Reduced host-plant specialization is associated with the rapid range expansion of a Mediterranean butterfly

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Abstract

Aim: Species ranges are highly dynamic, shifting in space and time as a result of complex ecological and evolutionary processes. Disentangling the relative contribution of both processes is challenging but of primary importance for forecasting species distributions under climate change. Here, we use the spectacular range expansion (ca. 1000 km poleward shift within 10 years) of the butterfly *Pieris mannii* to unravel the factors underlying range dynamics, specifically the role of (i) niche evolution (changes in host-plant preference and acceptance) and (ii) ecological processes (climate change).

Location: Provence-Alpes-Côte d'Azur, France; North Rhine-Westphalia, Rhineland-Palatinate and Hesse, Germany.

Taxon: Insect and angiosperms.

Methods: We employed a combination of (i) common garden experiments, based on replicated populations from the species' historical and newly established range and host-plant species representative for each distribution range, co-occurrence analyses and (ii) grid-based correlative species distribution modelling (SDM) using Maxent.

Results: We observed changes in oviposition preference, with females from the newly established populations showing reduced host-plant specialization and also an overall increased fecundity. These changes in behaviour and life history may have enabled using a broader range of habitats and thus facilitated the recent range expansion. In contrast, our results indicate that the range expansion is unlikely to be directly caused by anthropogenic climate change, as the range was not constrained by climate in the first place.

Main conclusions: We conclude that evolution of a broader dietary niche rather than climate change is associated with the rapid range expansion, and discuss potential indirect consequences of climate change as trigger for the genetic differences found. Our study thus illustrates the importance of species interactions in shaping species distributions and range shifts, and draws attention to indirect effects of climate change. Embracing this complexity is likely the key to a better understanding of range dynamics.

KEYWORDS

biogeography, host-plant preference, insect-plant interaction, niche evolution, niche following, *Pieris mannii*, range dynamics, species distribution modelling
1 | INTRODUCTION

Understanding the factors underlying species range dynamics is a key concern of ecology, evolutionary and conservation biology (Gillson et al., 2013; Hallatschek & Nelson, 2010; Rumpf et al., 2018). Typically, ecological processes have been implied as the principal drivers promoting shifts in species’ distribution and abundance (Caughley et al., 1988; Gallardo et al., 2020). Hence, range shifts are thought to mainly result from “niche following”, that is, species following their abiotic or biotic niche in response to changes in the environment (Guisan et al., 2017; Holt, 2009).

As all species are confined to a specific combination of climatic conditions, abundance and distribution patterns are strongly susceptible to climatic changes (Bennie et al., 2013; Hastings et al., 2020). Consequently, understanding the factors underlying range shifts has gained renewed and increasing interest in the current era of anthropogenic climate change (IPCC, 2014; Pinsky et al., 2020). Indeed, a multitude of studies from various taxa have attributed range contractions, shifts and expansions to current changes in climate (Mason et al., 2015; Parmesan & Yohe, 2003). Additionally, the crucially important role of biotic factors, including for instance food availability, for species range dynamics is becoming increasingly clear (Flores-Tolantino et al., 2020; Godsoe et al., 2017; Matthysen, 2012). The relevance of such factors is especially obvious in phytophagous insects such as butterflies, with their ranges depending strongly on the presence and abundance of specific host plants for larval feeding (Hill et al., 2009; Warren et al., 2001).

Despite widespread niche conservatism (Liu et al., 2020; Peterson, 2011; Wiens et al., 2010) range dynamics do not always result from niche following but alternatively from niche evolution (Pearman et al., 2008; Pfenninger et al., 2007; Stroud, 2021). Rapid genetic changes in range limiting traits such as host-plant use, dispersal ability or propagule pressure may promote range dynamics even in the absence of environmental change (Holt, 2003; Kirkpatrick & Barton, 1997). Evolutionary novelty may, amongst others, arise from hybridization and admixture events (Krehenwinkel et al., 2015; Lewontin & Birch, 1966; Springer & Gompert, 2020). Thus, range dynamics are often characterized by a complex interplay of evolutionary and ecological processes (Bush et al., 2016; Kubisch et al., 2014). While ecological processes have often been found to underlie range shifts, evidence for a crucial role of evolutionary processes is still relatively scarce (Benito Garzón et al., 2019; Hill et al., 2011). Most examples for rapid evolution associated with range shifts relate to dispersal-related morphology (Simmons & Thomas, 2004; Taylor-Cox et al., 2020), but also physiology (Leonard & Lancaster, 2020; Liebl & Martin, 2013), life history (Phillips et al., 2010) and behaviour including resource use (Lancaster, 2020; Singer & Parmesan, 2020; Thomas et al., 2001).

Disentangling the relative contribution of ecological and evolutionary factors though is difficult, especially as feedbacks between both occur frequently (Kubisch et al., 2014; Odling-Smee et al., 2013). Although empirical studies targeting this complexity, by investigating the causes underlying range dynamics at different levels, will greatly improve our abilities to better predict species responses to environmental change, there are still few such examples (Sexton et al., 2009; but e.g. Pfenninger et al., 2007; Turlure et al., 2016). Here, we use the Southern Small White butterfly, *Pieris manni* (Mayer, 1851), as a unique study system to explore ecological and evolutionary factors associated with range dynamics. This species has shown a spectacular range expansion in recent years, having moved poleward by approximately 1000 km within a period of 10 years (Wiemers, 2016). This range expansion is roughly 60 times faster than the global average range expansion rate of 16.9 km per decade (Chen et al., 2011), and thus unparalleled even among butterflies (Parmesan et al., 1999; Pöyry et al., 2009).

The range expansion of *P. manni* may have been caused by changes in climatic variables (niche following), niche evolution, for example, changes in host-plant specialization or life history, or a combination of both ecological and evolutionary factors (Forister et al., 2010; Thomas et al., 2001). Indeed, recent studies on Lepidoptera indicate that reduced host specialization and concomitantly broader dietary niches may play a crucially important role in range expansions (Lancaster, 2020; Singer & Parmesan, 2020) as they may relax species habitat associations (Pateman et al., 2012). Thus, niche evolution may have been an important factor for the rapid range expansion of *P. manni*. Note that concomitant evolutionary change in expanding populations may occur very rapidly, for example, based on (i) hybridization and admixture events (Krehenwinkel et al., 2015; Lewontin & Birch, 1966), (ii) non-random membership of edge demes through spatial sorting (Canestrelli et al., 2016; Chuang & Peterson, 2016) or (iii) strong genetic bases for traits like host-plant preference (Nylin et al., 2005; Thompson, 1988). We thus hypothesize that niche evolution is associated with the rapid range expansion of *P. manni* and predict that edge and core populations differ in dietary niche breadth, including host-plant preference and the degree of specialization (represented by a higher number of host plants accepted and a greater evenness of egg distribution across plant species; Schoonhoven et al., 2014). Alternatively, changes in climatic variables may have enabled the colonization of new areas at higher latitudes, as even very small changes in climatic variables can erase thresholds and thus enable rapid range expansions (Crozier, 2003; Paradis et al., 2008; Rochlin et al., 2013). However, the speed of the northward expansion of *P. manni* suggests that climatic change is not solely responsible. We use a combination of approaches including species distribution modelling to test for the impact of climatic variables, species co-occurrence analyses and common garden experiments based on replicated populations from historical and newly established sites to test for reduced host-plant specialization in the latter.

2 | MATERIALS AND METHODS

2.1 | Study organism

*Pieris manni* (Lepidoptera: Pieridae) is a widespread Mediterranean butterfly species, with a distribution ranging from Morocco across Mediterranean Europe to Turkey and Syria (Kudrna et al., 2011). The
species uses several host plants for larval development, all belonging to the family Brassicaceae (Lafranchis et al., 2015). Adults are nectar feeders, accepting a wide variety of species including the genera Lavendula and Syringa (Settele et al., 2015). Pieris mannii is polyvoltine, having up to five generations a year which tend to overlap (Wiemers, 2016). Diapause takes place in the pupal stage (Settele et al., 2015). Pieris mannii entails several subspecies (Ziegler & Eitschberger, 1999), including P. mannii alpigena (Verity, 1911) which is currently expanding its distribution range northwards (Hensle & Seizmair, 2015). Originating from south-east France, the species has successfully colonized large parts of Germany within a short period of time since 2008 (Figure 1).

**FIGURE 1** Range expansion of *P. mannii* ssp. *alpigena* since 2008 into Germany. Ranges at different time points are presented as alpha hull polygons (Burgman & Fox, 2003), based on point occurrences derived from GBIF.org (01.12.2020; https://doi.org/10.15468/dl.h7huwn), Reinhardt et al. (2020), Wiemers et al. (2020) and data sources outlined in Section 2.2. Black dots represent sampling sites of replicated *Pieris mannii* populations in Germany (G1-3) and southern France (F1-3)
2.2 | Population sampling and offspring rearing

In June and July 2018, we caught fresh, mated females in three replicated populations each in Southeast-France (historical range: F1: Valbonne 43.63°N/7.02°E; F2: Saorge 43.98°N/7.55°E; F3: Roquefort-la-Bédoule 43.26°N/5.65°E) and Germany (new range: G1: Verl 51.87°N/8.52°E; G2: Bad Kreuznach 49.84°N/7.87°E; G3: Habitzheim 49.85°N/8.88°E; Figure 1). The minimum straight distance between populations was 80 km. Females were transferred to climate chambers at Greifswald University for egg laying at 60% relative humidity, 25°C, and a photoperiod of 1L8:D6. These conditions were used throughout all experiments. Females were placed individually into breeding boxes (30 × 20 × 21 cm), being fed with a 20 vol% sugar solution and fresh flowers, which were replaced every other day. Boxes were further equipped with a leaf of greenhouse-grown rape (Brassica napus) as oviposition substrate. Resulting eggs were collected and kept separated by female. F1 offspring was reared individually in translucent plastic boxes (10.5 × 6 cm) equipped with a leaf of greenhouse-grown rape (Brassica napus) as oviposition substrate. Resulting eggs were collected and kept separated by female. F1 offspring was reared individually in translucent plastic boxes (10.5 × 8 × 4.5 cm) lined with moistened filter paper and ad libitum access to cuttings of rape for feeding. These caterpillars were used to perform larval host preference tests (see below). Afterwards, they were reared under the conditions outlined above until adult eclosion. Adult butterflies were mated randomly within populations, but excluding sib matings. To eliminate the potential environmental effects on behaviour, we reared a F2 generation as outlined above, which was used to explore female oviposition preference and host acceptance.

2.3 | Selection and growth of host plants

To compare host-plant preferences between populations from the historical and new range, we chose plant species assumed to be important in each type of range. Although the species uses multiple plant species of the Brassicaceae family across its historic distribution range, the distinct geographic subspecies differ in their host-plant use (Ziegler & Eitschberger, 1999). In Southern France, where the subspecies P. mannii alpigena is located, females are known to mainly use plant species of the genera Diplotaxis and Iberis as host plants (Lafranchis et al., 2015; Still, 2003). On this account, we selected Iberis sempervirens and Diplotaxis tenuifolia as host plants representative for the historical range. For the new range, faunistical observations suggest that the species still uses its historic host plants but additionally integrates new host plants such as Alliaria petiolata, Brassica oleracea and Sinapis arvensis into its diet (Geier, 2016; Hensle & Seizmair, 2020; Pähler, 2016). Based on these observations we here chose the aforementioned plant species, which are also commonly used by the closely related species Pieris rapae and Pieris napi (Tolman & Lewington, 1998), as potentially important hosts for the newly established populations. Note that, to date, even more plant species of the Brassicaceae family have been reported to be used as host plants by P. mannii within the new range (e.g. Lunaria annua and Alyssum murale; Köhler, 2021). Except for A. petiolata, which we collected in the wild (because of its obligatory seed dormancy; Lhotská, 1975), all plants used here were grown from seeds in a greenhouse. Phylogenetically, Diplotaxis tenuifolia, Brassica oleracea and Sinapis arvensis (Brassicaceae tribe) are close related to Alliaria petiolata (Thlaspiidaceae tribe) than to Iberis sempervirens (Iberidaceae tribe) (Al-Shehbaz et al., 2006).

2.4 | Larval host preference

In most Lepidopteran species the adult life stage is considered as the most important for host-plant choice, due to its high mobility (García-Barros & Fartmann, 2009). However, recent studies suggest that the larval life stage may still play an important role, as larvae can adjust or modify the females’ host choice. For example, larvae of the comma butterfly (Polygonia c-album) have been found to participate in host-plant choice by rejecting least favourable host species (Gamberale-Stille et al., 2014) and in experiments with Pieris brassicae, another member of the Pieridae family, larvae were able to adjust host preference in accordance with plant infestation status (with or without aphids), while adult females were not (Soler et al., 2012). The need for larval participation may become especially important when the mothers’ risk to make suboptimal choices is high, for example, through increased levels of stress or a generalist oviposition strategy (García-Barros & Fartmann, 2009 and references therein). To account for the share of the larval life stage in host-plant choice, we here performed a host-plant preference assay using 3rd and 4th instar larvae of P. manni. This way we ensured high mobility, reduced the risk of pupation before the end of the experiment, and minimized biases arising from larvae age (Chew, 1980). For testing, larvae were released individually in the centre of a feeding box (translucent plastic box, 15 × 10 × 6 cm), containing similar-sized leaves of plant species B. oleracea, D. tenuifolia, I. sempervirens and S. arvensis (A. petiolata was not used here), each provided at the same distance from the centre. After one hour, the choice of each larva for one of the plant species was recorded. If a larva was not found on a leaf (32% of the cases) but resting beneath or next to a leaf, typically after having fed on the respective leaf, this was also scored as preference. For every individual, we repeated this procedure on five consecutive days. Leaf cuttings were randomly arranged within boxes. We tested 123 larvae from France (F1: 53, F2: 45, F3: 25) and 118 from Germany (G1: 29, G2: 50, G3: 39).

2.5 | Oviposition preference and host acceptance

After mating, females were transferred individually to translucent boxes (30 × 20 × 21 cm) equipped with sugar solution and fresh flowers for feeding. Each box contained simultaneously one leaf of each of the five host-plant species given above, being placed individually in water-filled glass jars. Eggs were collected and counted daily for the following 10 days. Flowers and leaves were replaced each day, and the positions of leaves within boxes and boxes within the climate chamber were randomized daily to avoid position effects.
We used 75 females from France (F1: 26, F2: 22, F3: 27) and 65 from Germany (G1: 24, G2: 16, G3: 25).

### 2.6 | Co-occurrence analysis

To test whether possible changes in host use may have occurred prior to or during the range expansion, we ran a probabilistic co-occurrence analysis (Veech, 2013) of *P. mannii* and its most important host plants in the new range (*A. petiolata*, *D. tenuifolia* and *I. sempervirens*, based on the results of the oviposition preference experiment), using the R package "cooccur" (Griffith et al., 2016). This analysis allows to identify patterns of species interactions at a spatial scale (Veech, 2013). We here used it to explore changes in the co-occurrence between *P. mannii* and the aforementioned plant species. If the changes in female host-plant preference have occurred during the range expansion, we would expect the co-occurrence probability for *A. petiolata* and *D. tenuifolia* to increase and for *I. sempervirens* to decrease over time. In turn, if the preference changed beforehand, we would expect the co-occurrence probability to remain constant. We therefore compared the probability of *P. mannii* to co-occur with the aforementioned plant species between the early (2008–2013) and late phase (2014–2019) of the range expansion into Germany. We created two species-by-site presence–absence matrices (27 km² resolution) from species point occurrences in Germany, using the R command "lets.presab.points" from the ‘letsR’ package (Vilela & Villalobos, 2015). The matrices contained all available plant data and presence data of *P. mannii* from one of two time windows. The geographic area was restricted to the occurrence of *P. mannii* within the respective time window. Point occurrence data for plant species were obtained from GBIF (www.gbif.org; using the R command ‘bcc’ of the ‘spocc’ package; Chamberlain et al., 2021)).

### 2.7 | Distribution modelling

Grid-based correlative species distribution models, SDMs (Franklin, 2010), were used to predict the potential distribution of *P. mannii* prior to its recent range expansion (i.e. before 1991). For modelling, we compiled two data sets, namely (i) 148 geo-referenced occurrence data for *P. mannii* from its entire range prior to 1991 (www.gbif.org. license doi.org/10.15468/dl.oc2aa; www.ufz.de/lepidiv), and (ii) a subset of the above data set including all 55 records for the subspecies *alpigena*. The latter was used to investigate the potential distribution of the specific subspecies which is currently showing the massive range expansion. We acknowledge that *P. mannii alpigena* may not be a valid subspecies in a taxonomic sense (cf. Braby et al., 2012), which is not relevant in the given context as we simply wanted to generate a data set based on putative source populations. As ecological predictors we used high resolution climate data from the WorldClim 1.4 database (www.worldclim.org) for the period 1960–1990, with a spatial resolution of 30 arc sec (Hijmans et al., 2005). We used 6 of the 19 bioclimatic variables provided by WorldClim, selected via pairwise Pearson correlation analyses to avoid effects of multicollinearity (|r| > 0.7), which is important when projecting SDMs into new space (Dormann et al., 2013). The predictor set included Bio4 (temperature seasonality), Bio6 (minimum temperature of coldest month), Bio7 (temperature annual range), Bio11 (mean temperature of coldest quarter), Bio12 (annual precipitation) and Bio17 (precipitation of driest quarter).

'Maxent 3.4.1' (Elith et al., 2006; Phillips et al., 2006, 2017; Phillips & Dudík, 2008) was used for modelling (https://biodiversityinformatics.amnh.org/open_source/maxent/). It makes predictions on the suitability of a geographic area for a taxon by taking environmental data from geo-referenced species records and random background data (Phillips et al., 2006; Yackulic et al., 2013). Various settings for SDM building allow fine-tuning (Phillips et al., 2006; Phillips & Dudík, 2008), which requires some caution (Elith et al., 2006, 2011; Yackulic et al., 2013). In brief, we ran Maxent in two ways employing different feature types (linear + quadratic; hinge) to calculate response curves of the ecological predictors, here bioclimatic variables. We allowed Maxent to extrapolate response curves beyond the minimum and maximum values determined by the predictor values. Given the high number of species records, we used the subsample approach (100 replicates) with 25% of the records randomly set aside as test data. The background was chosen as a window enclosing all species records and the number of random background points was set to 100,000. All other settings were default (Merow et al., 2013; Phillips et al., 2017; Phillips & Dudík, 2008; Shcheglovitova & Anderson, 2013). As recommended (Elith et al., 2010), we performed a multivariate environmental similarity surface (MESS) analysis. Thereby, we explored if climatic conditions in the projection area (i.e. Germany) markedly varied from those in the area used for model training (i.e. at species presence in southern Europe). If so, the increased variation may cause misleading results (Elith et al., 2010), which was not the case here (Figure S1).

Maxent calculates the Area Under Curve (AUC), referring to the receiver operating characteristic curve, as a measure of predictive accuracy (Phillips et al., 2006). AUC values may range 0 to 1, that is, from no to high predictive ability; values ≥0.91 describe ‘high’, ≥0.71 ‘moderate’, ≥0.5 ‘low’ model accuracy (Swets, 1988). Although criticized (Yackulic et al., 2013), the AUC is a standard measure in ecological applications and considered informative as it mirrors the model’s ability to distinguish between species records and background points (Merow et al., 2013). To account for AUC critics, we also calculated True Skill Statistics (TSS; Allouche et al., 2006).

The Maxent default (complementary log-log) Cloglog output format was used for mapping SDMs in ‘DIVA-GIS 7.5’ (http://www.divagis.org; Hijmans et al., 2001). Cloglog values may range 0 to 1, and we explored four methods to identify limits (thresholds) for discriminating areas that are suitable versus unsuitable to the study (sub)species (Liu et al., 2005): minimum training presence, 10 percentile training presence, maximum training sensitivity plus specificity, and maximum test sensitivity plus specificity (Table 2). For evaluating SDM results, *P. mannii* distribution records in Germany since 1991 were gathered from various online sources (www.ufz.
de/lepidiv/, www.ufz.de/tagfalter-monitoring/, artenfinder.rlp.de, www.wanderfalter.org, org.falterfunde.de).

2.8 Statistical analyses

We tested for differences in the six bioclimatic predictor variables used among historical (before 1991) and new (after 1991) sites with Mann–Whitney-U tests as data were not normally distributed. Larval feeding (number of choices per plant; Poisson distribution with log-link function) and oviposition (egg numbers per plant; negative binomial distribution with log-link function, due to overdispersion of data) preferences were analysed with repeated measures generalized linear mixed models (GLMMs). We included country, host-plant species (repeated measure) and the country by host-plant interaction (all fixed) nested within population and country (for larval preference only as numbers per family were very low for oviposition preference) as random factors. Furthermore, we added population nested within country, and family (i.e. the offspring of an individual female) nested within country and population (for larval preference only as random effects. All families with <3 offspring were excluded from the analyses. To control for variation in testing days (e.g. due to mortality, pupation), we included the number of testing days per individual as covariate. For the oviposition experiment, we additionally calculated the total number of accepted plant species per individual female and the “evenness” (counting the number of eggs per plant as "individuals per species") of egg distribution across plant species. Both measures were analysed using GLMMs with the same random effect structure as outlined above, country as fixed effect (plant species accepted: gamma distribution; evenness: negative binomial distribution with log-link function). Differences among groups were located with the Tukey posthoc test. Best distribution fit of GLMMs was evaluated based on visual inspection. Test statistics for fixed effects and interactions were obtained by ANOVA “type-III” analyses and for random effects by pairwise model comparison via likelihood ratio tests (Bolker et al., 2009). To test for the consistency of female oviposition choice over the testing period, we calculated the repeatability $R$ as the proportion of the total variation that is reproducible among repeated measurements of the same individual (Nakagawa & Schielzeth, 2010). We used data on egg-laying choice on the different plant species (yes or no) from the second to the fifth day of egg-laying, as during this period females laid most eggs (69%). For the repeatability analysis, we used the ‘rpt’ command of the ‘rptR’ package with binary data and plant species as fixed factor, set to non-adjusted in order to calculate “enhanced agreement repeatability” (Stoffel et al., 2017). We ran the analyses separately for French and German females. All data were analysed using R. 3.6.2 with the packages ‘lme4’ to compute generalized mixed models, “car” to perform ANOVA analyses, ‘multcomp’ to perform posthoc tests, and ‘fitdistrplus’ to evaluate model distribution fit. Throughout, all means are given ± 1 SE (Bates et al., 2018; Delignette-Muller & Dutang, 2015; Fox et al., 2007; Hothorn et al., 2021; R Core Team, 2020).

3 RESULTS

3.1 Female oviposition and larval host preference

Daily egg numbers differed significantly among origins (Germany: 7.5 ± 0.5 > France: 6.7 ± 0.4) and host plants (Table 1). Overall, highest daily egg numbers were deposited on I. sempervirens (3.8 ± 0.3) followed by A. petiolata (1.6 ± 0.2), D. tenuifolia (1.1 ± 0.1), B. olerea (0.4 ± 0.01) and finally S. arvensis (0.2 ± 0.02; Figure 2a). However, German and French females showed strikingly different responses to specific host plants, indicated by the significant host plant by country interaction. French females laid significantly more eggs than German ones on host plant I. sempervirens, while it was the other way round on A. petiolata and D. tenuifolia. The pattern of reduced host specialization in German females was confirmed when testing for the total number of host-plant species accepted per female ($\chi^2 = 56.07, p < 0.001$) and the evenness of egg distribution across plant species ($\chi^2 = 65.32, p < 0.001$; Figure 3). Repeatability

| Factor                      | Larval preference | Oviposition preference |
|-----------------------------|-------------------|------------------------|
| Host plant                 | $\chi^2$ | df | $p$ | $\chi^2$ | df | $p$ |
| Country                    | 3 | 6.95 | 0.001 | 4 | 566.19 | 0.001 |
| Host plant * Country       | 3 | 23.12 | 0.001 | 4 | 199.01 | 0.001 |
| Days of observation        | 1 | 66.07 | 0.001 | 1 | 14.66 | 0.001 |
| Population [Country]       | 2 | 2.36 | 0.308 | 2 | 0.24 | 0.885 |
| Family [Country*Population] | 3 | 2.35 | 0.501 | - | - | - |
| Residual deviance          | 659.53, df = 842 | 693.26, df = 685 |

Marginal $R^2$ (marginal coefficient of determination for generalized mixed-effect models, representing the variance explained by fixed effect components; Nakagawa et al. (2017)) for larval preference (host plant: $R^2 = 0.18$, country $R^2 = 0.06$, host plant * country $R^2 = 0.21$) and oviposition preference (host plant: $R^2 = 0.27$, country $R^2 = 0.08$, host plant * country $R^2 = 0.40$). Significant $p$-values are shown in bold.
analyses revealed moderate but significant repeatability within German females ($R = 0.376$, CI $= 0.201–0.603$, $p < 0.001$), and low repeatability within French females ($R = 0.093$, CI $= 0.052–0.141$, $p < 0.001$). Larval feeding preferences also differed significantly among host plants but not by country of origin (Table 1). The most frequently chosen host plant was $I$. *sempervirens* ($44 \pm 2\%$) followed by $B$. *oleracea* ($25 \pm 2\%$), $S$. *arvensis* ($16 \pm 1\%$) and finally $D$. *tenuifolia* ($14 \pm 1\%$). These patterns prevailed in larvae from both origins, except that $D$. *tenuifolia* was more frequently chosen by French than German larvae (significant host plant by country interaction; Figure 2b).

### 3.2 Co-occurrence analysis

In the area occupied by *P. mannii* during the early phase of the range expansion, the highest co-occurrence probability was found with $A$. *petiolata* (40.5%), followed by $D$. *tenuifolia* (30%) and $I$. *sempervirens* (12%). A similar pattern was found for the late phase of the range expansion: $A$. *petiolata* (32.9%), $D$. *tenuifolia* (23.6%), $I$. *sempervirens*
The probability for *P. mannii* to co-occur with all plant species declined from the early to the late phase of the range expansion (Figure 4), likely caused by the larger area (more “sites”) covered in the late time window.

3.3 Distribution modelling

Accuracy of final SDMs was moderate to high (AUC 0.730–0.856; TSS 0.714–0.856). Under all four thresholds (Table 2), the modelled potential distributions, based exclusively on records from before 1991, extended widely into Germany, largely explaining the new records since 1991. This was true at both the species (Figure 5a) as well as subspecies levels (Figure 5b). Potential distribution analyses thus suggest that before 1991 the climate in Germany was already suitable for *P. mannii*. Accordingly, Bio4 (temperature seasonality), Bio6 (minimum temperature of coldest month) and Bio17 (precipitation of driest quarter) did not differ between historical and new range (Mann–Whitney-U tests; Bio4: U = 155610, p = 0.251; Bio6: U = 154062, p = 0.165; Bio17: U = 164278, p = 0.856). However, significant differences were found for variables Bio7 (U = 129280, p < 0.001), Bio11 (U = 148034, p = 0.021) and Bio12 (U = 133216, p < 0.001). Annual temperature range (Bio7: 27.3 ± 0.2 vs. 26.5 ± 0.1°C), mean temperature of the coldest month (Bio11: 2.13 ± 0.25 vs. 1.23 ± 0.08) and annual precipitation (Bio12: 858.4 ± 16.2 vs. 804.3 ± 7.0) were higher at historical than new sites.

4 DISCUSSION

4.1 Female oviposition preference

Females oviposited on all plant species offered in our choice tests, which all belong to the Brassicaceae family to which pierids are strongly linked (Munguira et al., 2009). Oligophagous species such as *P. mannii* often accept hosts closely related to their primary hosts (Scriber & Ording, 2005). Nevertheless, strong preference hierarchies often exist, ensuring that optimal hosts will be preferentially used without completely neglecting alternative ones (Wiklund, 1981). Considering the preference rank order found here, *B. oleracea* and *S. arvensis* were of low attractiveness for both German and French females, indicating a negligible role of those plant species for the range expansion of *P. mannii*. Interestingly, French females showed very little flexibility, evidenced by a strong preference for one of their native host plants, *I. sempervirens*. In contrast, and in line with our hypothesis on niche evolution, German females from the new range were much more flexible, that is, they showed reduced host-plant specialization, readily using *A. petiolata*, *D. tenuifolia* and *I. sempervirens*, generally accepting more plant species and distributing their eggs more evenly across them. These findings challenge the notion that the range expansion of *P. mannii* is related to the occurrence of *I. sempervirens*, commonly planted as garden ornament in central Europe for decades already (Hensle & Seizmair, 2015; Kratochwill, 2011). The reduced specialization of German females likely enables the use of a wider range of habitats in the new range. While *I. sempervirens* is typically found in artificial rock garden sites within settlements, comprising similar habitats to ones originally occupied by *P. mannii*, *A. petiolata* commonly grows at the edges of deciduous forests as well as at disturbed places, while *D. tenuifolia* is part of weedy plant communities (Dennis, 2010; Gupta, 2009; Wannig, 2016).

Our findings thus suggest that reduced host specialization may have enabled the use of a broader range of habitat types, which may in turn have facilitated the recent range expansion (Platts et al., 2019; Wilson et al., 2010). Similarly, the Short-tailed Blue (*Cupido argiades*) seems to have lost its association with specific habitats and host plants over the course of its range expansion (Landdeck et al., 2012). Likewise, the range expansion of the butterfly *Polygonia c-album* was associated with a broadening of its dietary range (Braschler & Hill, 2007; Pratt, 1986). Thus, successful range expansions in Lepidoptera seem to be often associated with increased generalism, in particular with regard to dietary niche breadth (Boy es et al., 2019; Lancaster, 2020; Singer & Parmesan, 2020; Warren et al., 2001; but e.g. Bridle et al., 2014).

Interestingly, German females showed a significantly higher fecundity than French ones. As data are based on F2 generation
offspring, this difference as well as the above outlined difference in oviposition preference must have a genetic basis. The fecundity data suggest a genetically increased reproductive effort in the newly established populations, which may contribute to establishing successfully in the new range (cf. Burton et al., 2010; Wolz et al., 2020). Propagule pressure has been frequently found to be a strong predictor of invasion success (Alzate et al., 2020; Lockwood et al., 2005). However, the increased reproductive effort is counter-intuitive, as range expansions and invasions typically entail an ‘r-selected’ phase (Burton et al., 2010). In any case, the current range expansion of P. mannii is associated with genetically based behavioural and life history differences among populations from the historic and new range.

4.2 Larval feeding preference

In contrast with above, German and French larvae strongly preferred I. sempervirens, while differences among origins were only marginal. Interestingly, results on oviposition and larval feeding preferences were in broad agreement for French individuals, but less so for German ones. Such potential mismatches between adult

| Taxon and modelling feature types | Minimum training presence | 10 percentile training presence | Maximum training sensitivity plus specificity | Maximum test sensitivity plus specificity |
|----------------------------------|---------------------------|--------------------------------|---------------------------------------------|----------------------------------------|
| P. mannii linear + quadratic     | 0.0317                    | 0.4387                         | 0.5651                                      | 0.5391                                 |
| P. mannii hinge                  | 0.1052                    | 0.3798                         | 0.4953                                      | 0.4709                                 |
| P. mannii alpigena linear + quadratic | 0.2119            | 0.3876                         | 0.3756                                      | 0.3804                                 |
| P. mannii alpigena hinge         | 0.2557                    | 0.4342                         | 0.4042                                      | 0.3954                                 |

Cloglog values range from 0 to 1. To assess the value (threshold) within this range, which divides suitable from unsuitable areas for the study (sub) species, various methods are available of which we used four (Liu et al., 2005; see Figure 5).
and immature preferences were frequently observed in butterflies (Chew & Robbins, 1984; Gratton & Welter, 1998), often entailing a broader host range in larvae than in adults (Singer, 1984; Wiklund, 1975). This probably indicates that caterpillars have only a secondary role in host-plant selection, owing to their low mobility (Munguira et al., 2009; but e.g. Gamberale-Stille et al., 2014). Thus, selection on host-plant preferences is expected to be stronger in the mobile females, which are in the first place responsible for finding suitable host plants for offspring development and thereby govern range expansions. However, note that A. petiolata, being most preferred by German females for oviposition, was not tested in larval feeding trials. Furthermore, these results may be affected by maternal effects, such that they need to be interpreted with caution.

Apart from preferences, offspring performance on different host plants has previously been shown to be important. Thus, while the ability to use novel hosts is clearly beneficial for range expansions, it may be detrimental to offspring performance (Scriber & Slansky, 1981; Tabashnik, 1983). Although female preference usually mirrors offspring performance (Garcia-Barros & Fortmann, 2009), as females should be selected for choosing plants that maximize larval fitness (‘mother knows best’ paradigm; Thompson, 1988), this is not always true (Jaenike & Holt, 1991; König et al., 2016; Kuczyn et al., 2021; Mayhew, 2001). While the successful range expansion of P. mannii does not suggest that this is the case here, offspring performance on different host plants should be evidently included in future studies.

### 4.4 Processes underlying the current range expansion of P. mannii

Our results suggest that the spectacular range expansion of P. mannii was not in the first place triggered by niche following in response to ongoing anthropogenic climate change. Instead, it seems to be associated with genetic adaptation in host use, namely the broadening of the host range, and in reproductive effort. In its historic range the species is restricted to xerothermic habitats and associated host plants (Lafranchis et al., 2015; Ziegler & Eitschberger, 1999), while German populations accept a much broader range of host plants, enabling the use of novel habitats such as moist meadows (Hensle, 2016; Hensle & Seizmair, 2015, 2017, 2020; Köhler, 2021; Pähler, 2016). Note that P. mannii did not show any obvious range expansions before 2008 (Friedrich, 2013; Schurian & Siegel, 2016). Changes in habitat and dietary niche breadth have been shown to play an important role for the range expansions in phytophagous insects also in other studies (Braschler & Hill, 2007; Bridle et al., 2014; Lancaster, 2020; Singer & Parmesan, 2020). In our case, substantial population differences must have evolved within a short period of time. However, it remains unclear whether the genetic changes in host-plant use and life history triggered the range expansion or occurred during the course of it (as it has been shown in the Mountain pine beetle; Cullingham et al., 2011). Indeed, recent, large-scale studies on Lepidopteran niche breadth showed that, for species undergoing poleward range expansions, young populations close to the northern edge of their range tend to have a broader niche breadth than “older” ones (Lancaster, 2020; Singer & Parmesan, 2020). Note that the broadening of niche breadth may also emerge as a non-adaptive consequence of range shifts (Lancaster, 2020; Singer & Parmesan, 2020), possibly because of a higher likelihood to include novel hosts with increasing geographic range (Forister & Jenkins, 2017). If this would similarly apply to the range expansion of P. mannii, we would expect temporal and spatial changes in host-plant use during the course of expansion. However, co-occurrence analyses showed no increase in the spatial co-occurrence of P. mannii with A. petiolata and D. tenuifolia over time. While the observed declines across plant species may comprise methodological artefacts, co-occurrence patterns seemed to be rather stable. Note, moreover, that the broader range of hosts used by females from expanding populations was consistent both at the population (indicated by the non-significant effect of population) and the individual level (indicated by the significant repeatability of female host choice).

We therefore speculate that some populations of the subspecies alpigena broadened their host-plant use within the original distribution area prior to the onset of range expansion. This may have different climatic conditions, as indicated by significant differences in some bioclimatic variables. The fact that other P. mannii populations, for example, in the Rhone Valley, northern France or Austria, are currently not expanding (Friedrich, 2013), provides further evidence against climate change as main driver.

### 4.3 Climate change as driver of the range expansion

Species distribution modelling indicated that the climatic conditions in central Europe, including Germany, were already suitable for P. mannii before 1991, as almost all new records outside the historical range are located inside the predicted distribution range based on climatic data before 1991 (Figure 5a). Consequently, climate does not seem to limit the species’ range in the first place. These findings are in sharp contrast with those of Settele et al. (2008), which did not even predict P. mannii to expand into Germany under future climate change scenarios. We suggest that such differences to the aforementioned study relate to larger grid size (i.e. 50 × 50 km UTM vs. 30 arc sec) and a more basic modelling approach (i.e. GLM versus Maxent) strongly affecting model performance (Franklin, 2010).

We obtained very similar results when only using the subspecies alpigena for model building, from which the expanding populations most likely originate (Hensle & Seizmair, 2015; Ziegler & Eitschberger, 1999). The fact that the highest suitability values for alpigena were found for mountain ranges within Germany might be due to a high proportion of records within the Alps and Pyrenees, where it only occurs at lower altitudes though (Ziegler & Eitschberger, 1999). Thus, these high values might be an artefact caused by a low resolution of species records. However, the recent range expansion, having started in 2008, is unlikely to be caused in the first place by climatic factors, even though populations in the new range encounter partly
resulted from genetic modifications, for example, novel mutations, chromosome inversions or admixture between individuals from different source populations. Already Lewontin and Birch (1966) could show for tephritid flies that hybridization caused the emergence of range expanding phenotypes, which may also apply to intraspecific hybridization of genetically differentiated populations. In our case, admixture of the subspecies alpigena and rossii seems plausible, with the latter occurring throughout much of Italy (Ziegler & Eitschberger, 1999). Perhaps, both subspecies came into contact through dispersal events (e.g. in response to extreme heat in the summer of 2007), which has subsequently boosted the range expansion. To confirm this assumption, large-scaled specimen collections of P. mannii across its historic and new distribution range and corresponding genetic analysis (using mitochondrial sequences, nuclear microsatellite and SNP markers; Krehenwinkel & Tautz, 2013) will be needed. An alternative explanation is that moister habitats became thermally suitable and / or xerothermic habitats are too hot and dry for successful larval development in the course of anthropogenic climate change (cf. Davies et al., 2004; Pateman et al., 2012, 2016). Indeed, evolution of host-plant preferences can occur rapidly in butterflies (Buckley & Bridle, 2014; Singer et al., 1993). Thus, potential host shifts within the historic range may have facilitated the subsequent range expansion.

Apart from reduced host specialization, evolutionary changes in other phenotypic traits, such as dispersal-related morphology (Hill et al., 1999) or thermal tolerance (Krehenwinkel & Tautz, 2013) may underlie the current range expansion of P. mannii. Changes in flight morphology though were not apparent among the populations sampled (though a detailed analysis is missing), and changes in thermal tolerance appear to be an unlikely explanation, because climate does not seem to be the limiting factor for the range of P. mannii in the first place. Similarly, unintentional introductions through commercial plant trade appear unlikely, considering the continuous expansion over time rather than a sudden occurrence at specific patches. Evidence suggests that the species expanded its range through the Swiss midlands (Hensle, 2016; Schanowski, 2013). Also note that I. sempervirens and D. tenuifolia were already available in Germany long before the range expansion started. Furthermore, changes in agricultural practices, as have been shown to underlie the rapid host range evolution of Edith’s checkerspot butterfly (Euphydryas editha) populations (Singer et al., 1993), cannot be expected as the driver of P. mannii’s shift in host-plant preference as the newly integrated plant species are rather representatives of uncultivated areas. Thus, although alternative explanations exist, they seem to be rather unlikely as drivers of the current range expansions.

4.5 | Conclusions

We explored the role of climate change as well as changes in host-plant preferences for the range expansion of the butterfly P. mannii. While the recent range expansion is unlikely to be directly caused by anthropogenic changes in climate, we document a broader host-plant use and increased fecundity in expanding populations. We conclude that reduced host specialization was likely the primary trigger of the fast range expansion. Thus, our results provide evidence for a central role of evolutionary shifts in insect–plant interactions during range expansions, and concurrently raise awareness for the high complexity of the causes underlying such phenomena. Though we can largely rule out a direct role of climate change, we assume that it has been involved in the documented host-plant shifts by facilitating hybridization, pointing towards indirect effects of climate change (Godsoe, Holland, et al., 2017). While our study provided some interesting first insights into the complexity of a spectacular range expansion, several issues warrant further investigation. These include (1) population genetic approaches to determine the origin of the range expansion, the degree of genetic differentiation and to test for hybridization among subspecies, (2) investigations of populations from the former distribution edge, and (3) preference-performance experiments scoring offspring fitness. Only if we are able to comprehend the factors promoting or preventing a species’ ability to establish new populations beyond the current range, we will have the fundamental knowledge needed for appropriate actions to protecting biodiversity, especially in the current era of anthropogenic global change (Hoffmann & Sgró, 2011).

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CONFLICT OF INTEREST

The authors declare no competing interests.

DATA AVAILABILITY STATEMENT

Data from this study have been deposited in Dryad Digital Repository: Oviposition, and larval choice data, data points used for species distribution modelling and the supporting information material are stored within the Dryad Data Repository at https://doi.org/10.5061/dryad.b8gth7d5.

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**BIOSKETCH**

Anika Neu is broadly interested in the ecological and evolutionary processes shaping species distribution patterns. This work represents a component of her PhD project that aims at uncovering the role of evolutionary and ecological factors for the recent and rapid range expansion of the Southern Small White butterfly (*Pieris mannii*), focusing on different behavioural and life-history traits. She and the other authors here collaborated to apply a multi-methodological approach, bringing together the expertise for fieldwork and laboratory experiments with Lepidoptera as well as species distribution modelling.

**Author contributions:** A.N. and K.F. conceived of the study. A.N. conducted the field work, analysed the data and performed, together with L.N., the laboratory experiments. S.L. performed the SDM. M.W. contributed to species records. A.N., K.F. and S.L. wrote the manuscript. All authors contributed critically to the drafts and approved the manuscript for publication.

**SUPPORTING INFORMATION**

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

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