Review

Effect of Life-History Traits and Habitat Condition on Genetic Diversity between Invasive and Native Plant Populations

Raquel Hernández-Espinosa [1,*], Jorge González-Astorga [1,*], Yessica Rico [2] and Juan B. Gallego-Fernández [3]

1   Red de Biología Evolutiva, Instituto de Ecología A. C. Carretera Antigua a Coatepec, No. 351, El Haya, Xalapa 91073, Mexico
2   Red de Diversidad Biológica del Occidente Mexicano, Instituto de Ecología A. C. Centro Regional del Bajío, Pátzcuaro 61600, Mexico
3   Departamento de Biología Vegetal y Ecología, Universidad de Sevilla, 41012 Sevilla, Spain
*   Correspondence: raquel.hernandez@posgrado.ecologia.edu.mx (R.H.-E.); jorge.gonzalez@inecol.mx (J.G.-A.)

Abstract: Plant invasions have a huge impact on the health of ecosystems and human well-being. The invasion risk varies with the introduction pathway, the propagule pressure, and the genetic diversity of the founding population. We performed a systematic review and meta-analysis of 30 studies reporting the genetic diversity of 31 plant species in their invasive and native ranges. We evaluated if patterns of genetic diversity differ between ranges and whether these responses are influenced by life-history traits, hybridization, polyploidization, and habitat condition. We found that invasive populations had significantly lower genetic diversity and higher inbreeding than native populations. In fragmented and degraded habitats, the genetic diversity of invaders was lower, but inbreeding was not affected. Polyploid invaders with hybrid capacity also showed lower genetic diversity. Invasive herbs with vegetative propagation were more sensitive to the loss of genetic diversity and had higher levels of inbreeding. Our synthesis showed that the genetic response in the invaded range could result from historical processes, such as founder and bottleneck events. Traits such as selfing are more likely to preserve the signatures of founder events and influence the genetic diversity in invasive populations. Additionally, clonality seems to be the predominant reproduction system in the invaded range.

Keywords: meta-analysis; biological invasions; genetic diversity; microsatellites; life-history traits

1. Introduction

One of the biggest threats to global biodiversity is biological invasions [1]. Several species of plants have become invasive in their non-native habitats due to human influence on the natural world [2]. Invasion begins with the transportation of plant propagules beyond their native range limits, their introduction into a new environment, and their establishment and spread [3]. However, only a fraction of the species introduced into a new habitat will become invasive due to the high probability of mortality at some stage of the invasion process [4]. The invasion risk also depends on the introduction pathway (i.e., intentionally or unintentionally introduced) [5], propagule pressure (i.e., the number of individuals introduced) [6], and genetic diversity of the founding population [7]. As for the last, it has been reported that small, founding, and expanding populations are more likely to lose genetic diversity by genetic drift and demographic bottlenecks [8,9]. However, while some species showed lower genetic diversity in the introduced range compared to their native range [10–15], others showed an opposite pattern, partially because of multiple introductions or the admixture of independent genetic stocks [16–20].

Plant life-history traits can influence levels of genetic diversity in the invasive range and can be crucial to the success or failure of an invasion [10,21,22]. Reproductive systems are the main determinant of plant genetic diversity [23]. For instance, there is evidence that genetic diversity may be reduced in invaded ranges because of a change in reproductive

strategies (e.g., clonality and selfing) [22]. Another factor determining genetic diversity in plants is the life form, with trees usually having traits that maintain high levels of genetic diversity compared to herbaceous plants [24]. Likewise, trees predominantly outcross, with a lower proportion of selfing than other life forms [25]. However, self-compatible trees sometimes exhibit high inbreeding, even if mixed, outcrossing, or predominantly selfing [26]. Low levels of inbreeding are also associated with perennial plants due to their longevity and overlapping generations [27]. In addition to life-history traits, interspecific hybridization and polyploidization (genome duplication) can influence genetic diversity [28,29]. Specifically, within a few generations, interspecific hybridization with native congeners may result in higher levels of standing genetic variation in the exotic population, thereby increasing its adaptive capacity in the new environment [19,30]. Additionally, polyploidization, which increases genome size, can prevent genetic erosion during the early stages of an invasion because polyploid genomes are less susceptible to drift [29,31].

Successful establishment in the invasive range might also depend on external factors, such as the interaction between the invader and the new environment [32]. Evidence suggests that human-disturbed habitats facilitate plant invasions [33]. Human-disturbed habitats can influence the distribution of genetic diversity by influencing propagule dispersal and reproduction [34–38]. For disturbed habitats, changes in habitat structure, resource availability, and community composition may reduce the diversity of pollinators and seed dispersers, resulting in changes in reproductive strategies (e.g., selfing and vegetative propagation), which, in turn, can reduce genetic diversity [39,40].

Systematic reviews comparing plant species in their invasive and native ranges have addressed the influence of fecundity-related traits on plant performance [41,42]. Meanwhile, meta-analytical approaches have evaluated performance-related traits, e.g., phenotypic plasticity, physiology, leaf-area allocation, shoot allocation, size, growth rate and fitness [43,44], life-history traits, and growth environment in species invasiveness [45]. So far, no previous studies have investigated the role of life-history traits, hybrid capacity, ploidy level, and habitat fragmentation and degradation in shaping genetic diversity in invaded ranges. In this study, we performed a systematic review and meta-analysis by comparing invasive and native ranges from empirical genetic studies in invasive plants to ask the following: (i) Is the genetic diversity of invasive populations lower relative to native populations? (ii) Are inbreeding levels higher in invasive populations than in native ones? (iii) Is genetic diversity and inbreeding within populations influenced by life-history traits in the invasive range? (iv) Does habitat fragmentation and degradation influence the invader's genetic diversity and inbreeding in the invasive range?

2. Materials and Methods

2.1. Study Selection and Coding

We searched for available scientific literature on invasive plant genetic diversity using a combination of the following keywords: invas * plants OR alien plants OR exotic plants OR introduced plants AND genetic diversity OR population genetic structure AND SSR OR microsatellite, in Web of Science, Scopus, Google Scholar, JSTOR, Wiley, and Science Direct databases. We chose studies that used microsatellite markers because they have been the most popular markers in the last decades in population genetic studies and to avoid marker bias by including other types of genetic markers [46]. The search was conducted from 1980 to 2021 and followed the PRISMA statement [47], which provides a standardized framework for meta-analysis and systematic reviews (Figure 1). To ensure that the gathered information was of high quality and that our results were replicable, we limited our search to peer-reviewed articles written in English. We excluded grey literature and previous reviews (which may duplicate the information). More than one study focused on these three species: *Ambrosia artemisiifolia* L. (Asteraceae), *Spartina alterniflora* Loisel. (Poaceae), and *Acacia dealbata* A. Cunn. (Fabaceae) and because the study sites were the same, we

included only the articles reporting all information needed to fill out our inclusion criteria. Each evaluated species was considered a case study.
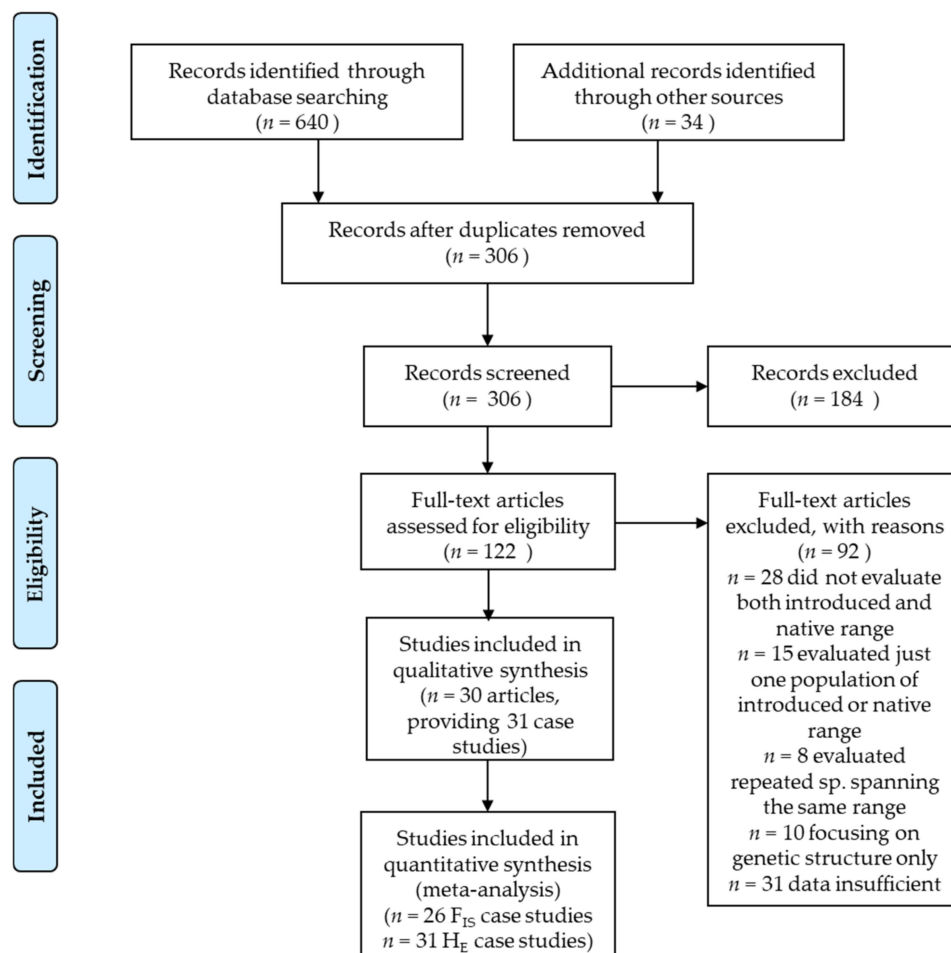
Figure 1. Flowchart of preferred reporting items for systematic reviews and meta-analysis (PRISMA), summarizing the sequence of information selected for this meta-analysis. *n* refers to the number of case studies used in each section.

We selected articles based on the following criteria: (i) included at least two invasive populations and two native populations of the same species; (ii) reported genetic diversity parameters of expected heterozygosity (H_E) [48], allelic richness (Ar), and inbreeding coefficients (F_{IS}) [49] for at least five microsatellite markers (with their dispersion measure (SD or SE), or provide original data to calculate them); (iii) reported the sample size (as the proportion of individuals to the number of populations following González et al. (2020) [50]; and (iv) reported if the habitat was conserved, fragmented, or degraded (hereafter habitat condition, see below).

The information recorded for each species included: (i) species ID, (ii) a reference number for each article, (iii) population type (invasive or native), (iv) number of populations per type, (v) number of microsatellite loci, (vi) distribution range, (vii) family and genus. We categorized habitat conditions into three human habitat modification categories following the definitions of Lindenmayer and Fischer (2013) [51]: (i) undisturbed, (ii) degraded habitat, and (iii) fragmented habitat (Table 1). Invasiveness was determined according to the Invasive Species Compendium (CABI) [52] (Table S1). Information on life-history traits was obtained from the article when available. Otherwise, the information was extracted from peer-reviewed descriptions for the evaluated species: (i) life form, (ii) lifespan, (iii) reproductive system, (iv) vegetative propagation, (v) ploidy level, and (vi) hybrid capacity.

Table 1. Habitat condition categories.

Category	Description
Habitat fragmentation	Continuous areas subdivided into smaller fragments that increase habitat isolation and edge effects, usually accompanied by habitat loss.
Habitat degradation	Areas with a reduction in habitat quality due to changes in vegetation structure, resource availability, and microclimate conditions but without experiencing fragmentation or loss.
Undisturbed habitat	Areas unaltered by humans.

2.2. Effect Size and Moderators

All the evaluated studies included invasive and native populations; thus, we compared the effect of the moderators on genetic diversity and inbreeding for both distribution ranges. We calculated Hedge's d as the unbiased, standardized mean difference in genetic diversity between the invasive (treatment) and native (control) groups using the population as the unit of analysis [53,54]. Hedge's d compares the two groups' means, standard deviations, and sample sizes [55]. We used a correction for small samples (five to ten studies) [56] and conducted separate analyses for the genetic diversity and inbreeding data sets. We defined eight moderators: (i) habitat condition, (ii) invasiveness (highly invasive or moderate invasive), (iii) hybrid capacity (yes or no), (iv) vegetative propagation (yes or no), (v) ploidy level (diploid or polyploid), (vi) mating system (self-compatible or self-incompatible), (vii) lifespan (perennial or annual), and (viii) life form (herbs, shrubs, or trees).

2.3. Effect Model and Publication Bias

The global effect sizes were estimated using mixed-effect models, considering each category in a moderator as a fixed subgroup and the variation between studies within categories as random [55]. To examine the heterogeneity among moderator levels, we estimated the between-group heterogeneity with the Q-between statistic and the X^2-distributed statistic, which compare the variation between and within moderators' levels and indicates a significant effect variation among moderator levels. Q-statistics are more appropriate for random-effect models than I^2 or r^2, which assume a fixed-effects model structure [57]. We examined the relationship between the effect and sample size with funnel plots to assess the potential publication bias [57]. We used Egger's test to assess funnel-plot asymmetry [58]. We also conducted a trim-and-fill analysis, which recalculated the mean effect and confidence intervals to verify the robustness of the results [59]. All analyses were conducted using Comprehensive Meta-Analysis 3.0 software (Borenstein et al., 2005) [60].

3. Results

An initial search resulted in 674 articles, and after filtering out duplicates and irrelevant results, the total retained was 122. We excluded 92 articles that did not meet our inclusion criteria (28 did not evaluate both distribution ranges, 15 evaluated just one single population of each range, 8 evaluated the same species within the same range, 10 were focused on genetic structure only, and 31 lacked the data (H_E/Ar/F_{IS} or SD) to estimate diversity and inbreeding parameters, resulting in 30 articles that provided 31 case studies (Table S2). The 31 species evaluated were from 17 families and 29 genera. The family with the largest number of species was Asteraceae (*n* = 9), followed by Fabaceae (*n* = 4), Apiaceae (*n* = 4), and then Rosaceae and Euphorbiaceae, with two species each. The remaining families had one representative. Only the genera *Senecio* L. (Asteraceae) and *Heracleum* L. (Apiaceae) had two species each. The number of populations included ranged from 4 to 50 in the invasive range and from 5 to 42 in the native range. The average number of individuals per population was 14, and the number of microsatellite loci ranged from 5 to 29. The dataset consisted of 19 herbs, 6 shrubs, 6 trees, 20 diploids, and 11 polyploids. Additionally, it

included 8 annual and 23 perennials, 20 self-compatible and 11 self-incompatible plants (Figure 2).
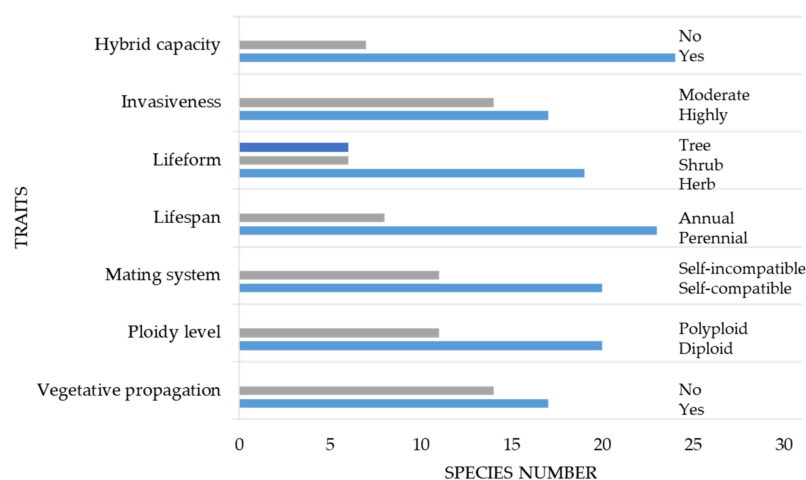

Figure 2. Plant species analyzed in the meta-analysis. The *X*-axis shows the number of species, and the *Y*-axis shows each of the seven moderators used. The bars show the categories within each moderator.

We could not include allelic richness (Ar) in the meta-analysis because the number of studies reporting it was insufficient to pass the publication bias tests (Figure S3). Thus, we only analyzed expected heterozygosity (hereafter genetic diversity), which provides an objective measurement of allelic richness and evenness in plants [50], for 31 case studies, whereas the inbreeding coefficient was obtained for 26 cases (hereafter inbreeding). Overall, the mixed effect models showed that invasive populations had a significantly lower genetic diversity (Z = −4.49, *p* = 0.0001) and higher inbreeding (Z = −2.24, *p* = 0.025) than the native populations. We found significant heterogeneity between study effect sizes for genetic diversity (QT = 179.356, df = 30, *p* = 0.0001) (Figure 3a) and inbreeding (QT = 100.56, df = 25, *p* = 0.0001) (Figure 4a).
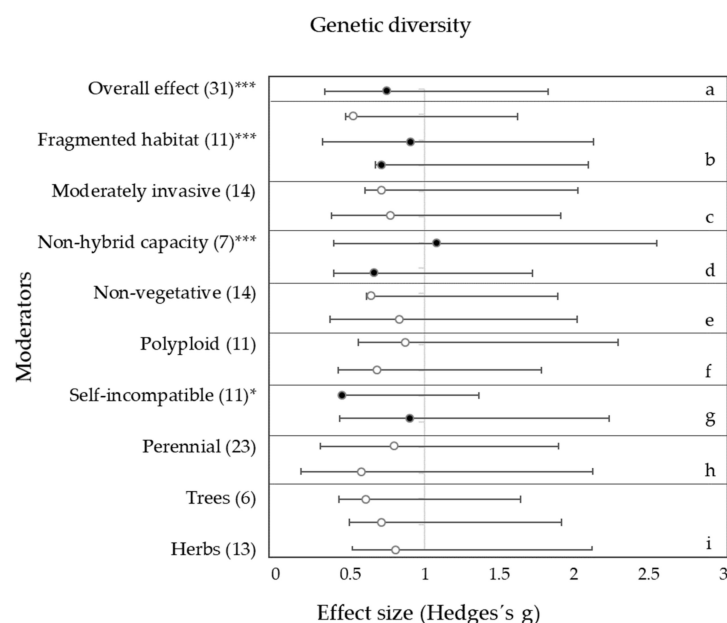
Figure 3. Effect sizes on genetic diversity: (**a**) overall effect, (**b**) habitat condition, (**c**) invasiveness, (**d**) hybrid capacity, (**e**) vegetative propagation, (**f**) ploidy level, (**g**) mating systems, (**h**) lifespan, (**i**) life form (mean and 95% CI; numbers in parentheses represent sample size; * *p* < 0.05, *** *p* < 0.001; not significant, *p* ≥ 0.05). Black dots represent a significant effect on genetic diversity.
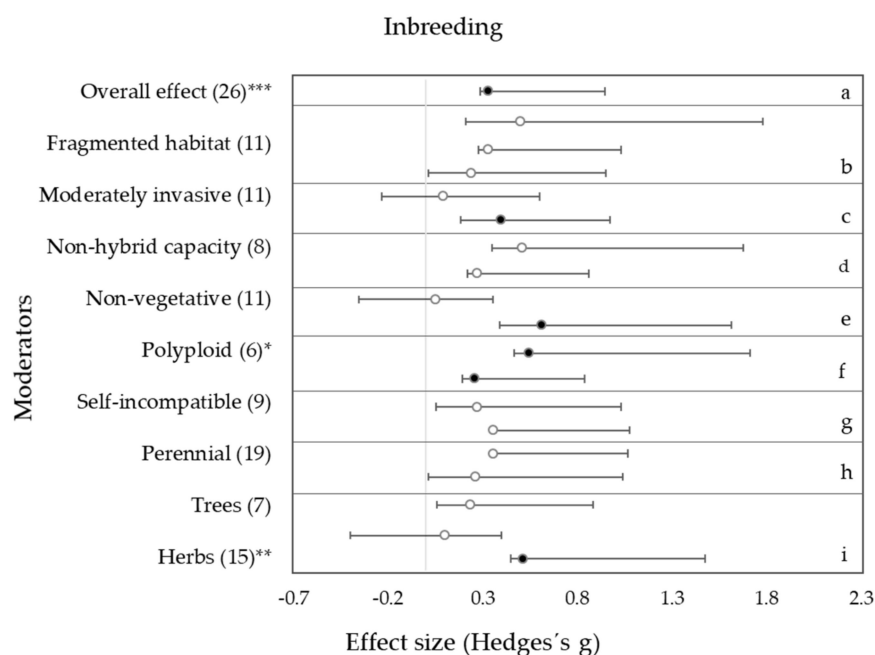
Figure 4. Effect sizes on inbreeding: (**a**) overall effect, (**b**) habitat condition, (**c**) invasiveness, (**d**) hybrid capacity, (**e**) vegetative propagation, (**f**) ploidy level, (**g**) mating systems, (**h**) lifespan, (**i**) life form (mean and 95% CI; numbers in parentheses represent sample size; * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$; not significant, $p \geq 0.05$). Black dots represent a significant effect on inbreeding.

3.1. Habitat Condition

Habitat condition had a significant negative effect on genetic diversity ($Z = -6.131$, $p = 0.0001$) and inbreeding ($Z = -2.271$, $p = 0.023$) in the invasive populations. Specifically, habitat fragmentation and habitat degradation had statistically significant negative effects on the genetic diversity of invasive populations (Q-between = 6.345, df = 2, $p = 0.042$) (Figure 3b), whereas no effect was found on inbreeding (Q-between = 0.309, df = 2, $p = 0.857$) (Figure 4b).

3.2. Invasiveness

The overall effect size showed that species invasiveness significantly influences genetic diversity ($Z = -4.370$, $p = 0.0001$) and inbreeding ($Z = -2.240$, $p = 0.025$). Species recorded as highly invasive had no significant effect on genetic diversity (Q-between = 0.008, df = 1, $p = 0.930$) (Figure 3c), but did have an effect on inbreeding (Q-between = 3.838, df = 1, $p = 0.050$) (Figure 4c).

3.3. Hybrid Capacity and Ploidy Level

When considering hybrid capacity, both genetic diversity ($Z = -4.465$, $p = 0.0001$) and inbreeding ($Z = -2.141$, $p = 0.032$) were negatively affected in invasive populations. The genetic diversity of invasive populations was negatively affected by both hybrid and non-hybrid capacity (Q-between = 8.72, df = 1, $p = 0.003$) (Figure 3d), but not inbreeding (Q-between = 0.37, df = 1, $p = 0.539$) (Figure 4d). When we evaluated ploidy level, genetic diversity ($Z = -4.393$, $p = 0.0001$) was lower and inbreeding higher ($Z = -2.252$, $p = 0.024$) in invasive populations. No ploidy-level categories showed a significant effect on genetic diversity (Q-between = 2.34, df = 1, $p = 0.126$) (Figure 3f), but both diploids and polyploid species showed high inbreeding in invasive populations (Q-between = 2.453, df = 1, $p = 0.020$) (Figure 4f).

3.4. Life-History Traits

The mean effect sizes for life-history traits (except vegetative propagation), showed significant effects on genetic diversity and inbreeding. Based on vegetative propagation, genetic diversity of invasive populations was negatively affected (Z = −4.388, *p* = 0.0001), but the direct comparison between categories did not reveal significant differences (*Q*-between = 1.708, df = 1, *p* = 0.191) (Figure 3e). Moreover, vegetative propagation had no effect on inbreeding (Z = −1.845, *p* = 0.065). However, the direct comparison between inbreeding categories revealed that the "YES" category had a significant effect (*Q*-between = 14.22, df = 1, *p* = 0.0001) (Figure 4e). For mating systems, genetic diversity of invasive populations was significantly lower for self-compatible and self-incompatible plants (*Q*-between = 13.87, df = 1, *p* = 0.0001) (Figure 3g), but inbreeding was not influenced by mating system (*Q*-between = 2.21, df = 1, *p* = 0.137) (Figure 4g). Regarding lifespan, perennial plants of invasive populations showed significant lower values of genetic diversity (Z = −4.078, *p* = 0.0001) (Figure 3h) and inbreeding (Z = −1.980, *p* = 0.048). (Figure 4h). For life form, genetic diversity (Z = −4.289, *p* = 0.0001) and inbreeding (Z = −2.239, *p* = 0.025) showed lower values in the invasive populations. However, a direct comparison between life forms did not reveal significant differences for genetic diversity (*Q*-between = 0.332, df = 2, *p* = 0.847) (Figure 3i), but did for inbreeding. Inbreeding was significantly higher in invasive herbs (*Q*-between = 8.845, df = 2, *p* = 0.012) (Figure 4i).

3.5. Publication Bias

Funnel plots showed some cases with large variances within the total distribution for genetic diversity. However, Egger's test showed no significant asymmetry (intercept = −2.68, df = 29, *p* = 0.181). Similarly, for inbreeding, the funnel plot showed some study cases with a large variation, but Egger's test showed no significant asymmetry (intercept = −2.20, df = 24, *p* = 0.211). The direction and significance of inbreeding results did not change after the trim-and-fill procedure, indicating that they were robust and uninfluenced by asymmetric bias. For genetic diversity, the direction did not change but the effect size estimated for the trim-and-fill procedure diminished (Figure S3).

4. Discussion

Population genetic studies on invasive plants have aimed to determine which factors (i.e., mating systems, life form, habitat condition) play a significant role in species' genetic diversity in the invaded range. However, there was no evidence of a general pattern. Our meta-analytical approach is the first to identify with statistical robustness the intrinsic (life-history traits) and extrinsic factors (human habitat modification) that influence the genetic response of invasive and native plant populations. Our global synthesis showed that invaders have lower genetic diversity and higher inbreeding relative to native populations. Empirical studies on invasive plants have reported low genetic diversity in the introduced range when populations experience genetic and demographic bottlenecks or colonization events [36,61]. Our results confirm that life-history traits, such as self-compatibility, vegetative propagation, and herbaceous life form, can significantly influence invaders' genetic diversity and inbreeding. For invasive species, historical processes are important determinants of genetic diversity, such as founder events and frequent genetic bottlenecks. Traits such as selfing are more likely to preserve the signatures of founder events in invasive populations [62]. Likewise, we confirmed that habitat condition is a stronger driver of invasive plant genetic diversity. Both fragmented and degraded habitats had a negative effect on invaders' genetic diversity.

4.1. Effects of Habitat Condition on Genetic Diversity and Inbreeding

We found a significant negative effect of fragmented and degraded habitats on invaders' genetic diversity, but not on inbreeding. Human-modified habitats are more prone to invasion than natural or semi-natural areas; the flora of urban areas and surroundings is usually richer in invasive species than natural areas [63]. Fragmented habitats are associ-

ated with a reduction in genetic diversity by a decrease in population size due to habitat isolation and matrix impermeability [64]. Fragmentation is also associated with higher selfing rates [50,65–67], which is consistent with our findings. We detected a significant reduction in invaders' genetic diversity in self-compatible species. We also found a significant negative effect of habitat degradation on invaders' genetic diversity. When an exotic species partially or totally replaces the native vegetation in the new area, the resulting habitat is usually composed of a mosaic of native and transformed stands [35]. Degraded habitats lack spatial discontinuities, but may impose restrictions to dispersal and gene flow [68]. The interruption of gene flow in altered habitats can affect invaders' genetic diversity [69] by changes in reproductive strategies, such as selfing or clonality, facilitating propagation. Habitat degradation also leads to changes in vegetation structure, source availability, and microclimate conditions [70], which can alter the diversity and behavior of pollinators and seed dispersers.

4.2. Effects of Interspecific Hybridization and Polyploidization on Genetic Diversity and Inbreeding

The formation of polyploids may be affected by environmental stress stimuli, as seen during an invasion. We found significantly low genetic diversity in polyploid invaders with hybrid capacity. Even if genome duplication may increase genetic variability, clonal propagation is often the strategy to spread, leading to extensive areas of genetic uniformity in the novel range [71]. Additionally, such invaders as *Tragopogon* L. (Asteraceae) [72] and *Spartina* L. (Poaceae) [73] have shown a marked reduction in the expression of duplicated genes with similar or redundant functions, which has led to genetic diversity loss in response to "genomic shock" by genomic incompatibilities and genetic redundancy during a polyploidization event [74,75]. Our results did not show a significant relationship between the mating system and inbreeding, suggesting that selfing does not favor inbreeding.

4.3. Effects of Life-History Traits on Genetic Diversity and Inbreeding

We found that genetic diversity and inbreeding were associated with specific plant traits in the invasive populations. For mating systems, we found a significantly low genetic diversity in self-compatible invasive populations. Selfing ability could promote invasiveness because it ensures reproduction even in the absence of pollinators [76]. Nevertheless, selfing can be harmful to reproductive success when inbreeding depression is present [26]. When we evaluated life forms, we found that herbs with vegetative propagation (clonality) had a negative effect on inbreeding. This result confirms what is expected when the reproductive system is predominantly vegetative in an invasion scenery. Clonal invasions in which sexual reproduction is limited or absent involve striking bottlenecks [22,28]. In many instances, invasion processes cause transitions to uniparental reproduction in the introduced range [23]. Although vegetative propagation appears to have ecological advantages in novel environments [23], extensive clonality can promote complete loss of sexual reproduction, increasing inbreeding in the populations [28].

Genetic studies, including the native range of an invader's species, have shown that selfing and inbreeding depression varied between life forms [26]. Herbaceous plants are frequently associated with early successional series in disturbed areas, where selfing is probably selected as a colonizing strategy when pollinators are scarce or inefficient [77]. Here, we found significantly higher inbreeding in invasive self-compatible herbs. Other studies evaluating selfing in herbaceous species have found that inbreeding may occur under various conditions, more frequently for taxa growing in stressful environments, as expected for invasive species [77–79]. Additionally, high levels of inbreeding depression are reported in tree invasions that are generally self-incompatible [80], although long-distance dispersal can ensure that some selfed progeny escape competition with outcrossed progeny [81,82]. In our meta-analysis, we did not find a strong relationship between trees and inbreeding, but we found a strong effect of self-compatibility on genetic diversity. Thus, despite high levels of inbreeding reported in tree invasions, there is a possibility that selfing promotes invasion or natural long-distance colonization. Invasive plants experienced

reductions in genetic diversity and an increase in inbreeding resulting from founder effects, genetic bottlenecks, autogamy, and reduced gene flow among isolated populations owing to habitat fragmentation. Such a combination of factors may reduce the invader's fitness due to the fixation of mildly deleterious recessive alleles, indicating potential genetic weakness, as reported in *Alliaria petiolata* [83]. Like *A. petiolata*, other invasive species may restore genetic variation by multiple introductions and genetic exchange among locally isolated populations. Still, once again, the strength of processes like this is highly dependent on the invasion history of species.

5. Future Research Recommendations

Despite the increasing number of genetic studies that include populations in the native and invasive range, few include all the necessary information to conduct a meta-analysis. For instance, parameters such as H_E and SD and F_{IS} and SD were lacking in 31 articles, whereas allelic richness (Ar) was reported only in a small number of studies. Ar is highly affected by demographic changes, being more sensitive to detect founder events. In a meta-analysis, the sample size is another constraint. We excluded 15 articles investigating only one invasive or native population and 8 that used less than five microsatellites, thereby drastically reducing our sample size.

Moreover, we found a lack of representativity of plant families, life forms, and lifespans. Perennial herbs were the most frequent, doubling the other categories. Increasing the number of empirical studies for diverse plant species is thus needed. Lastly, we evaluated studies based on microsatellites, which are codominant neutral markers, and, thereby, cannot directly inform selection and local adaptation. A future meta-analysis may consider including empirical studies based on functional genomic data, such as genome-wide association studies (GWAS) or next-generation sequencing (NGS). This information would shed light on traits under selection that influence the genetic response during a plant invasion.

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