

RESEARCH ARTICLE

Earlier flowering of winter oilseed rape compensates for higher pest pressure in warmer climates

Ute Fricke¹  | Sarah Redlich¹  | Jie Zhang¹  | Caryl S. Benjamin²  |
Jana Englmeier³  | Cristina Ganuza¹  | Maria Haensel⁴  | Rebekka Riebl⁴  |
Sandra Rojas-Botero⁵  | Cynthia Tobisch^{5,6}  | Johannes Uhler³  | Lars Uphus² |
Ingolf Steffan-Dewenter¹ 

¹Department of Animal Ecology and Tropical Biology, Julius-Maximilians-University Würzburg, Würzburg, Germany; ²Ecoclimatology, TUM School of Life Sciences, Technical University of Munich, Freising, Germany; ³Field Station Fabriktschleichach, Department of Animal Ecology and Tropical Biology, Julius-Maximilians-University Würzburg, Rauhenebrach, Germany; ⁴Professorship of Ecological Services, Bayreuth Center of Ecology and Environmental Research (BayCEER), University of Bayreuth, Bayreuth, Germany; ⁵Chair of Restoration Ecology, School of Life Sciences, Technical University of Munich, Freising, Germany and ⁶Institute for Ecology and Landscape, Weihenstephan-Triesdorf University of Applied Sciences, Freising, Germany

Correspondence

Ute Fricke

Email: ute.fricke@uni-wuerzburg.de**Funding information**

Bavarian Ministry of Science and the Arts;
JULIUS-MAXIMILIANS-UNIVERSITAET
WURZBURG

Handling Editor: Romina Rader**Abstract**

1. Global warming can increase insect pest pressure by enhancing reproductive rates. Whether this translates into yield losses depends on phenological synchronisation of pests with their host plants and natural enemies. Simultaneously, landscape composition may mitigate climate effects by shaping the resource availability for pests and their antagonists. Here, we study the combined effects of temperature and landscape composition on pest abundances, larval parasitism, crop damage and yield, while also considering crop phenology, to identify strategies for sustainable management of oilseed rape (OSR) pests under warming climates.
2. In all, 29 winter OSR crop fields were investigated in different climates (defined by multi-annual mean temperature, MAT) and landscape contexts in Bavaria, Germany. We measured abundances of adult pollen beetles and stem weevil larvae, pollen beetle larval parasitism, bud loss, stem damage and seed yield, and calculated the flowering date from growth stage observations. Landscape parameters (proportion of non-crop and OSR area, change in OSR area relative to the previous year) were calculated at six spatial scales (0.6–5 km).
3. Pollen beetle abundance increased with MAT but to different degrees depending on the landscape context, that is, increased less strongly when OSR proportions were high (1-km scale), interannually constant (5-km scale) or both. In contrast, stem weevil abundance and stem damage did not respond to landscape composition nor MAT. Pollen beetle larval parasitism was overall low, but

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occasionally exceeded 30% under both low and high MAT and with reduced OSR area (0.6-km scale).

4. Despite high pollen beetle abundance in warm climates, yields were high when OSR flowered early. Thereby, higher temperatures favoured early flowering. Only among late-flowering OSR crop fields yield was higher in cooler than warmer climates. Bud loss responded analogously. Landscape composition did not substantially affect bud loss and yield.
5. *Synthesis and applications*: Earlier flowering of winter OSR compensates for higher pollen beetle abundance in warmer climates, while interannual continuity of OSR area prevents high pollen beetle abundance in the first place. Thus, regional coordination of crop rotation and crop management promoting early flowering may contribute to sustainable pest management in OSR under current and future climatic conditions.

KEYWORDS

canola, climate-smart pest management, crop rotation, global warming, oilseed rape, pollen beetle, seed yield, stem weevil

1 | INTRODUCTION

Global climate change poses a major challenge for crop production (Lehmann et al., 2020; Molotoks et al., 2021; Pullens et al., 2019) and may result in lower yields, as reported for the world's dominant crops (Zhao et al., 2017). Some of the yield loss is indirectly caused by altered biotic interactions resulting from increasing temperatures, that is, changes in herbivory and predation (Lehmann et al., 2020; Vucic-Pestic et al., 2011). In addition, these interactions are also influenced by landscape composition (affects resource availability to insect pests and their antagonists) and its changes in connection with anthropogenic land use, that is, crop cultivation area, non-crop area and crop rotation (Rusch et al., 2011; Schneider et al., 2015; Skellern & Cook, 2018; Zaller et al., 2008b). Yet, too little is known about the combined direct and indirect (i.e. insect-mediated) impacts of temperature and landscape composition on crop production, despite an urgent need for sustainable crop and pest management strategies adapted to future climatic conditions.

Winter oilseed rape (OSR) is among the globally most important oilseed crops for oil production (see Zajac et al., 2016), with the pollen beetle *Brassicoglyphus aeneus* and the stem weevils *Ceutorhynchus napi* and *C. pallidactylus* being among its major pests in Europe (Williams, 2010). Yield losses to adult pollen beetles through bud damage can exceed 80% (see Ahuja et al., 2010). Besides, stem weevil larvae cause damage and yield loss through stem tunnelling (Williams, 2010; Zaller et al., 2008a). An important natural antagonist of the pollen beetle in the larval stage is the parasitoid *Tersilochus heteroceris* (Ulber et al., 2010). Thus, insects, both as pests and natural enemies, and their successful management are important for OSR production.

Higher long-term mean temperatures may exacerbate insect pest pressure in OSR in two ways. First, oviposition rates of pollen

beetles (Ferguson et al., 2014) and stem weevils (Reinhardt, 2014) increase with temperature. Consequently, regions with warmer climate, characterised by higher multi-annual mean temperature (MAT), may face higher pest pressure. Besides, temperature increase may partially release pollen beetles from natural control, for instance if warmer climates cause a phenological mismatch between the pollen beetle and its parasitoid *T. heteroceris*. This could occur, as the migration of both insects depends on different temperatures (Johnen et al., 2010). The resulting consequence of higher pest abundances in warmer climates on crop damage and yield, however, depends on the timing of pest migration (Junk et al., 2015) relative to crop development (Weymann et al., 2015), for example, as pollen beetle immigration is most damaging during bud stage (Seimandi-Corda et al., 2021; Williams, 2010). Thus, date of flowering may serve as proxy for vulnerability to pollen beetle damage and may modulate effects of high adult pollen beetle abundance on crop yield, yet evidence from field studies is lacking.

Landscape composition impacts resource availability to pests (Skellern & Cook, 2018) and pest regulation through natural enemies (Rusch et al., 2011; Thies et al., 2003). For instance, non-crop area enhanced both parasitism of pollen beetle larvae (Rusch et al., 2011; Thies et al., 2003) and adult pollen beetle abundance (Rusch et al., 2013; Zaller et al., 2008b), although neutral effects for pollen beetles were also observed (Skellern et al., 2017). Similarly, neutral (Zaller et al., 2008b) and negative effects (Rusch et al., 2013) of OSR area on pollen beetle abundance indicate context-dependent dilution effects, as also observed in response to changes in OSR area relative to the previous year (Schneider et al., 2015). For stem weevils, non-crop and OSR area had a neutral and negative effect on stem weevil larval abundance, respectively (Zaller et al., 2008b), while effects of interannual change in OSR area have not yet been investigated. Yet, evidence for landscape effects on OSR pests and

antagonists comes from studies focused on scales ≤ 2 km (e.g. Rusch et al., 2011, 2013; Zaller et al., 2008b), despite the ability of adult pollen beetles to disperse over distances up to 13.5 km (see Williams & Cook, 2010). In comparison, adult stem weevils are weak dispersers (see Zaller et al., 2008b). Thus, studying the effects of landscape composition at large spatial scales (>2 km) and of interannual change in OSR area on the abundances of multiple OSR pests improves our understanding of how landscapes affect abundances of OSR pests.

Landscape composition and temperature effects may synergistically influence pest abundance, which could be used in a climate-adaptation strategy utilising landscape management. Thus far, it is known that climate and habitat loss interactively influence biodiversity, for example, higher temperatures amplify biodiversity loss through habitat destruction (Mantyka-Pringle et al., 2012). More generally, effects of temperature and landscape composition may reinforce each other. However, the combined effects of temperature and landscape composition on pest abundances and the consequences for OSR yield are still unknown.

To identify strategies for sustainable and temperature-adapted pest management in winter OSR, we investigated the effects of multi-scale landscape composition (spatial scales 0.6–5 km) on pest abundances, larval parasitism, crop damage and yield along a MAT gradient (1981–2010), while also considering crop phenology. We tested the following predictions:

- (i) Reduced proportions of OSR area relative to the previous year lead to the concentration of OSR pests on OSR crop fields.
- (ii) Spatial scales of landscape-composition effects differ among pest species with different dispersal behaviour.
- (iii) Pest abundances but not larval parasitism rates are higher in regions with warmer climate.
- (iv) Effects of temperature on pest abundances are mitigated in landscapes with a large proportion of non-crop area or interannual continuity in OSR area.
- (v) Landscape and temperature conditions associated with high pollen beetle densities lead to lower bud loss in early compared to late flowering OSR crops.

2 | MATERIALS AND METHODS

2.1 | Study area and site selection

Data were obtained on 29 conventionally managed winter OSR crop fields within the study design of the LandKlif project. The LandKlif study design combined five 'climate zones' (based on MAT between 1981–2010; $<7.5^{\circ}\text{C}$, in 0.5°C steps until 9°C , $>9^{\circ}\text{C}$) and three regional land-use zones (near-natural, agriculture and urban) in four replicates selected from $5.8\text{ km} \times 5.8\text{ km}$ grid cells covering Bavaria, Germany (=60 grid cells; Redlich et al., 2021). In each selected grid cell, three plots were established adjacent to the dominating local habitat types (out of four possible: forest, grassland, arable field, settlement). Plots of the local habitat type 'arable field' were preferably

established in the vicinity to OSR, which are the sites selected for this study (Figure 1). Access to the study sites was granted by land owners or manager. No ethical approval was required for the conduct of this study.

2.2 | OSR growth stage observation and estimated Julian date of flowering

From April to August 2019, we recorded the OSR growth stage (BBCH stage) biweekly, which applied to at least 50% of the crop plants in the field, as described in Meier et al. (2001). Growth stages are indicated by two digits (Meier et al., 2001); the first digit indicates the principle growth stage (e.g. inflorescence emergence, flowering, development of fruit); the second digit refines the growth stage. We visually assessed the relationship of recorded growth stages over Julian dates and then modelled growth stages from inflorescence emergence (growth stage = 50) to crop senescence (growth stage = 97) using a linear mixed model from the R-package NLME (Pinheiro et al., 2020) and included site as random intercept term (see Figure S1 in Supporting Information). Using model slope and site-specific intercept, the Julian date of flowering (growth stage = 60) could be adequately calculated for crops with at least four growth stage records in the modelled period (27 out of 29 sites).

2.3 | OSR sampling at crop flowering and ripening

Oilseed rape was sampled around full flowering (growth stage 64–65; end-April to mid-May) and throughout crop ripening (growth stage 87–89; end-June to mid-August) along two parallel transects starting 1 m from one field edge (not bordering a forest) with $\geq 20\text{ m}$ (in two cases only $\geq 16\text{ m}$) to field edges on either side and $\geq 5\text{ m}$ distance between transects (Figure 1). Entire flowering OSR plants were cut at ground level every 3 m until 28 m into the field (10 samples per transect; total of 20 samples per site). When plant growth at the edge was poor, we started sampling a few metres into the field, for example, distance '1 m' was actually 6 m from field edge and so on. Cut flowering plants were bagged making sure adult pollen beetles that were on the plants were also bagged. Bags were tightly closed to prevent the escape of insect pests. Samples of flowering OSR plants were stored at -20°C until further processing.

Oilseed rape samples throughout crop ripening were taken in the same manner as described above, but sampling only every 6 m (total of 10 samples per site). Mature plants were stored in paper bags at a warm (23°C), dry and well-ventilated place until further processing.

2.4 | Pest abundances, crop damage and larval parasitism at crop flowering

Frozen flowering OSR plants were defrosted. Plants and the inside of bags were scanned for adult pollen beetles, which then were

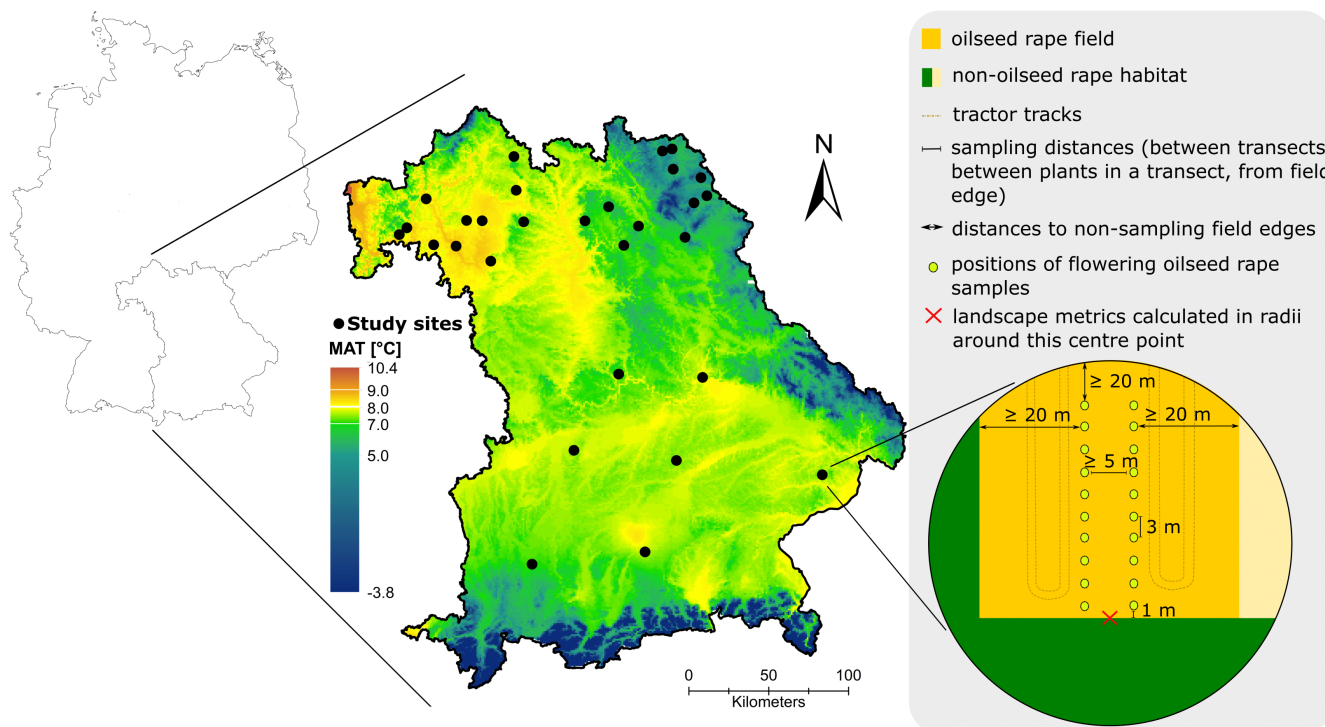


FIGURE 1 Locations of the 29 oilseed rape (OSR) crop fields studied in Bavaria, Germany (left: black dots), in-field sampling positions of OSR plants at flowering (right: yellow dots) and centre point for the calculation of landscape metrics (right: red cross). The climate map provides MATs (1981–2010).

counted (=pollen beetle abundance; 29 sites, 577 plants). To measure bud damage, all organs on the main raceme of flowering OSR were counted, distinguishing between 'lost buds' (stalks without buds or pods and stalks carrying dead buds), broken stalks (stalks with visibly moist tips at the breakage) and all other organs (pods, flowers, flower buds). Broken stalks were caused through transporting and handling of frozen samples so that the associated broken organs were loosely in the bags. However, broken organs could not be assigned to the broken stalks on the main raceme when organs broke all over the plant. Only 'lost buds' (in contrast to broken stalks) indicate reduction of potential yield, for example, due to pollen beetle infestation, stem weevil infestation, and nutrient or pollination deficiency (Jauker et al., 2012; Seimandi-Corda et al., 2021; Zaller et al., 2008a). The proportion of bud damage was calculated as the number of 'lost buds' relative to all organs on the main raceme (incl. broken stalks) per plant to account for differences between plants in the total number of organs. Broken stalks were mainly broken buds, flowers and pods but not exclusively. Thus, increasing proportions of broken stalks increasingly affected the precision of the measure 'proportion bud damage'. Therefore, data were excluded prior to analysis on plants with >5% broken stalks on the main raceme, and sites with values for less than three plants, to assure good data quality. This resulted in data on 321 plants and 25 sites.

For an estimate of pollen beetle larval parasitism, all flowers and flower buds >3mm of OSR plants were opened using tweezers—smaller buds are rarely used for oviposition by the pollen beetle (Hervé et al., 2015). Inside these flowers and buds, the number

of pollen beetle larvae >2mm was counted as potential oviposition resource for the pollen beetle parasitoid *T. heterocerus*, which prefers large over small pollen beetle larvae for oviposition (Ulber et al., 2010). We recorded the presence of black eggs of *T. heterocerus* inside large pollen beetle larvae (yes, no) and calculated the proportion of parasitised large pollen beetle larvae ('parasitism'). To standardise data quality before analysing parasitism data, we excluded plants with less than three large pollen beetle larvae and sites with values from less than three plants, which resulted in data on 207 plants and 20 sites.

To measure stem weevil larval abundance and stem damage, stems equal to or thicker than 5 mm were measured (length in cm) and cut open. Stem weevil larvae in opened stems were counted (=stem weevil abundance; 29 sites, 577 plants). Stem damage by stem weevil larvae was measured as the length of brown-orange-coloured pith (Zaller et al., 2008a), and the proportion of stem damage relative to total stem length was calculated. Before analysing the proportion of stem damage, data were excluded on plants without stem weevil larvae (to prevent zero-inflation due to the absence of stem weevil larvae), and sites with values from less than three plants. This resulted in data on 304 plants and 27 sites.

2.5 | OSR yields at crop ripening

To estimate plant yield, we counted all plant pods as well as the number of seeds in 20 pods, and we also measured seed mass.

Slightly compressing and shaking the ripe and air-dried plants released the majority of seeds. Seeds were manually cleaned from plant parts. In all, 400 seeds were counted per plant using a seed counter, and were dried in a drying oven at 60 °C until constant dry weight (ca. 24 h), and then weighed. Plant seed yield was calculated as the product of the average single seed weight, the average number of seeds per pod and the number of pods per plant (29 sites and 288 plants).

2.6 | Temperature and landscape parameters

We retrieved MAT based on monthly averaged mean daily air temperatures from 1981 to 2010 per site from the related 1 km × 1 km grid cell (Deutscher Wetterdienst, 2020).

Landscape parameters were calculated using ArcGIS Pro v. 2.2.0 (ESRI, 2018) at six radii (0.6 km, 1–5 km in 1-km steps) centred to the position at the field edge that falls in between the two transects used for OSR sampling (see Figure 1). Proportions of non-crop area (non-crop%: summed proportion of forest, permanent managed grassland and semi-natural habitat) were derived from detailed land-cover maps (combined ATKIS 2019, CLC 2018 and IACS 2019; see Appendix S1). Based on IACS data (2018, 2019), we calculated the proportion of OSR (OSR%) in the study year and the change in OSR% relative to the previous year ($\Delta\text{OSR}\%$) for each spatial scale by $(\text{OSR}_{\text{study year}} - \text{OSR}_{\text{previous year}}) / \text{OSR}_{\text{previous year}}$; positive values indicate an increase, while negative values indicate a decrease. When no OSR was cultivated in the previous year at a specific spatial scale, $\Delta\text{OSR}\%$ could not be calculated, which was the case for one site at scales <2 km. Data on this site were excluded before multimodel averaging (see below) to facilitate comparability across spatial scales. Candidate predictor variables are characterised in Table S1.

2.7 | Data analysis

Pest abundances (pollen beetles, stem weevils) on a per plant basis were analysed with negative binomial mixed effect models to cope with count data using the R-package GLMMTMB (Brooks et al., 2017) with R version 4.0.3 (R Core Team, 2020). Site was included as random intercept term to account for the study design. Unless stated differently, 'glmmTMB' and the random term 'site' were also used for all other mixed effect models described below (see also Appendix S2, Table S2, Figures S2–S7). Crop damage (proportion of bud loss and proportion of stem damage) were analysed using a binomial generalised linear mixed effect model to cope with proportions derived from count data and a beta mixed effect model to cope with proportions derived from continuous data, respectively (Douma & Weedon, 2019). In preparation of beta regression, the value 'one' was replaced by a slightly larger value than the largest non-one value (0.99; 2.6% of data). Pollen beetle parasitism was analysed with a binomial generalised linear mixed effect model. Due to an excess of zeros in the parasitism data (59%), a zero-inflation term was

introduced. Plant yield data were analysed with a gamma generalised linear mixed effect model to cope with positive continuous data.

As candidate predictors of pest abundances and parasitism, we considered landscape parameters (non-crop%, OSR% and $\Delta\text{OSR}\%$) at six spatial scales and MAT. Prior to analysis candidate predictors were z-transformed, while untransformed predictor variables were used for model presentation. To evaluate the importance of the predictor variables at various spatial scales, we employed multimodel averaging using the R-package MuMIn (Barton, 2020). Models with all possible predictor combinations at each spatial scale were created separately for pollen beetle abundance, stem weevil abundance and pollen beetle larval parasitism. From there, the sum of Akaike weights ($\sum w_i$, range: 0–low to 1–high) of each spatial scale and of each predictor at every spatial scale was calculated, which indicates the relative importance of a spatial scale (compared to other studied spatial scales) and of a predictor variable (compared to other studied predictors) at a certain spatial scale, respectively (Burnham & Anderson, 2002). To test for multicollinearity, we calculated variance inflation factors (VIFs). Furthermore, Pearson's correlation coefficients were calculated (Table S3) and model fit was assessed using the R-package DHARMA (Hartig, 2020). In the second step, we created a model on pest abundances including interactive effects of MAT and landscape parameters at the specific spatial scales, on which MAT and a specific landscape parameter contributed substantially to the best model. This was the case for pollen beetle abundance at 1-km (MAT, OSR%) and 5-km (MAT, $\Delta\text{OSR}\%$) scale. Relative goodness of fit was calculated based on Akaike's information criterion corrected for small sample size (AICc) using the R-package MuMIn (Barton, 2020). Models with lower AICc value were considered better, models differing by $\Delta\text{AICc} < 2$ were treated as equally good, and the more parsimonious model was selected.

As candidate predictors of crop damage and yield, we considered the same as for pest abundances, but additionally included Julian date of flowering and then proceeded as described above. Pearson's correlation coefficients are presented in Table S4. In the second step, we created models on crop yield including interactive effects of parameters that contributed substantially to the best pest abundance model (1 km: MAT, OSR%; 5 km: MAT, $\Delta\text{OSR}\%$) with Julian date of flowering. In a third step, the best crop yield model (date of flowering, MAT) was extended by site-averaged pest abundances or crop damage as candidate predictors of crop yield. Pest abundances and crop damage were included in separate models due to correlation coefficients ≥ 0.6 (Table S5).

To investigate the impact of MAT on the date of flowering, calculated Julian dates of flowering were also analysed using a linear model with MAT as predictor. Model selection was conducted using $\Delta\text{AICc} < 2$ and parsimony.

3 | RESULTS

Adult pollen beetles and stem weevil larvae were observed at all study sites, except for one with pollen beetles only. We counted

3.8 ± 0.4 (mean \pm se) adult pollen beetles and 4.6 ± 0.4 stem weevil larvae per plant (29 sites, 577 plants). In total, we observed 14.7 ± 1.1 pollen beetle larvae per plant (20 sites, 207 plants), of which on average 1.8 ± 0.3 were parasitised, resulting in relatively low proportions of parasitised pollen beetle larvae per plant ($14.4 \pm 1.6\%$). On three study sites, site-averaged pollen beetle larval parasitism exceeded 30%. On average, $43.5 \pm 1.4\%$ of buds on the main racemes of plants were lost to pollen beetle damage and other causes (25 sites, 321 plants) and $31.4 \pm 1.5\%$ of stem length was damaged on plants with stem weevil larvae (27 sites, 304 plants). OSR plants yielded 22.8 ± 0.9 g seeds (29 sites, 288 plants).

3.1 | Temperature and landscape effects on pest abundances and parasitism

The 1- and 5-km scale were identified as most relevant spatial scales of predictors for adult pollen beetle abundance based on the sum of Akaike weights (Figure 2a,b). Adult pollen beetle abundance per plant increased with increasing MAT. Besides, higher pollen beetle abundance was observed when OSR area was strongly reduced relative to the previous year at the 5-km scale (Figure 2, Table S6). It should be noted that a strong reduction in OSR area in the 5-km radius was accompanied by an equally strong reduction in the 3- and 4-km radius. The proportion of non-crop area did not substantially affect pollen beetle abundance (Table S6). Effects of MAT on pollen beetle abundance were amplified through lower proportions of OSR area and strongly reduced OSR area relative to the previous year (Figure 2e,f). However, interaction terms of landscape variables with MAT were not statistically supported (Table S7). In contrast to pollen beetles, the abundance of stem weevil larvae per plant was not affected by MAT nor any landscape parameter (Table S6, Figure S8).

Pollen beetle larval parasitism was not substantially affected by MAT but was occasionally high (>30%) under both low and high MAT (Figure 3a). The proportion of parasitised pollen beetle larvae increased when OSR area decreased relative to the previous year at 0.6-km scale (Figure 3b). Pollen beetle parasitism did not respond to other landscape predictors (Table S6, Figure S8).

3.2 | Temperature and landscape effects on crop phenology, damage and yield

OSR flowered on average 4.4 days earlier per degree Celsius higher MAT (Figure 4a, Table S6). However, variation in date of flowering was large, particularly among crop fields in warm compared to cool climates (19 vs 11 days between earliest and latest flowering crop field). Earlier flowering was associated with reduced bud loss, particularly in warm climates (Figure 4b, Table S6). In warm climates, late flowering was frequently associated with high bud loss, but not so in cooler climates, where bud loss was generally rather low (Figure 4b). In analogy, crop yield increased with earlier flowering of

OSR (Figure 4d and Figure S8, Table S6). Late flowering was associated with lower yields in warmer than cooler climates (Figure 4d). MAT alone did not explain crop yield (Figure 4c). When accounting for the combined effects of MAT and Julian date of flowering, OSR% and Δ OSR% did not add substantial explanation to bud loss nor crop yield (Table S6, Figure S9). Interaction terms of MAT or landscape composition with Julian date of flowering did also not substantially improve crop yield models (Table S8). In the next step, we analysed the direct effects of pollen beetle abundance and bud loss on yield variation. Higher mean abundance of adult pollen beetles and higher mean proportion of bud loss per plant were also related to lower crop yield, yet the combined effect of MAT and date of flowering still explained more variation in crop yield (Table S9, Figure S9).

Stem damage increased with Julian date of flowering (Figures S8 and S10), yet mean stem weevil larval abundance and mean stem damage did not affect crop yield (Table S9, Figure S9).

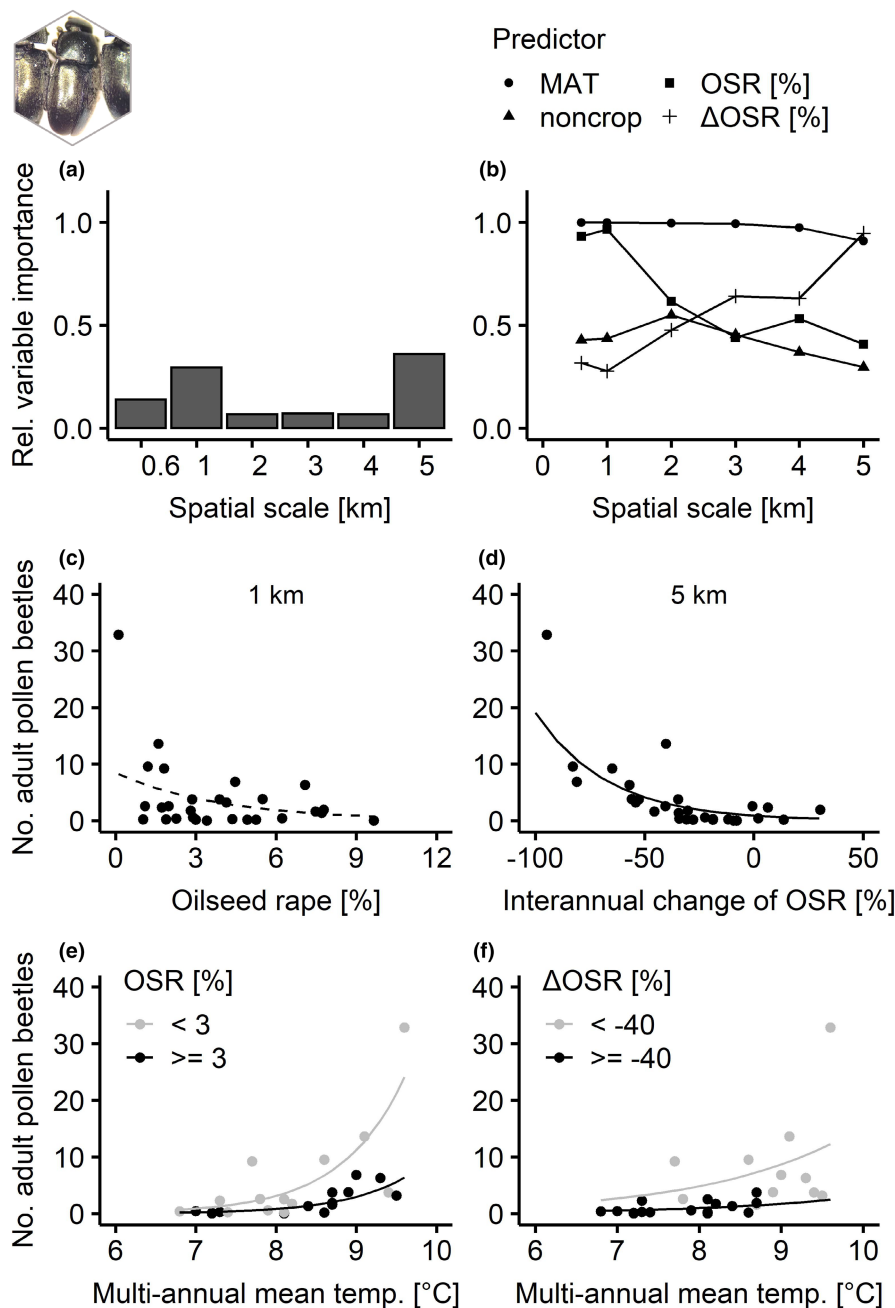
4 | DISCUSSION

We found that abundance of adult pollen beetles increased with MAT but less strongly depending on the landscape context, whereas abundance of stem weevil larvae was not substantially affected by any of the candidate predictors. Our results also show that despite the high abundance of adult pollen beetles at sites with warm climate (high MAT), crop yield was high—and the proportion of bud loss low—when OSR flowered early. Pollen beetle larval parasitism was overall low but occasionally exceeded 30% under both low and high MAT.

4.1 | Combined effects of MAT and landscape composition on pollen beetle abundance and parasitism

Adult pollen beetle abundance increased with increasing MAT, but less strongly when the proportion of OSR was high (>3%, 1-km scale), relatively constant compared to the previous year ($-40\% <$, 5-km scale) or both. This may result from increased oviposition rates over years of high temperature (Ferguson et al., 2014), which increases pollen beetle abundance, combined with dilution and concentration effects (spatiotemporal dynamics in OSR cover due to crop rotation, see also Schneider et al., 2015). However, in warmer regions, more farmers abstained from OSR cultivation in the study year due to drought around sowing in August–September of the previous year (personal communication with farmers in 2019: U Fricke). This probably led to the more frequent strong reductions in OSR area in warmer regions, which does not allow to clearly separate the two effects, but the best model supports both MAT and Δ OSR%. Thus, we provide first evidence that pollen beetle abundance may increase with increasing MAT under field conditions, while spatiotemporal dynamics of OSR area show great potential for sustainable management of the pollen beetle through regional coordination

FIGURE 2 Effects of landscape composition and multi-annual mean temperature (MAT) on adult pollen beetle abundance (28 sites); relative importance (= sum of Akaike weights) of (a) each spatial scale (0.6–5 km) and (b) each predictor; values range between zero (low) and one (high); Most relevant landscape parameters: (c) the proportion of oilseed rape area (OSR%) at 1-km scale—only contributed substantial explanation in combination with MAT—and (d) change in OSR area relative to the previous year (Δ OSR%) at 5-km scale (negative values: reduction, positive values: Increase). (e, f) Combined effects of MAT and the most relevant landscape parameters; here landscape parameters depicted as categorical variables (lighter colour: lower parameter range, darker colours: upper parameter range). In panels (c–f), dots indicate mean values per site and lines predictions from generalised linear mixed-effect models (solid: substantial contribution, dashed: no substantial contribution as single predictor).



of crop rotations, particularly when pollen beetle abundance is likely to be high, that is, at sites with warm climate.

Despite strong reduction in OSR area relative to the previous year at several spatial scales, concentration effects on pollen beetle abundance were only observed at 5-km scale, but not at 1-km scale, in contrast to Schneider et al. (2015). In principle, pollen beetles can disperse over distances up to 13.5 km (see Williams & Cook, 2010), despite a usual mean dispersal distance of 1.2 km (Juhel et al., 2017). Therefore, reduction in OSR area relative to the previous year at large spatial scales may have triggered long-distance dispersal of pollen beetles explaining concentration effects at large scales. Besides, reduction at larger spatial scales may mobilise more pollen beetles than reduction at smaller spatial scales, which represents reduction in a smaller area. Thus, strong reduction at large scales may

trigger a stronger spatial redistribution of pollen beetles and thus may dominate the concentration effect on pollen beetle abundance. By regional coordination of crop rotation, this finding may be used to either prevent concentration effects or to use them for spatially limited measures (i.e. application of mortality agents) to reduce pollen beetle abundance.

When OSR area is strongly reduced relative to the previous year at large spatial scales, the resulting concentration effect may conceal other landscape effects. This may explain the absence of non-crop effects in contrast to Rusch et al. (2013) and Zaller et al. (2008b), but see Skellern et al. (2017, neutral effect). In the case of non-crop area, however, the specific composition may also play a role as habitat properties such as litter thickness determine preference by pollen beetles for overwintering (Rusch et al., 2012). Thus, to provide

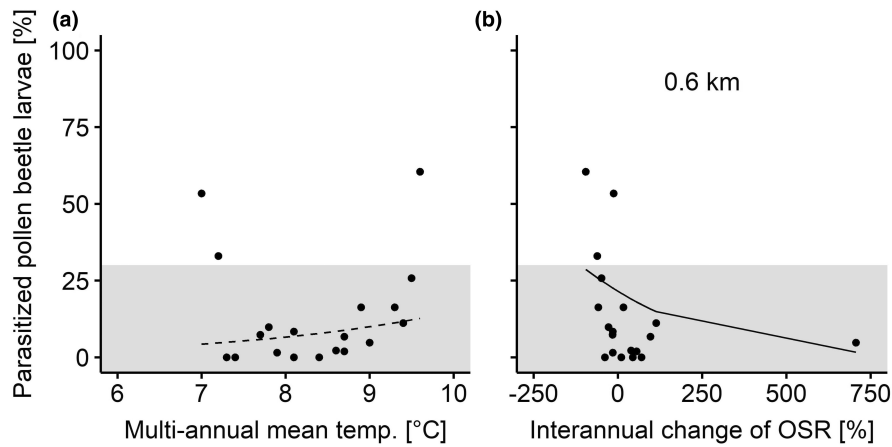


FIGURE 3 Relationship of the proportion of parasitised pollen beetle larvae with (a) multi-annual mean temperature (MAT) and (b) the change in oilseed rape (OSR) area relative to the previous year at 0.6-km scale; black dots: average values per site; lines: model predictions (solid: supported, dashed: no substantial effect); grey area: $\leq 30\%$ parasitism.

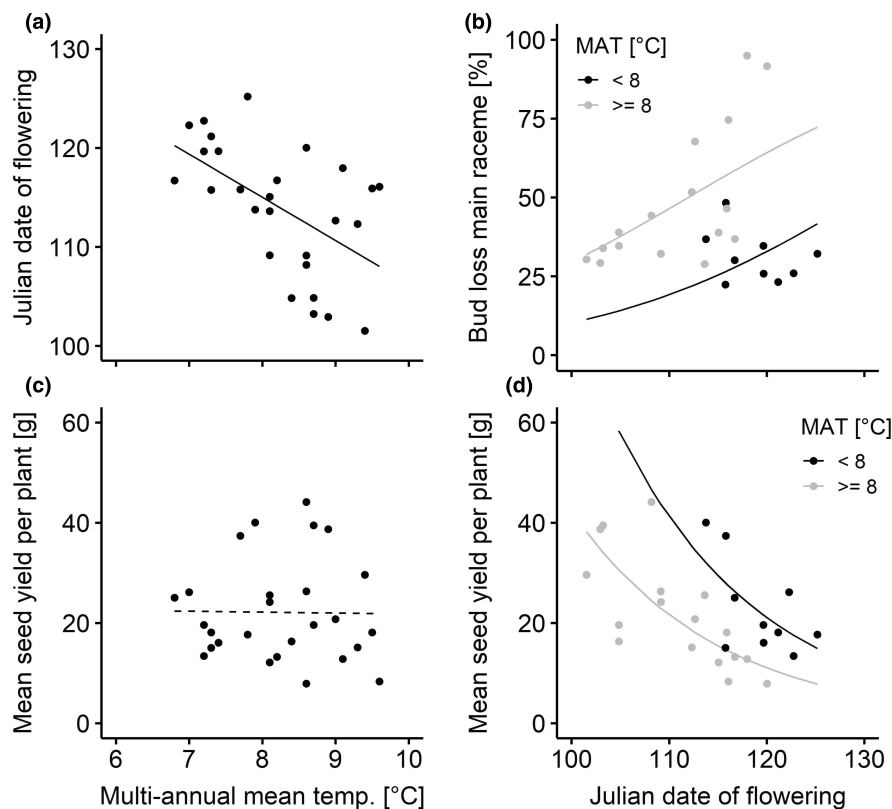


FIGURE 4 Relationships of Julian date of flowering (a, 27 sites), proportion of bud loss (b; 25 sites) and oilseed rape (OSR) yield (c, d; 27 sites) with multi-annual mean temperature (MAT; a, c) and Julian date of flowering while distinguishing between sites under low (black) and high MAT (grey). Dots indicate mean values per site. Lines present model predictions (solid: substantial contribution, dashed: no substantial contribution as single predictor).

sound advice for landscape management, efforts are needed to understand the conditions under which landscape effects apply. This may require refinement of some predictor variables and interpretation of landscape effects according to their spatiotemporal context.

The proportion of parasitised pollen beetle larvae was not affected by MAT, but increased with decreasing OSR area relative to the previous year at the 0.6-km scale. Thus, concentration effects may benefit pollen beetle parasitism, but possibly only at spatial scales < 1 km when considering that Schneider et al. (2015) did not observe such effects at 1-km scale. However, considerable variation remained unexplained, which suggests that other factors also affected parasitism, for example, insecticide use (Krimmer et al., 2021). Besides, parasitism of pollen beetle larvae was predominantly below the effective pest control threshold of about 30% (Hawkins & Cornell, 1994), although occasionally exceeding it at sites with both

cool and warm climates. This suggests that there is unused potential in natural pest control of pollen beetles irrespective of the prevailing mean temperature.

4.2 | Effects of MAT and landscape composition on stem weevil abundance

In contrast to adult pollen beetles, the abundance of stem weevil larvae did not respond to any of the candidate predictors. Stem weevils seem to be less responsive to landscape composition compared to pollen beetles (see also Zaller et al., 2008b), which may result from differences in pest species traits, for example, dispersal behaviour of the adults (Segoli & Rosenheim, 2012, addressing spatial crop cover). Stem weevils are known for relatively short

flights (see Zaller et al., 2008b), while pollen beetles can disperse over up to 13.5 km (see Williams & Cook, 2010). In case of strongly reduced OSR area relative to the previous year at large spatial scales, only a small proportion of stem weevils—particularly the ones close-by—may be able to reach OSR crops, which prevents concentration effects on stem weevils. Since high temperatures increase oviposition rates of stem weevils (Reinhardt, 2014), and consequently likely also abundance, occasional OSR crop rotations beyond the dispersal capability of stem weevils could reduce gradual increases in weevil abundance over several years of high temperatures. This could explain the absence of a MAT effect on this pest. Thus, some degree of spatiotemporal fluctuation in OSR area may benefit pest management of stem weevils in OSR crops, but more research is needed to confirm this.

4.3 | The role of MAT, landscape composition and crop phenology for bud damage and yield

At sites with warmer climate, bud loss decreased and crop yield increased with earlier flowering of OSR, while yield of late flowering OSR was higher at sites with cool than warm climate. This suggests that early flowering in warmer climates at least partially prevented pollen beetle immigration during the most vulnerable bud stage (Seimandi-Corda et al., 2021; Williams, 2010). Furthermore, lower pollen beetle abundance in cooler climates reduced the risk of yield loss to pollen beetles associated with late flowering. Beside temperature (see Weymann et al., 2015), other factors such as the genetically fixed differences among varieties influence the timing of flowering (Wang et al., 2011). This may explain the considerable variation in the date of flowering among crops in warm climates and could be used through cultivar selection and breeding to modify the timing of OSR flowering. Thus, although pollen beetles are predicted to migrate earlier with increasing temperatures (Junk et al., 2015), temperature effects on OSR development and actions such as selection of earlier flowering cultivars may limit bud loss and promote high OSR yield in current, and possibly also future, warm climates.

Date of flowering and MAT explained more variation in OSR yield than any of the landscape parameters or the abundance of pollen beetles. This highlights the importance of considering the risks of high pest abundance on crop yield loss in the context of crop phenology.

4.4 | Synthesis and management implications

Our study provides first evidence for increased adult pollen beetle abundance in warmer climates. This could also indicate increased pest pressure from pollen beetles on winter OSR in the course of global warming. Thus, although future reevaluation is needed, our study contributes important clues for sustainable pest management strategies under current and future climates. First, despite high pollen beetle abundance per plant, crop yield in warm climates

was high when OSR flowered early, suggesting that early flowering at least partially prevents the immigration of pollen beetles during the most vulnerable bud stage in warm climates (see also Seimandi-Corda et al., 2021; Williams, 2010). In addition to temperature-dependent earlier flowering, selection of early flowering cultivars could be used to promote high OSR yield in warm climates. Second, yield losses to pollen beetles were also lower when their abundance was low, for example, in cooler climates and when OSR area was not strongly reduced relative to the previous year. This could be harnessed through regional coordination of crop rotations either to use concentration effects for spatially limited measures to reduce pest abundances (e.g. application of mortality agents) or to prevent concentration effects, potentially with positive side effects on natural pest control due to increased interannual spatial continuity (see also Helenius, 1997). To prevent concentration effects on pollen beetle abundance, our results suggest some flexibility for regional crop rotation, as high pollen beetle abundance was only observed under strong reduction (>40%) in OSR area relative to the previous year so that other factors such as market prize or effects on other pests can also be considered. Highest pollen beetle abundance was observed when both OSR area was strongly reduced relative to the previous year and MAT was high. Therefore, greatest potential of coordinated crop rotation is expected in warm climates, and possibly also under other conditions favouring high pollen beetle abundance. Our results underpin the potential of targeted landscape management (e.g. through coordinated crop rotations) and timing of flowering (e.g. through cultivar choice) for sustainable pest management in winter OSR under current, and possibly also future, warm climates.

AUTHOR CONTRIBUTIONS

Ute Fricke, Sarah Redlich and Ingolf Steffan-Dewenter conceived the ideas; Ute Fricke, Jie Zhang and Ingolf Steffan-Dewenter designed the experiments; Ute Fricke, Sarah Redlich, Jie Zhang, Cynthia Tobisch, Sandra Rojas-Botero, Caryl S. Benjamin, Jana Englmeier, Cristina Ganuza, Maria Haensel, Rebekka Riebl, Johannes Uhler and Lars Uphus collected data; Ute Fricke analysed the data; Ute Fricke led the writing of the manuscript. All authors commented critically on the drafts and approved the final version.

ACKNOWLEDGEMENTS

The authors thank all farmers for facilitating this study and student assistants (Paul Geisendörfer, Konrad Güntner, Valentin Haberl, Jaqueline Johannsen, Annika Klein, Maren Prante, Annika Schöninger and Milena Sorger) for supporting OSR assessment. We acknowledge climate data provisioning by the Deutscher Wetterdienst (DWD) and land-cover data provisioning by the Bavarian Office for Surveying and Geographic Information (ATKIS 2019), the European Environment Agency of the European Union under the framework of the Copernicus programme (CLC 2018) and the Bavarian State Ministry of Agriculture and Forestry (IACS 2019). This study was performed within the *LandKlif* project (<https://www.landklif.biozentrum.uni-wuerzburg.de>) funded by the Bavarian Ministry of Science and the Arts via the Bavarian Climate Research Network

(bayklif, <https://www.bayklif.de>). Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.dfn2z355q> (Fricke et al., 2022b). R code available at Zenodo <https://doi.org/10.5281/zenodo.7324221> (Fricke et al., 2022a).

ORCID

Ute Fricke  <https://orcid.org/0000-0002-5284-4518>
 Sarah Redlich  <https://orcid.org/0000-0001-5609-0576>
 Jie Zhang  <https://orcid.org/0000-0003-2599-5983>
 Caryl S. Benjamin  <https://orcid.org/0000-0002-1704-4216>
 Jana Englmeier  <https://orcid.org/0000-0002-0559-1618>
 Cristina Ganuza  <https://orcid.org/0000-0002-4197-1829>
 Maria Haensel  <https://orcid.org/0000-0003-4530-8968>
 Rebekka Riebl  <https://orcid.org/0000-0002-8218-4717>
 Sandra Rojas-Botero  <https://orcid.org/0000-0002-0366-7383>
 Cynthia Tobisch  <https://orcid.org/0000-0002-2039-1462>
 Johannes Uhler  <https://orcid.org/0000-0003-3022-1229>
 Ingolf Steffan-Dewenter  <https://orcid.org/0000-0003-1359-3944>

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How to cite this article: Fricke, U., Redlich, S., Zhang, J., Benjamin, C. S., Englmeier, J., Ganuza, C., Haensel, M., Riebl, R., Rojas-Botero, S., Tobisch, C., Uhler, J., Uphus, L., & Steffan-Dewenter, I. (2023). Earlier flowering of winter oilseed rape compensates for higher pest pressure in warmer climates. *Journal of Applied Ecology*, 60, 365–375. <https://doi.org/10.1111/1365-2664.14335>