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Mohamed Diallo, Sébastien Ollier, Anaël Mayeur, Juan Fernández-Manjarrés, Alfredo García-Fernández, et al.. Plant translocations in Europe and the Mediterranean: Geographical and climatic directions and distances from source to host sites. *Journal of Ecology*, 2021, 109 (6), pp.2296-2308. 10.1111/1365-2745.13609 . hal-04311156

HAL Id: hal-04311156

<https://hal.science/hal-04311156>

Submitted on 31 Jan 2024

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16 To be cited as:

17 Diallo, M., Ollier, S., Mayeur, A., Fernández-Manjarrés, J., García-Fernández, A., Iriondo, J. M.,
18 Vaissière, A., & Colas, B. (2021). Plant translocations in Europe and the Mediterranean :
19 Geographical and climatic directions and distances from source to host sites. *Journal of Ecology*, 109,
20 2296-2308. <https://doi.org/10.1111/1365-2745.13609>

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25 **Abstract**

26 Although the number of plant translocations has been rapidly increasing for two decades, no study is
27 available to date that examines the directions and distances of plant displacements, which is essential
28 (though not sufficient) information for considering translocations as a management tool to enable
29 species to cope with the consequences of climate change. In this paper we study the geographic and
30 climatic directions and distances from source to host sites in 638 source-and-host site pairs of plant
31 translocations that aimed to achieve viable populations in the last decades in the Western Palearctic
32 (Europe and the Mediterranean). Translocation distances ranged from 0 to 661 km, but were generally
33 short, most (82%) being less than 25 km, due to both ecological considerations and legal and
34 administrative constraints. The host sites were not preferentially located in any geographic direction
35 or in any altitude relative to the source sites. In contrast, on a climate compass constructed from a
36 principal component analysis of seven bioclimatic variables, the host sites were slightly, but
37 significantly, under colder climatic conditions than the source sites. This observation appears to be
38 more the consequence of an effort to counteract already felt effects of climate change than to
39 anticipate future changes. The climatic distance between source sites and actual host sites was
40 generally smaller than between source sites and randomly selected host sites at a given distance or
41 within a given geographical area, which may be the result of a desire to minimise climatic differences
42 or differences in other ecological factors correlated with climatic differences.

43 Synthesis. This study is the first to compare, geographically and climatically, the source sites of
44 biological material and the host sites in translocations of wild plant species to obtain viable
45 populations. Past translocations are in line with mitigating the consequences of global warming on
46 plant species, because the host sites were in slightly cooler conditions than the source sites. Despite
47 this, climate considerations seem to have been little taken into account in plant translocation projects
48 and will certainly have to be much more so in a future with rapid anthropogenic climate change.

49 **Keywords:** reintroduction; reinforcement; plant conservation; biodiversity management; climate
50 change mitigation; climate distance; bioclimatic variable

1 | INTRODUCTION

Species translocations are increasingly used to restore communities or preserve or improve the conservation status of species (e.g., Soorae, 2018; Silcock et al., 2019). Indeed, anthropogenic pressures on natural habitats, due to agriculture, industry, transport and urbanisation, have led to a very high degree of fragmentation of natural habitats, which continues to increase, notably in Europe (European Environment Agency, 2011). Habitat fragmentation has two components: habitat patches are smaller and the distance between them is greater. The consequences for species living in these fragmented habitats are that population sizes are smaller and migration rates between populations are reduced. Small populations are more likely to suffer from demographic stochasticity, environmental stochasticity, Allee effects, inbreeding depression and low evolutionary potential due to loss of genetic variation, and accumulation of deleterious mutations (Lacy, 2000; Frankham, 2005). They then fall more easily into a dynamic that leads them to extinction (extinction vortex, Biere et al., 2002; Fagan & Holmes, 2006). When they are isolated, populations do not benefit from demographic or genetic rescue (Vilà et al., 2003; Hufbauer et al., 2015) to restore their viability by receiving individuals or gametes from neighbouring populations through migration. Although adaptive responses can mitigate its deleterious effects in a number of examples (Colas et al., 2004), habitat fragmentation is a major factor in altering the dynamics of metapopulations and the conservation status of species (Hanski et al., 2013; see also Fahrig, 2017 and Fletcher et al., 2018, for a controversy on the effects of habitat fragmentation on biodiversity).

Climate change is an added threat. In response to warming, species must adapt or migrate polewards, or to higher altitudes, or to more shaded slopes (Thomas et al. 2004; Lenoir et al., 2008; Lavergne et al., 2010; Urban, 2015; Román-Palacios & Wiens, 2020). However, in a context of habitat fragmentation, small populations have a reduced evolutionary potential to adapt to new conditions and fewer opportunities to reach new favourable habitat patches because of their isolation. Habitat fragmentation and climate change therefore have synergistic effects on the viability of

metapopulations (Brook et al., 2008), especially for plants whose dispersal is generally limited (Riba et al., 2005; Dullinger et al., 2015).

In this context, species translocations can allow (i) either demographic and genetic rescues that prevent the extinction of existing populations (reinforcements), or (ii) the colonisation of favourable patches that are difficult to reach by natural dispersal (reintroductions in formerly occupied sites or creation of populations in new sites within or beyond the extent of occurrence of the species). Plant translocations are now a common practice (e.g., Colas et al., 1997; Noël et al., 2011; Laguna et al., 2016). The main reasons for conducting translocation operations, beyond reaching the viability of the translocated populations, are the improvement of the conservation status of threatened species and the ecological restoration of degraded ecosystems. These actions can be underpinned by a legal framework (e.g. nature protection measures in the context of construction or development projects) or be triggered on a voluntary basis (e.g., cause defended by a non-profit organisation).

With climate change as an important concern for species conservation (Thomas et al., 2004; Thuiller et al., 2005; Bellard et al., 2012; Urban, 2015), translocations represent an opportunity for practitioners to contribute to the migration of populations towards the poles, or higher up in altitude, to cooler climatic conditions, thus mitigating the deleterious effects of warming (Fahselt, 2007; Brooker et al., 2011; Aitken & Whitlock, 2013). Review articles on plant translocations have focused on an assessment of the success of translocations, and the factors determining that success (Menges, 2008; Godefroid et al., 2011; Dalrymple et al., 2011; Silcock et al., 2019), although the criteria for success are themselves a subject of debate (Robert et al., 2015a, 2015b; Haskins, 2015; Seddon, 2015; Shier, 2015). Curiously, no studies are available that examine the geographic and climatic differences between the natural origins of translocated plant material and its final destination. This is probably because relatively few data on plant translocations are readily available in the scientific literature, and the grey literature describing them is widely scattered. In particular, data regarding the location of natural populations from which the plant material used for the translocation process was originally

harvested are difficult to find. In scientific articles and progress reports, information about botanical institutions that have stored or propagated plant material, and how they did it, is more frequent than information about the original natural populations.

Here, we propose to study the locations of source and host sites involved in translocations in the Western Palearctic (Europe and Mediterranean basin), by searching for geographical information on translocated populations of plants recorded in the TransLoc database (<http://translocations.in2p3.fr>). This will allow us to examine translocation distances and compare the geographical position and climatic conditions between the natural origin and the final destination of the plant material, regardless of the time it has spent *ex situ* (e.g. in cold storage or in cultivation) and the number of generations between the initial harvest and the final sowing or transplanting *in natura*.

We will specifically ask the following questions: (i) What is the distribution of plant translocation distances? (ii) Are the geographical directions of plant translocations randomly distributed around the compass rose? (iii) Do plant translocations generally occur to sites with climatic conditions that are different (e.g. colder) from the natural origins of the plant material? (iv) For given translocation distances, are plant translocations preferably to host sites with climatic conditions more similar to the source sites than is randomly expected for these distances?

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | The TransLoc database

Translocated plant and lichen populations were identified using the TransLoc database (<http://translocations.in2p3.fr>). This database has been developed using data on plant, lichen and

animal translocations in the Western Palearctic from ca. 1980 to 2019. The TransLoc database has a population basis. This means that the basic unit on which information is collected is a biological entity, the population, and not a restoration programme or action plan (such as the Plans Nationaux d'Action in France or Species Recovery Programmes in the UK), which may involve several species, or several sites for a species. A population is defined as a group of conspecific organisms that occupy a defined geographic area and between which ecological and reproductive interactions are more frequent than between them and other populations of the same species (Futuyma, 1986, p.554-555). To be included in the database, a population must contain a significant proportion of individuals that have been deliberately displaced (or the descendants of such individuals) in order to achieve population viability. The taxon must be identified and the date of translocation and the location of the population's host site must be known with some precision. The necessary objective of establishing a viable population or increasing the viability of an existing one may be accompanied by other objectives such as improving the conservation status of the species on a global or regional scale, or contributing to the restoration of a community, or a utilitarian objective for human well-being.

For every translocated population identified as explained above, optional information is collected when available. This information relates to the (i) context of the translocation (e.g., organizations involved, rationale for translocation, possible causes of taxon decline), (ii) type of translocation (reinforcement or reintroduction or creation of a population in a new site), (iii) characteristics of the host site (e.g., habitat type, distance to nearest population), (iv) biological material used (e.g., location of original population, diversity of life cycle stages), (v) various technical aspects (e.g., time spent ex situ in cold storage, greenhouse or garden, habitat preparation, post-translocation management), (vi) post-translocation monitoring effort (e.g., frequency and types of observations), and (vii) translocation results (e.g., population size, consequences on ecosystems). The sources of information are peer-reviewed scientific articles, books, theses, conference papers, presentations, reports, newspaper articles, maps, webpages, interviews, and personal communications.

2.1.2 | Geographical data

For every plant and lichen population in the database, we sought to locate the natural populations from which the biological material originated. For every identified original population, we delimited the geographical area in which it was located according to the available information. For some populations, this area was a round buffer of variable size around a fairly precise point such as a hamlet, a peak, or a cape, and for others it corresponded to a well-defined territory of variable size and shape such as an island, a pond, a nature reserve, a municipal territory, a province, etc. We then standardized all locations of original populations (henceforth, source site) by determining the latitude and longitude of the central point of the delimited area and by the maximum possible error between these coordinates and the actual position of the sampled population (the largest distance between the central point and the edge points of the area). These data were obtained by cross-referencing information from the documents relating to each translocation, Google Earth (Google Inc., 2017), the Database of Global Administrative Areas (GADM, 2018), and any document containing geographic information on the areas under consideration (e.g. web pages of municipalities, nature reserves, etc.). Similar work has been carried out to specify the location of the translocated populations (henceforth, host sites) as accurately as possible. We did not consider the ex situ locations where the biological material was kept or propagated between harvest from a natural population and transfer to the host site.

We were able to identify at least one source site for 613 populations among the 877 translocated populations of plants (867) and lichens (10) in the TransLoc database. This allowed us to generate a first array of 771 pairs of source and host sites, each associated with a taxon. From this array we removed all pairs of marine populations (of *Posidonia oceanica*, *Zostera marina*, and *Z. noltii*) because the analyses on the climatic differences between source and host sites (see below) were based on terrestrial data. We also removed pairs of sites for which the maximum possible error in the coordinates of either the source or host site was likely to result in an excessive bias in the geographic

or climatic distances between sites (see Supporting Information Figure S1). After these exclusions, the final array used for the analyses contained 638 pairs of source and host sites for 280 different taxa. In the final array, the maximum possible error was on average 1.81 km for hosts sites (range 0.1-11.0 km) and 2.31 km for source sites (range 0.1-14.0 km).

Source sites could appear several times in the array when they represented the place of origin of biological material translocated to several populations of the same species or of different species. Likewise, host sites could appear several times when they hosted translocated populations of several species or one population with several source sites. Source and host sites of one source-and-host site pair could be the same in the following cases: (i) when the translocation process consisted of a reintroduction attempt using biological material harvested from that specific locality prior to local extirpation, (ii) when the translocation process consisted of trying to reinforce an existing population with biological material previously harvested from the same population but propagated or cultivated ex situ to increase the number of individuals or make it pass a critical stage in the life cycle; (iii) when the two source and host sites were separate in the same area but the position of one of the sites could not be determined with sufficient precision, in which case the coordinates of both original and host sites have been degraded to the scale of the area (e.g., a municipal territory).

2.1.3 | Climatic data

We downloaded historical climate data with a 30-second spatial resolution ($\sim 1\text{km}^2$) from the WorldClim database version 2.1 (<https://www.worldclim.org/data/worldclim21.html>, Fick & Hijmans, 2017) using the *dismo* package of R (R Core Team, 2019). This database is the result of work initiated by Nix (1986) for the BIOCLIM package and its subsequent developments (Booth et al., 2014). It compiles monthly climate data from multiple weather stations and makes available bioclimatic variables, i.e. climate data believed to be biologically significant, the detailed description of which is available in O'Donnell and Ignizio (2012). We have selected seven bioclimatic variables based on climate averages for every month across the 1970-2000 span of years ('climate normals' sensu O'Donnell & Ignizio, 2012). They

reflect the climatic means, variability, and extremes that we thought were important for plants in temperate and Mediterranean regions. These variables are (naming after Fick & Hijmans, 2017, with additional information in brackets) BIO1 = annual mean temperature, BIO4 = temperature seasonality (standard deviation of monthly temperature averages x 100), BIO5 = max temperature of warmest month (monthly mean of daily maximum temperatures of the warmest month), BIO6 = min temperature of coldest month (monthly mean of daily minimum temperatures of the coldest month), BIO12 = annual precipitation, BIO15 = precipitation seasonality (coefficient of variation of monthly precipitation totals), BIO18 = precipitation of warmest quarter (total precipitation over the warmest 3-month time span).

2.2 | Data analyses

2.2.1 | Geographical distances and directions

All source and host sites were mapped and the geographic distance between sites for each pair of source and host sites was calculated using the `distGeo()` function of the `geosphere` package of R. The normality and variance homogeneity of translocation distances were improved applying the $x' = \log(x^{1/3} + 1)$ transformation. Each host site was plotted on a compass according to the differences in latitude and longitude compared to the source sites, using the transformed distances and grouping all the source sites into a single central point. We tested whether the translocations were significantly directed towards one cardinal point by bootstrapping the differences in latitude and longitude between sites and observing if the zero value was included within the 95%-confidence interval. All tests were done after removing site pairs with a geographical distance of zero, and prohibiting repetition of site pairs to avoid giving much weight to translocation programmes involving several species with the same source site on the one hand, and the same host site on the other hand. Differences in altitude were tested in the same way.

2.2.2 | Climatic distances and directions

Every bioclimatic variable was standardized to have a mean of 0 and a standard deviation of 1 over the whole set of pixels available in the study area (Western Palearctic). Then, for each bioclimatic variable and each pair of sites, a difference was calculated as the host site value minus the source site value. A climatic distance for each pair of sites was calculated as the Euclidian distance between source and host sites in the seven-dimensional space of normalized climatic variables. This distance was transformed to the power $1/7$ to normalize its distribution. We examined the correlation between Euclidian climatic and geographic distances on transformed data.

To understand the climate gradients of the study area, we applied a principal component analysis (PCA) on standardized data of the seven bioclimatic variables from the WorldClim database over the entire study area (Western Palearctic). This allowed us to summarize the climate data on two principal axes and visualize the largest fraction of each climatic distance between sites on a two-dimensional factorial map. By grouping the climatic coordinates of all source sites into a single central point, we were able to build a climatic compass (similar to the geographic compass described above) where the climatic positions of the host sites were plotted according to their total climatic distance (transformed data) from the source sites and a direction defined by the first two axes of the factorial map. We then tested whether the translocations significantly tended to any direction of the factorial axes by bootstrapping the differences in coordinates in the first and second axes between source and host sites, as for latitudes, longitudes, and altitudes, and observing if the zero value was included within the 95%-confidence intervals.

2.2.3 | Consequences of the choice of host sites on climatic distances

To examine whether the choice of host sites was made so as to somewhat minimize their climatic distance from the source sites, we compared the observed Euclidian climatic distances to the climatic distances between the source sites and random geographic points obtained in two different ways (see Supporting Information Figure S2). First, for each pair of source and host sites separated by more than 5 km, we simulated one hundred random points around the source site, at a distance equal to that where the host site was $\pm 5\%$, in any direction. The (transformed) climatic distance between the source

site and each simulated geographic point was recorded. We then determined the proportion of simulated points that gave a climatic distance lower than that of the true host site. Over all pairs of sites, this allowed us to see whether, for a given geographical distance, the geographical direction chosen between the source and host tended to minimize their climatic difference from what was expected with a random choice.

Second, we simulated one hundred random points around every host site within a radius equal to 0.25 times the distance separating source and host sites. Again, for each pair of source and host sites separated by more than 5 km, the climatic distance between the source site and each simulated geographic point was recorded, and the proportion of simulated points that gave a climatic distance lower than that of the true host site was determined. Over all pairs of sites, this allowed us to see if, in a given direction from the source site, the choice of the host site tended to reduce the climatic difference with the source site compared to what was expected with a random choice around the chosen site (within an area proportional to the square of the distance separating source and host sites). For both types of simulations, Student's t-tests allowed us to test whether the proportion of simulated geographic points with a lower climatic distance from the source site than the true host site was significantly less than 50%.

3 | RESULTS

3.1 | Geographical distances and directions

Source and host sites were located in fifteen different countries (Fig. 1). Translocation distances, from source to host sites, ranged from 0 to 661 km (mean: 28.9 km, median: 2.7 km); 202 (32%) were at less than 1 km, 320 (50%) were from 1 km to 25 km, and 116 (18%) were at longer distances (see Supporting Information Figure S3 for the distribution of translocation distances). Translocation distances were

longer in the northernmost operations than in the southernmost operations (see Supporting information Tables S1-S5 for details on geographic data). The host sites were distributed quite homogeneously on the geographic compass (Fig. 2), suggesting no preferred direction from source to host sites. This was confirmed by the bootstrap results on the differences in latitude and longitude between the source and host sites showing that the confidence intervals of the means of both differences included zero (Table 1). The difference in altitude was not significant either. The distributions of bootstrap means are available in Supporting Information Figure S4.

3.2 | Climatic distances and directions

The correlation between the Euclidian climatic and the geographic distances separating source and host sites was positive and highly significant (Fig. 3, $r(\text{Pearson})=0.91$; $P<10^{-3}$). Climatic distances are distributed similarly to geographic distances, with a bundle of short distances, where source and host sites often fall within the same climatic pixel, a group of medium distances distributed more or less normally, and a group of long distances with a near log-normal distribution (Fig. 3). As with geographic distances, climatic distances were greater in the northernmost operations than in the southernmost operations (Supporting information Table S6).

The PCA on climatic data of the Western Palearctic revealed two principal axes representing two important climate gradients for plants (Fig. 4). The first axis was related to a temperature gradient roughly oriented north-south. The second axis was related to an oceanic versus continental gradient roughly oriented west-east. The position of the host sites on the climate map was mainly in places where the climate was more oceanic than average in the Western Palearctic (negative coordinates on axis 2, Fig. 4).

The distribution of host sites on the climatic compass (Fig. 5) was less homogeneous than on the geographic compass. Indeed, there were more host sites on the left side of the compass, towards colder situations, than on the right side (194 versus 152, Fig. 5). Consequently, the bootstrap analysis

showed that the mean difference in coordinates of the host sites on the first factorial axis was significantly negative (Table 1). No significant difference was observed on axis 2 (oceanic-continental gradient). The distribution of bootstrap means is available in Supporting Information Figure S4.

Table 1. Bootstrap confidence intervals for the differences in geographic and climatic variables between host and source sites for plant translocations in the Western Palearctic (host site values minus source site values). Latitudes and longitudes are in decimal degrees, and altitudes in meters. Latitudes and longitudes on geographic compass are the coordinates on the geographical axes after transformation of the Euclidean distance between sites. Factorial axes derive from a principal component analysis (PCA) on all climatic data of host and source sites.

Variable	lower	upper
Latitude	-0.1097	0.0222
Latitude (on geographic compass)	-0.0438	0.1373
Longitude	-0.2811	0.0128
Longitude (on geographic compass)	-0.1420	0.0531
Altitude	-20.07	53.43
Coordinates on climatic compass, axis 1 (cold / hot)	-0.1377	-0.0080
Coordinates on climatic compass, axis 2 (oceanic / continental gradient)	-0.0390	0.0692

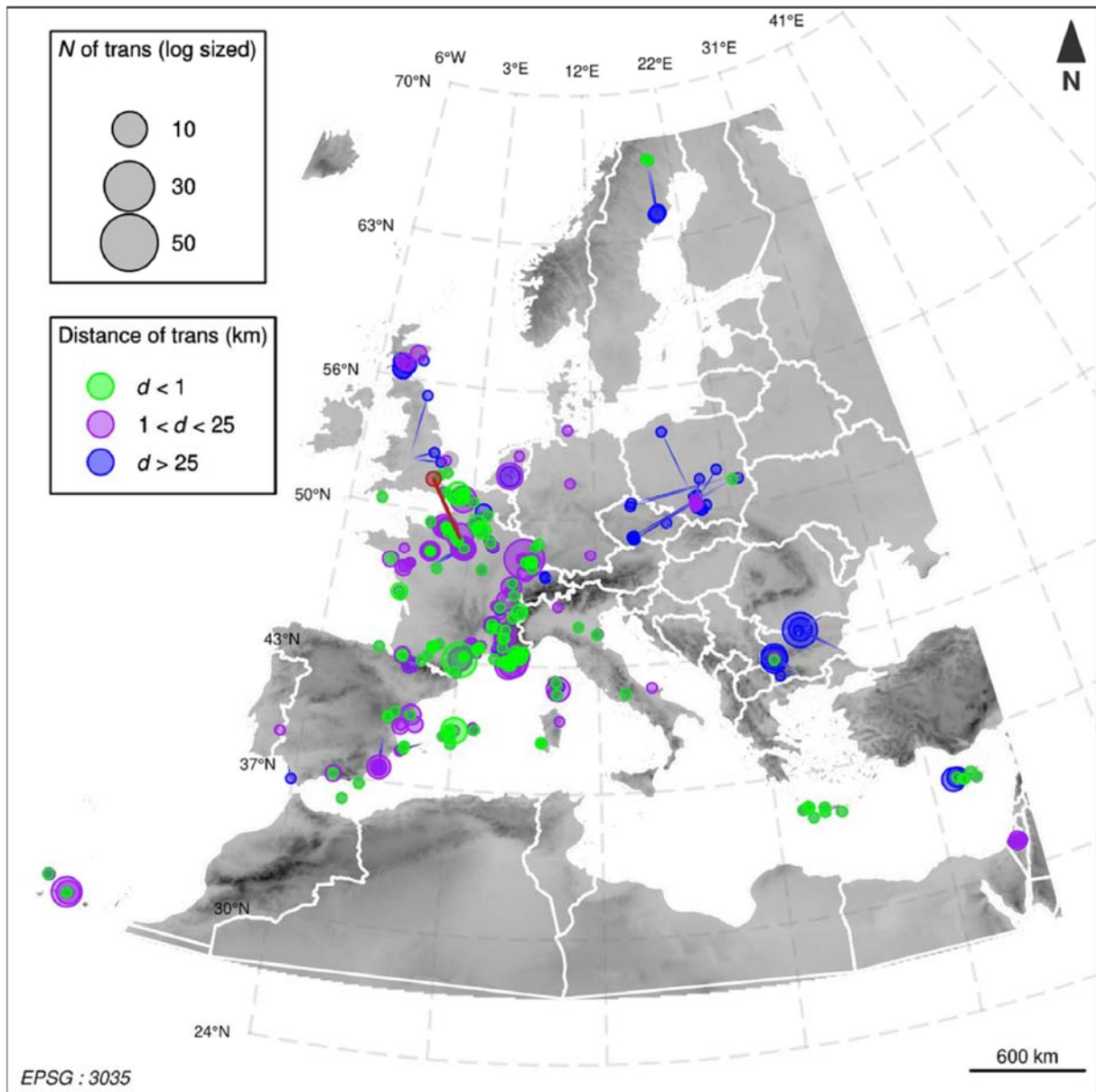


Figure 1. Location of host sites for plant translocations in the Western Palearctic. The size of the dots depends on the number of populations translocated in the site. The green dots correspond to translocations at a distance <1 km, the purple ones at distances between 1 and 25 km, and the blue ones at distances >25 km. The blue lines connect the host sites to their source sites for longer-distance translocations. The red line and dot symbolise a hypothetical translocation from Paris to London.

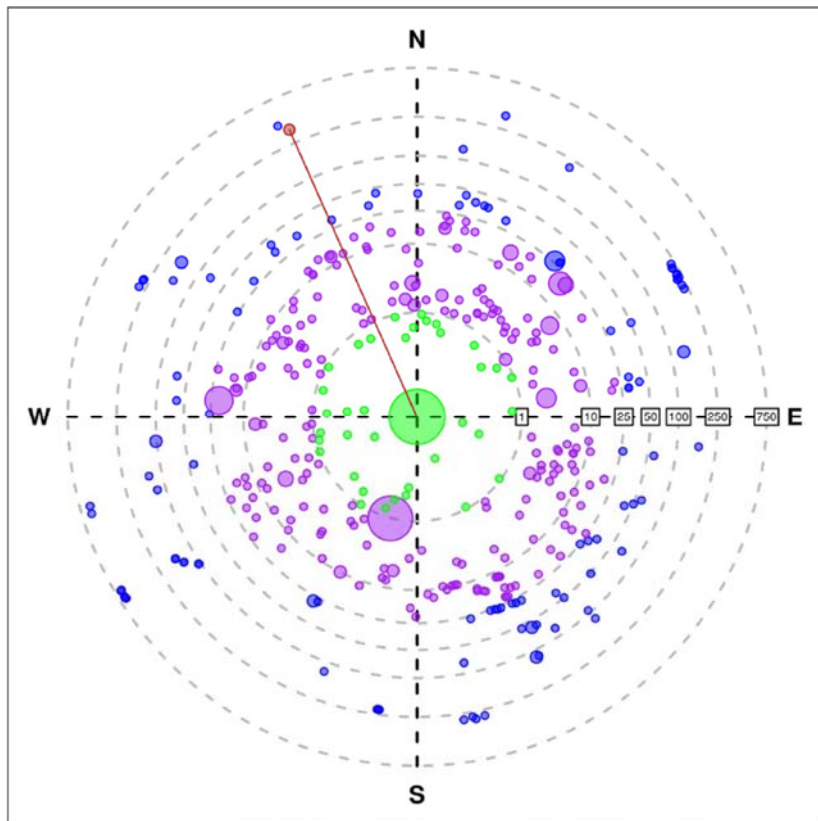


Figure 2. Location of host sites for plant translocations in the Western Palearctic on a geographical compass (with longitude and latitude axes) where all source sites have been grouped together at a single central point. The size of the dots depends on the number of populations with an identical origin translocated in the host site. The numbers on the dashed circles are the distances in kilometre between source and host sites (proportional in the figure to the transformed geographical distance, see text). The green dots correspond to translocations at a distance <1 km, the purple ones at distances between 1 and 25 km, and the blue ones at distances >25 km. The red line and circle symbolise a hypothetical translocation from Paris to London.

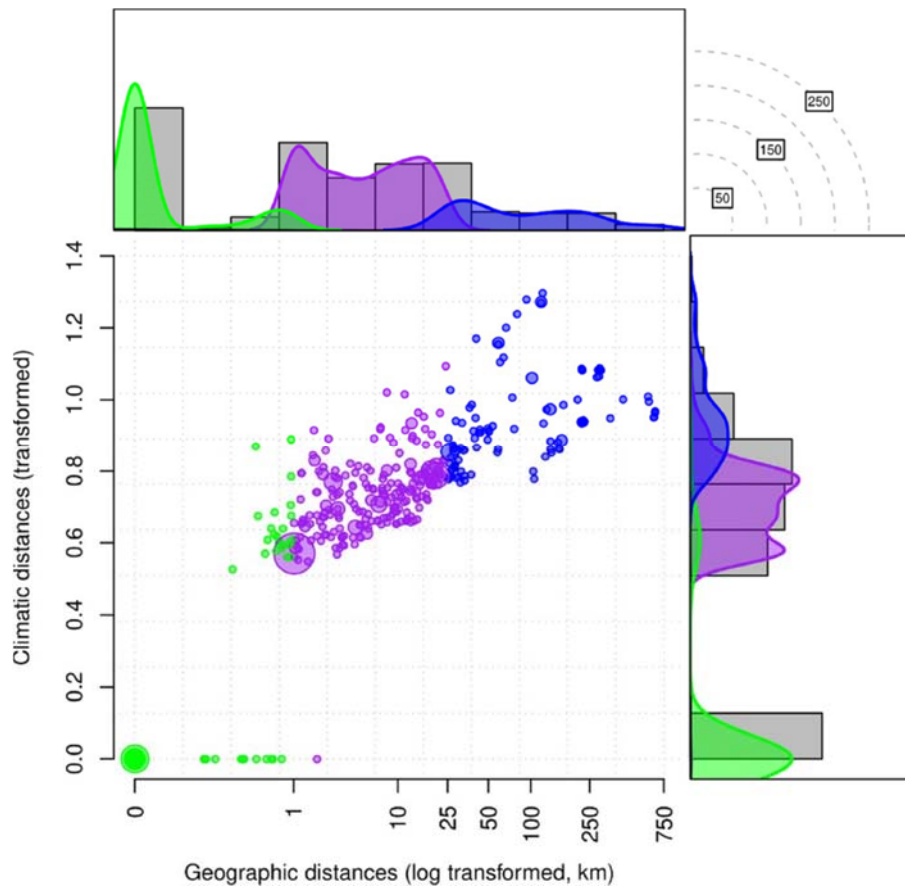


Figure 3. Relationship between the Euclidian climatic and geographical distances separating source and host sites in Western Palearctic plant translocations. The green dots correspond to translocations at a distance <1 km, the purple ones at distances between 1 and 25 km, and the blue ones at distances >25 km. The scatterplot is displayed with its two marginal histograms and kernel density estimations.

3.3 | Consequences of the choice of host sites on climatic distances

When random points were simulated in any direction around the source site (at the actual distance between the source and host sites $\pm 5\%$), the proportion of random points that resulted in a lower climatic distance value than the selected host site was significantly less than 50% when the host sites were located within 50 km of the source sites (Fig.6). When the host sites were located more than 50 km from the source sites, the proportion of random sites that gave a value of climatic distance less than that of the chosen host site did not differ from 50%. Thus, compared to random choices, the observed geographical directions from source sites to host sites tended to minimize their climatic difference for short and medium distances, but not for long distances.

The results were similar when random points were simulated around every host site within a radius equal to 0.25 times the distance separating source and host sites (Fig.6). Thus, in a given area (of ~ 0.2 times the square of the distance between the chosen source and host sites), the local positioning of host site tended to minimize the climatic difference with the source site for short and medium distances, but not for long distances.

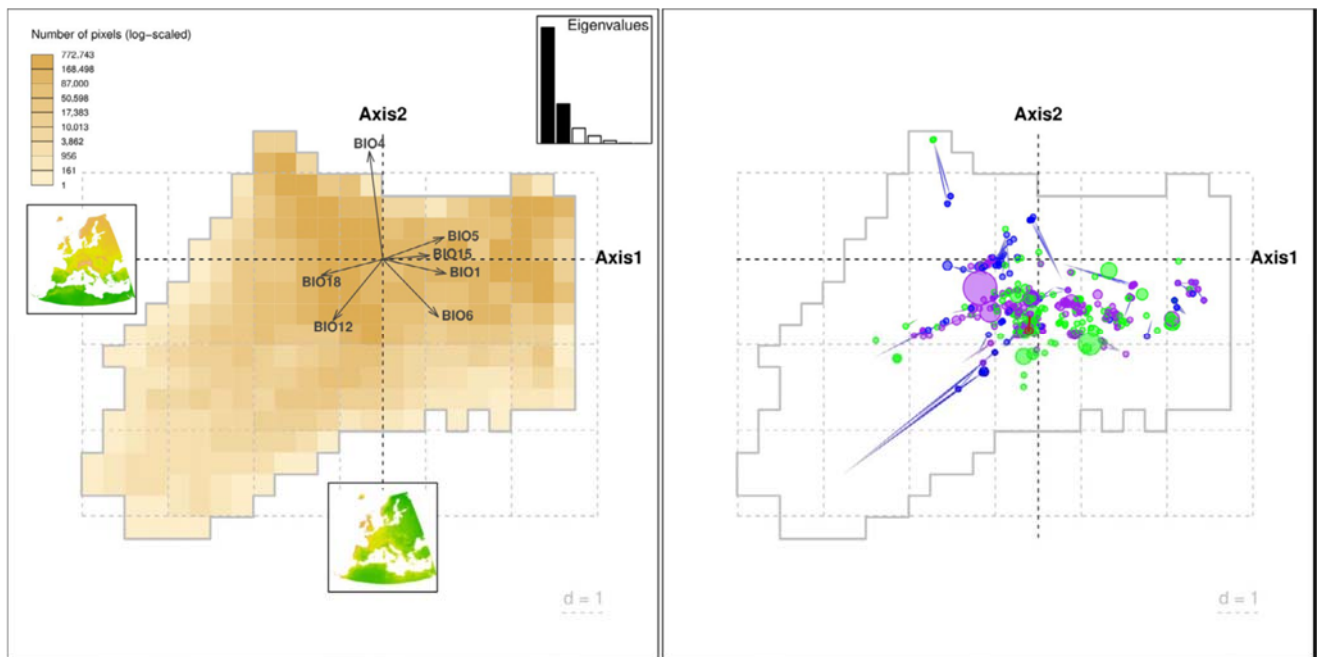


Figure 4. Principal component analysis of bioclimatic variables in the Western Palearctic. Left: Factorial climate space in the two main components (axes 1 and 2) and vectors corresponding to the seven bioclimatic variables. The mini maps show the geographical variation of the climatic coordinates on axis 1, which represents a temperature and humidity gradient, and on axis 2, which represents an oceanic/ continental gradient. Right: Location of host sites in the factorial climatic space, with symbolism is as in Figure 1.

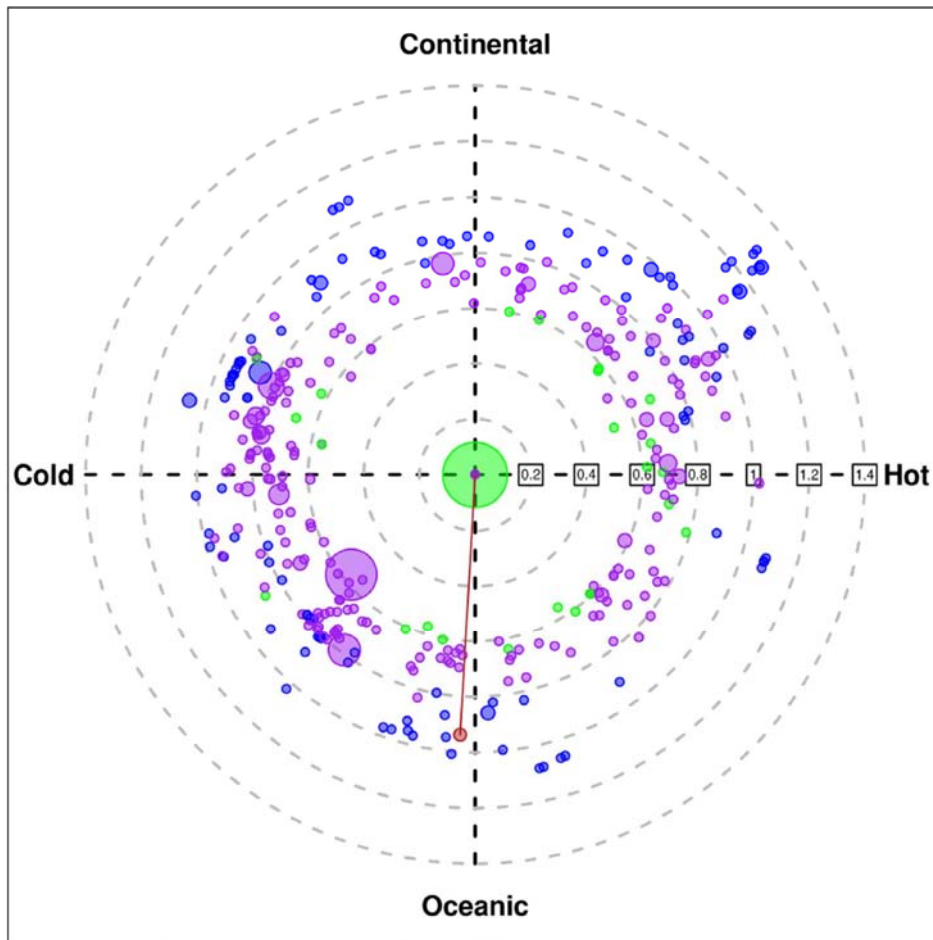


Figure 5. Position of host sites for plant translocations in the Western Palearctic on a climatic compass where all source sites have been grouped together at a single central point. The numbers on the dashed circles are the transformed climatic distances. The two axes are the principal axes of a principal component analysis performed on all data in seven bioclimatic variables in the Western Palearctic. The green circles correspond to translocations at a distance <1 km, the purple ones at distances between 1 and 25 km, and the blue ones at distances >25 km. The red line and circle symbolise a hypothetical translocation from Paris to London.

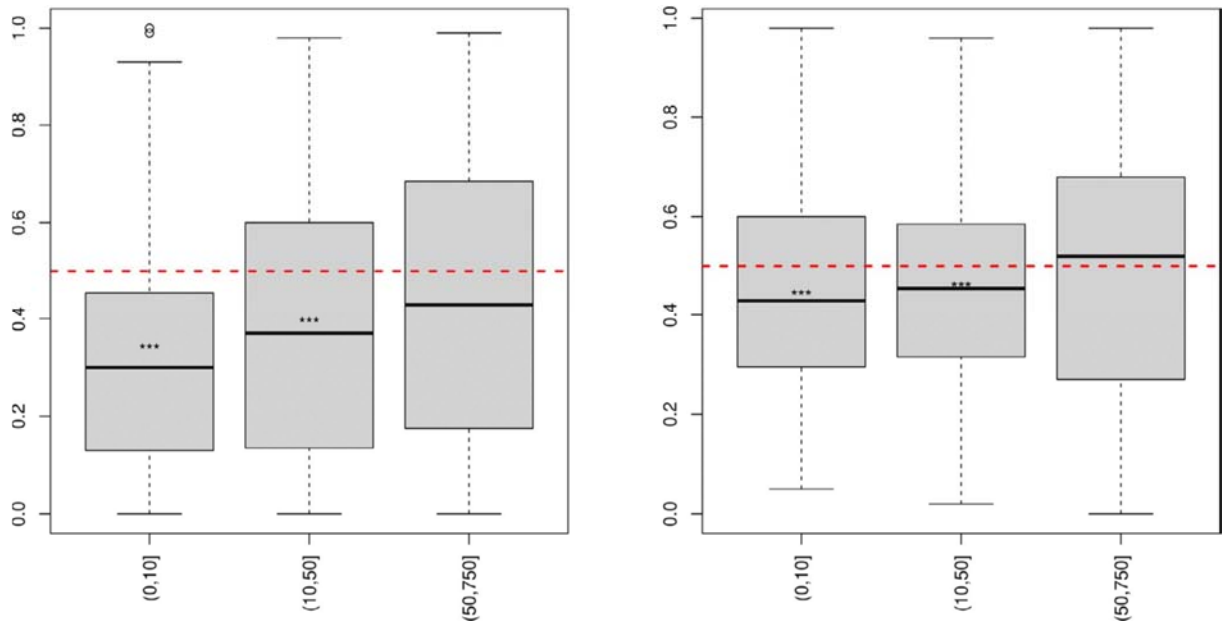


Figure 6. Boxplots showing the distributions of the percentages of simulated geographical points that have a Euclidian climatic distance to the source site lower than that of the true host site. Left: with random simulated points around the source site, at a distance equal to that where the host site is $\pm 5\%$, in any direction. Right: with random simulated points around the chosen host site, in an area with a radius equal to 0.25 times the distance separating source and host sites. The x-axis separates source–host pairs according to the distance between them (in km). *** indicates that the proportion of simulated geographical points with a lower climatic distance from the source site than the true host site was significantly less than 50% ($p < 0.001$, Student's t tests).

4 | DISCUSSION

4.1 | Geographical and climate distances and directions

In this paper we have compared the geographical locations and climatic conditions of host and source sites involved in translocations of plant species that aim to achieve viable populations in the Western Palearctic in the last decades. Most plant translocations were conducted at distances of less than 25 km. These distances are small when comparing them with the projected speed of climate change for the 21st century expressed in poleward shift per year in, e.g., Mediterranean forests, woodlands and scrub (0.26 km.yr⁻¹) or temperate broadleaf and mixed forests (0.35 km.yr⁻¹; Loarie et al., 2009). These short distances can be explained by the fact that it is easier to find similar habitats, likely to be suitable for the species, close to the source sites, but also by administrative and legal reasons, which we discuss below in the subsection about the many dimensions of site selection. In a very recent study, Skikne et al. (2020) estimated longer translocation distances in birds (median=105 km), using data from the Avian Reintroduction and Translocation database (Lincoln Park Zoo, 2012), including many translocations from New Zealand and the USA. Interestingly, they showed that the proportion of surviving birds one year after release decreased with longer distance translocations. As in our study, Skikne et al. observed that geographic and climatic distances between source and host sites were correlated, but not equivalent. But neither geographic nor climatic directions were documented in Skikne et al.'s study, and we are not aware of any such studies in plants.

In a context where climate change is an important concern for the conservation of species diversity (Thomas et al., 2004; Thuiller et al., 2005; Bellard et al., 2012; Urban, 2015), one would think that species translocations, whatever their main motivation, would represent an opportunity to move plant material (or the genetic information carried by this material) polewards, or higher in altitude, to cooler climatic conditions (Fahselt, 2007; Brooker et al., 2011; Aitken & Whitlock, 2013). We actually found that the translocations were not made preferentially in the direction of any cardinal point, nor towards a higher altitude. Yet on the climatic compass, the two axes of which are derived from the

PCA on the seven bioclimatic variables, the host sites were located on average in significantly cooler climatic positions than the source sites. We did not necessarily expect this result when we read the documents used for our database. While some documents suggested that global warming was one of the factors threatening the translocated species, none of them explicitly described the translocation project as a means of mitigating the negative effects of global warming. In addition, 82% of the source-host distances were less than 25 km, which limited the possibilities for climate differentiation. However, in a number of cases where managers had the choice between different candidate sites for the creation of new populations or reintroductions, they mentioned that they avoided sites where introduced individuals could suffer from excessive heat or drought (e.g., Fraga, 2000; Guyonneau & Amiotte-Suchet, 2019). This avoidance of sites with a relatively warmer and drier climate than other nearby sites (perhaps because of the slope, sun exposure, soil...) is probably the reason for our results. It is therefore fair to state that past translocations were more often made to sites where the effects of global warming on species could be limited rather than amplified. But in these cases, translocations were not considered in anticipation of future climate change to prevent the degradation of the conservation status of species whose populations could become extinct. It was within the framework of conservation programmes already underway to slow the decline of species that managers chose translocation sites in response to climate change, the effects of which were already tangible.

To go further, and possibly demonstrate that past translocations have helped to mitigate negative impacts of climate change on species conservation, it would be ideal to compare the viability of populations that have been translocated in contrasted climatic directions. Unfortunately, our post-translocation demographic data are currently too sparse and insufficiently standardised to allow such an analysis, even with a viability proxy.

The results of experiments in common gardens have shown an advantage of genotypes from warmer sites over local genotypes in *Mimulus guttatus* (Peterson et al., 2016) and *Clarkia pulchella* (Bontrager & Angert, 2019). Simulation results have shown that assisted gene flow is likely to reduce

maladaptation caused by climate change, despite outbreeding depression, in many cases (Aitken & Whitlock, 2013). All these results suggest that translocations can be a useful tool in species management to facilitate the adaptation of species to climate change (Aitken & Whitlock, 2013; Quigley et al, 2019), although some authors have pointed out that other local adaptation factors, such as soil or biotic interactions, may limit the interest of translocations and assisted gene flow (Bucharova, 2017). The identification of source sites currently experiencing the expected future climatic conditions in host sites is already included in translocation projects for long-lived trees, which may be part of productive forest plantation programmes (O'Neill et al., 2017) or ecological restoration programmes (Booth & Muir, 2020). It is likely (and hoped) that this approach will be more widely used in the future, notably for translocations of threatened species, although, in these cases, the choice of source and host sites is generally much more restricted than in the case of forest trees.

When we divided our dataset into four quartiles, according to the latitude of the host sites, we observed that compared to the most southern operations, the most northern operations tended to be at longer distances and further to the south (Supporting Information). The longer distances can be explained by the fact that there are fewer micro-endemic species of particular habitats, which tend to be translocated locally, in northern Europe than in the south. As for the more southerly directions, they could be related to the fact that from a certain latitude in northern Europe, human density and the associated frequency of degraded habitats decrease as one moves northwards. Habitat restoration and reintroduction of species may in these circumstances lead managers to bring back plant material from north to south. But these results and interpretations should be considered with great caution, since our dataset contains many more translocation operations carried out in Latin countries than in Northern Europe, where we have only had access to some (probably large) operations published in English (see subsection about the limits due to translocation practices and data availability).

4.2 | Extent of climatic differences between source and host sites

When translocation distances were less than 50 km, the climatic difference between the source and host sites was smaller than if the host sites had been randomly selected regardless of how the random selection was made, i.e. either at a given distance in any direction around the source site, or in a buffer zone locally centred around the actual host site. It would be tempting to interpret this result as the consequence of a choice aimed at minimising the climatic distance between host and source sites. But it is quite possible that this short climatic distance is only a secondary effect of the choice of a favourable habitat for the translocated species on other criteria. For example, when a plant living on coastal sand dunes is translocated, it is translocated to other coastal habitats, where sand dunes can be found, thus excluding inland, possibly mountainous, areas nearby. For a given geographical distance between them, two coastal sites are generally climatically closer to each other than a coastal site with a mountainous site, and therefore choosing a habitat favourable to the translocated plant on criteria other than the climatic criterion (such as soil texture or plant cover) may correlatively minimise the climatic distance without it having been included in the selection of the location of the sites.

Beyond 50 km, on the other hand, the climatic difference between the source sites and the actually selected host sites was no smaller than if the host sites had been selected at random, using both random selection methods. This result is intriguing, as the choice of habitat remains paramount over long distances. It could be related to the fact that microendemic species in Mediterranean coastal areas, including islands, have not been subject to long-distance translocations (see Figure 1). In regions where such translocations have taken place (Great Britain, northern France, Sweden, Eastern Europe), the landscapes are less heterogeneous and the climatic gradients are probably smoother, which may account for climatic distances that are not very different when host sites are randomly drawn in a buffer zone around the actual host site. However, this explanation is unconvincing when host sites are randomly drawn in any direction around the source site, where the actual host sites may be far away from the random host sites (see Supporting Information Figure S2, Simulation 1). On the whole, the

simulation results finally seem rather inconclusive, and do not allow us to affirm that the practitioners have endeavoured to minimise the climatic difference between the source and host sites.

4.3 | Limits due to translocation practices and data availability

We analysed a sample of translocations in Europe over the last 50 years. This sample is not random, and it might be biased in several ways. Firstly, the documents we relied on (peer-reviewed scientific articles, books, theses, conference papers, presentations, reports, newspaper articles, webpages, etc.) were mostly written in French, Spanish, Italian, and English, which excluded from our sample translocations for which the information we were looking for was only written in other languages. Secondly, many translocations are unknown to us. A number of them were carried out on individual initiatives by botanists, especially before the establishment of legal frameworks for these operations in Europe with the rise of the Natura2000 network. These attempts have generally been kept secret, whether or not they have resulted in persistent populations. Other translocations were carried out before the 2000s in a regulated and legal manner by nature management organisations, but their memory has more or less been lost because the reports concerning them have never been digitised or centralized. Thirdly, some translocations are known but we did not find sufficiently precise geographical information. This was either because people did not consider accurate location information (especially of source populations) to be very important, or to keep confidential the location of emblematic species to avoid too much frequentation or collection (for example the populations of *Cypripedium calceolus* in England or Switzerland, Joint Nature Conservation Committee, 2007; Parc Régional Chasseral, 2011).

Another limitation is that not all of our geographic data was very accurate. When they were not, the central coordinates of the territories we used (e.g. municipal territory, island, buffer around a village) did not necessarily correspond to the exact location of the population and might have distorted the geographical distances and directions calculated between source and host sites. Similarly,

imprecise geographic coordinates may have corresponded to climate pixels in the WorldClim database that were different from the actual climate pixels of the source and host sites. But there is no reason to believe that these inaccuracies biased our results in one direction or another. Finally, because there are no weather stations in every km² in Europe, the values provided for many climate pixels by the WorldClim database might be smoothed in gradients between weather stations, thus erasing local variations due for example to sunlight on slopes (see Scherrer et al., 2011, about the discrepancy between weather station data and temperature variation due to topography). But this phenomenon is probably limited by the fact WorldClim data were obtained from models using not only weather station data but also covariates such as elevation, distance to the coast and satellite-derived data (land surface temperature and cloud cover, Fick & Hijmans 2017).

4.4 | The many dimensions of site selection

A translocation program must deal with many parameters. These parameters depend in part on the objectives of the translocation. Even if the translocations included in our database were all aimed at leading to a viable population, they sometimes contain other objectives such as experimentation (e.g., Sainz-Ollero & Hernández-Bermejo, 1979; Colas et al., 2008; Dalrymple & Broome, 2010), ecological restoration (Kiehl & Pfadenhauer, 2007), or ecosystem service supply (Arnold et al., 2005; Walter, 2005). In addition, the way in which sites are selected varies. Sometimes the source site is determined in advance because it is itself at the origin of the translocation project. This is the case when a natural area containing protected species is degraded for the needs of a human activity and a host site is sought for the implantation of these species so that their conservation status is not unduly altered (e.g., *Cochlearia polonica*, Cieślak et al., 2010). Sometimes, the project comes directly from a desire to reintroduce a taxon to a site from which it has disappeared or to reinforce an existing population. In such cases, one or more sites of origin are searched for and selected (Adamec & Lev, 1999). In other cases, finally, the project, focusing on a taxon whose populations are to be

increased, offers the possibility of selecting both one or more source site(s) and one or more host site(s) from a range of possibilities (Guyonneau & Amiotte-Suchet, 2019).

The selection of source and host sites depends of course on ecological considerations: population size, similarity of habitat, geographical and climatic distances, etc. However, many other aspects, including socio-economic and legal ones, probably guide this selection but were not considered in our analysis. Access to land depends on its ownership and relies on the owner's willingness to sell the land or sign a contract to host the taxon. Other aspects might include its status as protected or not, the probable evolution of its use, and other administrative or legal constraints. Some countries might favor short distance translocation in the implementation of some specific public policies, which might partly explain why a significant number of translocations are implemented at short geographic distance from the source site. This is the case for France and Spain, which have small translocation distances compared to the whole dataset (Supporting information Table S2). For example in France, in the context of the mitigation hierarchy (i.e., avoiding, reducing and, as a last resort, offsetting for damages to biodiversity) that developers are supposed to follow when proposing a new project, translocations were considered as offsetting measures until recently and were thus supposed to follow the corresponding guidelines requiring to keep the measures at a functional proximity from the impacted area (MEDTL, 2012, now Art. L. 163-1 II of the French environmental code). In Spain, another country that provided many entries in the database, the competence on environmental matters have been transferred to sub-national structures (Autonomous Communities in Spain). This organisation forces de facto translocations to take place preferentially within the territories governed by sub-national structures. It is still possible to undertake translocations that involve two sub-national territories, but it is obviously a lot more difficult as they have to be approved and coordinated by the authorities of both entities (see the unpublished Spanish guide for translocations approved by the Comisión Estatal para el Patrimonio Natural y la Biodiversidad in 2013, available at https://www.miteco.gob.es/es/biodiversidad/temas/conservacion-de-especies/doc_directrices_reintroduccion_tcm30-198128.pdf).

The reduction of site availability due to these non-ecological dimensions might lead to a situation where the remaining sites do not allow stakeholders to consider climate change predictions (Fahsel, 2007). Further research based on enquiries among translocation practitioners should deserve considerations to identify the overriding factors for the selection of sites that might explain part of our observations.

5 | CONCLUSIONS

Past translocations have, for the most part, been conducted by skilled practitioners who were committed to finding the most favourable ecological conditions possible to achieve viable populations. Climate change is a factor that must be taken into account in the choice of sites, among other important factors such as soil texture, pH and moisture, competition with other plant species, predation, human frequentation, land ownership, management method, administrative, legal and economic constraints, etc. The considerations are therefore often very complex. Although past translocations have been to slightly cooler sites, climate change does not appear to have been a major consideration. We are now in a time of rapid anthropogenic climate change, and it is likely that this factor will need to be taken into account to a much greater extent over the next few decades if translocations are to improve the viability of plant populations that generally have limited dispersal ability.

Acknowledgements

This study was financially supported by the Initiative de Recherche Stratégique ACE-ICSEN from Université Paris-Saclay, by the “Partenariats” projects from LabEx BASC, and by a PEPS project from CNRS-INEE. The authors would like to thank the many people who contributed to the data collection.

Author's contributions

MD, SO, JFM, ACV and BC conceived the ideas and designed methodology; MD, AM, AGF, JMI and BC collected the data; SO, MD, and JFM analysed the data; BC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Data availability

The data used in this paper are locations of plant species, many of which are endangered. Some precise locations are publicly available in scientific articles or non-confidential reports. Others were given to us by providing confidential reports or during interviews, and we have no right to make them public. Degraded data (e.g. to the municipality level) of all locations are accessible through the TransLoc website (<http://translocations.in2p3.fr/index.php>). R-scripts used for data analyses are available in Supporting information.

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Supporting information

Additional supporting information may be found online in the Supporting Information section.

