



Plant ecotype affects interacting organisms across multiple trophic levels

Anna Bucharova^{a,*}, Mark Frenzel^b, Karsten Mody^c, Madalin Parepa^a,
Walter Durka^{b,d}, Oliver Bossdorf^a

^aPlant Evolutionary Ecology, Institute of Evolution & Ecology, University of Tübingen, Tübingen, Germany

^bDepartment of Community Ecology, Helmholtz Centre for Environmental Research-UFZ, Halle, Germany

^cEcological Networks, Department of Biology, Technische Universität Darmstadt, Darmstadt, Germany

^dGerman Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Germany

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Abstract

In plant conservation and ecosystem restoration, plants are often translocated to ensure or enhance plant survival and performance. While the effects of ecotype origin on the performance of translocated plants are increasingly acknowledged among researchers and practitioners, ecotype effects on associated communities and ecosystems have hardly been studied. This is critical because plants also constitute the habitat for a large number of interacting organisms, and many of them might be influenced by plant ecotype characteristics. Here, we studied different ecotypes of *Centaurea jacea* L., a plant species commonly used in grassland restoration, and their effects on seed herbivores and their parasitoids. We grew eight *C. jacea* ecotypes originating from different regions in Germany in a common garden and found that the ecotypes differed up to three-fold in the frequencies of seed herbivores. These differences appeared to be mainly driven by ecotype differences in flowering phenology. We also found that there were up to four-fold differences in the frequencies of parasitoids, and even up to nine-fold differences in the abundances of parasitoids among ecotypes. In summary, plants from different origins substantially differed in their effects on interacting organisms, potentially reflecting coevolutionary relationships across trophic levels. The introduction of foreign ecotypes in restoration projects may thus not only affect the plants themselves, but it may also disrupt the balance of their biotic interactions.

Zusammenfassung

In Artenschutzprojekten wie auch bei der Renaturierung von Ökosystemen werden Pflanzen häufig gebietsfremd angesiedelt, um ihr Überleben zu sichern oder ihr Gedeihen zu fördern. Während die Bedeutung der Herkunft des Ökotypen für das Gedeihen der umgesiedelten Pflanzen von Wissenschaftlern und Naturschutzpraktikern zunehmend anerkannt wird, wurden die Auswirkungen der Pflanzenherkunft auf Pflanzen-assoziierte Lebensgemeinschaften sowie Ökosysteme bisher kaum

*Corresponding author at: University of Tübingen, Institute of Evolution & Ecology, Plant Evolutionary Ecology, Auf der Morgenstelle 5, 72076 Tübingen, Germany.

E-mail address: anna.lampe-bucharova@uni-tuebingen.de (A. Bucharova).

weitergehend untersucht. Dies ist problematisch, da Pflanzen Habitat und Nahrungsressource für eine große Zahl an interagierenden Organismen darstellen, von denen viele von Merkmalen der Pflanzen-Ökotypen beeinflusst werden können. In dieser Studie untersuchten wir die Beziehung verschiedener Ökotypen der Wiesen-Flockenblume (*Centaurea jacea*)-einer Pflanzenart, die häufig bei der Renaturierung von Grasland verwendet wird-zu Samenherbivoren und ihren Parasitoiden. Wir kultivierten acht Ökotypen von *C. jacea* aus unterschiedlichen Herkunftsregionen in Deutschland in einem common-garden-Experiment und fanden ein bis zu dreifach höheres Auftreten von Samenherbivoren auf einzelnen Ökotypen. Diese Unterschiede schienen hauptsächlich durch Unterschiede in der Blüh-Phänologie der Ökotypen erklärt zu werden. Wir fanden außerdem, dass sich das Auftreten von Parasitoiden bis zu vierfach und die Häufigkeit von Parasitoiden bis zu neunfach unterschieden. Zusammenfassend lässt sich feststellen, dass sich Pflanzen aus unterschiedlichen Herkunftsregionen deutlich in ihrer Auswirkung auf interagierende Organismen unterscheiden können, was möglicherweise koevolutionäre Beziehungen über verschiedene trophische Ebenen hinweg widerspiegelt. Die Einbringung gebietsfremder Ökotypen in Renaturierungsprojekten kann daher nicht nur die Pflanzen selbst beeinflussen, sondern auch zur Störung biotischer Wechselbeziehungen führen.

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Introduction

Environmental change can threaten natural populations in several ways. Habitat loss can reduce population sizes (Swift & Hannon 2010), habitat fragmentation can restrict migration, gene flow, and the colonization of new suitable habitats (Bijlsma & Loeschcke 2012; Holderegger & Di Giulio 2010; Honnay et al. 2002), and climate change can disrupt habitat adaptation of populations (Parmesan 2006). To help the affected organisms survive, a number of practical measures have been suggested, from the creation of new habitats with the help of seed introduction (Hölzel et al. 2012) to the transfer of organisms to more suitable habitats (Gallagher et al. 2015) or moving individuals to ensure gene flow (Sgrò et al. 2011). Many of these activities involve the translocation of plants or genetic material over large geographical distances.

The main goal of organism translocations is to enhance the performance of a target population. Based on substantial empirical evidence of local adaptation (Hereford 2009; Leimu & Fischer 2008), many researchers and practitioners currently prefer the use of regional diaspores for ecosystem restoration, where seed transfer is confined to within specific regions (Bucharova et al. 2016a; Vander Mijnsbrugge, Bischoff, & Smith 2010). Others argue that because of climate change, many local populations may soon be maladapted, and seed sources from other regions might be more suitable for ecosystem restoration (Kreyling et al. 2011; Sgrò et al. 2011).

So far the debate on plant translocations is largely focused on the performance of the translocated plants themselves, and its dependence on ecotype origin (Breed et al. 2012; Broadhurst et al. 2008; Sgrò et al. 2011). However, it is important to consider that plants also create a habitat for a large number of other species. Interactions between plants and pollinators, herbivores, pathogens and organisms on higher trophic levels like parasitoids, are known to be shaped by long-time coevolutionary processes and are often geographically differentiated (Abrahamson & Weis 1997; Leimu et al. 2012). A number of previous studies have demonstrated how

plant genotype identity can affect the structure of interacting communities across multiple trophic levels (Abdala-Roberts & Mooney 2013; Bischoff & Trémulot 2011; Gols et al. 2009; Johnson 2008; Moreira & Mooney 2013), sometimes with genotype effects of the same order of magnitude as the effects of species identity (Mooney et al. 2010; Singer et al. 2012). Thus, if plants are generally genetically differentiated across geographic regions (Duminil et al. 2007; Harter et al. 2015), the introduction of plant ecotypes from other regions are likely to disrupt the coevolutionary balance of regional biotic interactions. Still, the effects of foreign genotypes on biotic interactions have hardly been studied or discussed in the context of seed sourcing for ecological restoration (Breed et al. 2012; Broadhurst et al. 2008; Vander Mijnsbrugge et al. 2010).

Here, we studied eight different ecotypes of *Centaurea jacea*, a plant species commonly used in grassland restoration, and their effects on seed herbivores and their parasitoids in a common-garden experiment. The plants used in this study were shown to be genetically as well as phenotypically differentiated (Bucharova et al. 2016b; Durka et al. 2016). In the present study, we extend this work to biotic interactions, specifically seed herbivores and their parasitoids living in the flower heads of *C. jacea*. We asked whether ecotypes differed in (1) overall rates of infestation by seed herbivores, (2) the frequency and abundance of specific seed herbivores and (3) the frequency and abundance of parasitoids associated with the herbivores.

Materials and methods

Study system

Centaurea jacea L. (Asteraceae) is a perennial plant common in European grasslands. Its flower heads are, as in many other species of the family, frequently attacked by seed herbivores, among others tephritid flies belonging to the genera

Acanthiophilus and *Chaetorellia* (Merz 1994), here specifically *A. helianthi* and *Ch. jaceae* (White 1988). Both *A. helianthi* and *Ch. jaceae* are generalists and feed on a wide variety of plants from the Asteraceae family. Consequently, the flying period of adults spans from spring to summer, as long as there are any flowering host plants (Saeidi et al. 2015, Bucharova, personal observation). Females lay one to few eggs between the outer bracts of flower buds (*Ch. jaceae*) or young flowers (*A. helianthi*). The larvae induce no galls and feed on the soft parts of flower heads, developing seeds and achenes (Al-Ali et al. 1977). Pupation takes place within the flowerhead. Both species have one to two generations per year (Zwölfer 1983; Bucharova, personal observation), the hibernating stage is a pupae or larvae and the adults emerge next spring at the time when host plants start to flower (Al-Ali et al. 1977; White 1988).

The larvae and pupae of tephritid flies are attacked by various parasitoid wasps. In our study, two species were common enough to allow quantitative analysis: *Pteromalus elevatus* (Pteromalidae, Pteromalinae) and an unidentified species from family Tetrastichinae (Eulophidae). *P. elevatus* females lay their eggs into larvae of the second and third larval stage of the host by stinging the ovipositor through the wall of the flower head. The parasitoid larvae are endoparasites, feed on the host larvae and pupate within host puparia. They have two generations with the second one hibernating as pupae in the flower head (Janzon 1986). The wasps from the family Tetrastichinae are very small and they feed as gregarious endoparasites, with up to 20 parasitoid larvae feeding on one host. They have two generations per year, with the second one hibernating as larvae in the dry skin of the host (Varley 1947).

Experimental design

In Germany, a regional seed provenancing approach for grassland restoration has recently been established, where the country is divided hierarchically into eight larger and 22 smaller regions, within which seed transfers for grassland restoration takes place (for details see Bucharova et al. 2016b; Durka et al. 2016). Native seeds of many common grassland species are now commercially available for each region. The seeds are collected from multiple large wild populations in a given region to ensure genetic variability, regionally farm-propagated for up to five generations, and then used in restoration and other projects.

We worked with eight ecotypes (referred to as E1–E8 below) of the perennial plant *Centaurea jacea* L. (Asteraceae), which corresponded to eight regions of seed origin in Germany (Fig. A1 in online Appendix, see also Bucharova et al. 2016b). We obtained the seeds from a commercial producer of regional seeds for nature restoration (Rieger-Hofmann GmbH, Blaufelden-Raboldshausen, Germany). In 2013, we grew all ecotypes in three common gardens 150–400 km apart from each other (Tübingen, Halle and Freising; details on planting in Bucharova et al. 2016b). In

each garden we grew 12 plants from each of the eight ecotypes, altogether 288 plants. As a measure of plant phenology, we recorded the onset of flowering for each plant individual.

In September 2013, we harvested flower heads from all flowering plants. We collected only mature flower heads that were fully open and had already begun to wither. We dissected all flower heads and recorded the presence of herbivores or feeding traces. In one of the gardens, Tübingen, three flower heads from each plant, altogether 198 flower heads, were not dissected but kept individually in glass tubes of 2 cm diameter, closed with an air-permeable plug and stored at room temperature. This allowed the development of adult seed herbivores and their parasitoids. One year later, in September 2014, we examined all glass tubes for emerged adults, pupae and larvae of seed herbivores and their parasitoids. We determined all herbivore adults, pupae and larvae to the species level, whereas two morphospecies of parasitoids could only be determined to the genus or subfamily.

In this study, we focused on the overwintering generation of all the species.

Data analysis

We analyzed our data in three steps related to the three study questions outlined above. First, we used presence/absence of herbivores to test for overall differences in herbivore infestation rates among ecotypes and gardens. We ran a generalized linear model with quasibinomial error that tested for the effects of garden, ecotype and their interaction, on the proportion of flower heads with presence of herbivores or feeding traces. Second, we analyzed the occurrence of individual herbivore species within each garden, using GLMMs with a binomial error distribution that included ecotype identity as fixed effect and individual plant identity as random effect. Third, we analyzed the occurrence of parasitoid species with the same GLMMs as above, using only the flower heads where herbivores or parasitoids were present. One of the parasitoid species (an unidentified Tetrastichinae species) was gregarious, i.e. multiple parasitoids could develop within a host. For this species, we additionally analyzed the number of hatched individuals per flower head (GLMM as above, but with Poisson error), using only flower heads where this parasitoid was present. Finally, since we were suspecting that ecotype effects could be driven by the phenological differences between plant ecotypes, we re-ran all of the models described above also with onset of flowering as an additional continuous explanatory variable. All analyses were carried out in R version 3.2.0 (R Development Core Team 2013).

To test the significance of fixed model factors, we used 95% credible intervals (CrI), a Bayesian analogue of confidence intervals, which are considered to be more reliable than likelihood ratio tests in GLMMs (Bolker et al. 2009). For each response variable and factor of interest (e.g. herbivore infestation rates of the different ecotypes), we obtained the model estimates from the back-transformed

effect sizes. The associated 95% CrIs were then calculated from 10,000 simulations of the mean and variance of each estimate, using the *sim* function in the R package *arm* with non-informative priors (Korner-Nievergelt et al. 2015). If the CrI of a group did not overlap with the mean of the other group, we considered the difference between these groups to be significant. Likewise, for the continuous variable phenology we used the CrI of the regression slope to assess significance: if the CrI of the slope estimate did not include 0, the phenology effect was considered to be significant.

Results

Overall rates of infestation by seed herbivores

Only five out of the eight ecotypes of *C. jacea* that we planted in the different gardens flowered early enough to produce more than five withered flower heads per plant (Fig. A2). Therefore, we could only include these ecotypes in all subsequent analyses (E4–E8).

Herbivore infestation rates differed among the three gardens, with highest overall infestation rates in Freising and somewhat lower ones in Halle and Tübingen. Only in the Tübingen garden there were differences between ecotypes, where two ecotypes, including the regional one, were approximately 25% less infested than the other three ecotypes (Fig. 1).

Frequency and abundance of specific seed herbivores

We found two herbivore species in the flower heads from the Tübingen common garden: the tephritid flies *Acanthiophilus helianthi* (Rossi, 1794) and *Chaetorellia jaceae* (Robineau-Desvoidy, 1830). Infestation rates of both herbivore species differed up to threefold between plant ecotypes

(0.10–0.33 in *A. helianthi*; 0.24–0.65 in *Ch. jaceae*; Fig. 2A and B). There were also differences in the composition of the herbivore community: ecotypes E5 and E6 were much more attacked by *Ch. jaceae* than by *A. helianthi*, while in other ecotypes the infestation by the two tephritid flies tended to be equal. When the flowering phenology of the plants was added to the models, this turned out to explain half of the variability previously assigned to ecotype identity (ecotype alone: 10% of variability; phenology alone: 16%; ecotype identity fitted after phenology: 5%). *A. helianthi* occurred more frequently on early-flowering plant individuals, whereas *Ch. jaceae* was more frequent on later-flowering plants (Fig. 2C and D).

Frequency and abundance of parasitoids

Four species of parasitoids (*Eurytoma* sp., *Microdonotomerus annulatus*, *Pteromalus elevatus*, and an unidentified species from the Tetrastichinae subfamily) hatched from the flower heads. Only two parasitoid species (*P. elevatus* and the Tetrastichinae species) occurred in more than 10 flower heads, so we restricted quantitative analyses to these two. There were significant differences among ecotypes in the presence of *P. elevatus* in flower heads, with infestation rates ranging from 0.13 in ecotype E4 to 0.5 in ecotypes E7 (Fig. 3A). There were no differences in the infestation rate of the Tetrastichinae species, but the number of individuals of the Tetrastichinae species that hatched per flower head differed up to nine-fold among ecotypes (Fig. 3B). Neither the rate of occurrence nor the abundance of the two parasitoids was influenced by plant phenology. Interestingly, parasitoids were generally most successful on ecotype E7, the ecotype originating from the same region as the Tübingen garden (Fig. A1), with the highest infestation rates of *P. elevatus* and the highest abundance of Tetrastichinae individuals on this ecotype (Fig. 3).

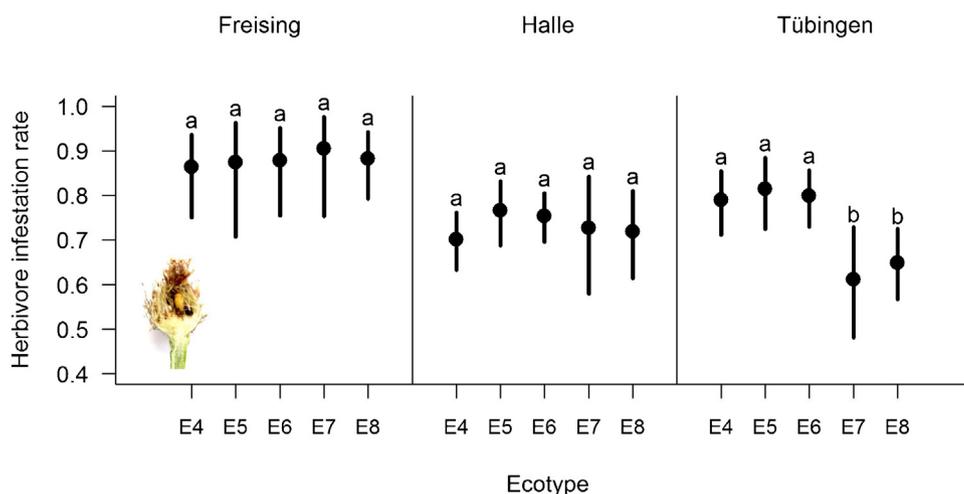


Fig. 1. Herbivore infestation rates of flower heads in five *Centaurea jacea* ecotypes (E4–E8) grown in three common gardens. The symbols and whiskers indicate the means and 95% credible intervals estimated from statistical models (see Section “Methods” for details). Differences are indicated within gardens only.

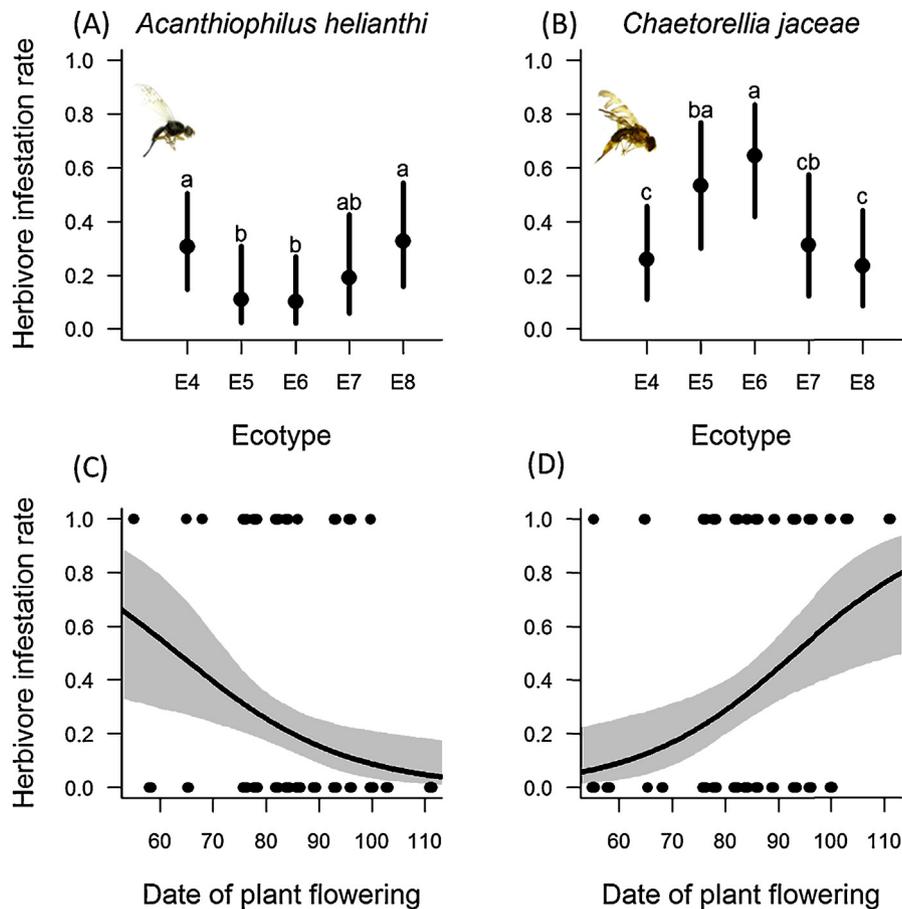


Fig. 2. Frequencies of two flower head herbivores, the tephritid flies *Acanthiophilus helianthi* and *Chaetorellia jaceae*, in five different ecotypes (E4–E8) of *Centaurea jacea* when grown in the Tübingen common garden. (A) and (B) show the estimated mean infestation rates (whiskers: credible intervals) of each ecotype, (C) and (D) the cross-ecotype relationships between plant phenology and herbivore infestation rates.

Discussion

There is currently much debate about seed origins in ecological restoration, but effects on other trophic levels have hardly been explored. Here, we found that different ecotypes of *C. jacea* differed strongly in the frequencies of flower head herbivores, as well as in the frequencies of the parasitoids that parasitize these herbivores, when compared in a common garden environment.

Herbivores feed on plants and are therefore directly influenced by all differences among ecotypes that affect plant quality (Awmack & Leather 2002). Several previous studies found similar ecotype effects on herbivores (e.g. Cronin et al. 2015; Horner & Abrahamson 1992; Lehndal & Ågren 2015; Mcguire & Johnson 2006; Mody et al. 2015). Effects on flower head herbivores might be driven by several factors, from differences in chemical defence to morphological differences in flower head size and toughness, which influence the success of ovipositing females, and differences in phenology (Münzbergová et al. 2015). Phenology is important because in order to maximize reproductive success by attacking the suitable stage of the flower or the bud,

herbivores must synchronize their life cycles with the host plants (e.g. Both et al. 2009; De Vries et al. 2010; Mopper 2005). Particularly in plants with a short flowering period the time window for the females to lay eggs can be very short (Straw 1991; Yukawa 2000), and therefore flower head herbivores should coevolve with regional plant ecotypes if these differ in phenology. We know that the latter is true for the studied *C. jacea* ecotypes (Bucharova et al. 2016a), and since phenology explained most of the ecotype effects in our analyses of herbivore infestation, it is very likely that in our study phenological differences between plant ecotypes were a key driver.

Besides affecting herbivores, plant ecotypes could also affect higher trophic levels. One group of interacting organisms that are usually highly specialized and that might be particularly affected, either directly or indirectly, by host plant ecotype or genotype identity, are parasitoids (Mody et al. 2012; Sarfraz et al. 2008). We found large differences among *C. jacea* ecotypes in the success of two parasitoid species. These differences in parasitoid presence and abundance were not related to phenology, and they were not driven by the presence of the herbivore hosts, since we considered

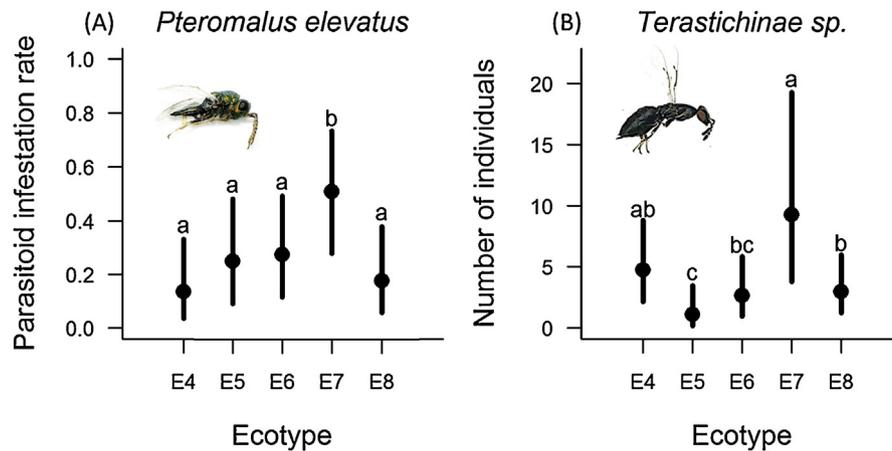


Fig. 3. Variation in parasitoids on different ecotypes of *Centaurea jacea* grown in the Tübingen common garden. (A) Frequency of occurrence of *Pteromalus elevatus*. (B) Average abundance per flower head of an unidentified species from the Terastichinae subfamily. Symbols and whiskers represent estimated means and credible intervals (see Section “Methods” for details).

only flower heads with herbivores (or their leftovers) in our analyses. Clearly, a mechanistic explanation of these results would require further research, but one possibility would be that plants attracted parasitoids directly through volatiles induced by herbivore feeding (Lill et al. 2002; Wist et al. 2015).

A key issue in the debate about species translocations is local adaptation. It is therefore important to not only test for overall ecotype differences, but also to contrast local and foreign ecotypes. In our study, the *C. jacea* ecotype E7 originated from the same region where our experimental garden was situated. Interestingly, both parasitoid species showed the highest performance on this regional ecotype, which suggests that the regional ecotype may indeed have unique characteristics also with regard to its biotic interactions. To what degree these patterns truly reflect regional adaptation can only be answered with more detailed studies of the biology of these interactions, together with plant fitness. We know from other studies though that biotic interactions are an important part of local adaptation (Garrido et al. 2012).

In summary, our study demonstrates that plant ecotype identity affects biotic interactions across multiple trophic levels. It is likely that this ecotype specificity of biotic interactions reflects the shared coevolutionary histories of plants and insects (Abrahamson & Weis 1997; Leimu et al. 2012). This is very relevant to current conservation and restoration practice, which often involves the translocation of plant ecotypes across large spatial scales. Our study indicates that an introduction of foreign ecotypes may not only affect the plants themselves, but it will also disrupt their biotic interactions. Because of this, regional seed sources should generally be the first choice in restoration projects. In cases where the introduction of foreign ecotypes is desired, researchers and practitioners must also consider and evaluate the effects of such introductions on other organisms in the target ecosystems.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.09.001>.

References

- Abdala-Roberts, L., & Mooney, K. A. (2013). Environmental and plant genetic effects on tri-trophic interactions. *Oikos*, *122*, 1157–1166.
- Abrahamson, W. G., & Weis, A. E. (1997). *Evolutionary ecology across three trophic levels. Goldenrods, gallmakers, and natural enemies*. Princeton University Press.
- Al-Ali, A. S., Al-Neamy, I. K., Abbas, S. A., & Abdul-Masih, A. M. E. (1977). On the life-history of the safflower fly *Acanthophilus helianthi* Rossi (Dipt., Tephritidae) in Iraq. *Zeitschrift für Angewandte Entomologie*, *83*, 216–223.
- Awmack, C. S., & Leather, S. R. (2002). Host plant quality and fecundity in herbivorous insects. *Annual Review of Entomology*, *47*, 817–844.
- Bijlsma, R., & Loeschcke, V. (2012). Genetic erosion impedes adaptive responses to stressful environments. *Evolutionary Applications*, *5*, 117–129.
- Bischoff, A., & Trémulot, S. (2011). Differentiation and adaptation in *Brassica nigra* populations: Interactions with related herbivores. *Oecologia*, *165*, 971–981.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H., et al. (2009). Generalized linear mixed

- models: A practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135.
- Both, C., van Asch, M., Bijlsma, R. G., van den Burg, A. B., & Visser, M. E. (2009). Climate change and unequal phenological changes across four trophic levels: Constraints or adaptations? *Journal of Animal Ecology*, *78*, 73–83.
- Breed, M. F., Stead, M. G., Ottewell, K. M., Gardner, M. G., & Lowe, A. J. (2012). Which provenance and where? Seed sourcing strategies for revegetation in a changing environment. *Conservation Genetics*, *14*, 1–10.
- Broadhurst, L. M., Lowe, A., Coates, D. J., Cunningham, S. A., McDonald, M., Vesk, P. A., et al. (2008). Seed supply for broadscale restoration: Maximizing evolutionary potential. *Evolutionary Applications*, *1*, 587–597.
- Bucharova, A., Durka, W., Hermann, J.-M., Hölzel, N., Michalski, S., Kollmann, J., et al. (2016). Plants adapted to warmer climate do not outperform regional plants during a natural heat wave. *Ecology and Evolution*, <http://dx.doi.org/10.1002/ece3.2183>
- Bucharova, A., Michalski, S. G., Hermann, J. M., Heveling, K., Durka, W., Hölzel, N., et al. (2016). Genetic differentiation and regional adaptation among seed origins used for grassland restoration: Lessons from a multi-species transplant experiment. *Journal of Applied Ecology*, <http://dx.doi.org/10.1111/1365-2664.12645>
- Cronin, J. T., Bhattarai, G. P., Allen, W. J., & Meyerson, L. A. (2015). Biogeography of a plant invasion: Plant–herbivore interactions. *Ecology*, *96*, 1115–1127.
- De Vries, H. H., Ens, S. H., de Graaf, G., Teunissen, L., van der Velde, R., Vogelaar, L., et al. (2010). Synchronisation of egg hatching of brown hairstreak (*Thecla betulae*) and budburst of blackthorn (*Prunus spinosa*) in a warmer future. *Journal of Insect Conservation*, *15*, 311–319.
- Duminil, J., Fineschi, S., Hampe, A., Jordano, P., Salvini, D., Vendramin, G. G., et al. (2007). Can population genetic structure be predicted from life-history traits? *American Naturalist*, *169*, 662–672.
- Durka, W., Michalski, S., Berendzen, K., Bucharová, A., Hermann, J., Hölzel, N., et al. (2016). Genetic differentiation among multiple common grassland plants supports seed transfer zones for ecological restoration. *Journal of Applied Ecology*, <http://dx.doi.org/10.1111/1365-2664.12636>
- Gallagher, R. V., Makinson, R. O., Hogbin, P. M., & Hancock, N. (2015). Assisted colonization as a climate change adaptation tool. *Austral Ecology*, *40*, 12–20.
- Garrido, E., Andraca-Gómez, G., & Fornoni, J. (2012). Local adaptation: Simultaneously considering herbivores and their host plants. *New Phytologist*, *193*, 445–453.
- Gols, R., van Dam, N. M., Raaijmakers, C. E., Dicke, M., & Harvey, J. A. (2009). Are population differences in plant quality reflected in the preference and performance of two endoparasitoid wasps? *Oikos*, *118*, 733–742.
- Harter, D. E. V., Jentsch, A., & Durka, W. (2015). Holocene re-colonisation, central–marginal distribution and habitat specialisation shape population genetic patterns within an Atlantic European grass species. *Plant Biology*, *17*, 684–693.
- Hereford, J. (2009). A quantitative survey of local adaptation and fitness trade-offs. *American Naturalist*, *173*, 579–588.
- Holderegger, R., & Di Giulio, M. (2010). The genetic effects of roads: A review of empirical evidence. *Basic and Applied Ecology*, *11*, 522–531.
- Hölzel, N., Buisson, E., & Dutoit, T. (2012). Species introduction – A major topic in vegetation restoration. *Applied Vegetation Science*, *15*, 161–165.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B., & Hermy, M. (2002). Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, *5*, 525–530.
- Horner, J. D., & Abrahamson, W. G. (1992). Influence of plant genotype and environment on oviposition preference and offspring survival in a gallmaking herbivore. *Oecologia*, *90*, 323–332.
- Janzon, L. A. (1986). Morphometric studies of some *Pteromalus Swederus* species (Hymenoptera: Chalcidoidea) with emphasis on allometric relationships; or: Are ratios reliable in chalcid taxonomy? *Systematic Entomology*, *11*, 75–82.
- Johnson, M. T. J. (2008). Bottom-up effects of plant genotype on aphids, ants, and predators. *Ecology*, *89*, 145–154.
- Korner-Nievergelt, F., Roth, T., von Felten, S., Guelat, J., Almasi, B., & Korner-Nievergelt, P. (2015). *Bayesian data analysis in ecology using linear models with R, BUGS, and Stan*. Elsevier.
- Kreyling, J., Bittner, T., Jaeschke, A., Jentsch, A., Jonas Steinbauer, M., Thiel, D., et al. (2011). Assisted colonization: A question of focal units and recipient localities. *Restoration Ecology*, *19*, 433–440.
- Lehdal, L., & Ågren, J. (2015). Latitudinal variation in resistance and tolerance to herbivory in the perennial herb *Lythrum salicaria* is related to intensity of herbivory and plant phenology. *Journal of Evolutionary Biology*, *28*, 576–589.
- Leimu, R., & Fischer, M. (2008). A meta-analysis of local adaptation in plants. *PLoS ONE*, *3*, e4010.
- Leimu, R., Muola, A., Laukkanen, L., Kalske, A., Prill, N., & Mutikainen, P. (2012). Plant–herbivore coevolution in a changing world. *Entomologia Experimentalis et Applicata*, *144*, 3–13.
- Lill, J. T., Marquis, R. J., & Ricklefs, R. E. (2002). Host plants influence parasitism of forest caterpillars. *Nature*, *417*, 170–173.
- Mcguire, R. J., & Johnson, M. T. J. (2006). Plant genotype and induced responses affect resistance to herbivores on evening primrose (*Oenothera biennis*). *Ecological Entomology*, *31*, 20–31.
- Merz, B. (1994). Diptera Tephritidae. *Insecta Helvetica, Fauna*, *10*, 1–198.
- Mody, K., Collatz, J., & Dorn, S. (2015). Plant genotype and the preference and performance of herbivores: Cultivar affects apple resistance to the florivorous weevil *Anthonomus pomorum*. *Agricultural and Forest Entomology*, *17*, 337–346.
- Mody, K., Spoerndli, C., & Dorn, S. (2012). How parasitoid sex ratio, size and emergence time are associated with fruit tree cultivar, within-orchard tree position and ants. *Biological Control*, *60*, 305–311.
- Mooney, K. A., Halitschke, R., Kessler, A., & Agrawal, A. A. (2010). Evolutionary trade-offs in plants mediate the strength of trophic cascades. *Science*, *327*, 1642–1644.
- Mopper, S. (2005). Phenology – How time creates spatial structure in endophagous insect populations. *Annales Zoologici Fennici*, *42*, 327–333.
- Moreira, X., & Mooney, K. A. (2013). Influence of plant genetic diversity on interactions between higher trophic levels. *Biology Letters*, *9*, 1–4.
- Münzbergová, Z., Skuhrovec, J., & Maršík, P. (2015). Large differences in the composition of herbivore communities and seed

- damage in diploid and autotetraploid plant species. *Biological Journal of the Linnean Society*, 115, 270–287.
- Parnesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, 37, 637–669.
- Saeidi, K., Mirfakhraei, S., & Mehrkhou, F. (2015). Population dynamics of safflower capsule flies (Diptera: Tephritidae) in Kohgiluyeh safflower farms of Iran. *Journal of Entomological and Acarological Research*, 47, 50–55.
- Sarfraz, M., Dossdall, L. M., & Keddie, B. A. (2008). Host plant genotype of the herbivore *Plutella xylostella* (Lepidoptera: Plutellidae) affects the performance of its parasitoid *Diadegma insulare* (Hymenoptera: Ichneumonidae). *Biological Control*, 44, 42–51.
- Sgrò, C. M., Lowe, A. J., & Hoffmann, A. A. (2011). Building evolutionary resilience for conserving biodiversity under climate change. *Evolutionary Applications*, 4, 326–337.
- Singer, M. S., Farkas, T. E., Skorik, C. M., & Mooney, K. A. (2012). Tritrophic interactions at a community level: Effects of host plant species quality on bird predation of caterpillars. *American Naturalist*, 179, 363–374.
- Straw, N. A. (1991). Resource limitation of tephritid flies on lesser burdock, *Arctium minus* (Hill) Bernh. (Compositae). *Oecologia*, 86, 492–502.
- Swift, T. L., & Hannon, S. J. (2010). Critical thresholds associated with habitat loss: A review of the concepts, evidence, and applications. *Biological Reviews of the Cambridge Philosophical Society*, 85, 35–53.
- Vander Mijnsbrugge, K., Bischoff, A., & Smith, B. (2010). A question of origin: Where and how to collect seed for ecological restoration. *Basic and Applied Ecology*, 11, 300–311.
- Varley, G. (1947). The natural control of population balance in the knapweed gall-fly (*Urophora jaceana*). *Journal of Animal Ecology*, 16, 139–187.
- White, I. M. (1988). *Tephritid Flies (Diptera: Tephritidae)*. pp. 134. *Handbooks for the identification of British insects* (10 (5a)) London: Royal Entomological Society.
- Wist, T. J., Greis, R., & Evenden, M. L. (2015). Differential parasitism by a generalist parasitoid is mediated by volatile organic chemicals of the herbivore's host. *Arthropod-Plant Interactions*, 9, 515–527.
- Yukawa, J. (2000). Synchronization of galls with host plant phenology. *Population Ecology*, 42, 105–113.
- Zwölfer, H. (1983). Life systems and strategies of resource exploitation in tephritids. In R. Cavalloro (Ed.), *Fruit flies of economic importance. Proceedings of the CEC/IOBC International Symposium, Athens, November 1982, Rotterdam* (pp. 16–30).

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