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Abstract

Agri-environment schemes are the most widely adopted political measure to maintain and restore farmland biodiversity in Europe. However, abiotic and biotic factors often limit the success of ecological restoration. Among the biotic factors, the size of the local and regional species pool is a major constraint. This is only well documented for plants. We therefore wanted to know if a small regional species pool can also limit restoration efforts of invertebrates. Specifically, we tested if by relocating grasshoppers from further away, we could overcome regional species pool limitations on hay meadows under the Swiss agri-environment scheme, so-called Ecological Compensation Area meadows (ECA meadows). All meadows had been under restoration for 6 years and were formerly intensively used hay meadows. Two grasshopper species, Euthystira brachyptera and Mecostethus parapleurus, were selected; E. brachyptera was not found in the regional species pool and M. parapleurus had nearly disappeared. In 2004, 1,400 grasshopper individuals of each species were taken from the nearest large source populations and distributed equally on seven ECA meadows and seven control meadows. In 2005, we evaluated whether the species had successfully established. Only one individual of M. parapleurus was found. We conclude that a small regional species pool is not the only constraint for the reestablishment of grasshoppers on restoration meadows. Also, other factors such as habitat quality appear to constrain the reestablishment of grasshoppers on restoration meadows. Additional restoration efforts specifically targeted at grasshopper restoration are needed, and innovative techniques have to be developed to overcome the relocation constraints.
Impact of regional species pool on grasshopper restoration in hay meadows

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Abstract

Agri-environment schemes are the most widely adopted political measure to maintain and restore farmland biodiversity in Europe. However, abiotic and biotic factors often limit the success of ecological restoration. Among the biotic factors, the size of the local and regional species pool is a major constraint. This is only well documented for plants. We therefore wanted to know if a small regional species pool can also limit restoration efforts of invertebrates. Specifically, we tested if by relocating grasshoppers from further away we could overcome regional species pool limitations on hay meadows under the Swiss agri-environment scheme (ECA meadows). All meadows had been under restoration for six years and were formerly intensively used hay meadows. Two grasshopper species, *Euthystira brachyptera* and *Mecostethus parapleurus*, were selected; *E. brachyptera* was not found in the regional species pool and *M. parapleurus* had nearly disappeared. In 2004, 1400 grasshopper individuals of each species were taken from the nearest large source populations and distributed equally on seven ECA meadows and seven control meadows. In 2005 we evaluated whether the species had successfully established. Only one individual of *M. parapleurus* was found. We conclude that a small regional species pool is not the only constraint for the re-establishment of grasshoppers on restoration meadows. Also, other factors such as habitat quality appear to constrain the re-establishment of grasshoppers on restoration meadows. Additional restoration efforts specifically targeted at grasshopper restoration are needed, and innovative techniques have to be developed to overcome the relocation constraints.

Introduction

Agri-environment schemes are the most widely adopted political measure to maintain and restore farmland biodiversity in Europe (OECD 2003). However, results of previous restoration under agri-environment schemes have been inconsistent (Kleijn & Sutherland 2003; Kleijn et al. 2006). In
order to understand the reasons for this, it is important to consider possible limitations on ecological restoration.

Limitations of ecological farmland restoration might consist of abiotic and biotic factors (Bakker & Berendse 1999; Suding et al. 2004). Among the biotic factors, the size of the local and regional species pools is a major constraint. For plants, for example, it has been shown that the restoration of species-rich grassland is sometimes severely limited by a lack of propagules of some species, both in the local and regional seed bank (Hutchings & Booth 1996; Bekker et al. 1997; Partel et al. 1998). In addition to the species pools, shifts in species dominance, trophic interactions or invasions by exotics might hamper the restoration process (Suding et al. 2004). Among the abiotic factors, high residual soil fertility is likely to slow enhancement of species richness in restored grassland (Janssens et al. 1998). Atmospheric deposition of nutrients accentuates this effect (Bobbink et al. 1998).

Various approaches have been explored to reduce abiotic and biotic restoration constraints. For example, a variety of techniques attempt to reduce residual soil fertility (Marrs 1993). In addition, sowing of desired plant species is a frequently used technique to overcome species-pool limitations (Pywell et al. 2002). Regarding animals, introductions of species are not an established practise in restoration ecology; relocations of animals, however, have been conducted for the purpose of conserving specific species. Of the published examples, 75% dealt with mammals and birds and thus were applied on a larger scale than the restoration of a single field (Fischer & Lindenmayer 2000). Only a few relocation attempts have been made with invertebrates (New 1994; Wagner et al. 2005).

Most European agri-environment schemes do not explicitly include measures to overcome restoration constraints and often they do not even have a clear restoration objective with regard to biodiversity targets (see review by Kleijn & Sutherland 2003). However, there are exceptions. In the UK, for example, the sowing of wild flower margins is a frequently adopted measure. Also in
Switzerland, some of the measures of the agri-environment scheme are specifically targeted to overcome restoration constraints. For hay meadows under the agri-environment scheme (ECA meadows), regulations aim to reduce residual soil fertility by strongly limiting fertilization and requiring that the grass must be cut and removed at least once a year, but not before the 15th of June (or later depending on altitude and agricultural zone) (Bundesrat 1998). Implicitly, the Swiss agri-environment scheme relies on the local and regional species pools of plants and animals still being present in the surroundings of ECA meadows. It is expected that the species are able to re-colonize the meadows within the contract period of six years. Mowing techniques and frequencies after the postponed first cut are not considered as potential restoration constraints and are not regulated by the scheme.

In general, ECA meadows increase species richness of plants and arthropods (Herzog et al. 2005; Knop et al. 2006); however, diversity levels are still significantly lower than in "unimproved", i.e. never intensified, grassland (Herzog & Walter 2005). Moreover, the effectiveness of ECA meadows differs between regions and species groups (Herzog et al. 2005; Knop et al. 2006). In some regions, ECA meadows increase biodiversity successfully, in others they do not.

This study, therefore, tested if the effectiveness of ECA meadows may be limited by the availability of invertebrate colonists. Specifically, we investigated if relocating grasshoppers from the nearest large source population could overcome regional species-pool limitations of ECA meadows. The study was motivated by the results of Knop et al. (2006), who found that grasshopper diversity was significantly increased on ECA meadows in regions with a presumably larger regional pool of grasshopper species, whereas there was no effect in a region with a depleted species pool of grasshoppers.

**Methods**
The investigation was carried out in a grassland farming region of the Canton of Lucerne, Central Switzerland. In this region the restoration management of hay meadows had no effect on species diversity of grasshoppers (Knop et al. 2006). The grasshopper species pool of the study area consisted of 16 species and was dominated by *Chorthippus parallelus* Meadow Grasshopper, *Chorhippus albomarginatus* Lesser Marsh Grasshopper, *Gomphocerippus rufus* Rufous Grasshopper and *Tetrix subulata* Slender Ground-hopper (Walter et al. 2005). In a previous sampling campaign (August 2000), the entire area (approximately four square kilometres) had been systematically searched for grasshopper species and their presence had been noted (Walter et al. 2005).

To test the species pool hypothesis, two grasshopper species, *Euthystira brachyptera* Small Gold Grasshopper and *Mecostethus parapleurus* Leek Grasshopper, were selected. Both species are typical species of extensive grassland of the Swiss lowlands (CSCF 2006). During the surveys of the entire study area in 2000 (Walter et al. 2005), *M. parapleurus* had been found once, and *E. brachyptera* had not been found. We therefore do not know whether *E. brachyptera* occurred in the region before the intensification of agriculture. However, the nearest population of this species was only 15 km away from the study site (CSCF 2006).

In 2004, 1400 grasshopper individuals of each species were taken from nearby large source populations and distributed equally on seven ECA meadows and seven control meadows. In 2005, we evaluated whether the species had successfully established. Species names follow the nomenclature of Coray (2001).

**The species**

*Euthystira brachyptera* is a small species (females 19–22mm; males 14–17mm) (Coray 2001). The wings of the female are reduced. The wings of the male cover approximately half of the abdomen length (Bellmann 1993). Both sexes therefore have poor flying abilities, although macropterous specimens have been found in both sexes (Detzel 1998). The species occurs in northern, western
and eastern Europe (Detzel 1998). *E. brachyptera* feeds preferentially on grasses, but species from other plant families also have been observed as food plants (Ingrisch & Köhler 1998). Eggs are laid between two leaves folded together, 20–50 cm above ground (Detzel 1998). In Switzerland, adult individuals occur in late summer, with the highest abundance in August (Thorens & Nadig 1997). Species tolerate both dry and wet habitat conditions (Detzel 1998). *E. brachyptera* is currently not threatened in Switzerland (BUWAL 1994), but nevertheless, intensive agricultural practices, bush encroachment and urbanisation have been reducing its distribution (Detzel 1998).

*Mecostethus parapleurus* is a large species (females 24–30 mm; males 17–21 mm) (Coray 2001). The wings of both sexes reach approximately the end of the abdomen (Bellmann 1993); thus, the species is able to fly short distances. *M. parapleurus* is distributed across southern, western and eastern Europe (Detzel 1998). Preferences with respect to food plants are not known (Ingrisch & Köhler 1998). Eggs are laid into the ground (Detzel 1998). In Switzerland, adult individuals occur in late summer, with maximum abundance at the beginning of September (Thorens & Nadig 1997). *M. parapleurus* occurs in dry and wet meadows; in addition, it is found in reeds (Detzel 1998). The Red List of Switzerland classifies the species as threatened (BUWAL 1994), due to similar reasons for the reduction of *E. brachyptera* populations (Detzel 1998).

**Specimen collection and translocation**

*E. brachyptera* was collected on sunny days between the 15th and the 20th of July 2004. In total, 1400 specimens (896 males and 504 females) were collected. The 1400 individuals (770 females and 630 males) of *M. parapleurus* were collected between the 27th of July and third of August 2004. For details regarding site locations and specimens collected per site see Table 1.

To collect grasshoppers, insect nets such as Bioquip 7112NA student nets (BioQuip Products, Rancho Dominguez, CA) were used. Each individual was placed in a separate plastic tube, stored over night in a cool house (approximately 12° C) and on the subsequent day released at the new site. Individuals from different sites and sexes were distributed equally among the 14 translocation
sites. Consequently, 100 individuals were released per meadow (*E. brachyptera*: 64 females and 36 males; *M. parapleurus*: 55 females and 45 males). The individuals were released at ten different points along a transect in the centre of the meadow. The points were 10 m apart from each other, starting in the centre of the meadow.

Before releasing the animals, the meadows were searched for the two species during 15 minutes on a 100 m transect and during 15 minutes on the entire meadow.

Table 1: Origin and number of specimens collected per site and sex.

<table>
<thead>
<tr>
<th>Species</th>
<th>Site</th>
<th>Elevation (m a.s.l.)</th>
<th>Number of specimens</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>females</td>
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<tr>
<td><em>E. brachyptera</em></td>
<td>Egerkingen</td>
<td>580</td>
<td>98</td>
</tr>
<tr>
<td></td>
<td>Oberbuchsitten</td>
<td>720</td>
<td>294</td>
</tr>
<tr>
<td></td>
<td>Erzberg</td>
<td>500</td>
<td>504</td>
</tr>
<tr>
<td><em>M. parapleurus</em></td>
<td>Flaach</td>
<td>350</td>
<td>770</td>
</tr>
</tbody>
</table>

**Release habitat**

Grasshoppers were released on 14 meadows of the adjacent municipalities of Ruswil and Buttisholz (Canton Lucerne). The region is characterized by dairy and arable farming. The meadows were situated within an area of approximately four square kilometres and were located at an altitude of approximately 600 m.

The 14 meadows were paired: the two meadows within one pair were close to one another, experienced similar abiotic conditions (e.g. soil type, water table, exposition, inclination, landscape structure), but differed in terms of management. One meadow in each pair served as a control and was conventionally managed according to common agricultural practices in Switzerland (conventional meadow). The other meadow in a pair was under the ECA management prescribed by
the Swiss agri-environment scheme for hay meadows (ECA meadow) (Bundesrat 1998). ECA meadows were thus not fertilized and the first cut was on or after the 15th of June. According to interviews with farmers, the ECA meadows were cut 2.4 ± 0.5 times per year and they had been under ECA management for 7.1 ± 2.0 years. On average, ECA meadows were 0.5 ± 0.2 ha in size and conventional meadows 1.4 ± 0.9 ha.

**Population monitoring**

During 2005, in mid June, at the end of July and at the beginning of September, three transect surveys were conducted on each of the 14 meadows. A transect survey consisted of noting all species that were observed or recorded by sound on a one-meter wide transect over a 15-minute period (Ingrish & Köhler 1998). In addition to the species census, the numbers of specimens per meadow were estimated for the two target species *E. brachyptera* and *M. parapleurus*. Sampling was carried out on sunny days between 10:00 and 16:00.

**Control cages**

To assess whether individuals were caught at the beginning of the reproductive period and whether they survived the transport, nine additional individuals of each species were put into cages (22 x 30 x 36 cm) after translocations (two females and one male per cage). The cages had a wooden frame covered with a wire net (1 mm) and an opening door for handling the grasshoppers. For practical reasons, they were placed in a yard in Neu-Affoltern (Canton Zurich). The cages were kept outdoors to simulate natural conditions and contained vegetation plots that were randomly taken from meadows nearby. In October, the cages were searched for egg pods, these were put in plastic vials containing moist vermiculite, and incubated at approximately 20° C for 50 d which allows the embryos to reach the diapause stage (van Wingerden et al. 1991). After this, the clutches were stored at approximately 4° C. In April, the clutches were retrieved from the cool house and kept at approximately 20° C under natural light conditions until hatchlings emerged.
Results

Release habitat

Before relocation in 2004, both species were not present on the meadows. In 2005, the repeated transect surveys revealed $3.0 \pm 1.0$ grasshopper species on ECA meadows and $2.1 \pm 0.4$ on conventional meadows ($N = 7$ per meadow type) (Fig. 1).

Translocated specimens

*M. parapleurus*

A total of 16 egg pods of *M. parapleurus* had been laid in the control cages. Hatchlings emerged successfully from three of these. However, only one individual of *M. parapleurus* was re-found in an ECA meadow in 2005.

*E. brachyptera*

In the control cages, a total of 4 egg pods were laid. Hatchlings emerged successfully from three of these. Despite this breeding success, no individual of *E. brachyptera* was re-found in either type of meadow in 2005.
Figure 1. Number of meadows on which grasshopper species were found one year after the relocation (N = 7 per meadow type). Only one individual of *M. parapleurus* was found to persist on one meadow.

**Discussion**

Our results suggest that, in addition to the lack of regional species pool, other constraints hamper grasshopper re-establishment on restoration meadows. Berggren (2001) proposes that successful grasshopper introduction is largely influenced by propagule size, predation, interspecific competition and habitat quality. Our propagule size was at least three times larger than in a previous successful introduction of grasshoppers (Berggren 2001). The most important predators of grasshoppers are web-spiders, birds and lizards (Ingrisch & Köhler 1998); all three predators were also present in the original habitat of the translocated specimens (E. Knop, Agroscope ART, Zürich, CH, 2004, personal observation). Still, the high abundance of the two dominant grasshopper species, *C. albomarginatus* and *C. parallelus*, at the release sites (Walter et al. 2005) indicated that predation pressure on grasshoppers was not particularly high. Interspecific competition was probably also not a main factor contributing to the lack of relocation successes. The two dominating grasshopper species, *C. albomarginatus* and *C. parallelus*, were found on both ECA meadows and conventional meadows. We do not expect these two species to have competed with the relocated species because all four grasshopper species are food generalists and use different niches for oviposition (Detzel 1998).

Regarding habitat quality, sufficient food plants and suitable breeding sites might be most important for grasshoppers (Wagner et al. 2005). With respect to food plants, habitat quality was probably suitable since the two species have general food requirements (Detzel 1998). For *E. brachyptera*, the availability of breeding sites was probably still insufficient on the ECA meadows and this might have been one of the main reasons for the failure of the relocation. The eggs, which
are laid 20–50 cm above ground (Detzel 1998), were probably removed when the ECA meadows were cut in summer and autumn. The Swiss agri-environment scheme only prescribes a postponed first cut in June; it makes no prescriptions regarding mowing frequency after the first cut or regarding mowing techniques and machines that are used (Bundesrat 1998). Additional measures, such as a minimum residual grass height after a cut or a restriction of parts of the meadow to only one cut per year would probably improve the habitat quality for *E. brachyptera*. This would also benefit other invertebrates that depend on standing vegetation throughout the growing season. *M. parapleurus* lays its eggs below ground, so breeding sites are influenced only indirectly through altered microclimate conditions after each cut.

In addition to ecological factors, methodological constraints such as the technique and length of post-release monitoring might also have influenced the result of the study. Firstly, due to the low visibility of relocated invertebrates, monitoring is difficult (New 1994). Secondly, the density of invertebrates may vary strongly between seasons. Therefore, after relocation long-term monitoring is needed, and repeated relocations might be required for successful restoration (New 1994). Thirdly, experiences from related species cannot be easily transferred and species have to be tested individually (New 1994). Berggren (2001), for example, successfully relocated only two individuals of *M. roesli*, whereas the relocation of Wagner et al. (2005) using 32 individuals of *O. germanica* failed. In order to improve the technique of grasshopper relocations, it therefore is important that the various attempts, failures and successes, are properly reported. Our results for *E. brachyptera* and *M. parapleurus* will contribute to the literature on Orthoptera population restoration.

We conclude that a small regional species pool is not the only constraint for the re-establishment of grasshoppers on restoration meadows. Other factors, such as habitat quality, appear to constrain the re-establishment of grasshoppers on restoration meadows. Additional restoration efforts specifically targeted at grasshopper restoration are needed, and innovative techniques have to be developed to overcome the relocation constraints.
Implications for Practice

- Species pool limitations cannot be overcome simply by transferring the desired species to the restoration meadows.
- Ecological constraints of grasshopper re-establishment on restoration meadows have to be identified for individual species separately.
- Methodological constraints of grasshopper relocation need further investigation.

Acknowledgements

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