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COMPARISON OF GENETIC DIVERSITIES IN NATIVE AND ALIEN POPULATIONS OF HOARY MUSTARD (*HIRSCHFELDIA INCANA* [L.] LAGREZE-FOSSAT)

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Increased selfing and inbreeding and, consequently, depauperate genetic diversities are commonly expected for alien colonies. We compared RAPDs data for native (southern Europe) and alien (British Isles) populations of hoary mustard (*Hirschfeldia incana*). This species is normally out-breeding, but it is capable of self-fertilization. Contrary to the common expectations, genetic diversities in native and alien populations were similar, without any strong evidence of decreased levels of genetic diversities in alien populations. A variety of factors may have contributed to this observation, including high variation in founding groups, founders originating from multiple *H. incana* source populations, and high rates of past and/or current gene flow. A review of other studies showed that this pattern of similar genetic diversities in native and alien populations was not unusual but has been regularly observed in other invasive plant species.

Keywords: alien, Brassicaceae, invasive, population genetic structure, RAPDs.

Introduction

The establishment and spread of invasive alien plants is viewed as a threat to biodiversity at global and local levels (Lövei 1997; Cox 1999), and because of this, it is useful to identify features shared by successful invaders. Attributes such as self-fertilization, vegetative reproduction, reduced levels of genetic variation, and greater degrees of interpopulation differentiation are often associated with invasive plants (Barrett and Shore 1989). As a general rule, inbreeding and/or single-parent reproduction are assumed to be beneficial for rapid and successful range expansion (Williamson and Brown 1986). A further advantage of inbreeding and/or single-parent reproduction is that it conserves coadapted gene complexes that have been selected for optimum fitness in the novel habitat (Novak and Mack 1993; Williams et al. 1995).

Colonizing populations are also likely to suffer loss of variation due to bottleneck or founder effects. Genetic theory predicts a reduction in the average heterozygosity per locus when population size decreases suddenly (Wright 1931), and recovery to original levels of genetic diversity is expected to be slow (Nei et al. 1975). Whether or not inbreeding or founder effects occur will be contingent upon the history of introduction. For example, where there have been multiple and frequent introductions, one might expect high genetic diversities in alien colonies (Stepien et al. 2002). Founder effects specifically require situations where dispersal events are rare and founder groups are small. A reduction in genetic variation could result from either one or a combination of founder effects, inbreeding, and single-parent reproduction. Previous reviews have drawn attention to low or uniform genetic diversity in colonizing populations (Barrett and Shore 1989 and references therein). However, in most studies alien species have only been investigated within their introduced range. A more convincing approach in establishing if loss of genetic diversity has occurred in the course of colonization would be a comparison of native and alien populations.

Here we investigate the genetic diversity of native and alien populations of hoary mustard (*Hirschfeldia incana* [L.] Lagreze-Fossat), a member of the Brassicaceae native to southern Europe that is undergoing an impressive range expansion in Britain and North America, where it is an alien invader. In the British Isles, recent surveys show that more than 50% of plant species established in the flora are aliens that been introduced during the last 500 years (Preston et al. 2002). In spite of this, there have been relatively few studies of the genetic diversities of such populations in Britain (compared with other areas of the world; Cox 1999), particularly in the context of commonly held assumptions about the biology of invasion.

Hirschfeldia incana in Britain is a typical example of a recently established alien. Many South Wales populations were recorded by the 1950s, whereas most other populations in England appeared only later, after the 1970s. The plant has several attributes that make it suitable for the purposes of this study. Although described as an out-breeding species (Rich 1991), experimental evidence (Darmency and Fleury 2000) indicated that a small proportion of *H. incana* plants are capable of self-fertilization. Observations of *H. incana* in South Wales indicate that selfing can indeed occur among the aliens (C. R. Hipkin, personal observation). Relatively low genetic variation in alien populations compared with out-breeding native populations would be expected if there were comparatively high selfing rates, inbreeding, and/or founder effects. We tested this expectation in *H. incana* by comparing the genetic diversities of native and alien populations. We further compared our results with those of similar studies.

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Material and Methods

Sample Collection

Samples were obtained from 19 locations in the United Kingdom, consisting of 13 locations in South Wales and six locations in England (fig. 1; table 1). Almost all South Wales populations (except wPBD) were recorded by the 1950s, whereas most English populations (except eKEN) only appeared in the 1970s or later. Populations can therefore also be grouped by their relative age since introduction: an older group consisting of mainly South Wales populations and a younger group of mainly English populations.

Most South Wales material was collected by us, and other British samples were received on request from Vice County recorders (see "Acknowledgments"). Samples received from other collectors or botanical gardens (see "Acknowledgments") for four southern European locations (table 1) situated within the native distribution of the species (Mielke 1977; Jallas et al. 1996) south of 40°N latitude were a broad representation of the native range equivalent to more than 30° of longitude. This covers the westernmost edge of southern Europe (Portugal) through the easternmost edge of the region (Cyprus).

Leaves or seeds were collected from natural populations, and up to 10 samples per location were used in RAPDs analysis (table 1). For all locations except cPOR and cCYP, leaves or seeds were from different individual plants (i.e., each sample used in the RAPDs analysis represented a different individual). Seeds from cPOR and cCYP were sent by botanical gardens and were assumed to be mixed material from various plants, so it is possible that by chance some seeds may have been from the same individual plant. However, examination of within-population relatedness values (Lynch and Milligan 1994) confirmed that these were indeed comparable with those of other southern European seed known to be from different individuals (Mann-Whitney U-test: $z = -0.458$, $P = 0.647$). Leaf samples taken from wild plants or from plants grown from seed under greenhouse conditions were frozen at −20°C until DNA was extracted.

DNA Extraction and PCR Amplification

DNA was extracted from leaf material with a genomic DNA isolation kit (Gentra Systems, Minneapolis, Minn.). Using a pipette tip as a pestle, ca. 25 mg of leaf tissue was macerated in 300 μL of cell lysis solution (Puregene, Gentra). The extraction procedure followed the manufacturer's protocol for plant tissue. Precipitated DNA was rehydrated in

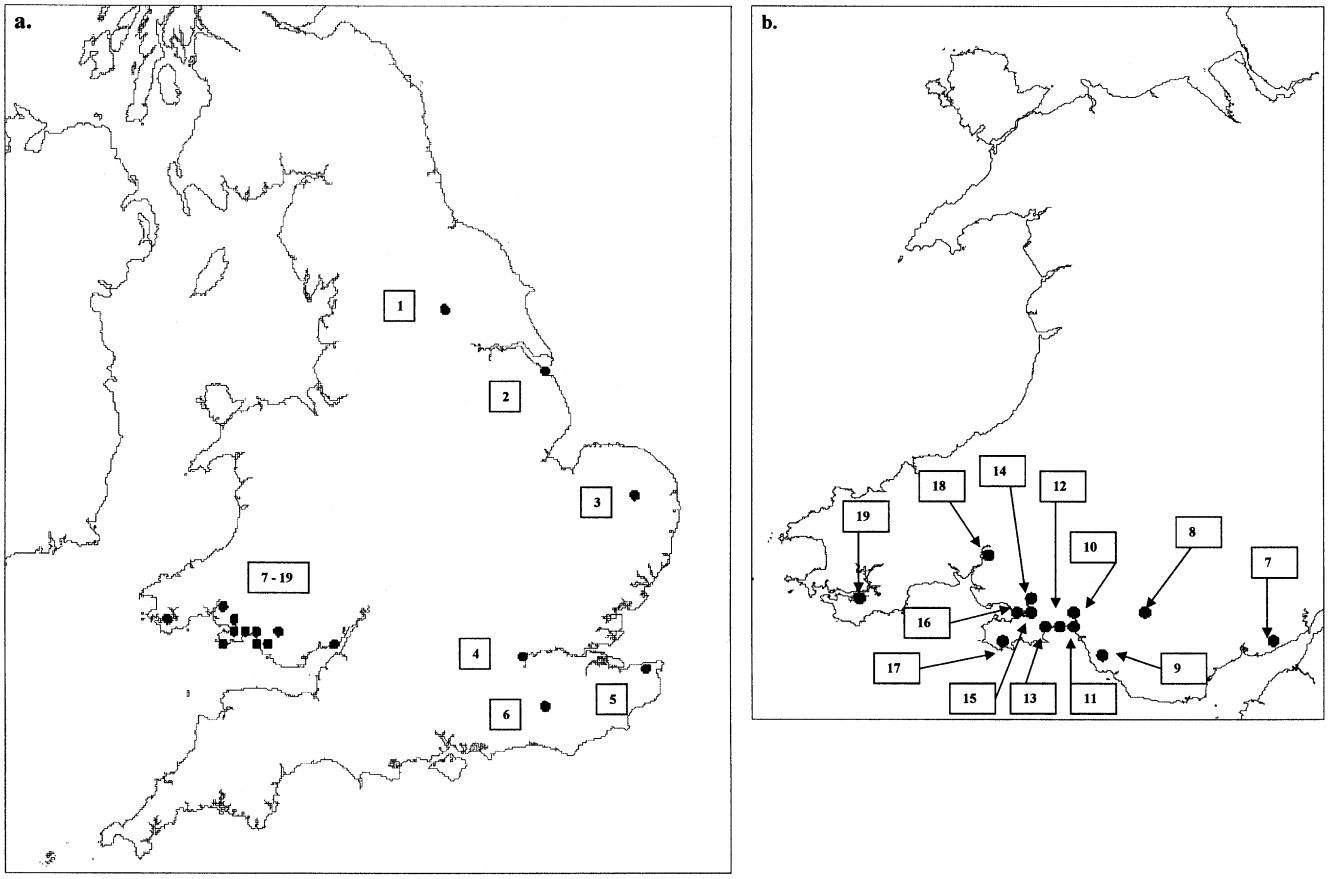

Fig. 1 Sampling locations in (*a*) England and (*b*) South Wales. *a*, England: *1*, eYOR; *2*, eLIN; *3*, eENK; *4*, eMDX; *5*, eKEN; *6*, eSUX; *7–19*, sites in Wales. *b*, South Wales: *7*, wMON; *8*, wEGL; *9*, wBR1; *10*, wNP2; *11*, wNP1; *12*, wSW1; *13*, wSW2; *14*, wPON; *15*, wGO2; *16*, wGO1; *17*, wGO3; *18*, wCM3; *19*, wPBD. For location codes, see table 1.

Table 1

Gene Diversities Averaged over Loci (with SE) for *Hirschfeldia incana* Samples Collected from Locations in Southern Europe and the United Kingdom

Code	Location	Sampled material	N	Polymorphic loci (%)	H_j (SE)	H_j' (SE)
South Wales:						
wBR1	Bridgend	Leaves	10	83.3	0.276 (0.029)	0.398 (0.074)
wCM3	Carmarthen	Leaves	10	83.3	0.299 (0.031)	0.420 (0.081)
wEGL	East Glamorgan	Leaves	9	96.7	0.377 (0.021)	0.554 (0.074)
wGO1	Gower 1	Leaves	9	83.3	0.288 (0.032)	0.470 (0.068)
wGO2	Gower 2	Leaves	9	90.0	0.354 (0.028)	0.558 (0.073)
wGO3	Gower 3	Leaves	8	100	0.467 (0.019)	0.682 (0.062)
wMON	Monmouthshire	Leaves	10	100	0.438 (0.018)	0.778 (0.050)
wNP1	Neath Port Talbot 1	Leaves	10	80.0	0.352 (0.031)	0.552 (0.083)
wNP2	Neath Port Talbot 2	Leaves	10	80.0	0.319 (0.034)	0.493 (0.078)
wPON	Pontardulais	Leaves	10	80.0	0.315 (0.032)	0.450 (0.079)
wPBD	Pembroke Dock	Leaves	10	90.0	0.394 (0.027)	0.598 (0.069)
wSW1	Swansea 1	Leaves	10	93.3	0.352 (0.023)	0.606 (0.072)
wSW2	Swansea 2	Leaves	10	90.0	0.395 (0.024)	0.593 (0.077)
England:						
eENK	East Norfolk	Seeds	10	100	0.485 (0.011)	0.787 (0.033)
eKEN	Kent	Seeds	10	93.3	0.365 (0.025)	0.537 (0.076)
eLIN	Lincolnshire	Seeds	10	96.7	0.412 (0.023)	0.612 (0.072)
eMDX	Middlesex	Seeds	10	100	0.439 (0.016)	0.651 (0.071)
eSUX	Sussex	Seeds	9	100	0.408 (0.022)	0.725 (0.058)
eYOR	York	Seeds	10	100	0.425 (0.011)	0.908 (0.022)
Southern Europe:						
cCRE	Crete	Seeds	10	100	0.435 (0.016)	0.818 (0.035)
cPOR	Portugal	Seeds	10	80	0.416 (0.022)	0.799 (0.031)
cMCA	Mallorca	Leaves	10	100	0.350 (0.034)	0.492 (0.080)
cCYP	Cyprus	Seeds	9	100	0.394 (0.023)	0.744 (0.050)

50 μL of DNA hydration solution (Puregene). DNA concentrations of the rehydrated DNA samples were assessed with a Genequant spectrophotometer (Pharmacia, Amersham Biosciences, Little Chalfont, U.K.). Samples were diluted with DNA hydration solution (Puregene) to a concentration of 20 ng/μL prior to use in PCR (polymerase chain reaction).

For all PCR reactions, 50 ng of extracted DNA was used in 25 μL reaction mixes. Other components were 0.25 μM of primer, 250 μM of each dNTP, 2 mM of $MgCl_2$, 2.5 μL of Buffer IV (ABGene: 750 mM Tris-HCl [pH 8.8], 200 mM $[NH_4]_2SO_4$, 0.1% [v/v] Tween 20), and 1 unit *Taq* DNA polymerase (ABGene, Surrey, U.K.). Reactions were carried out in a DNA Engine thermocycler (MJ Research, Waltham, Mass.). Five RAPDs 10-mer primers from Operon (Qiagen, Hilden, Germany) were used: OPA-08, OPA-16, OPC-11, OPE-01, and OPE-14. All thermocycling reactions were carried out with the following protocol: 94°C for 5 min to denature the DNA, followed by 45 cycles of 94°C for 1 min, 36°C for 1 min, and 72°C for 2 min, and ending with a final extension step of 72°C for 5 min. The PCR products were resolved by electrophoresis on a 1% agarose gel. These were stained with ethidium bromide, visualized under UV irradiation, and digitally documented (Gel Doc 2000 system, Bio-Rad Laboratories, Hercules, Calif.). To check reproducibility, all procedures were repeated for 18 arbitrarily chosen samples; the replicated procedure included using a different leaf of the same plant for DNA extraction. Only reproducible polymorphic bands were scored, and sizes were estimated with a 2-log DNA ladder (New England Biolabs, Beverly, Mass.). Each RAPD band retained for analysis was considered an individual locus. A total of 30 loci for each sample were scored for the presence or absence of a band.

Data Analysis

Dominant data such as that of RAPDs presents analytical challenges because most approaches must compensate for the unknown heterozygosity. For example, the inbreeding coefficient has to be assumed or measured by other means (Lynch and Milligan 1994). Methods based on assumed Hardy-Weinberg equilibrium may lead to greater biases in estimations of genetic diversity compared with estimations based on codominant data, particularly in cases of small samples sizes (Lynch and Milligan 1994; Isabel et al. 1999). However, a Bayesian method providing nearly unbiased estimates of heterozygosity has been developed (Zhivotovsky 1999). This estimates allele frequencies for each locus from the sample size and the number of individuals lacking the RAPD fragment and also estimates the distribution of allele frequencies based on the variation of the RAPD frequencies over loci. The program AFLP-SURV (Vekemans et al. 2002) was used for this procedure. Both Hardy-Weinberg genotypic proportions and a fixed deviation from Hardy-Weinberg ($F_{IS} = 0.5$) were used: this allows the effect of inbreeding on the estimated statistics to be examined. Statistics on the genetic diversities for the Bayesian-estimated allele frequencies

followed the methods of Lynch and Milligan (1994), where H_j is the mean gene diversity per population (expected heterozygosity), H_w is the average gene diversity within populations, and H_t is the total gene diversity in the data set.

Genetic diversities were also estimated using Shannon's Index, following the method explained by Bussell (1999) (to differentiate statistics estimated using Shannon's Index, the prime symbol is used). Genetic diversity per RAPD locus and per population was calculated as $H_j' = -\Sigma p_i \log_2 p_i$ (p_i = the frequency of the presence or absence of the RAPD locus). Diversity averaged over all populations was $H_{pop}' = (1/n)\Sigma H_j'$ (n = the number of populations). Total diversity for each locus was calculated as $H_{sp}' = -\Sigma p_s \log_2 p_s$ (p_s = the frequency of the presence or absence of the RAPD locus for all samples). The proportion of genetic diversity found within populations is calculated as H_{pop}'/H_{sp}'. This approach is a useful comparison because it does not require estimates of allele frequencies or assumptions about Hardy-Weinberg equilibrium.

The hierarchical structure of genetic data in multiple nested populations can be described in terms of *F*-statistics (Wright 1951). G_{ST}, the proportion of total gene diversity that occurs among as opposed to within populations (Lewontin 1972), can be interpreted as F_{ST}. To calculate F_{ST} based on the Bayesian-estimated allele frequencies, G_{ST} is $(H_w - H_t)/H_t$ (AFLP-SURV; Vekemans et al. 2002). To test if there were significantly greater degrees of genetic differentiation than expected from random assemblages of individuals, 500 permutations were performed on the data set. Shannon's Index of gene diversities provides G_{ST}' values that are free of assumptions about Hardy-Weinberg equilibrium and are not based on estimates of allele frequencies (the prime symbol differentiates statistics estimated using Shannon's Index). The overall partitioning of genetic diversities between populations (G_{ST}') was calculated from average per-primer values for H_j', H_{pop}', and H_{sp}' (Chalmers et al. 1992), where $G_{ST}' = (H_{sp}' - H_{pop}')/H_{sp}'$.

In addition, we used the alternative Bayesian method of Holsinger et al. (2002) for calculating θ^B as an estimate of the fixation index (F_{ST}) under a random-effects model of population sampling, using the program Hickory, version 0.8, with default settings and noninformative priors (Holsinger et al. 2002; free software is available at http://darwin.eeb.uconn.edu/hickory/hickory.html). This incorporates the uncertainty of the degree of inbreeding (Hardy-Weinberg equilibrium is not assumed) into the estimate of θ^B and has been shown to provide accurate F_{ST} estimates even for small sample sizes (Holsinger et al. 2002). The Bayesian model can be used in calculating *f*, but this should only be interpreted as an estimator of the inbreeding coefficient (F_{IS}) with caution (Holsinger et al. 2002). The full model estimates both θ^B and *f* and the $f = 0$ model estimates θ^B under the assumption of no inbreeding, whereas the $\theta^B = 0$ model estimates *f* under the assumption of no population differentiation. There is also an "*f*-free" model where *f* is not estimated but is chosen at random from its prior distribution. The Hickory analyses include estimations of the fit of the models to the data ($\overline{D}$) (Spiegelhalter et al. 2002). The Deviance Information Criterion (DIC) is the Bayesian measure of fit that takes into account the complexity term p_D (p_D being the approximate number of parameters being estimated), where smaller DIC or ($\overline{D}$) values indicate better fit (Spiegelhalter et al. 2002). This allows a qualitative evaluation of the different models under consideration; differences of six or fewer units between models is not sufficient to differentiate between models, but where differences in DIC or ($\overline{D}$) values are more substantial, the model with the smallest values may be favored (Spiegelhalter et al. 2002).

Pairwise θ^B (F_{ST}) values were estimated for use in Mantel tests (Mantel 1967) of correlations with geographic distances (km). Ln-transformed geographic distances and values for $F_{ST}/(1 - F_{ST})$ were used (Rousset 1997). Pairwise genetic distances and Nei's *D* (Nei 1972), calculated with the Bayesian-estimated allele frequencies in AFLP-SURV (Vekemans et al. 2002), were also used in tests of spatial autocorrelation. Bootstrapped pairwise genetic distances were further used in neighbor-joining cluster analyses as implemented in PHYLIP (Felsenstein 1993).

Results

Genetic Diversities

Estimates of diversity were similar regardless of the value of F_{IS} used (cf. H_w results in table 2). The Shannon's Index method provided higher values of genetic diversities, but the patterns of diversity were similar to those found with the other estimation methods: there were significantly lower diversities in populations from South Wales compared with those of English populations (Mann-Whitney *U*-test: $z = -2.280$, $P = 0.023$ for H_j' and $z = -2.368$, $P = 0.018$ for H_j) but no significant difference in genetic diversities between British and southern European samples (Mann-Whitney *U*-test: $z = -1.460$, $P = 0.144$ for H_j' and $z = -0.487$, $P = 0.626$ for H_j). Also, there was a significant association with colony age, Mann-Whitney *U*-test of genetic diversities in younger (those recorded only after the 1970s) versus older (those recorded by the 1950s) populations: $z = -2.719$, $P = 0.007$ for H_j' and $z = -2.543$, $P = 0.011$ for H_j.

Genetic Differentiation

Populations for all locations and for each region (South Wales, England, and southern Europe) were more genetically differentiated than random arrangements of individuals (i.e., G_{ST} values in table 2 were significantly greater than zero for all groups). Further evidence of genetic differentiation among populations was provided by the comparatively high DIC values for the $\theta^B = 0$ model for all analyses, indicating that this model has the worst fit in all cases (table 3).

Table 2

Partitions of Gene Diversities for Various Geographical Groupings of Locations

	H_w		G_{ST}			
Groups	$F_{IS} = 0$	$F_{IS} = 0.5$	$F_{IS} = 0$	$F_{IS} = 0.5$	H_{pop}'/H_{sp}'	G_{ST}'
All	0.380	0.372	0.149	0.189	0.657	0.343
South Wales	0.356	0.336	0.188	0.242	0.586	0.413
England	0.422	0.422	0.080	0.098	0.766	0.234
Southern Europe	0.399	0.413	0.101	0.122	0.739	0.239

Table 3

Summary of Statistics Estimated by Bayesian Methods for F_{ST} Estimation

Model	Mean θ^B (95% credible interval)	Mean f (95% credible interval)	$\overline{D}$	p_D	DIC
All locations:					
Full	0.2557 (0.2238, 0.2867)	0.6982 (0.3556, 0.9709)	2050.8232	407.9816	2458.8048
$f = 0$	0.1968 (0.1737, 0.2224)	...	2051.9330	445.2067	2497.1397
f free	0.2468 (0.2078, 0.2823)	...	2081.3103	438.3332	2519.6435
$\theta^B = 0$	...	0.7354 (0.3491, 0.9845)	3884.3058	29.3758	3913.6816
South Wales only:					
Full	0.3139 (0.0.2617, 0.3623)	0.6142 (0.1632, 0.9565)	1042.2812	220.1566	1262.4377
$f = 0$	0.2558 (0.2178, 0.2954)	...	1040.0790	246.8197	1286.8987
f free	0.3087 (0.2587, 0.3573)	...	1055.7471	235.5842	1291.3314
$\theta^B = 0$	...	0.7167 (0.3316, 0.9813)	2290.0808	28.8148	2318.8956
England only:					
Full	0.1423 (0.0971, 0.1912)	0.6483 (0.2223, 0.9676)	580.7322	101.2167	681.9489
$f = 0$	0.1091 (0.0754, 0.1481)	...	579.9811	111.2048	691.1859
f free	0.1410 (0.0972, 0.1899)	...	588.7633	112.5633	701.3266
$\theta^B = 0$	...	0.6728 (0.2877, 0.9741)	818.4795	28.4891	846.9686
Southern Europe only:					
Full	0.1564 (0.1031, 0.2178)	0.7081 (0.3095, 0.9810)	394.6135	73.9345	468.5480
$f = 0$	0.1204 (0.0762, 0.1739)	...	392.2736	79.3944	471.6679
f free	0.1512 (0.0969, 0.2139)	...	399.1253	80.4252	479.5505
$\theta^B = 0$	...	0.7826 (0.4388, 0.9891)	565.9477	28.5660	594.5137

Note. θ^B is the estimator for F_{ST}, and f is the estimator for F_{IS}, with the 95% credible interval for each in parentheses. $\overline{D}$ is a measure of the fit of the model to the data, and the approximate number of parameters being estimated is p_D. The Deviance Information Criterion (DIC) is the Bayesian measure of fit that takes into account the complexity term p_D.

Both G'_{ST} and G_{ST} were greater for South Wales populations than for other groups, whereas those for English samples were similar to those obtained for native southern European locations (table 2). Although not as high as the G'_{ST} estimates, the average θ^B values were generally higher than G_{ST} values. With our data, the difference was particularly pronounced for South Wales populations. In contrast, the θ^B and G_{ST} values were more comparable for the English and southern European samples, with the G_{ST} values lying within the 95% credible intervals of θ^B (cf. results of $G_{ST}[F_{IS} = 0]$ with θ^B [$f = 0$ model], and that of G_{ST} [$F_{IS} = 0.5$] with θ^B [full model] in tables 2 and 3).

Spatial Relationships

Both pairwise θ^B and D values yielded similar results. A significant but negative correlation was found with Ln-transformed distance measures ($g = -1.7767$, $r = -0.2969$, $P < 0.05$ and $g = -1.7069$, $r = -0.282$, $P < 0.05$, respectively). The negative correlation was caused by higher degrees of genetic structure among South Wales populations as compared with those in England (see previous sections) and geographical distances within South Wales (average of 39.446 km) being significantly lower than distances within England (average of 196.171 km; $t = -6.529$, df = 14.577, $P = 0.000$). Indeed, when English and South Wales groups were tested separately, there was no longer any correlation with geographic distances ($g = 0.1282$, $r = 0.029$, $P > 0.05$ and $g = -0.5586$, $r = -0.1176$, $P > 0.05$, respectively, for pairwise θ^B values). Overall, therefore, there was no evidence of isolation by distance affecting patterns of genetic differentiation. Similarly, cluster analysis (fig. 2*a*) showed little bootstrap support (< 50%) and did not display any pattern of geographical assemblages. Removal of southern European samples from the analysis and analysis of South Wales samples only resulted in consensus trees with low bootstrap support for most clusters (results not shown). But when the analysis was restricted to English samples, a consensus tree with good bootstrap support for all clusters was found (fig. 2*b*). Nevertheless, the pattern of clusters remained inconsistent with the spatial arrangement of locations; for example, although eSUX is geographically closest to eKEN and eMDX (fig. 1), it was grouped with eYOR in the cluster analysis.

Discussion

A single introductory event would mean a single original founding group, with all other populations in the alien region originating from this founding group. The lack of spatial correlation means that there was no support for such a pattern of introduction of *Hirschfeldia incana* into Britain. Perhaps current migration has ameliorated this by reshuffling genetic variation. Alternatively, there could have been a history of either multiple founding groups originating from different source populations or heterogeneous founding groups with members originating from different source populations.

If founding groups had been small and limited, then genetic bottlenecks would be expected to have led to reduced genetic diversity in the new colonies. Also, genetic differentiation is expected to be independent of the age of a colony, when observed genetic distances are more strongly affected by reduced population sizes (Hedrick 1999). However, the

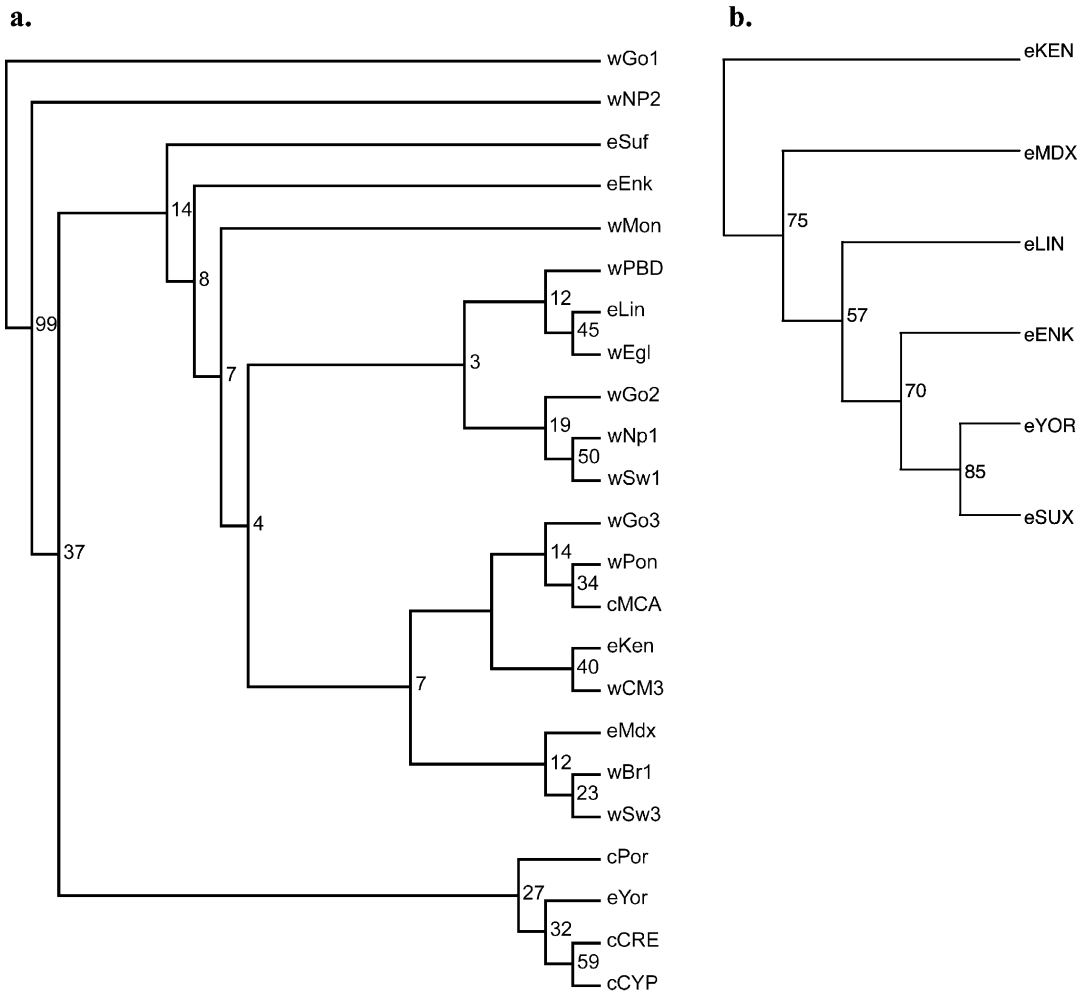

Fig. 2 Majority rule consensus of neighbor-joining trees for (*a*) all data and (*b*) English samples only

degrees of genetic diversity in the alien *H. incana* populations in Britain, although variable, were found to be comparable with the range of genetic diversities observed for native populations. Diversities appeared to be associated with the age of the alien colonies, the older, mainly South Wales group, having significantly lower diversities than the newer, mainly English group of colonies. These observations are contrary to those expected for colonies established from small, limited founding groups. Alternatively, it is possible that the number of native samples included in this study was too few or that some of these were in themselves also genetically depauperate due to recent demographic changes.

In considering whether founding groups could have been from single source populations or, alternatively, were heterogeneous mixes, it may be useful to consider metapopulation theory (Levins 1970; Slatkin 1977). Metapopulation models include rates of colonization and extinction as explicit factors (McCauley 1991; Hanski 1998). Factors include whether founding groups consisted of individuals selected at random from the entire range of source populations (migrant pool model) or whether each colony originated from a single population selected at random from the range of source populations (propagule pool model) (Slatkin 1977; Wade and McCauley 1988). In the propagule pool model, colonization leads to increased genetic differentiation among populations (Wade and McCauley 1988; Whitlock and McCauley 1990). F_{ST} for the migrant pool model may also increase, but if the founding group was large relative to the rate of migration and the current population size, then F_{ST} may decrease (Wade and McCauley 1988; Whitlock and McCauley 1990).

The genetic structure of *H. incana* showed a pattern more consistent with the migrant pool model, where the F_{ST} of newly founded populations was similar to that observed in native populations. In contrast, all methods indicated that the South Wales populations were more differentiated from each other than those within England or southern Europe. For example, the 95% credible intervals of θ^B for the South Wales group do not overlap those of the other groups (table 3). In time, genetic drift or selection has perhaps resulted in gradual reduction of diversity and increased differentiation among the older alien populations. Alternatively, higher degrees of genetic differentiation within the South Wales group may be caused by greater degrees of inbreeding (Hartl and Clark 1997). Initially, this appears to be a plausible explanation

since the South Wales group had lower genetic diversities within populations and *H. incana* is known to be capable of self-fertilization (Darmency and Fleury 2000). Also, f values were estimated to be 0.6 or higher in the full models. The DIC values for the South Wales $f = 0$ model were substantially higher than that for the full model, with a difference of 24 units, which may be interpreted to mean that the full model (where f is allowed to vary from zero) should be favored over $f = 0$. In comparison, the differences between the DIC values of full and $f = 0$ models for populations in England and southern Europe were much smaller (10 units or less). However, examination of the $\overline{D}$ values (table 3) reveals that there were few differences between the full and $f = 0$ models for all groups, even for South Wales. This indicates that the differences in DIC values can be attributed to differences in the complexity (p_D) rather than the actual fit of the models (Spiegelhalter et al. 2002), and there is no strong evidence for f being greater than zero for any of the groups, including the South Wales populations. However, the similar $\overline{D}$ values also mean that either model could be accommodated. Therefore, we can neither favor the model where f is allowed to vary from zero nor discount it. Caution must be taken in interpreting f values as estimates of F_{IS} (Holsinger et al. 2002), particularly since the 95% credible intervals were rather large and, therefore, the average f values may not be very informative. Nevertheless, if it is presumed that the average f values from the full model were correct in terms of precision (although not necessarily accurate) and if the estimated f values are merely considered for comparative purposes within this data set, we find that the South Wales f values are actually similar to those for England and southern Europe (table 3). Again, this does not support higher levels of inbreeding in the South Wales group of populations.

It could be argued that the apparent association with age is only coincidental: perhaps English and South Wales colonies had separate histories of introductions with English colonies founded according to the migrant pool model and South Wales colonies established through a propagule pool model. According to Giles and Goudet (1997), if isolation by distance can be demonstrated among populations, this would suggest that the founders were drawn from a limited number of source populations (propagule pool model). The lack of spatial autocorrelation for the South Wales samples, however, does not support the propagule pool model. Thus, the migrant pool model appears more likely, even for South Wales samples.

It is known that hoary mustard was cultivated in Britain in the eighteenth century and was first recorded growing wild in 1837 (Preston et al. 2002). Evidence indicates it also arrived as a contaminant in imported seed (Dunn 1905) and wool (Hayward and Druce 1919). Dockland sites are also a significant feature of early records, where introduction was often associated with seed arriving in ballast. Thus, it appears that hoary mustard indeed was brought to Britain via diverse routes, and the colonies are therefore likely to have originated from multiple sources.

The genetic diversities (H_j' and H_j) and partitions of genetic diversities between populations (G_{ST}' and G_{ST}) of British *H. incana* compared well with those for other out-crossing plants and were dissimilar to those reported for self-fertilizing plants (Schoen and Brown 1991). Furthermore, estimates of the genetic diversities of both native and alien populations were similar, indicating comparable levels of outbreeding. Thus, even though *H. incana* may be self-compatible, the genetic data did not reveal any evidence that the British populations were more inbred than native populations. In addition, heuristic comparison of the $\overline{D}$ values of full and $f = 0$ Bayesian models, as well as the similar average f values obtained for both native and alien populations, did not provide any evidence for higher levels of inbreeding in British *H. incana*.

Comparison with Other Studies

A search of the literature (table 4) places our results for *H. incana* in context with other studies in which native and alien populations had been compared. Reduced diversities in alien populations have indeed been reported for many of the predominantly inbreeding or selfing species that have been studied (table 4, pt. A). Some introduced populations of normally outbreeding species also appear to be reproducing clonally or with high levels of selfing/inbreeding (table 4, pt. B). However, there is also a variety of normally out-breeding species, in addition to *H. incana*, for which there was no suggestion of a change in reproductive strategy (table 4, pt. C).

Of the out-breeding aliens that do not appear to have altered their reproductive method (table 4, pt. C), genetic diversities in native and introduced populations were similar in half of these species. Of those alien populations exhibiting differences in genetic variation, only one was genetically depauperate. For the other species in table 4, part C, for which there was a difference in genetic variation, the opposite results were reported: introduced populations of *Epipactis helleborine* (Squirrell et al. 2001) and *Trifolium hirtum* (Molina-Freaner and Jain 1992) had higher genetic diversities relative to native populations. The similar case of *Raphanus raphanistrum* was attributed to large founding populations and multiple introductions caused by human dispersal of seeds as an agricultural contaminant (Kercher and Conner 1996).

In these studies, genetic differentiation between alien populations was also lower (in table 4 see G_{ST} or F_{ST} in "Genetic differentiation"), perhaps because the original founding population was a heterogeneous sample with high polymorphism (Molina-Freaner and Jain 1992). In contrast, the degree of genetic differentiation among English *H. incana* samples was similar to that found for southern European populations, whereas that of South Wales samples was higher. Since most of the South Wales populations have been established longer than the English colonies, there had been perhaps more time for genetic drift or selection to increase genetic differentiation.

Possible Genetic Factors Contributing to Successful Invasion

Human-mediated migration will increase the likelihood of founders of mixed origin, multiple introduction events, or a continued input of migrants. There are possible genetic benefits. Admixture of genotypes from different, genetically isolated source populations could lead to heterosis. This has been demonstrated experimentally (Saccheri and Brakefield 2001), and there are reports of population recovery following

Table 4

Studies That Compare Genetic Diversities in Native and Alien Populations for Various Plants of Different Breeding Systems

Organism	Method	Genetic diversity			Genetic differentiation			Reference
		Native	Difference	Alien	Native	Difference	Alien	
A. Inbreeding/selfing/asexual breeding system:								
Avena barbata	Isozyme	Western Mediterranean		California	...	...	...	Clegg and Allard 1972
		$A = 2.4$	$>$	1.02–2.2				
		$H_t = 0.435$	$\gg$	0.001–0.180				
	Isozyme	Spain		California				Garcia et al. 1989
		$G_t = 45$	$\gg$	3	...	...	...	
Bromus tectorum	Isozyme	Eurasia and North Africa		North America				Novak and Mack 1993
		$A = 1.01$	$=$	1.05	$G_{ST} = 0.754$	$>$	0.478	
		$P = 52\%$	$>$	28%				
		$H_j = 0.009$	$\ll$	0.046				
Capsella bursa-pastoris	Isozyme	Europe		North America				Neuffer and Hurka 1999
		$G_t = 83$	$\gg$	41	...	...	...	
Chondrilla juncea	Isozyme	Turkey		Australia				Chaboudez 1994
		$G_t = 91$	$\gg$	3	...	...	...	
B. Outbreeding system in natives but shift to inbreeding/asexual in aliens:								
Eichhornia paniculata	Isozyme	Brazil		Jamaica				Glover and Barrett 1987
		$A = 1.27$	$>$	1.07	$F_{ST} = 0.324$	$\ll$	0.633	
		$P = 23.8\%$	$\gg$	7.6%				
		$H_o = 7.8$	$\gg$	2.0				
		$H_j = 0.09$	$\gg$	0.03				
		$H_t = 0.15$	$\gg$	0.06				
Fallopia japonica var. *japonica*	RAPD	Asia		Europe and North America				Hollingsworth and Bailey 2000
		$G_t = 12$	$\gg$	1	...	...	...	
Rubus alceifolius	AFLP	Southeast Asia		Indian Ocean islands, Australia				Amsellem et al. 2000
		SI = 0.73–0.99	$<$	0.83–0.99	...	...	...	
C. Outbreeding:								
Alliaria petiolata	ISSR	Europe		North America				Meekins et al. 2001
		$H_t = 0.940$	$=$	0.910	...	...	...	
Apera spica-venti	Isozyme	Europe		Canada				Warwick et al. 1987
		$P = 62\%$	$=$	57%	$G_{ST} = 0.024$	$\gg$	0.010	
		$A = 2.53$	$=$	2.54				
		$H_o = 0.228$	$=$	0.230				
		$H_j = 0.203$	$=$	0.209				
		$H_t = 0.208$	$=$	0.211				
Echium plantagineum	Isozyme	Europe		Australia				Burdon and Brown 1986[a]
		$A_p = 2.6$	$=$	2.7	...	...	...	
		$P = 82\%$	$<$	94%				
		$H_o = 0.29$	$=$	0.32				
		$H_j = 0.35$	$=$	0.34				

		$H_t = 0.38$	=	0.39				
Epipactis helleborine	Isozyme	Europe		North America				Squirrell et al. 2001
		$A = 1.77$	=	1.9	$F_{ST} = 0.20$	≫	0.09	
		$A_p = 2.4$	=	2.54				
		$P = 55\%$	=	58%				
		$H_j = 0.230$	=	0.232				
	cpDNA	$PP = 24\%$	≪	92%	$F_{ST} = 0.506$	>	0.367	
Hirschfeldia incana	RAPDS	Southern Europe		England				This study
		$H_j = 0.400$	=	0.422	$G_{ST} = 0.112$	=	0.080	
				South Wales				
			=	0.356		<	0.188	
Ligustrum robustum ssp. *walkeri*	RAPDS	Sri Lanka		La Reunion				Milne and Abbott 2004
		$H_j = 12.084$	=	10.470	...	...	...	
Lolium perenne	Isozyme	Italy		Corsica			...	Balfourier and Charmet 1994
		$A = 2.84$	=	2.79	...	...	...	
		$P = 87\%$	=	85%				
		$H_j = 0.326$	=	0.347				
Raphanus raphanistrum	Isozyme	England†		North America‡				Lewis-Jones et al. 1982;† Kercher and Conner 1996‡
		$P = 13.3\%$	≪	75%–100%				
		$H_j = 0.133$[b]	≪	0.27–0.58	...	...	$F_{ST} = 0.14$	
Trifolium hirtum	Isozyme	Turkey		California				Molina-Freaner and Jain 1992
		$A = 1.07$	=	1.18	$G_{ST} = 0.82$	≫	0.30	
		$A_p = 1.19$	<	1.97				
		$H_j = 0.0144$	≪	0.0549				
		$H_t = 0.0820$	=	0.0784				
Turnera ulmifolia	Isozyme	Latin America		Caribbean				Barrett and Shore 1987[c]
		$A = 2.1$	=	2.0	...	...	...	
		$P = 46\%$	≫	20%				
		$H_o = 0.11$	>	0.07				
		$H_j = 0.12$	≫	0.04				

Note. Symbols indicate the qualitative direction and extent of the difference between genetic diversity measures or estimates of genetic differentiation between native and alien populations:=indicates similar degrees of genetic diversity/differentiation; < or > indicate that genetic diversity/differentiation is smaller or larger, respectively, in the native as compared with introduced populations; double symbols (≪ or ≫) indicate that the magnitude of the difference is twice or more. Estimators of genetic diversity: A=mean number of alleles per locus; A_p=mean number of alleles per polymorphic locus; G_t=total number of genotypes; H_o=mean observed heteroxygosity, H_j=mean genetic diversity within populations (also known as H_s or average expected heterozygosity); H_t=mean total genetic diversity; P=percentage of loci polymorphic; PP=percentage of polymorphic populations; SI=similarity index. See respective references for definitions of the estimators used in each study. Estimators of genetic differentiation between populations: F_{ST}=F-statistics; G_{ST}=proportion of genetic diversity between populations. See respective references for definitions of the estimators used in each study.

[a] Data from Barrett and Husband (1990) and Molina-Freaner and Jain (1992).

[b] Unspecified whether this is observed or expected heterozygosity.

[c] Data from Barrett and Husband (1990).

immigration (Westemeier et al. 1998; Madsen et al. 1999; Vilà et al. 2002). Admixture would lead to new genetic combinations and the possibility of new "adaptive systems" that may be advantageous in novel ecological niches (references in Ellstrand and Schierenbeck 2000). Ellstrand and Schierenbeck (2000) proposed that such admixture could catalyze the evolution of invasiveness, suggesting that this could explain commonly reported observations that aliens become invasive only after multiple introductions or a long lag period after arrival. Indeed, *H. incana* in Britain displays the typical lag pattern (Preston et al. 2002).

High genetic variation may also be an advantage or even a necessity for colony expansion in novel and strongly variable environments (Nevo 1983; Williamson 1996). Outbreeding would be an important strategy to increase or maintain the variability of a limited number of founders (Carlquist 1966). High genetic variation is thought to be particularly important in competitive and demanding environments. For example, sexual species are often in more competitively demanding environments (Lynch 1984), and there are suggestions of correlations between colonizing ability and increased out-breeding or increased genetic variation (Jain and Martins 1979; Williamson 1996; Lambrinos 2001).

There is now a greater appreciation that the history of introduction plays a significant role in the success of alien establishment (Lonsdale 1999). Human transportation increases the diversity of alien populations beyond levels achieved through natural (nonanthropogenic) migration. With human-assisted migration, perhaps species that cannot "normally" attain the prerequisite of high genetic diversity for successful invasion are released from this restriction. Hoary mustard, for example, is often associated with routes of human transportation such as disturbed roadside verges, docks, and railways. In these locations, plants flower profusely and produce large amounts of fruit and huge numbers of seed that are likely to be dispersed effectively by wind and traffic vortices. Human transportation is not the sole factor. A review of examples of contemporary adaptation identified anthropogenic disturbance or changes as a common feature of invaded environments (Reznick and Ghalambor 2001). In considering the availability of disturbed habitats, together with increased transportation by humans, species that would not normally have the opportunity to gain a foothold in alien habitats or to enjoy the genetic advantages of admixture and high levels of variation in founding groups are perhaps now able to proceed beyond the limitations of natural modes of dispersal. Future studies comparing populations in their native and introduced ranges will be an invaluable approach to understanding this problem.

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