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Population dynamics of the butterfly *Pyrgus armoricanus* after translocation beyond its northern range margin

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Abstract. 1. Translocation experiments can be used to study the factors limiting species' distributions and to infer potential drivers of successful colonisation during range shifts.

2. To study the expansion dynamics of the butterfly *Pyrgus armoricanus* in southern Sweden and to find out whether its distribution was limited by climate, translocation experiments were carried out within and 50–60 km beyond its natural range margin. Populations were monitored for 8 years following the translocation.

3. Although most translocation attempts failed, *P. armoricanus* was able to survive in two sites north of its current range limit. One of them eventually led to expansion and establishment of a viable metapopulation. Translocation success appeared to be independent of latitude, suggesting that climate is not the main factor determining the current northern distribution limits of this butterfly.

4. Population growth and secondary spread in the expanding population were positively related to patch area and connectivity, while local habitat quality seemed to be less important.

5. The successful translocation and the importance of a well-connected patch network suggest that the current distribution of *P. armoricanus* is limited by its low dispersal ability combined with the fragmentation of its habitat, making it unlikely to track its changing climatic niche. Assisted migration could be an effective tool for such species, but long-term evidence for its effectiveness is not yet available.

Key words. assisted migration, butterflies, climate change, dispersal ability, lepidoptera, metapopulation, range shift, temperature, translocation experiment.

Introduction

Climate is generally assumed to be the main factor limiting the latitudinal margins of species' ranges (but see Sexton *et al*., 2009; Lee−Yaw *et al*., 2016). In a context of climate change, although most species will probably suffer from a drastic change of climatic conditions (Urban, 2015), populations at the poleward margins of a species' range are predicted to be favoured by a warmer climate and may expand their distribution as a consequence (Parmesan, 2006; Pateman *et al*., 2012). However, the relative importance of climate and other drivers in shaping range limits and population dynamics at species' range margins remains unclear for most species. While, overall, there is evidence that climate limits the range of many butterfly species (Schweiger *et al*., 2012), other studies have pointed out the crucial importance of local habitat quality and of the reachability of suitable patches (e.g. Fourcade *et al*., 2017).

Host plant distributions have been shown to be an essential driver of butterflies' distributions and responses to climate change (Pelini *et al*., 2009; Romo *et al*., 2014). In addition, land use changes have recently been singled out as the primary factor contributing to the current worldwide decline of insects (Sánchez-Bayo & Wyckhuys, 2019). As only those habitats that are actually reachable can be occupied (Soberón & Nakamura, 2009), species' dispersal ability and habitat connectivity

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are also important factors in their current and future distributions (Thomas *et al*., 2004). The potential dispersing individuals are mostly found in the range margins of the species (Hampe & Petit, 2005), where dispersal distance can be lower than in core populations, as an adaptation to the scarcity of habitat patches which makes dispersal more costly (Dytham, 2009). At the same time, it has been observed that range expansions and shifts due to climate change act as a selective pressure that favours good dispersers (Hill *et al*., 2011). Habitat fragmentation may significantly decrease opportunities for colonisation of patches and, as a consequence, for range shifts (Burrows *et al*., 2014). On a more local scale, patches in a habitat network that have a larger size and a higher connectivity are more likely to be occupied by butterflies (Hanski, 1994). Generally, population dynamics at range margins are driven by a complex interaction of multiple factors at different spatial and temporal scales, e.g. climate and temperature regime, biotic interactions and dispersal opportunities (Soberón, 2007). Disentangling the contribution of these respective effects in shaping species' range limits appears thus necessary to anticipate the effect of global changes.

Translocation experiments can be used to test hypotheses on factors limiting species distribution. By moving individuals beyond the current range margin of the species, and monitoring their fitness and establishment success, we can infer the relative importance of climate, dispersal and biotic interactions in shaping species distributions, and hence predict the species' fate in a changing climate (Marsico & Hellmann, 2009; Pelini *et al*., 2009; Willis *et al*., 2009). Assisted colonisation, i.e. translocation with the aim of establishing populations in regions that the species could not reach by itself, has been proposed as a possible tool to help species colonise new suitable habitats they would have been unable to reach otherwise. Assisted colonisations are heavily debated (Hoegh-Guldberg *et al*., 2008; Richardson *et al*., 2009; Thomas, 2011) but rarely studied empirically (Hewitt *et al*., 2011; but see Mueller & Hellmann, 2008). There is also a lack of clear set goals of translocations and evaluation of their effectiveness (Chauvenet *et al*., 2013). Nonetheless, identifying the factors driving the success or failure of translocations can be a valuable way to gain insights into the limiting factors of species ranges, especially when individuals are relocated beyond their natural range margins.

Here, we report on a translocation of Oberthür's grizzled skipper butterfly *Pyrgus armoricanus* (Oberthür, 1910) north of its current range margin, albeit not as a conservation measure, but solely for experimental purposes. Modelling suggests that if climate were the only factor driving the distribution of the species, the climatic niche of the species would strongly shift to the north in the future as a result of climate change (Fourcade *et al*., 2017). This, in turn, would make *P. armoricanus* a species of high conservation concern if the butterfly would be found unable to track its climatic niche accordingly (Settele *et al*., 2008). Observations from the northern range margin in Germany suggest that the species has expanded its range drastically in parts of Germany (Bolz, 2006) and seemed to have profited notably from the hot summers of 2003 (Ulrich, 2005) and 2018 (Kettermann et al., 2020). However, we previously found that the local abundance, distribution and colonisation-extinction dynamics of *P. armoricanus* in Sweden were largely explained by patch isolation and quality in form of host plant density (Fourcade *et al*., 2017; Fourcade & Öckinger, 2017). The observation that colonisation of high-quality habitat patches is inhibited if these are too isolated suggests that *P. armoricanus* might not be able to fill its entire potential climatic niche (Fourcade *et al*., 2017). To gain insight into the limitations of the distribution of *P. armoricanus*, we translocated individuals in 2009 to six previously uninhabited sites about 70 km beyond their northern range margin in southern Sweden, and to six sites within the current range. After a failure of the translocations in all sites but one during the first attempt, three sites were restocked in 2010. Subsequently, we monitored translocation success for 8 years with regard to various patch properties (see Table 1).

Table 1. Different translocation sites, sorted by category (north of the current distribution range or south within the current distribution range) with the number of translocated individuals on the first and second attempt and success of translocation in the year following the respective attempts. Numbers in brackets indicate that in this patch, individuals have been found in subsequent years, but it is unclear whether they were present because of the first translocation or because of an expansion from another site.

Site	Category	Translocated individuals in 2009 (all females)	Established after 2009 translocation	Translocated individuals in 2010 (females + males)	Established after 2010 translocation
Mosslunda	North	4	(Yes)		(Yes)
Skepparslöv	North	2	No		-
Landön	North	4	No		-
Edenryd	North	2	No	5 + 2	Yes
Ugerup	North	4	No	5 + 2	Yes
Tosteberga	North	2	No		-
Stavsten	South	4	No		-
Skarviken	South	2	No	5 + 3	No
Glemmingebro	South	4	No		-
Backåkra	South	2	Yes		-
Beden	South	4	Yes		-
Mellby	South	2	No		-

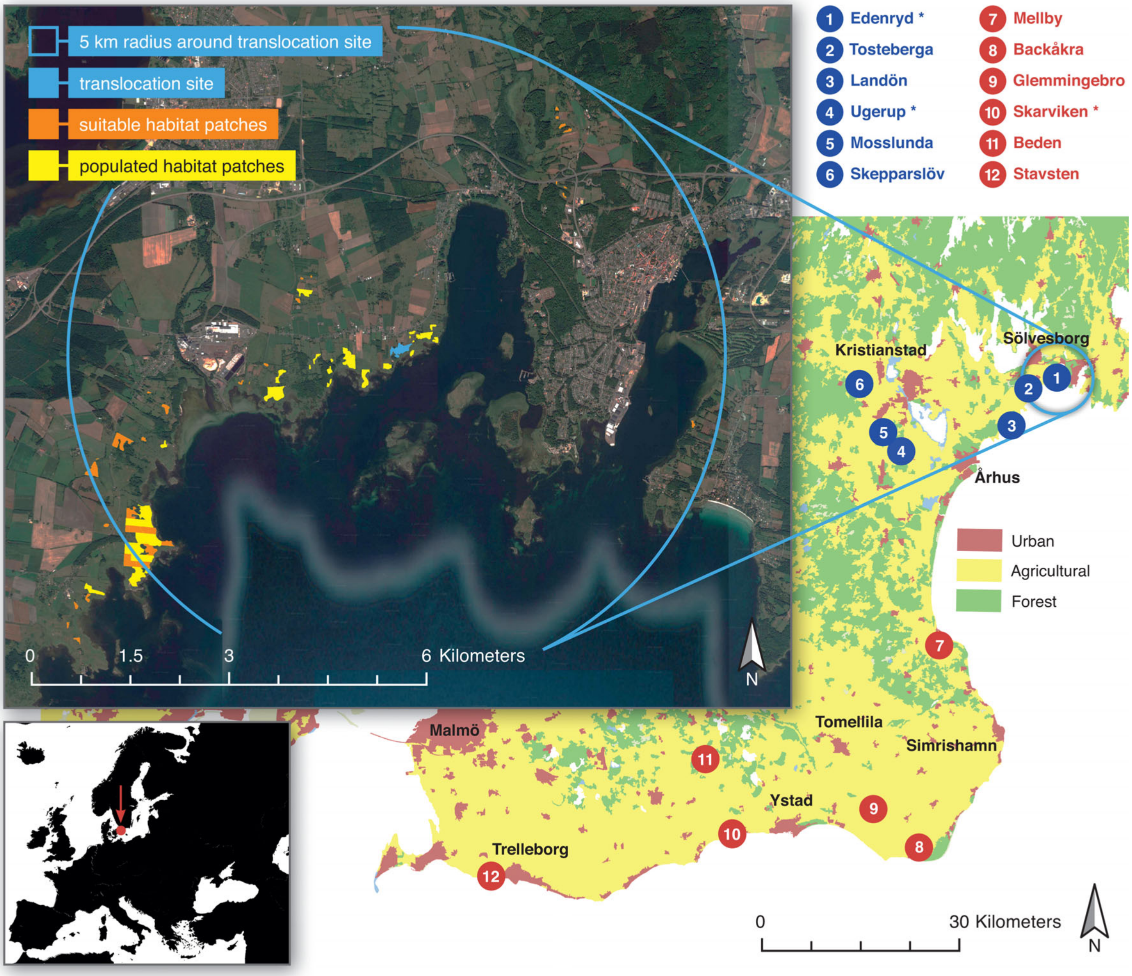

Figure 1. Translocation sites of *P. armoricanus* in southern Sweden. Sites south of its range margin are marked in red, sites north of the margin in blue. An asterisk (*) marks the sites where a second translocation has been carried out. The close-up around Edenryd shows the patch network around the translocation site and the sites the butterfly has spread to since the translocation. The map to the bottom left shows the location of the translocation sites within Europe. [Color figure can be viewed at wileyonlinelibrary.com]

First, we assumed that the long-term establishment of a population in the translocation area would indicate that climate is not the primary limiting factor of the distribution of *P. armoricanus* at its northern range margin. Second, in the case of a successful translocation, we hypothesised that the secondary spread was limited by patch connectivity. Functional connectivity is not only the result of geographical distance but also of barriers to movement and habitat permeability (Baguette *et al.*, 2013). Therefore, we expected a negative correlation between patch occupancy or abundance and the occurrence of barriers to dispersal or intensely managed farmland in the close vicinity of the patch. Finally, given the recognised importance of temperature for butterfly survival and reproduction (Fischer *et al.*, 2003; Crozier, 2004), and the observation that the annual variation in *P. armoricanus* abundance is strongly correlated with temperature during the larval development period (Fourcade *et al.*, 2017), we tested whether the abundance of *P. armoricanus* in the occupied patches could be explained by weather conditions.

Material and methods

Study species

Pyrgus armoricanus is a bivoltine butterfly with occurrences throughout most of central and southern Europe, the northern range limit being in southern Sweden and Denmark (Kudrna *et al.*, 2011). In our study region, *Filipendula vulgaris* and *Helianthemum nummularium* are the most important larval host plants (Eilers *et al.*, 2013), which occur in dry, unimproved calcareous meadows. *P. armoricanus* is relatively sedentary with an average lifetime movement distance of 295 m (maximum = 7447 m) (Fourcade *et al.*, 2017). Due to its small area

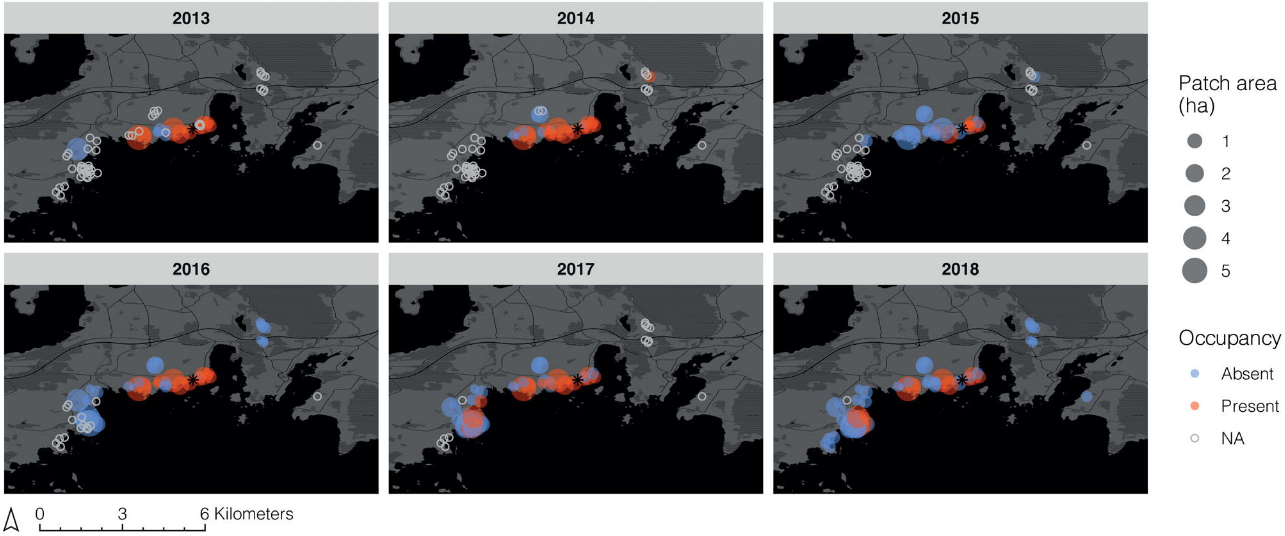

Figure 2. Time series of the spread of *P. armoricanus* to suitable habitat patches around the translocation patch in Edenryd in each year since the start of the monitoring of the expansion in 2013 ($N = 45$). Sites that have been monitored and where *P. armoricanus* has been confirmed or been found absent are shown as well as sites that have not been monitored in the respective year. The translocation site, where *P. armoricanus* has always been present since the translocation event, is marked with a black asterisk (*). Water is displayed in black. [Color figure can be viewed at wileyonlinelibrary.com]

of occurrence and the large variation in abundance between years, *P. armoricanus* is listed as endangered on the red list of Sweden (Artdatabanken, 2015).

First translocation experiment

In order to test whether climate alone determines the northern margin of the distribution of *P. armoricanus*, we carried out a first translocation experiment in 2009. We translocated adult butterfly individuals from existing populations to 12 previously uninhabited sites. Six of these sites were located approximately 50–60 km north of the northernmost known *P. armoricanus* population, and six control sites were located at the same latitude as the existing native populations in southern Sweden (Figure 1). These will be referred to as northern and southern translocation sites, respectively. Butterflies to be translocated were collected from two large, established populations where *P. armoricanus* has been monitored since 2004. We collected young female butterflies, which could be assumed to have been mated but still carried most of their eggs. In order to test for effects of propagule size, we translocated two adult female butterflies to six of the sites (three in the north and three in the south), and four adult female butterflies to rest of the sites (Table 1). We deliberately kept the number of translocated individuals low, both because we wanted to simulate natural colonisation events, and also because *P. armoricanus* is a rare species and most source populations are relatively small, so the number of individuals available for translocation was limited.

We identified potential target sites for the translocation based on (i) their spatial location and (ii) the presence of at least one of the two larval host plants, *F. vulgaris* and *H. nummularium*. The information on the presence of these plants was extracted from a nation-wide inventory of valuable semi-natural grasslands taken from the TUVA database (Jordbruksverket, 2015). In this inventory, *F. vulgaris* and *H. nummularium* were two of the indicator plant species that should be recorded if present in a certain grassland. We selected the final set of translocation sites based on their habitat quality for *P. armoricanus*, which we assessed in the field as having (i) a high abundance of at least one of the host plants, and (ii) management in the form of grazing. These factors were previously identified as key aspects of *P. armoricanus* habitat quality (Fourcade & Öckinger, 2017). *Pyrgus armoricanus* is not legally protected in Sweden. Nevertheless, we contacted the Swedish Environment Protection Agency (Naturvårdsverket) to make sure no special permits were required, and informed the County Administration (Länsstyrelsen) in Skåne as well as the Swedish Species Information Centre (Artdatabanken) about the project and the location of the translocation patches.

Second translocation experiment

After 1 year (i.e. in 2010), it appeared that most of the translocations had failed. Therefore, we attempted a second translocation in August 2010, with fewer sites but a higher number of individuals per site. Adult female and male butterflies were collected from the same sites as in the first experiment. We translocated five females and two to three males each to three sites of high habitat quality (high host plant abundance, high abundance of floral resources, large habitat area), two in the north and an additional one in the south (Table 1; Fig. 1).

Habitat quality in the translocation sites

We assessed the habitat quality in the translocation sites by estimating the cover of the two host plants (*F. vulgaris*, *H.*

Table 2. Habitat quality variables in the native occupied patches and the translocation sites (including mean, median, minimum and maximum values).

	Native occupied patches				All translocation sites			
	Mean	Med.	Min.	Max.	Mean	Med.	Min.	Max.
Vegetation height (cm)	8.6	8.1	5	16.3	14.7	13.1	3.8	42.4
Filipendula density (%)	51	3.4	0.05	33.4	1.4	0.5	0	6.6
Helianthemum denisty (%)	0.2	0	0	3.5	0.02	0	0	0.2
Bare ground cover (%)	2.3	1.4	0	10.4	4.1	2.7	0.7	10.2

Table 3. Total abundance (N) of *P. armoricanus* in the initial translocation patch in Edenryd monitored from 2011 to 2018 and in all monitored patches in Edenryd and Ugerup including the respective translocation patch from 2013 to 2016. The number of occupied patches and mean temperature (°C) during the flight (May 15 to June 15) and larval (August 1 to May 15) periods of the spring generation are given.

Year	N in Edenryd translocation patch	No. of occupied patches in Edenryd	Total N (in all monitored patches) around Edenryd	Total N in Ugerup	Average temperature (°C) during flight period	Average temperature (°C) during larval period
2011	1		1	1	14.58	4.34
2012	5		5	1	13.08	6.04
2013	24	9	72	11	14.94	4.39
2014	78	17	280	7	14.90	6.83
2015	21	8	46	3	12.50	6.98
2016	60	15	218	2	15.17	6.61
2017	26	18	72	4	14.89	6.43
2018	54	15	92	0	17.03	10.05

nummularium), the cover of bare ground and vegetation height. These variables have previously been found to be good predictors of *P. armoricanus* habitat quality (Christensen, 2000; Eilers *et al*., 2013; Fourcade *et al*., 2017; Fourcade & Öckinger, 2017). We estimated host plant cover and the cover of bare ground in ten 1 × 1 m plots placed along a transect in each site. We measured the vegetation height next to the border of the plot.

Mapping of potential habitats

After 2 years (i.e. in 2012), it became evident that *P. armoricanus* had spread to patches adjacent to some of the translocation patches, and from 2013 onwards we initiated a monitoring programme for these areas. Potential grasslands with *P. armoricanus* habitat were first identified from the TUVA database (Jordbruksverket, 2015) based on the observed presence of the larval host plants *F. vulgaris* or *H. nummularium* followed by field visits to confirm this. In addition, we visited semi-natural grassland sites in the vicinity of the translocation patches that were missing from the database and identified potential suitable habitat patches for *P. armoricanus* by occurrence of *F. vulgaris* or *H. nummularium* occurred in these sites.

If host plants were not present in the entire grassland site, we mapped their distribution and defined discrete habitat patches as either separated from other patches by non-grassland habitat (e.g. forest, arable land), or at least 15 m of grassland habitat without any of the host plants. One exception to this was the Tosteberga nature reserve, where the host plants occurred more or less continuously in an area that would have been too large to define habitat characteristics. Therefore, we here used stone walls as an additional factor delimiting habitat patches. For this reason, we repeated all of our analyses with and without the sites in Tosteberga nature reserve. The results were however very similar in both cases. Here, the results including the sites at Tosteberga are reported.

Vegetation mapping. Within each mapped area, we recorded vegetation characteristics, using the same methods as described under "Habitat quality in the translocation sites" above.

Solar irradiance. Using ArcGIS Version 10.2.1 (ESRI, Redlands, CA, USA), we calculated some additional patch characteristics to the ones recorded manually. We calculated solar irradiance of each patch with the Area Solar Radiation Tool based on the digital elevation model (2 m resolution, vertical accuracy of 0.5 m) of the Swedish Land Survey (Lantmäteriet). We later included mean and SD of solar irradiance per habitat patch in the analysis, since these two factors had been shown to have an effect on the abundance of this butterfly in a previous study (Fourcade & Öckinger, 2017).

Land cover. To analyse the influence of land cover surrounding each patch, we created areas surrounding the respective patch (buffers) with a radius of 100, 250 and 500 m, though only the data from the 100 m buffers were included in the final analysis. This was because the larger buffers had a very large overlap

Table 4. Results of a binomial GLM of the association of five landscape-scale and local habitat factors with occupancy in all patches in a 5 km radius around the translocation patch in Edenryd, ranked by AICc ($N = 45$), with number of visits to each patch included as frequency weights (adj. $R^2 = 0.82$).

Explanatory variable	Estimate	Std. Error	*P* value
Connectivity	0.0702	0.0113	<0.0001***
Log-transformed patch area	0.9766	0.1881	<0.0001***
Percentage of agricultural area in 100 m buffer	−2.5573	1.4444	0.0766
Percentage of barriers in 100 m buffer	0.6109	1.3876	0.6595
Percentage of host plant cover in patch	−0.0525	0.0404	0.1938
Mean solar irradiance	<0.0001	<0.0001	0.2990
Standard deviation of solar irradiance	<0.0001	0.0001	0.3677

Significance is indicated by $P < 0.0001$***.

between patches, and yielded similar results to the 100 m buffer in a preliminary analysis. We used the Svenska Marktäckedata database, which is the Swedish version of the CORINE database and is administrated by the Swedish Environmental Protection Agency, as a source for land cover types. We extracted the area of two land cover categories in the buffers. First, we merged forested areas and water bodies as a 'barrier' category since these two land cover types do not constitute much of the land cover by themselves (no patch was surrounded by more than 30% forest cover in the buffer). Second, we extracted the area of agricultural land because it is the main land use around the translocation patch in Edenryd.

Patch connectivity and distance to translocation site. We measured connectivity of each habitat patch according to the *Si* index of Hanski (1999).

$$S_i = \sum_{j \neq i} e^{-\alpha d_{ij}} N_j$$

where *Si* describes the connectivity of patch *i*, d_{ij} is the Euclidian distance between patches *i* and *j*, N_j the population size of patch *j*, and α a constant describing the decrease in immigration probability from patch *j* with increasing distance. In this case, we used $\alpha = 0.0034$, derived from a previous analysis of mark-recapture data of *P. armoricanus* (Fourcade *et al.*, 2017). In our models, we used the average connectivity across all years for each patch. Since translocation is a special situation where there is just one initial point (i.e. the translocation patch) from which individuals can spread, we also calculated for each patch the distance to the initial translocation patch. Distance tables were calculated with the *R*-packages rgeos and rgdal (Bivand & Rundel, 2018; Bivand *et al.*, 2018).

Temperature. We obtained daily temperature data from the Swedish Meteorological and Hydrological Institute (SMHI) from the weather station in Kristianstad. We extracted for each year the mean temperature during the larval (August 1 of previous year until May 15 of current year) and adult periods (May 15 until June 15). In a preliminary analysis we tested for any correlations with precipitation, but since this did not explain any of the observed patterns in abundance or patch occupancy, we chose to include temperature as the only climatic variable.

Butterfly monitoring

Pyrgus armoricanus occurrence and abundance was monitored in the translocation sites from 2010 to 2018 and in suitable habitat patches in the surrounding landscape in Edenryd and Ugerup from 2013 to 2018. As it became apparent that the butterfly expanded further away from the translocation patch, more patches were gradually added to the monitoring. In 2010 and 2011, translocation sites were monitored in both June and August, i.e. during the flight periods of both generations of this bivoltine species. To assess secondary spread, we monitored habitat patches in the landscape surrounding the Edenryd translocation site annually between mid-May and mid-June, corresponding to the flight period of the spring generation. The two generations differ systematically in abundance (with lower abundance in the spring generation) and are thus difficult to compare directly, but the abundance of both generations seems to respond to the same environmental factors (Christensen, 2000; Fourcade & Öckinger, 2017). The monitoring process consisted of first actively searching for any *P. armoricanus* individuals in each monitored patch to establish their presence or absence. In patches where *P. armoricanus* was observed, the observer thereafter walked slowly through the patch in transects with approximately 5 m distance in between, thus covering the whole patch area, and documenting all sightings of *P. armoricanus* in order to estimate abundance.

Analyses

Habitat quality in the translocation sites. To evaluate whether translocation sites were of similar quality as sites where *P. armoricanus* has been observed to persist within its native distribution, we compared the habitat quality (vegetation height, cover of the two host plant species and cover of bare ground) between the 12 translocation sites and occupied habitat patches in the native distribution of the species, where presence/absence of *P. armoricanus* had been monitored in 50 habitat patches from 2004 to 2017 (Fourcade *et al.*, 2017; Fourcade & Öckinger, 2017). Habitat quality was recorded in these patches in 2010, using the same methods as described above for the translocation sites. We compared the median values of the four habitat quality variables between all translocation sites and native

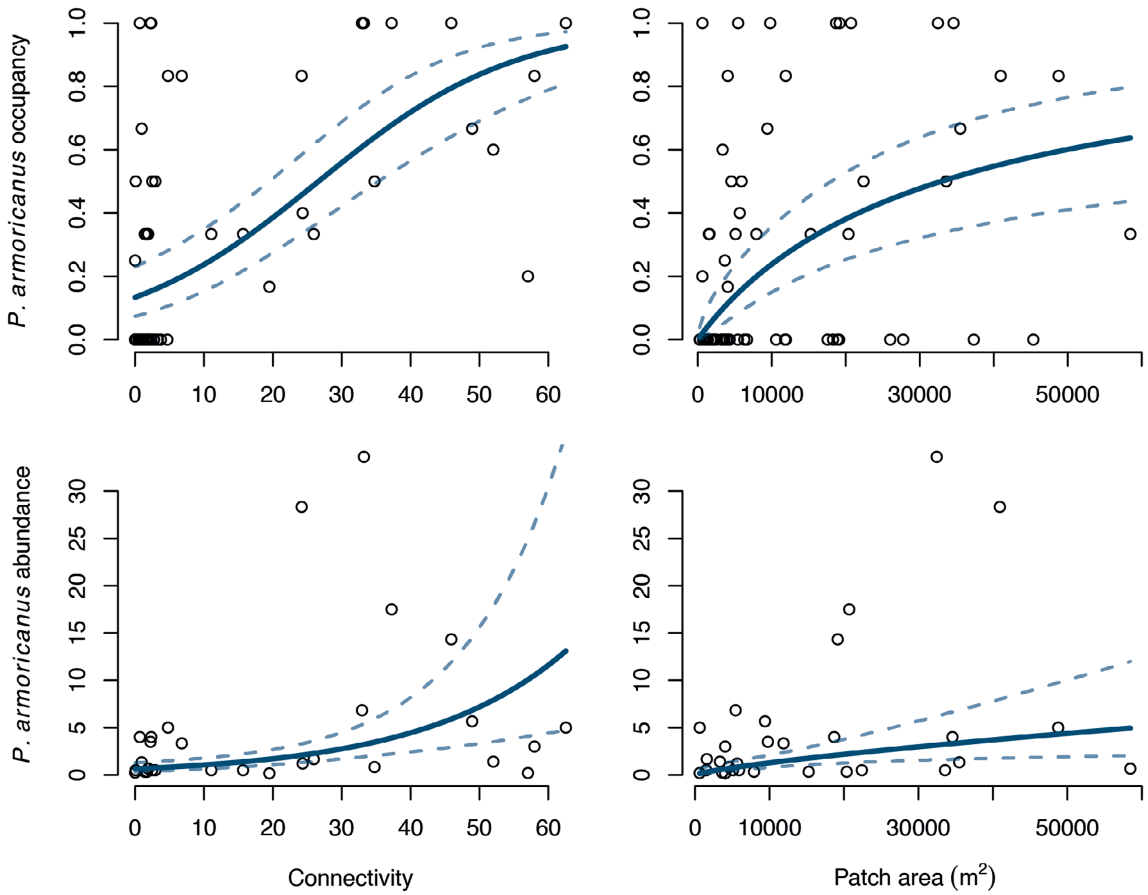

Figure 3. Relationship between *P. armoricanus* occupancy ($N = 45$) as well as mean abundance in occupied sites ($N = 29$) and connectivity (left) as well as patch area (right). The solid and dashed lines show the mean model predictions and 95% confidence intervals, respectively, when all other variables are kept at their median value. [Color figure can be viewed at wileyonlinelibrary.com]

Table 5. Results of two models describing the abundance of *P. armoricanus* in all patches in Edenryd. (1) Linear regression model of three landscape-scale and local habitat factors with averaged and log-transformed *P. armoricanus* abundance in all patches in Edenryd that were populated in at least 1 year between 2013 and 2018 ($N = 29$). (2) Generalised linear mixed model of the association of mean temperature during the flight and larval periods, occupancy of the respective patch in the previous year and time since the translocation event (quadratic effect) with the annual abundance of *P. armoricanus*.

Explanatory variable	Estimate	Std. Error	P Value
(1) Effects of landscape-scale and local habitat factors on mean abundance (adj. $R^2 = 0.58$).			
Connectivity	0.0479	0.0108	0.0002***
Log-transformed patch area	0.7643	0.2196	0.0020**
Percentage of host plant cover in patch	−0.0929	0.0404	0.0310*
Percentage of agricultural area in 100 m buffer	2.4529	1.5480	0.1268
Average vegetation height	0.0224	0.0517	0.6687
Mean solar irradiance	<−0.0001	<−0.0001	0.1863
(2) Effects of temperature and time since translocation on annual abundance			
Mean flight temperature	0.7101	0.0535	<0.0001***
Mean larval temperature	0.2621	0.0716	0.0003**
Time since translocation	1.5108	0.1797	<0.0001***
Time since translocation^2	−0.2061	0.0204	<0.0001***
Occupancy in previous year	0.0656	0.1096	0.5496

Significance is indicated by $P < 0.05$*, $P < 0.01$**, $P < 0.0001$ ***.

patches that had been occupied in more than 50% of the years from 2004 and 2017 using Mann–Whitney U-tests. Since only 2 out of 12 translocations in the first translocation experiment were successful, it was not possible to compare habitat quality in the successful vs. the unsuccessful translocation sites statistically. Instead, the differences were simply described in terms of mean values. In addition, we also tested whether temperatures differed between the two translocation attempts (2009 vs. 2010) because we hypothesised that it could be an important factor of establishment success. For this purpose, we extracted temperatures – using the Kristianstad weather station described above, close to the only translocation site that has seen population expansion – during the adult period of the translocation years and during the following larval period. We compared values in 2009 and in 2010 using Mann–Whitney tests to test differences in medians, and Fligner-Killeen tests to test differences in variances.

Secondary spread. The translocation patch in Edenryd was occupied by *P. armoricanus* in every year since the translocation event. In addition, the newly established population has also expanded to neighbouring patches (Fig. 2). The questions addressed in the analysis were aimed at discovering factors associated with the expansion dynamics. Prior to analyses, we checked for correlation between all explanatory variables with a correlation matrix as well as with the variance inflation factor (vif) from the HH package (Heiberger, 2018). We found no correlation above 29% for the explanatory factors in the matrix, and variance inflation factors were below 1.23. All statistical analyses were performed using R (Version 3.1.1). Model diagnostics in the form of residual plots were performed using the DHARMa R package (Hartig, 2019) that creates scaled residuals from a simulation-based approach for easier interpretation. In all models described below, residual plots showed no deviations from assumptions. Where appropriate, we also performed tests of overdispersion and zero-inflation using functions from the same package.

Occupancy of patches. We investigated whether the probability for a patch to be occupied by *P. armoricanus* during the time after the translocation was related to any local habitat characteristics and landscape factors. To conduct the analysis, all suitable patches with a 5 km radius around the translocation site of Edenryd were taken into account. We considered variables that had proved important for occupancy and abundance in previous studies of *P. armoricanus* and other butterfly species at their northern species range margins (Öckinger *et al*., 2012; Eilers *et al*., 2013; Kuussaari *et al*., 2015; Fourcade & Öckinger, 2017). This resulted in three landscape-scale factors (area of barriers and agricultural land within a 100 m buffer and mean patch connectivity across all years), and six local habitat factors (average vegetation height, average percentage of host plant cover, average cover of bare ground, patch area, mean solar irradiance, SD of solar irradiance). We used binomial generalised linear models (GLMs) with occupancy as response variable and all possible combinations of local habitat and landscape variables as explanatory variables. Occupancy was modelled as the ratio of the number of times a patch had been occupied out of the number of years it had been surveyed, with the latter included as frequency weights in the model to meet the assumptions of a binomial regression. The resulting models were ranked by Akaike's Information Criterion corrected for small sample sizes (AICc) using the dredge function from the MuMIn package (Barton, 2018). The explanatory variables found in all models with ΔAICc <2 were retained and we interpreted results based on a reduced model containing these remaining variables. Since we did not detect strong evidence of overdispersion in the model (observed-to-simulated residuals ratio = 1.20; $P = 0.12$), we did not attempt to account for it.

Abundance in occupied patches. We further investigated whether the mean abundance in the patches that were occupied in at least 1 year, was related to the same landscape-scale and local habitat factors as above. The model selection was similar as for patch occupancy. Abundance data were log-transformed prior to analyses to meet the assumption of normality of a linear model.

Effect of temperature on population dynamics. The temporal variation in the abundance of *P. armoricanus* has been found be strongly related to temperature in a given year (Fourcade *et al*., 2017). To test how this factor influenced population growth after translocation, we analysed the relationship between annual temperature and the abundance in each patch and each year using a GLM effects model with a Poisson distribution and a log link. To account for the fact that a few patches were not monitored every year, we excluded patches that were only monitored in 1 year ($N = 7$) or had a monitoring break of more than 1 year in between recordings ($N = 1$) and assumed that the abundance in a certain patch was always 0 in the year before this patch was monitored for the first time. For a few patches that were monitored in 2016 and 2018 but not in 2017 and had 0 abundance in 2016 and 2018, we assumed that the abundance was 0 also in 2017 ($N = 7$). Our results were robust to uncertainties in these assumptions, since model coefficients remained highly similar if we assumed that non-surveyed patches, including before the first year of monitoring, were occupied with abundance = 1 (Supporting information, Fig. S1). Temperature during the larval period, temperature during flight period and occupancy of each patch in the respective previous year were included as explanatory variables, and patch identity as random intercept. Since we were also interested in testing how abundance changed with time, we added time since the second translocation event as an explanatory variable. However, since we had no *a priori* reason to assume that abundance would increase linearly, we compared a linear effect of time since translocation, a quadratic effect, and a spline smooth in a generalised additive mixed model (GAMM). Since there was evidence, based on their AICc, that the best fit was provided by the quadratic model (ΔAICc with the GAMM model = 12.42, ΔAICc with the linear model = 131.22), we retained the quadratic effect of time, modelled by the inclusion in the model of both the time since translocation and its squared value. We found no evidence that this model was affected by overdispersion (observed-to-simulated residuals ratio = 1.25; $P = 0.42$) or zero-inflation (observed-to-simulated residuals ratio = 1.11; $P = 0.57$). In this analysis, we considered *P. armoricanus* abundance recorded not only in the colonised patches monitored from 2013 but also in the original translocation site that was monitored from as early as 2011. The model was fitted using the lme4 (Bates *et al.*, 2015) and lmerTest (Kuznetsova *et al.*, 2017) R packages.

Results

Habitat quality of translocation sites

Translocation sites had on average slightly lower density of the host plant *F. vulgaris* (Mann–Whitney U-test: $Z = 2.6$, $P = 0.01$) and taller vegetation ($Z = 2.3$, $P = 0.03$) compared to occupied sites in the native distribution, but there were no statistically significant differences in the density of *H. nummularium* ($Z = 1.2$, $P = 0.21$) or in the cover of bare ground ($Z = 1.6$, $P = 0.11$; Table 2).

Establishment of the translocated populations

After re-visiting the translocation sites in June and August 2010, a population appeared to have established in only one of 12 translocation sites (Backåkra, Fig. 1; Table 1). However, in 2013, a few *P. armoricanus* individuals were observed in one additional translocation site where no second translocation had taken place (Beden, Fig. 1; Table 1). This site is situated 12 km from the nearest known *P. armoricanus* population (which is very small), and 14 km from the nearest larger population, while the maximum observed dispersal distance is 7.4 km. Therefore, we assume that this population was established through the translocation but had remained undetected during the following 3 years, rather than through spontaneous colonisation from a native population. The two populations established through the first translocation were, however, short-lived, and no further *P. armoricanus* observations were made in any of the sites after 2011 and 2013, respectively. In 2013, and 2015–2017, *P. armoricanus* individuals were also observed in a third translocation site (Mosslunda, Fig. 1; Table 1). Because this site was located only 4 km from Ugerup, one of the sites where the translocation survived after the 2010 translocation, this is more likely to represent a secondary colonisation than a population that was undetected for 3 years.

One of the two sites where populations had established after the first translocation had received two, and the other site had received four translocated individuals (Table 1). The values of the habitat quality variables in the two successful translocation sites were within the range of values for all other translocation sites. The host plant cover (for both plant species combined) in the two successful translocation sites was 3.2% and < 0.1%, compared to 1.4% (min 0.0%, max. 6.6%) for all other translocation sites. The vegetation height was 16.1 cm and 8.8 cm in the successful translocation sites compared to 15.2 cm (min. 3.8 cm, max. 42.4 cm), and the average cover of bare ground was 1.9% and 10.2% compared to 3.3% (min. 0.7, max. 10.2).

After the second translocation (in 2010), populations established in both of the two northern translocation sites (Edenryd and Ugerup), but not in the southern translocation site (Table 1). There was no significant difference in the median and variance of temperature recorded in the weather station close to these sites between 2009 (failed translocation) and 2010 (successful translocation), either during the adult period (Mann–Whitney: $P = 0.63$, Fligner-Killeen: $P = 0.40$) or the following larval period (Mann–Whitney: $P = 0.69$, Fligner-Killeen: $P = 0.09$).

Secondary spread

The year following the second translocation, *P. armoricanus* populations had expanded from the translocation site in Edenryd to other habitat patches in the surrounding landscape (Fig. 2; Table 3). The total number of observed individuals and the number of occupied patches increased rapidly until 2014, but after this, the population size appeared to have stabilised, although it fluctuated depending on temperature (see below). All suitable patches closer than about 1200 m to the translocation patch were occupied by *P. armoricanus* 5 years after the translocation (Fig. 2). Up to 2018, a total of 29 patches out of the 45 potential patches within a 5 km radius around the original translocation patch were occupied during at least 1 year (Fig. 1; Table 4), with a mean of 13 patches occupied per year. In the final model, we found that occupancy was strongly positively related to both average connectivity and to patch area (Fig. 3; Table 4).

The abundance of *P. armoricanus* in all patches that were occupied at least once during 4 years of monitoring was also strongly positively related to connectivity and log-transformed patch area Fig. 3; Table 5). Surprisingly, *P. armoricanus* abundance was negatively related to host plant cover. However, if one habitat patch with a very high *F. vulgaris* cover but a very low butterfly abundance was removed from the data set, the relationship, while still visible graphically, was no longer statistically significant ($P = 0.08$).

Butterfly abundance was positively related to the temperature during both the adult and larval periods (Table 5). In particular, there was a strong association between abundance and increasing temperature during the adult period (Supporting Information Fig. S2). There was a quadratic relationship between the time since the translocation and abundance. Specifically, abundance increased rapidly after the translocation, then started to decrease after ca. 2015 (Supporting Information Fig. S2). There was no relationship between the occupancy of a patch in the previous year and abundance in the respective patch (Table 5).

Discussion

By translocating *P. armoricanus* individuals beyond its northern range margin, it was possible to establish new populations that have persisted for 8 years so far. This suggests that habitat availability and dispersal capacity, rather than climatic conditions, were limiting the regional distribution of *P. armoricanus* at the northern margin of its global distribution. This conclusion is supported by the observed secondary expansion from both of the translocated populations, where the spatial distribution of the butterfly's habitat was correlated with both patch occupancy and abundance. All patches situated within a 1200 m distance from the translocation patch in Edenryd were colonised at some point during the first 5 years after the translocation. The species was later, in 2017, able to reach a nature reserve with great habitat opportunities about 5 km from Edenryd translocation site, after having established a viable metapopulation around the translocation site. During the expansion, patch occupancy and local abundance were related to both patch area and distance to the translocation patch. Some patches were occupied continuously after they had first been colonised, while in other patches *P. armoricanus* went extinct again after colonisation. This conforms well to the occupancy patterns observed in the native distribution of this butterfly, where colonisation-extinction dynamics are frequent, and connectivity to adjacent habitat patches is one of the most important factors explaining patch occupancy (Fourcade *et al.*, 2017; Fourcade & Öckinger, 2017), as is characteristic for a metapopulation (Hanski, 1994). Moreover, observed dispersal from a mark-recapture study revealed an average movement distance of 295 m, with only very rare occurrences of movements up to 7.4 km (Fourcade *et al.*, 2017). This suggests that, although colonisation at relatively long distance might occasionally occur, such events may be too rare to allow the establishment of viable populations far away from the translocation site within only a few years.

As expected, larger habitat patches were more likely to be occupied and had higher average abundance. Since habitat patches were defined based on the host plant occurrence, larger patches did on average contain higher abundance of host plants, even though the density of host plants did not explain patch occupancy. After removal of one outlier, we found a statistically non-significant, yet still visible negative relationship between host plant cover and *P. armoricanus* abundance ($P = 0.08$). While this is surprising at first sight, it is worth considering that not all individual plants of the two species considered are equally suitable as larval hosts. For oviposition, females prefer *F. vulgaris* plants that are surrounded by low vegetation (Eilers *et al.*, 2013). This could mean that if the vegetation is particularly tall and dense, only a small fraction of the host plants in a patch might actually be suitable.

Population dynamics in the colonised habitat patches was characterised by rapid population growth after establishment. Apparently, the carrying capacity was reached after the first few years and after this, the population sizes tended to oscillate around that level or even to decrease. Interestingly, neither the overall abundance nor the number of occupied patches increased after 2014 even though the population expanded spatially. This is because the colonisation of new patches at the periphery of the distribution was balanced against local extinctions of previously occupied patches, closer to the Edenryd translocation site, as expected from metapopulation dynamics (Hanski, 1999). This balance between extinctions of populations that have already reached their carrying capacity and establishment of new local populations that initially were small can also partly explain why we observed a decrease of abundance in the occupied sites after 2015.

Following the initial phase of population growth, population dynamics is mainly correlated with temperature, as was also observed in the native range of this species (Fourcade *et al.*, 2017). This can probably be attributed to a higher winter survival rate of the larvae, a typical pattern in ectotherm species like butterflies (Crozier, 2004). However, since the exact time of the larval diapause is unknown, it is also possible that temperature affects larval growth instead of winter survival. Butterfly abundance was also positively correlated with temperature during the adult period. This might be due to a lower detection probability when temperature is below the threshold that allows individuals to fly. However, it is noteworthy that a time series of only 8 years of data is available from this experiment, and that this pattern is largely explainable by the exceptionally cold spring of 2015 (on average 2°C colder than other years), which may have affected adult survival as well.

In the first translocation, the attempt to establish persistent populations in any of 12 translocation sites was not successful. One possible explanation is that the translocation sites were not of high enough quality, but this is contradicted by the fact that we could later establish viable populations in two of these sites. Instead, a more likely explanation is that the number of translocated individuals was too low. Accordingly, the second translocation attempt was successful in establishing populations in two of the translocation sites, even though temperatures, which are associated with *P. armoricanus* population fluctuations (Fourcade *et al.*, 2017), were not statistically different between these years. These findings are in accordance with two translocation attempts of the clouded Apollo butterfly *Parnassius mnemosyne* in Finland (Fred & Brommer, 2015; Kuussaari *et al.*, 2015). These studies highlighted (i) that translocation success is rare, sometimes for unknown reasons, and (ii) that the successful establishment of a (meta)population is linked to the presence of the species' host plant in sufficient amount. More generally, a recent study found that the key factor explaining the success or failure of translocations of terrestrial insects was the number of individuals released (Bellis *et al.*, 2019).

We demonstrated that *P. armoricanus* is able to survive and spread in regions north of its current range margin, indicating that its native regional distribution is not limited by climate alone. However, the species has not managed to reach those sites by natural means, due to its limited dispersal ability combined with high habitat fragmentation. It is impossible to exclude the possibility that the species will be able to reach these areas in the future. For example, the species may still be in a process of postglacial recolonisation and may not yet have had time to fill its entire potential niche (Dullinger *et al.*, 2012; Marta et al., 2016). However, there is evidence that the current range limit has not advanced northwards considerably for at least a century (Nordström, 1955), which suggests that the current northern edge is stable over time. Even though our study regions are not near the northern ranges of either of the host plants of *P. armoricanus* (Hultén, 1971), there is a chance that the translocation patches and surrounding patches have only recently become inhabitable due to recent climate change, and that *P. armoricanus* would have reached them eventually. These observations counter traditional expectations of latitudinal range boundaries being defined by climatic factors (Pearson & Dawson, 2003). However, the observations are in accordance with modern niche theory that acknowledges dispersal as a key limiting factor of species distributions (Soberón & Nakamura, 2009; Wilson *et al.*, 2009).

Conservation implications. Calcareous grasslands, the habitat of *P. armoricanus*, are among the richest in Europe in terms of insect species (Polus *et al*., 2007), but their biodiversity is seriously threatened by fragmentation, nitrogen deposition (Stevens *et al*., 2004) and climate change. For many species including *P. armoricanus*, considerable parts of their current distribution will become uninhabitable in the future due to climate change (Settele *et al*., 2008), emphasising the conservation value of maintaining well-connected networks of suitable habitat in northern Europe. Some other butterfly species associated with dry grassland, e.g. *Aricia agestis* and *Hesperia comma*, have managed to profit from warmer conditions in the northern parts of their distribution range (Davies *et al*., 2005; Pateman *et al*., 2012). In contrast to this, *P. armoricanus* appears to be highly constrained by habitat fragmentation, and furthermore most likely unable to shift its range to track its climatic niche. Understanding how *P. armoricanus* and other specialised grassland butterflies are likely to respond to global changes is key to anticipating their conservation in a changing world.

The suitability of assisted migration as a tool for conservation has been the subject of intense discussion (Hoegh-Guldberg *et al*., 2008; Marris, 2008; Richardson *et al*., 2009; Thomas, 2011; Hewitt *et al*., 2011; Hill *et al*., 2011). For some species, however, it might be the only solution since for many species, habitat-based measures such as improving protected area management, establishing corridors, and improving the landscape matrix cannot fully compensate the negative impact of climate-induced range shifts (Wessely *et al*., 2017). Assisted migration should be considered in particular if dispersal ability is low or if the species has a limited ability to persist in unfavourable conditions (Early & Sax, 2011). We found that *P. armoricanus* can indeed be translocated to areas north of its current population range and establish viable populations. Translocation might hence be a potential conservation method for this and other species with similar life histories and habitat requirements in the future. This is, however, conditional upon habitat and landscape conditions, since a network of high-quality habitat patches appears necessary for the long-term survival and expansion of translocated populations.

Compliance with ethical standards

No legal permits were required for the translocation experiment. The translocation of butterflies was reported to the County Administration (Länsstyrelsen) in Skåne as well as the Swedish Species Information Centre (Artdatabanken).

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Conflict of interest

The authors declare that they have no conflict of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Sensitivity analysis of the model describing abundance as a function of time since translocation, mean larval and flight temperature and occupancy in previous year. In blue are shown coefficients (± 95% confidence intervals) of the original model described in the main text, while coefficients in red correspond to a model in which abundance was assumed to be 1 in non-surveyed sites/years.

Figure S2 Modelled relationships between *P. armoricanus* annual abundance per site and the time since translocation (here 2011), the mean temperature during the flying period and the mean temperature during the larval period.

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