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Modelling potential success of conservation translocations of a specialist grassland butterfly

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ABSTRACT

Success rates for conservation translocations of species are low and there is a need for increased understanding of how this activity is best applied. Here, using static species distribution models and a spatially-explicit dynamic simulation model, RangeShifter, we examine the impacts of habitat cover in recipient landscapes, allocation of individuals into multiple sites and species trait characteristics on the long-term fate of hypothetical translocations of a grassland specialist butterfly, *Maniola jurtina*, in Finland. While persistence of populations introduced to climatically suitable locations northwards of the current range can be increased by selecting sites with increasing habitat cover and by allocation of individuals to multiple release sites, local population growth rate is shown to be the key parameter in determining likely translocation success. We conclude that the long-term persistence of translocated habitat specialist butterflies, particularly with low growth rates, appears to be uncertain in modern-day fragmented grassland networks and that translocation activities should prioritize management that improves local growth rate.

1. Introduction

Conservation-oriented translocations (Seddon et al., 2007), i.e. assisted movements of organisms from one area to another, are a controversial tool (McLachlan et al., 2007; Loss et al., 2011) which nevertheless hold much potential for species conservation (Chauvenet et al., 2013a). In particular, carefully planned translocations can aid habitat specialists with limited mobility to track spatial changes in suitable areas (Willis et al., 2009a; Gallagher et al., 2015).

The two main types of conservation translocations are (i) reintroductions where species are released within their indigenous range and (ii) assisted colonization (referred to also as assisted migration and managed relocation) where species are moved beyond their historical range (McLachlan et al., 2007; Seddon et al., 2014). These have certain common key features (Olden et al., 2011). First, the success rate of both reintroductions (Griffith et al., 1989; Armstrong and Seddon, 2008) and assisted colonization (Gallagher et al., 2015) has been low, resulting from insufficient consideration of species biology and ad hoc selection of release sites (Seddon et al., 2007; Schultz et al., 2008; Chauvenet et al., 2013b). Second, translocation resources are often limited and only a few options can be implemented. Thus potential success of different alternatives should be scrutinized with appropriate tools (Rout et al., 2007; Schultz et al., 2008; Lewis et al., 2012). Indeed, increasingly sophisticated approaches are available for assessing factors determining the success of population establishment (Fordham et al., 2012; Chauvenet et al., 2013a). Systematic application of such tools helps in developing both reintroduction and assisted colonization planning (Armstrong and Seddon, 2008; Chauvenet et al., 2013b). A promising avenue is the use of species distribution models (SDMs) to determine the broad-scale suitability of recipient areas in conjunction with dynamic population models, which provide estimates of the translocation success (Fordham et al., 2012; Lewis et al., 2012).

In this study we examine the potential success of butterfly translocations at the northern range margin. We consider a habitat specialist, *Maniola jurtina*, which inhabits sparsely occurring managed grasslands in SW Finland (Heikkinen et al., 2014). With SDMs we determine the climatically suitable area for the species which is currently unoccupied, apparently due to difficulties in dispersing across fragmented landscapes (Warren et al., 2001; Pöyry et al., 2009). Within this focal area we use the dynamic model RangeShifter (Bocedi et al., 2014a) to explore potential success of simulated introductions in relation to (1) regional availability of suitable habitat (Chauvenet et al., 2013a; Seddon et al., 2014) and (2) allocation of introduced individuals in one vs. multiple sites (Rout et al., 2007; Armstrong and Seddon, 2008). We also examine the role of three key life-history parameters, growth rate, carrying capacity and length of long-distance dispersal events, in determining the introduced populations' persistence and spread. We conclude with recommendations for

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the development of reintroduction and assisted colonization programmes for habitat specialist species in modern-day agricultural landscapes.

2. Materials and methods

2.1. Study species

The Meadow Brown butterfly, *M. jurtina* (Linnaeus, 1758) (Lepidoptera, Nymphalidae) is a grass-feeding grassland generalist in many parts of Europe (Van Swaay, 2003; Dennis, 2004). However, the northern range margin of *M. jurtina* is in southernmost Finland (Fig. 1) where the species favors sparsely occurring managed dry unimproved (i.e. semi-natural, unploughed, non-fertilized, traditionally managed) grasslands over other types of grasslands (Schulman et al., 2005). Thus in our study area the species behaves as a grassland habitat specialist.

Despite possibilities provided by recent climatic warming (Pöyry et al., 2009) the species has not managed to expand its range northwards. As such, it represents a suitable candidate for an experimental climate change-related translocation (cf. Carroll et al., 2009). We used the National Butterfly Recording Scheme in Finland (NAFI) (Saarinen et al., 2003) data for 2001–2010 to determine 10 × 10 km cells with recent populations of *M. jurtina* in our study area (Fig. 1; Supplementary material, Text A1).

2.2. Recent climatically suitable areas

We determined the area that had recently become climatically suitable for *M. jurtina* by generating three SDMs (generalized linear models (GLM), generalized additive models (GAM) and generalized boosting method (GBM)). These SDMs were based on European-wide butterfly (Kudrna et al., 2011) and climate data, recorded using a regular 30′ × 30′ grid system and averaged across the time period of 1971–2000 (for details see Supplementary material, Text A1). In SDMs, the European range of *M. jurtina* was related to four climate variables, found to be ecologically important predictors for the broad-scale distributions of butterflies: mean temperature of the coldest month (MTCO), annual daily temperature sum above 5 °C (growing degree days, GDD5), annual water deficit (WD) and mean annual precipitation (PREC). The calibrated SDMs were then fitted to 10 × 10 km resolution climate data for Finland for the period 2001–2010, providing three different (GLM-, GAM- or GBM-based) projections of climatic suitability across the whole country. These model-based probabilities of suitability were converted into three maps where each 10 × 10 km cell was predicted to be either climatically suitable or unsuitable, and climatically favorable cells were determined by agreement of at least two of the models (see Supplementary material). Overlaying these 10 × 10 km cells with NAFI records revealed climatically suitable but currently unoccupied areas in SW Finland (Fig. 1).

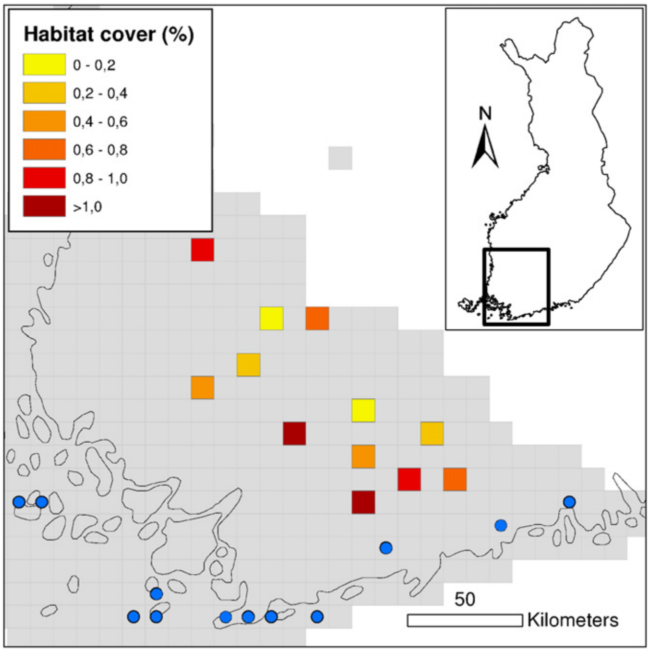

Fig. 1. Distribution of the selected twelve 10 × 10 km grid cells ("10 × 10 km landscapes") used in the modelling of translocation potential of *Maniola jurtina* butterfly in SW Finland. Cover of suitable habitat in the selected 10 × 10 km cells is shown using a 6-level scale. Grey shading indicates climatically suitable area for the species and blue dots (midpoints of 10 × 10 km grid cells) known occurrences in 2001–2010.

2.3. Land cover data and selection of recipient landscapes and sites

The amount of suitable habitat (i.e. 'habitat cover') for *M. jurtina* was determined for all unoccupied but climatically suitable 10 × 10 km cells and for all potential release sites (200 × 200 m cells) using CORINE 2006 Land cover data, available at 25 × 25 m resolution, by summing up the categories 'Pastures' and 'Natural grassland' — the two CORINE categories deemed suitable for *M. jurtina* (Heikkinen et al., 2014). In these calculations climatic suitability, as determined by SDMs, was not considered, only the habitat cover. Next we selected twelve 10 × 10 km cells as recipient landscapes, two for each of six habitat cover classes (<0.2%; 0.2–0.4%; 0.4–0.6%; 0.6–0.8%; 0.8–1.0% and >1.0% cover), in order to represent a gradient in habitat cover (Table A1). Two selection rules were used: no neighboring 10 × 10 km cells were selected for simulated release sites and all selected cells were located inland, separated by at least one empty 10 × 10 km cell from known occurrences (Fig. 1). From each of the twelve 10 × 10 km landscapes, we then selected as release sites, the one, four or eight 200 × 200 m cells with the highest habitat cover. Habitat calculations were conducted using ArcMap software (Version 10.2.2, ESRI Inc., Redland, CA, USA).

2.4. Species parameterization, founder population persistence and spread

The long-term persistence and spread of translocated *M. jurtina* populations were projected using RangeShifter v1.0, a platform for individual-based modelling of species' population dynamics and dispersal (Bocedi et al., 2014a). We used a female-only and non-overlapping generation population model, requiring information on growth rate (r_{max}) and carrying capacity (K; i.e. equilibrium population density) (Bocedi et al., 2014a). We assumed density-dependent dispersal probability (Heikkinen et al., 2014) and sampled the dispersal distance from a double negative exponential distribution in order to account for rare long distance dispersal events (i.e. simulating a combination of more common short dispersal events and rarer long distance dispersal events) (Nathan et al., 2012). We modelled population dynamics at a 200 × 200 m resolution, recording local population abundances for 50 years following each initial translocation. The 'released' butterfly populations were allowed to spread outside the focal 10 × 10 km cells, potentially throughout the whole climatically suitable area (grey-shaded grid cells in Fig. 1).

Biological parameters were extracted from literature, long-term butterfly monitoring surveys and expert assessments (for details see Supplementary material, Text A1 and Heikkinen et al., 2014). We conducted a sensitivity analysis to evaluate the effects of varying three key life-history traits on the simulated population dynamics (Carroll et al., 2003; Naujokaitis-Lewis et al., 2013): carrying capacity, population growth rate and the mean distances of long-distance dispersal events (McInerny et al., 2007; Willis et al., 2009b; Heikkinen et al., 2014). A default intermediate value and one alternative lower and one higher parameter value were used for each parameter, such as $K = 100/150/200$ individuals/ha ("K100", "K150" and "K200"), for $r_{max} = 1.5/2.0/2.5$, and mean long-distance dispersal = 1500/3000/5000 m ("D1500", "D3000" and "D5000"). For a 200 × 200 m cell with 100% habitat cover, we therefore assumed a default carrying capacity of 600 individuals (cf. Van Swaay, 2003). The mean short-distance dispersal distance was set at 200 m and the probability of individuals dispersing according to the long-distance dispersal kernel to 0.1 based on observations of Öckinger and Smith (2007). For the double negative exponential kernel, only one value for the mean of short-distance dispersal events, 200 m, was used based on information from literature (e.g. Schneider, 2003; Öckinger and Smith, 2007).

We included both environmental stochasticity affecting carrying capacity and probabilistic local population extinction into our RangeShifter analyses. First, to mimic impacts of annually varying regional climate conditions we implemented temporal environmental stochasticity acting globally on the carrying capacity of the 200 × 200 m cells (Bocedi et al., 2014a). Environmental stochasticity is implemented by adding $\varepsilon_t K$ to the initial K of the cell, where ε_t is the noise value sampled through a first order autoregressive process (for more details see Supplementary material, Text A1). Here, we assumed temporally uncorrelated fluctuations between years (i.e. white noise). Second, we set the probability of random local population extinction to 0.2. As there were no directly applicable studies available for *M. jurtina*, we selected this value based on comparisons with data on *Melitaea cinxia* in Finland (Hanski et al., 1995).

2.5. Translocation simulation design and analysis

We first simulated the translocation of 40 (female) individuals into each of the twelve recipient landscapes using the default life-history trait values, by 'releasing' 5 individuals into eight sites (200 × 200 m cells), 10 individuals into four sites, or all 40 individuals into one site. Forty individuals were deemed a realistic target both for specialist butterflies based on expert assessments and for species' translocations in general (Griffith et al., 1989). Next, we repeated the simulations varying the life-history trait values (K, r and long-distance dispersal) one by one (i.e. only one parameter was changed at a time), testing both one lower and one higher alternative. Each simulation was repeated 300 times.

The persistence and spread of translocated populations were assessed with two descriptors: (1) probability of translocation success (percentage of simulations surviving 50 years) and (2) spatial spread after 50 years, measured as the mean number of occupied 200 × 200 m cells (calculated for surviving replicates). Impacts of habitat cover, allocation of the translocated individuals and life-history parameters on the two descriptor statistics were analyzed using SPSS version 22 and ranked ANOVA tests (Thomas et al., 1999). To gain a balanced number of factors for the ANOVA tests, we agglomerated the data into three habitat cover categories: <0.4%, 0.4–0.8% and >0.8%, (Table A1). Additionally, we report the mean number of individuals remaining in each of our translocation simulation setting after 50 years in Supplementary material.

3. Results

Growth rate critically affected the persistence of introduced *M. jurtina* populations (data averaged over the 12 recipient landscapes; $F_{2,\,99} = 57.004$, $p < 0.001$; Table 1), showing a stronger impact than the two other life-history traits (Table 2). Higher growth rates resulted in substantially higher survival probability and spread of translocated populations after 50 years (Figs. 2–3). For example, with $r_{max} = 2.5$, populations persisted in 56.9% of replicates and those that survived had spread to an average of 57.6 200 × 200 m cells. By contrast, with $r_{max} = 1.5$, populations survived in only 5.9% of replicates and those that persisted had spread an average of 9.8 200 × 200 m cells (Table A2, Table A3). The impact of the other two life-history parameters was weaker. Neither varying K nor D showed a statistically significant impact (after Bonferroni correction; Table 2) on population survival probability or number of occupied 200 × 200 m cells.

As expected, increasing habitat cover in the recipient landscape results in a significantly higher survival probability (Fig. 2, Table 2) and the total number of occupied 200 × 200 m cells (Fig. 3, Table A3). With the default growth rate ($r_{max} = 2.0$), the probability of population survival often drops below 50% when the habitat cover is less than 1% (Table A2). However, spreading the translocation effort into multiple release sites and particularly increasing the growth rate can notably increase the simulated population survival probability for a given amount of habitat cover (Fig. 2).

Allocation of translocated individuals into multiple sites systematically increases the population survival probability (Fig. 2, Table 2). Populations persisted in 47.1% versus 22.4% of replicates when introduced into 8 versus 1 site (Table A2). However, if the founder population survived, the number of introduction sites did not have any significant effect on the number of occupied 200 × 200 m cells after 50 years (Fig. 3, Table A3). The mean number of individuals remaining in persistent simulations varied from less than 100 to over 16,000 (Fig. A1, Table A4). Only landscapes with >1.0% habitat cover were simulated to have constantly (except with $r_{max} = 1.5$) more than 1000 individuals after 50 years.

4. Discussion

Species translocation is a controversial and expensive conservation tool and it is challenging to know when and how it is best applied (Carroll et al., 2003; Rout et al., 2007; Schwartz and Martin, 2013). Modelling tools have the potential to increase the understanding of factors underlying translocation success and aid avoiding management options with low likelihood of success (Lewis et al., 2012; Chauvenet et al., 2013b; Schwartz and Martin, 2013). While static species distribution models yield useful assessments of the overall climatic suitability of introduction areas (Carroll et al., 2009; Willis et al., 2009a), our study, alongside some earlier ones (McIntire et al., 2007; Fordham et al., 2012), shows the important role spatially-explicit dynamic models can play in forecasting survival and spread of introductions under alternative translocation scenarios, before these are actually implemented in the field.

Several factors may affect the success of translocations, ranging from number of individuals released to the quality of recipient sites and genetic effects (Griffith et al., 1989; Rout et al., 2007; Armstrong and Seddon, 2008). Here we demonstrated that habitat availability in the landscape, allocation of translocated individuals in one vs. multiple sites and life-history traits significantly affect the fate of translocations. Considering habitat cover (and default growth rate and single release site), ≥1% of suitable habitat in the landscape appears as a general threshold for reaching the 50% probability of persistence in released *M. jurtina* populations in our study area. However, even in our landscape

Table 1
Mean survival probability (i.e., percentage of replicate simulations where the translocated population persisted 50 years) of translocated *Maniola jurtina* populations (mean ± SD). Probability values are averaged over the twelve recipient landscapes and shown in relation to the number of release sites (one, two or eight 200 × 200 m grid cells within the twelve recipient 10 × 10 km landscapes) and the three life-history parameters: growth rate (r_{max}), carrying capacity (K) and mean distance for long-distance dispersal events (D).

	Number of release sites		
	1	4	8
Default life-history parameters			
r_{max}2.0–K150–D3000	0.23 ± 0.15	0.38 ± 0.22	0.49 ± 0.26
Alternative life-history parameters			
r_{max}2.0–K100–D3000	0.23 ± 0.17	0.36 ± 0.23	0.47 ± 0.28
r_{max}2.0–K200–D3000	0.23 ± 0.16	0.40 ± 0.22	0.52 ± 0.24
r_{max}1.5–K150–D3000	0.04 ± 0.04	0.06 ± 0.06	0.08 ± 0.07
r_{max}2.5–K150–D3000	0.37 ± 0.22	0.60 ± 0.26	0.74 ± 0.28
r_{max}2.0–K150–D1500	0.23 ± 0.17	0.38 ± 0.23	0.51 ± 0.26
r_{max}2.0–K150–D5000	0.23 ± 0.16	0.38 ± 0.22	0.49 ± 0.26

Table 2
Results for three-factor analysis of variance based on the rank order of original values (three-way ANOVA on ranks; Thomas et al., 1999), conducted separately for each life-history trait. (A) Survival probability (percentage of persistent populations) of translocated *Maniola jurtina* populations (P_{Surv}) and (B) mean number of occupied 200 × 200 m grid cells (N_{Cells}) at the end of a 50 year dynamic simulation with 300 replicate runs. (B) was calculated based on replicate runs where the translocated population persisted after 50 years. Factors included were: (i) habitat area (area; grouped into three main size classes), (ii) number of release sites (N_{Sites}; three classes, 1, 4 and 8) and (iii) life-history parameters (P) used. For each life-history parameter (carrying capacity (K), population growth rate (r), mean length of long-distance dispersal events (D)) a default value and one lower and one higher alternative value were applied.

	Life-history parameter (P)											
	K				R				D			
	MS	df	F	p-Value	MS	df	F	p-Value	MS	df	F	p-Value
(A) P_{Surv}												
Area	32,514.15	2, 81	181.28	<0.001	14,412.76	2, 81	85.59	<0.001	32,873.44	2, 81	193.47	<0.001
N_{Sites}	11,028.42	2, 81	61.49	<0.001	3867.44	2, 81	22.97	<0.001	11,242.59	2, 81	66.17	<0.001
P	285.19	2, 81	1.59	0.210	25,509.05	2, 81	151.49	<0.001	27.76	2, 81	0.16	0.850
(B) N_{Cells}												
Area	43,008.05	2, 81	214.20	<0.001	28,754.09	2, 81	128.52	<0.001	43,812.34	2, 81	228.85	<0.001
N_{Sites}	333.15	2, 81	1.66	0.197	437.52	2, 81	1.96	0.148	495.44	2, 81	2.59	0.081
P	697.72	2, 81	3.48	0.036	12,537.65	2, 81	56.04	<0.001	5.44	2, 81	0.03	0.972

MS = Mean square; df = degrees of freedom; Bonferroni-corrected level for statistically significant p-value, 0.05/6 = 0.008.

which includes the single largest aggregation of semi-natural grasslands in Southern Finland the projected probability of long-term population persistence remained below 85%..

Examination of the habitat cover in the 10 × 10 km grid cells where the species has been recorded in the year 2001 and afterwards reveals interesting patterns. While the two easternmost inland landscapes with the species indeed have habitat more than 1%, the mean habitat cover in the other occupied 10 × 10 km grid cells – located all except one in the archipelago – is 0.5%. These discrepancies may be caused by the improved local climate conditions in the archipelago compared to the inland (milder winters and longer growing season) or by differences in the spatial configuration of the habitats (patches being more

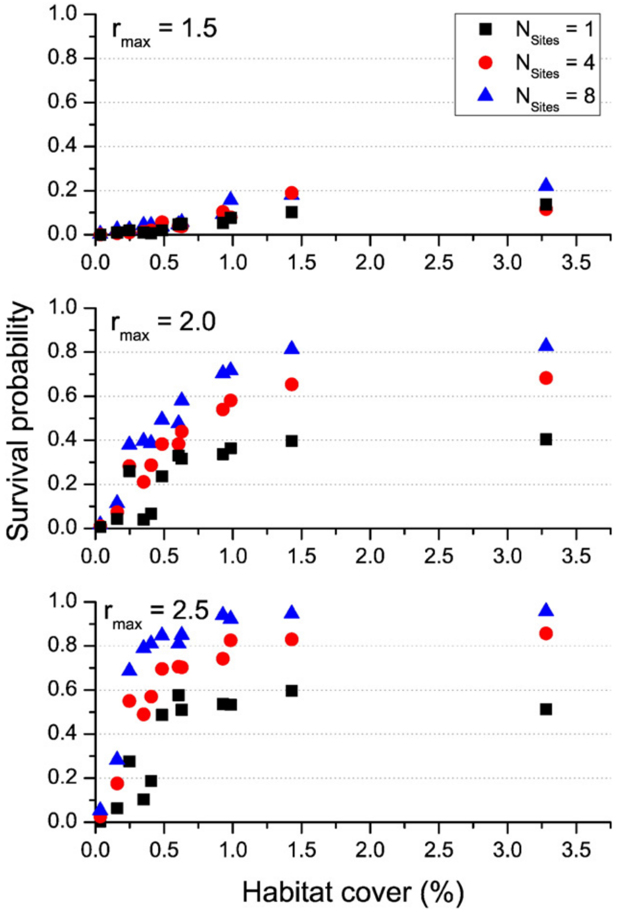

Fig. 2. Survival probability of translocated *Maniola jurtina* populations in relation to the amount of suitable habitat in the recipient landscapes (10 × 10 km grid cells) and the number of release sites (one, two or eight 200 × 200 m grid cells). Survival probability = the percentage of the simulations among 300 replicate runs where the introduced population persisted 50 years. Upper panel, lower growth rate (r_{max} = 1.5); middle panel, default growth rate (r_{max} = 2.0); lower panel, higher growth rate (r_{max} = 2.5). Simulation results for alternative K and long-distance dispersal parameters are excluded from the figure.

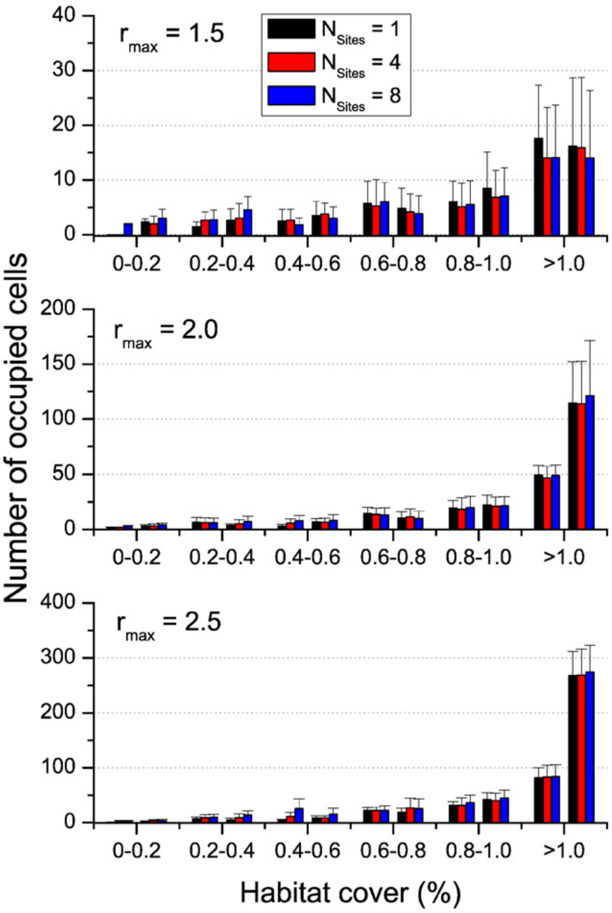

Fig. 3. Number of 200 × 200 m grid cells occupied by *Maniola jurtina* at the end of a 50 year dynamic simulation exercise in relation to the amount of suitable habitat for the species in the recipient landscapes (10 × 10 km grid cells) and the number of release sites (one, two or eight 200 × 200 m grid cells). The number of occupied grid cells is calculated as the mean of simulation replicates where populations persisted 50 years. The results for the three different growth rate values are shown. Note that the scale of the y-axis varies between different growth rate values.

agglomerated and better connected in large islands than in inland areas) which enable persistence in 10 × 10 km grid cells with less overall habitat. However, we highlight one difference here: while the RangeShifter simulation projections for population persistence show assessments based on a 50-year long period, the records of *M. jurtina* in the butterfly atlas data may represent temporally sporadic observations. To improve possibilities for empirical testing of the simulation results we need surveys of the long-term dynamics and survival of butterfly populations where the same areas are monitored systematically over several consecutive years (cf. Van Swaay et al., 2012; Oliver and Roy, 2015).

There is much variation in the simulated number of occupied 200 × 200 m cells for a given set of parameters. This is likely due to stochastic expansion–retraction processes determined by the environmental stochasticity in carrying capacity and the relatively low dispersal ability (Boggs et al., 2006). Our results suggest that if the founder population persists, it may increase in abundance even in the poorest landscapes. However, in such landscapes only a few introductions establish (<10% of simulation replicates persisted), because these butterfly populations are constrained to the introduction sites and thus highly susceptible to extinction.

Few studies have examined the impacts of spreading the translocation effort. Using a dynamic population viability model, Lewis et al. (2012) showed that introduction success of Fisher (*Martes pennanti*), a mid-sized carnivore, increased with the number of release sites. Griffith et al. (1989) described an asymptotic relationship showing that there may be little additional benefit from extra individuals when translocation includes a large number (>100) of individuals. Under such circumstances, splitting the individuals into two sites reduces the risk of translocation failure. Our results suggest that spreading the translocation even with fewer individuals into multiple sites enhances the population persistence, if the population growth rate is not too low. This is an interesting result because such a risk-spreading tactic would lead to small founder (sub)populations with only 5 or 10 individuals. Notably, certain translocations have established successfully from <15 founders (Taylor et al., 2005) and new butterfly populations may successfully start from very few dispersing females (Hanski, 2011). Nevertheless, small populations have inherent risks including genetic bottlenecks (Krauss et al., 2002; Armstrong and Seddon, 2008). Weeks et al. (2011) argued that the founder population should reach an effective size of 1000 individuals to guarantee maintenance of genetic variation. Among our persistent simulations, absolute population sizes of this magnitude were reached only in landscapes where the habitat cover was 0.8% or more (Table A4). Further work is required, ideally using spatially explicit population models that are extended to incorporate genetics, to explore these additional potential complexities. Further work is also required not only to experiment via real-life translocation trials (Carroll et al., 2009; Willis et al., 2009a; Kuussaari et al., 2015) the validity of the RangeShifter simulations developed here for *M. jurtina*, but also to assess how widely the revealed importance of spreading the translocation effort and habitat cover levels on introduction success can be applied to other grassland species and other areas (cf. Baguette et al., 2000; Lindenmayer et al., 2003; McIntire et al., 2007). This is because species often differ in their ecological characteristics and there may also be within-species variation in certain life-history traits between different regions, and thus findings from single-species studies should be generalized only with caution.

Moreover, uncertainties in parameterization of dynamic models may substantially affect their results (Minor et al., 2008; Heikkinen et al., 2014), highlighting the importance of sensitivity analysis (Carroll et al., 2003; Naujokaitis-Lewis et al., 2013). The sensitivity analysis conducted here showed that the translocation success of *M. jurtina* is affected differently by the variation in the three studied life-history traits. Contrary to a priori expectations (Boggs et al., 2006; McInerny et al., 2007), alterations in the length of long-distance dispersal did not affect the success of translocations. This is at least partly due to the severely fragmented network of grasslands in Finland, where the potential for longer distance dispersal does not guarantee a successful colonization of small isolated habitat patches (cf. Mair et al., 2014). However, along with the vast majority of similar modelling exercises, we used here a simple kernel based approach for modelling dispersal; this has the advantage of being easier to parameterize but lacks mechanistic realism that may alter conclusions (Travis et al., 2013). Recent theoretical work demonstrated that species with strong dispersal ability (i.e. can survive for lengthy periods while crossing matrix) may actually have higher rates of spread when habitat is more fragmented (Bocedi et al., 2014b). Such complex results are challenging to capture with the simple kernel-based approach. This highlights the need for future work on modelling translocation success, where gathering the empirical data that would allow models to incorporate a more mechanistic based approach for representing dispersal has a central role (Travis et al., 2012).

A striking feature in the present results was the critical role of growth rates. Some earlier studies have considered high growth rates as an important determinant for the translocation success (Griffith et al., 1989; Taylor et al., 2005) and for the rate of range expansion in butterflies (Willis et al., 2009b). Recently, Mair et al. (2014) examined simultaneously the importance of habitat availability, abundance trends and dispersal ability for the range shifting of 25 British butterfly species. These authors showed that positive population growth has a fundamental role for species' range expansion, and this role may be more central than that of habitat availability and dispersal during unfavorable climate periods. It appears that when species show low growth rates or declining abundances even long-established populations will not produce many migrants and may fail to colonize new sites. In agreement with Mair et al. (2014), our results underscore that if the population growth rates are low, as often is the case close to range margins, the probability of translocation success may decrease drastically even in landscapes with seemingly sufficient amount of suitable habitat.

4.1. Conservation planning for grassland butterflies

Earlier studies have shown that habitat specialist butterflies have difficulties in spreading into new areas across modern-day agricultural landscapes (Warren et al., 2001; Pöyry et al., 2009). Indeed, the drastic loss and fragmentation of traditionally managed grasslands have in many parts of Europe caused severe challenges for the conservation planning of grassland biota, reflected as the replacement of specialists by generalists in species assemblages and blocking of dispersal and colonization (Critchley et al., 2003; Polus et al., 2007; Willis et al., 2009a). One potential approach to support grassland species is constructing networks of patches and ecological corridors across human-dominated landscapes to facilitate species spread to new suitable areas (Nuñez et al., 2013). In Europe, such corridors might be built via increased adaptation of low-intensity farming practices and maintenance and restoration of grassland patches valuable for biodiversity based on agri-environment schemes (AES) (Donald and Evans, 2006; Arponen et al., 2013; Tainio et al., 2014). However, this approach may be unrealistic, as the evidence for corridors promoting insect dispersal is equivocal (Öckinger and Smith, 2008; Baur, 2014; but see Loss et al., 2011) and because the construction of corridors with habitat patches as stepping stones can be very expensive (Tainio et al., 2014).

Translocations are potentially a logistically more feasible and cost-effective solution to help species colonize new areas than constructing ecological corridors in severely fragmented areas (Loss et al., 2011; Baur, 2014). However, planning translocations requires detailed understanding of the species' biology as well as a priori assessments of the factors affecting their success, such as present-day habitat availability. Our study landscapes may represent typical examples of agricultural landscapes for much of Europe (cf. Critchley et al., 2003; Littlewood et al., 2012). Given this, our results suggest that the habitat loss often hampers also the translocation success of grassland butterflies, as the probability of long-term persistence of founder populations was less than half in most of our landscapes. Corresponding obstacles for translocations are likely also in other highly fragmented habitat types (McIntire et al., 2007) and in other species groups (Fordham et al., 2012). These problems concern especially many habitat specialists and also clearly translocated species with low population growth rates may face difficulties to establish successfully.

In modern-day agricultural landscapes, a more successful conservation strategy for grassland butterflies than ecological corridors might be the planning of local networks of restored grasslands, agglomerated to include sufficient amount of habitat. Such agglomerations would provide focal "translocation centers", where introductions of species with similar climatic requirements might be targeted. Modelling tools, particularly spatially-explicit dynamic models equipped with more mechanistic representation of species' population dynamics and dispersal, may aid assessing whether habitat patches available in target landscape are sufficient for species persistence or if new restoration efforts are required to promote the success of translocations (McIntire et al., 2007). Again, AES and especially biodiversity-related AES measures could have a key role in such restoration planning (Donald and Evans, 2006; Tainio et al., 2014).

The persistence of released populations may be enhanced also by selecting target landscapes based on criteria additional to habitat cover. Firstly, management and restoration planning associated with species translocations can benefit landscape-scale planning (Helm, 2015). In particular, sufficient habitat connectivity in target landscapes is essential (McIntire et al., 2007; Loss et al., 2011). Spatially-explicit dynamic models inherently capture elements of habitat connectivity in their simulations but importance of connectivity can be examined also more directly, e.g. with certain spatial conservation planning tools such as the Zonation software (Arponen et al., 2013). Alarmingly, Arponen et al. showed that grassland habitat connectivity has received very little attention in the spatial allocation of agri-environment schemes, and concluded that improving conservation planning for grasslands of conservation value would benefit of integrating connectivity into AES.

Secondly, areas between habitat patches (i.e. "matrix") can affect the persistence of species' populations in the patches (Sweaney et al., 2014). Characteristics of the matrix which are likely to be supportive for grassland butterflies include land use and habitat heterogeneity, rugged topography, adjacent woodlands providing shelter, nectar and host plant resources, and uncultivated grassy elements increasing matrix permeability and supporting between-patch movements of species (Littlewood et al., 2012; Sweaney et al., 2014; Villemey et al., 2015). It is increasingly argued that government schemes aiming to promote grassland biodiversity (particularly AES) should support maintaining and restoring these beneficial elements in the landscapes around the actual grassland patches (Donald and Evans, 2006). Thirdly, habitat quality in the translocation sites is important, as low quality has been one of the primary limiting factors for the success of species reintroductions (Schultz et al., 2008). Habitat quality could be examined also at the landscape-scale level, by considering the characteristics (e.g. soil nutrient status; Critchley et al., 2003) of the existing grassland patches in the network, as well as the quality of low-quality grasslands available for enhancement and sites where re-creation of new grassland patches might be attempted (Littlewood et al., 2012). Finally, heterogeneous and low-intensity management actions should be prioritized in the implications of AES, simply because different species groups can have notably different responses to grassland management e.g. by grazing or mowing (Littlewood et al., 2012; Baur, 2014).

4.2. Conclusions

It is evident that developing successful translocations for declining, rare and at-risk habitat specialist grassland butterflies requires a multi-faceted planning system with several important steps requiring careful consideration. These include gathering a detailed knowledge of the focal species' life-history and ecology to support building more complex models, and identifying release sites with sufficient amounts of habitat to generate large source populations for further dispersal (McIntire et al., 2007). Release sites should be located in heterogeneous landscapes and preferably adjacent to wooded patches (Villemey et al., 2015). They should also be embedded in landscapes showing a strong connectivity of grassland patches and including elements in the matrix which are likely to support the spread and persistence of grassland species (e.g. permeability) (Sweaney et al., 2014). Moreover, where the current habitat network appears marginal in terms of potential translocation success, realistic possibilities for restoration and rehabilitation of suitable grassland habitats based on AES should be considered (Critchley et al., 2003; Littlewood et al., 2012). Different target locations and landscapes are likely to support different introduced species populations to a varying degree (Baguette et al., 2000; Lindenmayer et al., 2003; Baur, 2014). This study, alongside earlier ones (McIntire et al., 2007; Fordham et al., 2012), shows that conservation and management planning based on spatially-explicit dynamic models can provide useful comparisons of the persistence potentiality of species in the same or different target landscape(s) and thereby have a valuable role in successful translocation interventions.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2015.09.028.

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