–1309. doi:10.1111/ele.13527.

Fontúrbel, F.E., González-Ancin, H., Rojas-Hernández, N., and Vega-Retter, C. 2024. Effects of selective logging on genetic diversity and population structure of a keystone mistletoe. Population Ecology **66**(2): 86–92. doi:10.1002/1438-390X.12170.

Freund, F., Wirtz, J., Zheng, Y., Schäfer, Y., and Wiehe, T. 2025. Muller's ratchet and gene duplication. Theoretical Population Biology **164**: 12–22. doi:10.1016/j.tpb.2025.04.002.

Gargiulo, R., Budde, K.B., and Heuertz, M. 2025. Mind the lag: understanding genetic extinction debt for conservation. Trends in Ecology & Evolution **40**(3): 228–237. doi:10.1016/j.tree.2024.10.008.

Gegear, R.J., Heath, K.N., and Ryder, E.F. 2021. Modeling scale up of anthropogenic impacts from individual pollinator behavior to pollination systems. Conservation Biology **35**(5): 1519–1529. doi:10.1111/cobi.13754.

Goudet, J., and Jombart, T. 2004, August 14. hierfstat: Estimation and Tests of Hierarchical F-Statistics. doi:10.32614/CRAN.package.hierfstat.

González, A.V., Gómez-Silva, V., Ramírez, M.J., and Fontúrbel, F.E. 2020. Meta-analysis of the differential effects of habitat fragmentation and degradation on plant genetic diversity. Conservation Biology **34**(3): 711–720. doi:10.1111/cobi.13422.

Grossenbacher, D., Briscoe Runquist, R., Goldberg, E.E., and Brandvain, Y. 2015. Geographic range size is predicted by plant mating system. Ecology Letters **18**(7): 706–713. doi:10.1111/ele.12449.

Hejda, M., Pyšek, P., and Jarošík, V. 2009. Impact of Invasive Plants on the Species Richness, Diversity and Composition of Invaded Communities. Journal of Ecology **97**(3): 393–403.

Helm, A., Oja, T., Saar, L., Takkis, K., Talve, T., and Pärtel, M. 2009. Human Influence Lowers Plant Genetic Diversity in Communities with Extinction Debt. Journal of Ecology **97**(6): 1329–1336.

Hill, W.G. 1981. Estimation of effective population size from data on linkage disequilibrium. Genetics Research **38**(3): 209–216. doi:10.1017/S0016672300020553.

Hood, K.W., Fabbro, F., and Karp, D.S. 2025. Mistletoe-bearing trees positively influence bird foraging patterns across urban and natural environments. Urban Ecosystems **28**(3): 112. doi:10.1007/s11252-025-01714-6.

Karachaliou, E., Schmidt, C., de Greef, E., Docker, M.F., and Garroway, C.J. 2025. Urbanisation Is Associated With Reduced Genetic Diversity in Marine Fish Populations. Molecular Ecology **34**(7): e17711. doi:10.1111/mec.17711.

Kinnunen, R.P., Fraser, K.C., Schmidt, C., and Garroway, C.J. 2025. Structural and socioeconomic features of cities predict migratory bird species richness. Journal of Avian Biology **2025**(1): e03189. doi:10.1111/jav.03189.

Jombart, T., Kamvar, Z.N., Collins, C., Lustrik, R., Beugin, M.-P., Knaus, B.J., Solymos, P., Mikryukov, V., Schliep, K., Maié, T., Morkovsky, L., Ahmed, I., Cori, A., Calboli, F., Ewing, R.J., Michaud, F., DeCamp, R., Courtiol, A., Clark, L.V., Dimens, P., Coulter, M., and Krylov, I. 2025, February 6. adegenet: Exploratory Analysis of Genetic and Genomic Data. Available from https://cran.r-project.org/web/packages/adegenet/index.html [accessed 3 September 2025].

Librán-Embid, F., Grass, I., Emer, C., Ganuza, C., and Tscharntke, T. 2021. A plant–pollinator metanetwork along a habitat fragmentation gradient. Ecology Letters **24**(12): 2700–2712. doi:10.1111/ele.13892.

Lososová, Z., Horsák, M., Chytrý, M., Čejka, T., Danihelka, J., Fajmon, K., Hájek, O., Juřičková, L., Kintrová, K., Láníková, D., Otýpková, Z., Řehořek, V., and Tichý, L. 2011. Diversity of Central European urban biota: effects of human-made habitat types on plants and land snails. Journal of Biogeography **38**(6): 1152–1163.

Majewska, A.A., and Altizer, S. 2020. Planting gardens to support insect pollinators. Conservation Biology **34**(1): 15–25. doi:10.1111/cobi.13271.

Makowski, H., Lamb, K., and Galloway, L.F. 2024. Support for Baker's law: Facultative self-fertilization ability decreases pollen limitation in experimental colonization. American Journal of Botany **111**(6): e16351. doi:10.1002/ajb2.16351.

Malécot, G. 1955. La Génétique de population: Principes et applications. Population (French Edition) **10**(2): 239–262. Institut National d'études Démographiques. doi:10.2307/1525149.

McElreath, R. 2020. *Statistical Rethinking: A Bayesian Course with Examples in R and STAN*. In 2nd edition. Chapman and Hall/CRC, Boca Raton, FL. doi:10.1201/9780429029608.

Miedaner, T., and Garbelotto, M.M. 2024. Human-mediated migration of plants, their pathogens and parasites. Journal of Plant Pathology **106**(2): 301–325. doi:10.1007/s42161-024-01589-0.

Mitchell, C.E., Blumenthal, D., Jarošík, V., Puckett, E.E., and Pyšek, P. 2010. Controls on pathogen species richness in plants' introduced and native ranges: roles of residence time, range size and host traits. Ecology Letters **13**(12): 1525–1535. doi:10.1111/j.1461-0248.2010.01543.x.

Mittell, E.A., Nakagawa, S., and Hadfield, J.D. 2015. Are molecular markers useful predictors of adaptive potential? Ecology Letters **18**(8): 772–778. doi:10.1111/ele.12454.

Moreira, H., Kuipers, K.J.J., Posthuma, L., Zijp, M.C., Hauck, M., Huijbregts, M.A.J., and Schipper, A.M. 2023. Threats of land use to the global diversity of vascular plants. Diversity and Distributions **29**(6): 688–697.

Nei, M. 1973. Analysis of Gene Diversity in Subdivided Populations. Proceedings of the National Academy of Sciences **70**(12): 3321–3323. Proceedings of the National Academy of Sciences. doi:10.1073/pnas.70.12.3321.

Palumbi, S.R. 2001. Humans as the World's Greatest Evolutionary Force. Science **293**(5536): 1786–1790. American Association for the Advancement of Science. doi:10.1126/science.293.5536.1786.

Perrin, A., Khimoun, A., Ollivier, A., Richard, Y., Pérez-Rodríguez, A., Faivre, B., and Garnier, S. 2023. Habitat fragmentation matters more than habitat loss: The case of host–parasite interactions. Molecular Ecology **32**(4): 951–969. doi:10.1111/mec.16807.

Rossetti, M.R., Tscharntke, T., Aguilar, R., and Batáry, P. 2017. Responses of insect herbivores and herbivory to habitat fragmentation: a hierarchical meta-analysis. Ecology Letters **20**(2): 264–272. doi:10.1111/ele.12723.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., and Woolmer, G. 2002. The Human Footprint and the Last of the Wild: The human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not. BioScience **52**(10): 891–904. doi:10.1641/0006-3568(2002)052%5B0891:thfatl%5D2.0.co;2.

Schlaepfer, D.R., Braschler, B., Rusterholz, H.-P., and Baur, B. 2018. Genetic effects of anthropogenic habitat fragmentation on remnant animal and plant populations: a meta-analysis. Ecosphere **9**(10): e02488. doi:10.1002/ecs2.2488.

Schmidt, C., Domaratzki, M., Kinnunen, R.P., Bowman, J., and Garroway, C.J. 2020. Continent-wide effects of urbanization on bird and mammal genetic diversity. Proceedings of the Royal Society B: Biological Sciences **287**(1920): 20192497. doi:10.1098/rspb.2019.2497.

Schmidt, C., and Garroway, C.J. 2021. The population genetics of urban and rural amphibians in North America. Molecular Ecology **30**(16): 3918–3929. doi:10.1111/mec.16005.

Sokal, R.R., and Oden, N.L. 1978. Spatial autocorrelation in biology: 1. Methodology. Biological Journal of the Linnean Society **10**(2): 199–228. doi:10.1111/j.1095-8312.1978.tb00013.x.

Springer, Y.P. 2009. Edaphic Quality and Plant-Pathogen Interactions: Effects of Soil Calcium on Fungal Infection of a Serpentine Flax. Ecology **90**(7): 1852–1862.

Stebbins, G.L. 1957. Self Fertilization and Population Variability in the Higher Plants. The American Naturalist **91**(861): 337–354. doi:10.1086/281999.

Tilman, D., May, R.M., Lehman, C.L., and Nowak, M.A. 1994. Habitat destruction and the extinction debt. Nature **371**(6492): 65–66. Nature Publishing Group. doi:10.1038/371065a0.

Tufto, J. 2010. Gene Flow from Domesticated Species to Wild Relatives: Migration Load in a Model of Multivariate Selection. Evolution **64**(1): 180–192. doi:10.1111/j.1558-5646.2009.00807.x.

The IUCN Red List of Threatened Species. 2024. Available from https://www.iucnredlist.org/search?query=Vascular%20Plants&searchType=species [accessed 19 October 2024].

van Dijk, L.J.A., Ehrlén, J., and Tack, A.J.M. 2021. Direct and insect-mediated effects of pathogens on plant growth and fitness. Journal of Ecology **109**(7): 2769–2779. doi:10.1111/1365-2745.13689.

Van Kleunen, M., Weber, E., and Fischer, M. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. Ecology Letters **13**(2): 235–245. doi:10.1111/j.1461-0248.2009.01418.x.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., and Pyšek, P. 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecology Letters **14**(7): 702–708. doi:10.1111/j.1461-0248.2011.01628.x.

Wagner, A. 2008. Robustness and Evolvability: A Paradox Resolved. Proceedings: Biological Sciences **275**(1630): 91–100.

Waples, R.S. 2006. A bias correction for estimates of effective population size based on linkage disequilibrium at unlinked gene loci*. Conservation Genetics **7**(2): 167–184. doi:10.1007/s10592-005-9100-y.

Weed Seeds Order. 2016. SOR/2016-93. Government of Canada, Ottawa, Ontario, Canada. Available from https://laws-lois.justice.gc.ca/PDF/SOR-2016-93.pdf. [accessed 25 March 2026].

Wildlife Conservation Society (WCS) and Center for International Earth Science Information Network (CIESIN), Columbia University. 2005. Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). Available at: http://dx.doi.org/10.7927/H4M61H5F [Accessed 2 September 2025].

Winfree, R., Aguilar, R., Vázquez, D.P., LeBuhn, G., and Aizen, M.A. 2009. A Meta-Analysis of Bees' Responses to Anthropogenic Disturbance. Ecology **90**(8): 2068–2076.

Zaffarano, P.L., McDonald, B.A., and Linde, C.C. 2008. Rapid Speciation following Recent Host Shifts in the Plant Pathogenic Fungus Rhynchosporium. Evolution **62**(6): 1418–1436.

Zeitler, L., Parisod, C., and Gilbert, K.J. 2023. Purging due to self-fertilization does not prevent accumulation of expansion load. PLoS Genetics **19**(9): e1010883–e1010883. doi:10.1371/journal.pgen.1010883.