# What limits the spread of two congeneric butterfly species after their reintroduction: quality or spatial arrangement of habitat?

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## Abstract

Population growth and spread of recently reintroduced species is crucial for the success of their reintroduction. We analysed what limits the spread of two congeneric butterfly species *Maculinea teleius* and *Maculinea nausithous*, over 10 years following their reintroduction. During this time, their distributions appeared to be limited to a few sites although it was thought that more suitable habitats were available. Thus, we question, does the quality or the spatial arrangement of their habitat limit their spread? Although adult individuals of both species can select high-quality plots, we show that selection of suitable plots in the area of reintroduction is spatially constrained. A low colonization probability of unoccupied distant plots of high quality was found for both species. The abandonment of occupied plots in *Ma. teleius* was also found to be dependent on the distance to occupied plots. We conclude that the spatial distribution of the two species during the 10 years following reintroduction was limited by the spatial arrangement of their habitat, rather than by the availability of high-quality plots. The spatial constraints in movement can explain observed source–sink structures when female butterflies deposit their eggs on low-quality plots. We conclude that although these species have very similar life histories, they require different approaches to their conservation due to subtle differences in adult habitat use and movement. Conservation of *Ma. teleius* should concentrate on improving local habitat quality, whereas conservation of *Ma. nausithous* is predicted to be more effective by creating a spatial network of suitable habitat plots, such as along road verges.

## Introduction

Populations of many species are declining worldwide due to habitat loss and habitat degradation (Schipper *et al.*, 2008). Many approaches to conservation of endangered or extinct species recommend reintroduction as a vital component (e.g. Fritts *et al.*, 1997; Schultz, Russell & Wynn, 2008). A key consideration limiting the success of reintroductions is low habitat quality. In their guidelines, IUCN therefore state that sufficient suitable habitat should be available, and the conditions that caused the extinction in the past should no longer be present (IUCN, 1995). However, even when sufficient suitable habitat is available, reintroduced populations do not always establish. Population growth and spread of the reintroduced species are crucial if the reintroduction is to be successful, especially for species with large fluctuations in population size from year to year, for example many invertebrate species (Schultz *et al.*, 2008). We studied the spread of two congeneric butterfly species, scarce large blue butterfly *Maculinea teleius* and dusky large

blue butterfly *Maculinea nausithous*, in the Netherlands for a period of 10 years following their reintroduction. In 1990, the two butterfly species were reintroduced in the Moerputten nature reserve after they became nationally extinct in 1976 (Wynhoff, 1998). Their reintroduction can be rated as successful because both butterfly species have established themselves at the sites where they were released (Wynhoff, 2001). However, although sufficient suitable habitat seems to be available, the distribution of the two butterflies is limited: *Ma. teleius* occurs only on the meadows where it was reintroduced, while *Ma. nausithous* has established populations on the railway embankment in the nature reserve and the surrounding road verges (Wynhoff, 1998). The two butterflies are strictly sedentary, with *Ma. nausithous* moving, on average, larger distances than *Ma. teleius* (Settele, 1998; Nowicki *et al.*, 2005a, 2007). The presence of both butterfly species largely depends on the occurrence of two larval resources. Both *Ma. teleius* and *Ma. nausithous* deposit their eggs only on the host plant *Sanguisorba officinalis* (Thomas, 1984; Elmes & Thomas,

1987; Wynhoff, 2001). First, the early instar caterpillars feed on developing seeds of this host plant. Second, both species are myrmecophilous because later instars are found in *Myrmica* ant nests, where they feed on ant larvae. *Maculinea teleius* is mainly found in the nests of the ant *Myrmica scabrinodis*, while *Ma. nausithous* can be found in nests of *Myrmica rubra* (Wynhoff, 2001; however, see also Pech, Fric & Konvicka, 2007; Tartally & Varga, 2008). Habitat selection studies of these butterflies, which measure the oviposition behaviour and the occurrence of adults, show that females of both butterflies are able to select those host plants for oviposition that are in the proximity of nests of their specific ant host (Wynhoff, Grutters & Van Langevelde, 2008). Although the butterflies are able to preferentially lay their eggs in these plots, the species do not seem to have a high rate of colonization of more distant plots where both resources also co-occur. Thus, is it the quality or the spatial arrangement of their habitat that limits the spread of these two butterfly species? We addressed this question by investigating distribution shifts in the two species since their reintroduction and establishment.

If random dispersal is assumed, the colonization of unoccupied suitable plots largely depends on the ability of the butterflies to reach these plots, which is determined by the distance to these unoccupied plots from those that are occupied. This distance is a measure of the connectivity of these unoccupied plots (Van Langevelde, Van der Knaap & Claassen, 1998; Van Langevelde, 2000). Plots have a low connectivity when they are located at a large distance from occupied ones relative to the movement ability of the animals, resulting in a low colonization probability of these plots. For the two butterfly species, we test whether the colonization of unoccupied plots is related to their connectivity, which suggests that the movement of these butterflies over their release area is spatially constrained. We should, however, be sure that the quality of the unoccupied plots at large distances from the release sites is not lower. Therefore, we estimated habitat quality for both butterfly species by analysing the relationship between their presence and absence and a number of habitat characteristics. For both species, we expect individuals to be more commonly found in plots that are suitable for oviposition: plots that contain both the host plant *S. officinalis* and nests of their respective host ant. Regarding the abundant host plant distribution and the low nest density of the host ants, the quality of the habitat of both species is thought to be largely determined by the presence of the ant nests (Nowicki *et al.*, 2007; Wynhoff *et al.*, 2008).

After colonization, plots can again become unoccupied, a general phenomenon in spatially distributed populations such as metapopulations (Hanski, 1999). Besides the quality of the habitat, we test whether the probability that a plot becomes unoccupied depends on the distance to occupied plots as the influx of individuals from other occupied plots might prevent abandonment. If true, this supports the argument that the movement of these reintroduced butterflies is spatially constrained.

## Materials and methods

### Data collection

The study area covers the nature reserve of Moerputten (116 ha) and its surroundings, situated in the centre of the Netherlands in the province of Noord-Brabant (51°41′N, 5°15′E, altitude 2 m a.s.l.; Fig. 1). Moist meadows provide the habitat for the butterflies. In 1990, the founding butterflies were released on the meadows at the southern border of the reserve. *Maculinea teleius* colonized the release sites and expanded to a few meadows further west. However, after only 3 years, this species was restricted to the release site, where it still occurs today (Fig. 1a). *Maculinea nausithous* seemed to have left the nature reserve after release, but was found a year later on the railway embankment crossing the reserve. This population increased rapidly and gave rise to the establishment of a new local population at a distance of *c*. 600 m on the verges of a minor road (Fig. 1b). The embankment population remained rather constant for several years and then decreased in numbers, while the new local population increased rapidly (Wynhoff, 1998).

Since the reintroduction in 1990, both *Ma. teleius* and *Ma. nausithous* were monitored thoroughly over a period of 10 years. We captured and marked butterflies of each species in several years (*Ma. teleius* during 1990, 1991, 1992, 1995, 1996 and 1997; and *Ma. nausithous* during 1990, 1992, 1993, 1995 and 1996). The minimal population size in each year was estimated using the minimal number alive (MNA) method (Amler *et al.*, 1999). The net displacement of the individuals between captures was analysed by hand only for *Ma. teleius* in 1991.

During each visit, the location of all observed butterflies was mapped in 1 m$^2$ plots (Wynhoff, 1998). Plots of 1 m$^2$ were used as this size represents the scale at which a female decides whether or not to deposit an egg. Behavioural observations show that once a *Maculinea* female has found a suitable flowerhead by sight she relies on other cues (Wynhoff, 2001). If the presence of ants plays a role in her decision to deposit eggs, it is likely that chemical cues are involved. It could be the scent of the volatile pheromones or the odour of the *Myrmica* host ant nests (Cammaerts *et al.*, 1978; Cammaerts, Evershed & Morgan, 1981; Hölldobler & Wilson, 1990). For *My. rubra* and *My. scabrinodis*, a number of volatile and non-volatile pheromones from the Dufour gland have been identified and their function in interspecific communication has been partly clarified (Cammaerts *et al.*, 1978, 1981). While the very volatile compounds are not species specific, the less volatile compounds used for marking of territories are. We assume that within a 1 m$^2$ plot, we cover the ant nest-related olfactory characteristics of the habitat plot.

The nature reserve and the colonized road verges were visited at least once a week, but where possible every second to third day, during the whole flight period of both species. Each year the populations were studied for a total of 25–30 days, depending on the weather conditions. After the peak of the flight period, all road verges and ditch sides

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(a)



(b)

**Figure 1** Distribution of (a) *Maculinea teleius* over all years, and (b) *Maculinea nausithous* over all years, in $1\,m^2$ plots in and around the nature reserve Moerputten (the Netherlands). Occupied plots are in black and unoccupied plots are in white.

surrounding the Moerputten reserve were also searched for *Maculinea* butterflies.

For our analyses, we used 587 randomly selected $1\,m^2$ plots that contained at least one individual of the host plant *S. officinalis* (Fig. 1, see figures in Wynhoff *et al.*, 2008). In each plot, the presence or absence of an adult butterfly was recorded from the detailed field maps in each year during the 10 years following reintroduction (1991–2000). Colonization was recorded when a plot was unoccupied in a certain year and occupied in the next year, and abandonment was recorded when a plot was occupied in a certain year and unoccupied the next. For *Ma. teleius*, all years of observations were used in this study. For the colonization analysis, the year of reintroduction was excluded because the butter-

flies could not spontaneously colonize the first-year occupied plots. *Maculinea nausithous* passed through a bottleneck of small numbers in 1991 and, therefore, the analysis began with the census in 1992.

The connectivity of a plot was measured as the Euclidean distance (in m) to the nearest neighbour plot that was occupied (from centre to centre). To determine the relationship between the probability of both colonization and abandonment of a plot in year $t$ and its connectivity, the distance to its nearest neighbour that was occupied in year $t-1$ was used.

In the $587\,1\,m^2$ plots, we recorded the presence or absence of different ant species by attracting them with sugar cubes (Elmes & Thomas, 1992). In the middle of the plots at the

foot of a *Sanguisorba* plant, a sugar cube was placed on a concave glass plate covered with black plastic. This was carried out in the early hours of the morning (before 8 AM) before the ants start their first activity period. After at least 1 h, the bait was checked for worker ants visiting the sugar. From each species, several ants were collected for identification in the laboratory. Empty baits were left in the field and checked again later. In the evening, all baits were removed. We assume that the plots with sugar cubes undetected by ants represent ant-free environments at the scale of our $1 \text{ m}^2$ plot.

From these 587 plots, we randomly selected 251 plots to collect the following data: (1) plant species composition according to the Braun–Blanquet method (involves identifying all plant species and estimating their abundances in each plot); (2) vegetation structure measurements, such as maximum height, density of vegetation cover and *S. officinalis* plants, and the number of *S. officinalis* flowerheads and their phenology. In the remaining $3361 \text{ m}^2$ plots, only vegetation structure during the flight period of the butterflies was determined.

## Statistical analysis

The data on vegetation composition were analysed using a Detrended Correspondence Analysis (DCA) in CANOCO (Ter Braak & Smilauer, 1998), in which samples and species are ordinated along canonical axes according to similarities in occurrence. Plant species recorded in just one plot were excluded from the analysis. To interpret the ordination axes, we calculated the mean Ellenberg values per plot for humidity, productivity and acidity. Ellenberg values are plant species-specific indicator values (Ellenberg, 1982; Ertsen, Alkemade & Wassen, 1998; Schaffers & Sýkora, 2000).

To estimate habitat quality for both butterfly species, we first analysed the relationship between the presence and absence of each of the butterfly species and habitat characteristics using logistic regression. Population size of the butterflies was included as we predicted that when the population size increases, the number of less suitable plots occupied would also increase. The total number of butterflies we found on the occupied plots was used as a proxy for the overall population size. We correlated this total with the calculated MNA from the mark–recapture study to test whether this number can indeed be used as a proxy. The combined effect of the habitat characteristics in this analysis provided us with an estimate for habitat quality.

The colonization of unoccupied plots and the abandonment of occupied plots by the two butterfly species were analysed using logistic regression. We again included population size, as the probability that a plot of certain habitat quality is colonized or abandoned in a certain year depends, among other factors, on the population size in that year. In the regression analyses of both colonization and abandonment, the variables for habitat quality and population size were first added. Then, the distance to the nearest neighbouring occupied plot was added. Because of the constant management of the nature reserve and the surrounding habitat, the vegetation composition and structure and the presence of ant nests were considered constant over all years

in the analyses (Elmes & Thomas, 1992). We used the software SAM (Rangel, Diniz-Filho & Bini, 2006) for calculating Moran's *I* to analyse whether our data were spatially autocorrelated. Moran's *I* for the residuals of all regression models were very low, suggesting that spatial autocorrelation was not an issue.

## Results

After reintroduction, the population sizes of the newly introduced butterflies both increased and decreased over the years (Table 1). The average population size (expressed as geometric mean) of *Ma. teleius* is 222.2 individuals, and that of *Ma. nausithous* is 503.9 individuals. Also, the number of occupied plots (expressed as arithmetic mean) fluctuated considerably between sequential years: for *Ma. teleius*, the average number of occupied plots is 75.3, with a standard deviation of 29.9 ($n = 9$), while *Ma. nausithous* has an average of 41.3 occupied plots, with a standard deviation of 21.2 ($n = 7$). We found that the calculated MNA correlated with the total number of butterflies on the occupied plots in both species (for *Ma. teleius*: Pearson's correlation, $r = 0.862$, $n = 5$, $P < 0.1$; for *Ma. nausithous*: Pearson's correlation, $r = 0.964$, $n = 4$, $P < 0.05$). Therefore, we used the number of butterflies in the occupied plots as a proxy for population size. In the study area, during the investigation period of 10 years, 274 colonizations of a total of 1920 unoccupied plots were observed for *Ma. teleius*, while 256 of a total of 590 occupied plots were abandoned the next year. *Maculinea nausithous* colonized 50 of 1849 unoccupied plots. From 144 occupied plots, 51 were abandoned the following year. We found that *Ma. teleius* had an average net displacement of $< 1 \text{ m}$ per day. The maximum net displacement found was 260 m in 10 days for males and 639 m in 7 days for females.

We found that the probability that an adult butterfly was present in a plot is related to the size of the butterfly population, the presence of the *Myrmica* host ant, the

**Table 1** Parameters of the populations as revealed by the mark–recapture study

| Year | Individuals marked | Sex ratio (males:females) | % Recapture | Population size (MNA) |
|------|------|------|------|------|
| *Maculinea teleius* | | | | |
| 1990* | 86 | 0.431 | 38.37 | 86* |
| 1991 | 103 | 0.689 | 48.54 | 137 |
| 1992 | 318 | 0.882 | 20.75 | 785 |
| 1995 | 148 | 0.644 | 20.27 | 296 |
| 1996 | 58 | 1.522 | 17.54 | 126 |
| 1997 | 118 | 0.934 | 32.20 | 229 |
| *Maculinea nausithous* | | | | |
| 1990* | 70 | 0.458 | 28.57 | 70* |
| 1992 | 83 | 0.482 | 42.17 | 123 |
| 1993 | 103 | 0.778 | 18.45 | 286 |
| 1995 | 398 | 0.598 | 23.87 | 751 |
| 1996 | 249 | 0.847 | 27.31 | 592 |

*Year of reintroduction, so population size was exactly known.

**Table 2** Results of the logistic regression analyses of the presence and absence of *Maculinea teleius* and *Maculinea nausithous*

|  | *M. teleius* | | | | *M. nausithous* | | | |
|---|---|---|---|---|---|---|---|---|
| Number of cases | 1900 | | | | 1520 | | | |
| % Predicted correctly | 71.4 | | | | 92.7 | | | |
| Variables | $\beta_i$ | SE | Wald | Significance | $\beta_i$ | SE | Wald | Significance |
| Constant | −3.215 | 0.371 | 75.263 | <0.001 | −6.893 | 0.490 | 197.580 | <0.001 |
| Population size | 0.005 | 0.001 | 78.775 | <0.001 | 0.002 | 0.001 | 17.701 | <0.001 |
| DCA axis | 4.211 | 0.684 | 37.863 | <0.001 | 1.788 | 0.170 | 101.593 | <0.001 |
| (DCA axis)$^2$ | −3.067 | 0.420 | 53.250 | <0.001 | | | | |
| Ant presence ($A_{scab}$) | 0.436 | 0.130 | 11.236 | 0.001 | | | | |
| Ant presence ($A_{rub}$) | | | | | 1.481 | 0.262 | 31.874 | <0.001 |
| Vegetation height | 0.027 | 0.011 | 5.719 | 0.017 | −0.016 | 0.005 | 9.104 | 0.003 |

Only factors with significant effect are presented. The regression coefficients ($\beta_i$ and $\gamma_i$, used in equations 1a and 1b), their standard errors (SE), the Wald statistics and their significance levels are given. The DCA axis represents the first axis of the Detrended Correspondence Analysis of the vegetation relevés (see text), $A_{scab}$ and $A_{rub}$ is the presence or absence of a host ant nest (*Myrmica scabrinodis* and *Myrmica rubra*, respectively). The probability of observing a butterfly of either one or the other *Maculinea* species is given by $e^{regression\ equation}/(1+e^{regression\ equation})$.

vegetation height and vegetation composition as represented by the first DCA axis (Table 2; see also Wynhoff *et al.*, 2008). Based on these results, the quality of the habitat for each of the butterfly species could be estimated as follows:

$$Q_{tel} = \beta_0 + \beta_1 A_{scab} + \beta_2 D + \beta_3 D^2 + \beta_4 V \quad \text{for } Ma.teleius$$
(1a)

$$Q_{naus} = \gamma_0 + \gamma_1 A_{rub} + \gamma_2 D + \gamma_3 V \quad \text{for } Ma.nausithous \quad (1b)$$

where $\beta_i$ and $\gamma_i$ are the regression coefficients (Table 2), $A_{scab}$ and $A_{rub}$ the host ant presence of, respectively, *My. scabrinodis* and *My. rubra*, $D$ the first DCA-axis scores and $V$ the vegetation height. The term $D^2$ implies a unimodal relationship between the probability of finding *Ma. teleius* and the first DCA axis. The first DCA axis correlates with the Ellenberg productivity (Pearson's correlation, $n = 234$, $r = 0.887$, $P < 0.001$), acidity (Pearson's correlation, $n = 229$, $r = 0.723$, $P < 0.001$) and moisture (Pearson's correlation, $n = 236$, $r = -0.626$, $P < 0.001$). Note that population size (Table 2) is not included in these proxies for habitat quality.

The probability that an unoccupied plot is colonized is significantly related to the recorded habitat quality of the plot, the butterflies' population size and the connectivity of this plot (Table 3). For each butterfly species, a similar set of variables yielded significant effects for the colonization probability. Increasing habitat quality leads to an increase in colonization probability. However, plots with habitat of high quality can remain unoccupied when they have a low connectivity shown by a decrease in colonization probability with increasing distance to the nearest neighbouring occupied plot. Figure 2 gives the predictions for the colonization probability of unoccupied plots for each butterfly species. This figure shows the distances that individuals of each species covered to colonize unoccupied plots: *Ma. teleius* showed on average shorter distances than *Ma. nausithous*. Colonization distances are highly positively skewed, especially for *Ma. teleius*, indicating that the majority of butterflies only disperse over short distances (Fig. 2). *Maculinea teleius* has a clumped

**Table 3** Results of the logistic regression analyses of the colonisation of unoccupied plots by *Maculinea teleius* and *Maculinea nausithous*

|  | *M. teleius* | *M. nausithous* |
|---|---|---|
| Number of cases | 1920 | 1849 |
| % Predicted correct | 87.6 | 97.3 |

| Variable | Regression coefficient | SE | Wald | Significance |
|---|---|---|---|---|
| *M. teleius* | | | | |
|   Habitat quality ($Q_{tel}$) | 0.578 | 0.100 | 33.177 | <0.001 |
|   Population size | 0.006 | 0.001 | 76.451 | <0.001 |
|   Log(distance) | −1.211 | 0.087 | 194.546 | <0.001 |
| *M. nausithous* | | | | |
|   Constant | −6.996 | 1.073 | 42.536 | <0.001 |
|   Habitat quality ($Q_{naus}$) | 0.618 | 0.083 | 54.984 | <0.001 |
|   Population size | 0.002 | 0.001 | 10.893 | 0.001 |
|   Log(distance) | −0.406 | 0.142 | 8.213 | 0.004 |

Only factors with significant effect are presented. The regression coefficients, their standard errors (SE), the Wald statistics and their significance levels are given. $Q_{tel}$ and $Q_{naus}$ represent the habitat quality for *M. teleius* and *M. nausithous*, respectively (equations 1a and b). The distance refers to the distance to the nearest neighbour plot that was occupied in the previous year (in m).

distribution in the study area, resulting in many examples of larger distances to apparently suitable, but unoccupied plots (Table 4). The highest mean and maximum colonization distances were measured in years following population increase, for example, in 1991 after reintroduction. Although a high population size increases the probability of colonization, we could not find evidence that movement distances are density dependent: individuals do not cover larger distances to colonize unoccupied plots when the population size is high. We tested this by adding the interaction between connectivity and population size to the regression model for *Ma. teleius*, but it was not significant. For *Ma. nausithous*, colonizing plots at larger distances, the distances to unoccupied plots are
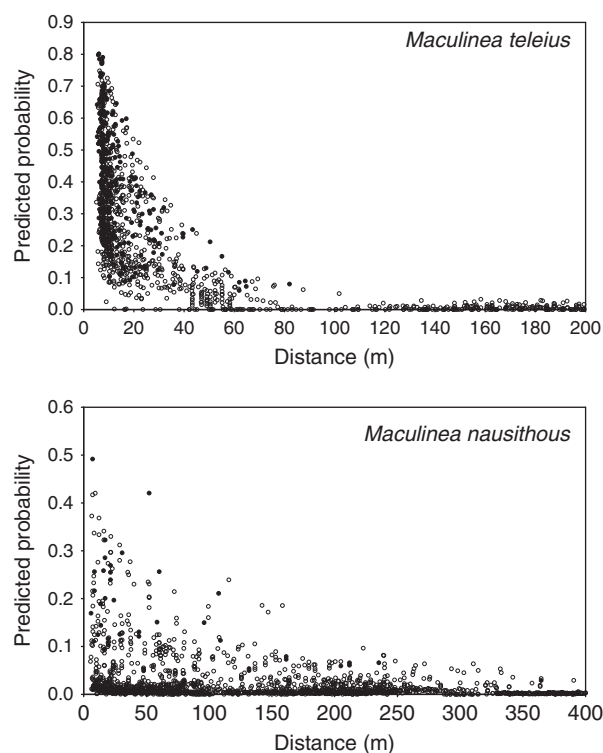
**Figure 2** Predictions of the colonization probability plotted against the observed distances of each unoccupied plot to its nearest neighbouring plot that was occupied the previous year. Black dots denote colonized plots and white dots refer to plots that remained empty.

**Table 4** Characteristics of the connectivity of plots that remain unoccupied or are colonised by *Maculinea teleius* and *Maculinea nausithous* in the study area

| | # Plots | Median distance | Minimum distance | Maximum distance | Skewness | $SE_{SK}$ |
|---|---|---|---|---|---|---|
| *M. teleius* | | | | | | |
| All | 1920 | 81 | 5 | 922 | 1.19 | 0.06 |
| Empty | 1646 | 171 | 5 | 922 | 1.011 | 0.06 |
| Colonized | 274 | 9.8 | 5 | 263 | 7.9 | 0.30 |
| *M. nausithous* | | | | | | |
| All | 1849 | 143 | 5 | 655 | 0.62 | 0.06 |
| Empty | 1799 | 147 | 5 | 655 | 0.061 | 0.06 |
| Colonized | 50 | 42 | 6 | 442 | 1.56 | 0.34 |

The connectivity is expressed as the distance (in m) to the nearest neighbour plot that was occupied in the previous year. The skewness is a measure of the asymmetry of a distribution: a large positive skewness (more than twice its standard error $SE_{SK}$) indicates a long right tail.

shorter (Table 4). Again, no significant density-dependent colonization distances were found.

The probability that an occupied plot is abandoned increases for both butterfly species when the quality of the habitat is lower. The probability of abandonment in *Ma. nausithous* could only be related to habitat quality (Table 5).

**Table 5** Results of the logistic regression analyses of the abandonment of occupied plots by *Maculinea teleius* and *Maculinea nausithous*

| | *M. teleius* | | | *M. nausithous* | |
|---|---|---|---|---|---|
| Number of cases | 590 | | | 144 | |
| % Predicted correct | 63.6 | | | 71.5 | |

| Variable | Regression coefficient | SE | Wald | Significance |
|---|---|---|---|---|
| *M. teleius* | | | | |
| Constant | −2.028 | 0.831 | 5.960 | 0.015 |
| Habitat quality ($Q_{tel}$) | −0.596 | 0.206 | 8.362 | 0.004 |
| Population size | −0.006 | 0.001 | 33.680 | <0.001 |
| Log(distance) | 1.850 | 0.330 | 31.437 | <0.001 |
| *M. nausithous* | | | | |
| Constant | 5.791 | 1.512 | 14.667 | <0.001 |
| Habitat quality ($Q_{naus}$) | −0.648 | 0.152 | 18.253 | <0.001 |

The regression coefficients, their standard errors (SE), the Wald statistics and their significance levels are given. $Q_{tel}$ and $Q_{naus}$ represent the habitat quality for *M. teleius* and *M. nausithous*, respectively (equations 1a and b). The distance refers to the distance to the nearest neighbour plot that was occupied in the previous year (in m).

For *Ma. teleius*, habitat quality of the plot, the overall population size and its connectivity have an effect on the abandonment probability. When the distance to the nearest neighbouring occupied plot increases, the probability that a plot is abandoned by *Ma. teleius* also increases (Table 5).

## Discussion

Our results show that the spatial arrangement of habitat limits the spread of the two congeneric *Maculinea* butterfly species following reintroduction, rather than availability of a suitable habitat. Although selection of this suitable habitat might be problematic as the two species critically depend on their ability to select plots with both host plants and host ant nests as larval resources, *Ma. teleius* and *Ma. nausithous* seem to be able to select for *S. officinalis* in the proximity of host ant nests to deposit their eggs (Wynhoff *et al.*, 2008), and a higher butterfly population density on sites with a higher host ant density has been shown for both species (Anton *et al.*, 2008; Batáry *et al.*, 2008; Nowicki *et al.*, 2005b). For both *Ma. nausithous* and *Ma. teleius*, we show that suitable plots further away from occupied plots have a lower probability of being occupied. To date, many studies on spatial population dynamics have assumed equal quality of patches of habitat (Moilanen & Hanski, 1998; Armstrong, 2005), whereas this study shows that incorporation of differences in habitat quality can improve our understanding of spatial and temporal population dynamics.

The colonization events of *Ma. teleius* took place mainly within the meadow where the butterflies have occurred since their release in 1990. The very small colonization steps (Fig. 2; Table 4) indicate an expansion–retraction process. The retraction is most likely caused by stochastic demography

due to weather conditions, whereas the expansion is slow due to limited movement. The latter is supported by Hovestadt & Nowicki (2008), showing that *Ma. teleius* probably establishes home ranges. Distances between captures were shorter than expected based on the random walk model and habitat size. The probability that an individual will leave this meadow for surrounding plots is low. This agrees with the displacement of individuals in our mark–recapture study. Even though the butterflies are quite active, they tend to stay at particular sites within the meadow. Similar data supporting high site fidelity have been found in other populations (Settele, 1998; Stettmer, Binzenhöfer & Hartmann, 2001; Nowicki *et al.*, 2005*b*), with a single displacement of more than 5 km. These data and our findings suggest that movement to unoccupied, suitable habitat plots at longer distances is constrained and this is likely to limit the distribution of *Ma. teleius*. Comparable results have been found for the closely related *Maculinea rebeli* (Körösi *et al.*, 2008).

*Maculinea nausithous* has been found to colonize unoccupied plots less frequently, but on average it covers longer distances. The latter is shown by the longer colonization distances (Fig. 2; Table 4). Displacements exceeding 1 km have only rarely been found, but more frequently than in *Ma. teleius* (Settele, 1998; Binzenhöfer & Settele, 2000; Nowicki *et al.*, 2005*b*). Thus, we conclude that spatial arrangement of habitat also limits the distribution of *Ma. nausithous*.

The results in *Ma. teleius* show that the probability that a plot becomes unoccupied decreases with both the population size and the distance of an occupied plot to the nearest other occupied plot. With increasing population size, more individuals tend to move to a particular plot nearby, which leads to an increase in its local density and hence a decrease in the probability of abandonment of this plot. The spatially constrained movement could explain observed patterns in habitat selection. With respect to the presence of the host ant, Wynhoff (2001) found a positive relationship between ant nest presence and oviposition of *Ma. teleius* at the beginning of the flight period; however, this relationship disappeared at the end of the flight period, as has been found by Van Dyck *et al.* (2000) for *Maculinea alcon*. This positive relationship can be explained by oviposition behaviour, whereby *Ma. teleius* females select exclusively for empty flowerheads, avoiding those that are already occupied. They seem to be restrained to cover large distances in search of empty flowerheads in the proximity of ant nests. Therefore, they oviposit at the end of the flight period relatively more frequently on plants without ant nests. Our findings suggest that these butterflies have to utilize lower quality plots (related to the presence of the host ant or to the composition and height of the vegetation), because better plots are located too far away. In such low-quality plots, abandonment will be recorded unless the searching females visit such plots in the next year again and deposit their eggs on these flowerheads. These plots may act as a sink. Our results agree with theory that predicts the occurrence of source–sink structures when there is some form of constraint on movement (Diffendorfer, 1998; Boughton, 2000). Source–sink structures may be more obvious in *Ma. teleius* than in *Ma. nausithous* because the latter can oviposit several eggs on the same flowerhead.

Based on our findings, we expect that *Ma. teleius* is less widely distributed than *Ma. nausithous* because they cover smaller distances (Fig. 2). This agrees with the observed distribution pattern over the years. The distribution of the more dispersive *Ma. nausithous* seems to be more closely related to habitat quality than the less dispersive *Ma. teleius*, which is much more constrained to using habitat close to where adults emerge, even if that habitat is of poor quality. We therefore conclude that these two species with very similar life histories require different approaches to their conservation because of subtle differences in adult habitat use and movement. *Maculinea teleius* and especially *Ma. nausithous* are typical butterfly species occurring nowadays in fragmented habitats (Stettmer *et al.*, 2001; Nowicki *et al.*, 2007; Batáry *et al.*, 2008). Conservation of *Ma. teleius* in these landscapes should concentrate on improving local habitat quality. The constrained movement in this butterfly species resembles the almost flightless moth *Itame andersoni* (Doak, 2000) and the flightless moth *Orgyia vetusta* (Harrison, 1994). Given such low movement abilities, expansion of the resident population can only be expected on high-quality patches in the close proximity. Plots with high-quality habitat at longer distances are more likely to be colonized if high-quality stepping stones are available in between (Haddad, 2000). For *Ma. teleius*, local habitat quality can be improved by a mowing regime of one cut every year, either some weeks before or some weeks after the flight period. This prevents vegetation succession with a herb layer developing into tall and rough vegetation types. Additionally, incidental mechanical disturbance of the soil is required to improve vegetation structure and is beneficial for the ants and their prey, small soil-dwelling organisms. Our results suggest that this species can bridge distances around 250 m; thus, if several patches with suitable habitat are available, they should be connected with stepping stones at distances not longer than 250 m.

For *Ma. nausithous*, creating a spatial network of suitable habitat plots, for example along road verges, seems to be a more effective method of conservation because this species is able to cover longer distances. Local populations of this species are generally smaller and seem to depend more on the exchange of individuals. These butterflies can bridge distances around 450 m. In the Netherlands, the host ant *My. rubra* shows a preference for sites along vegetation edges, for example at forest edges, reed fields, bushes, hedges and rough vegetation in general. Habitats for the butterflies should therefore consist of taller vegetation types that are mown once every 3–5 years. To create the right microclimate, these spots should be located next to yearly mown open vegetation, such as meadows or grassy road verges. Because road verges and channel borders are property of municipalities, this places an extra challenge to the management of public places. Also, these linear elements are declining and distances between these patches of habitat are increasing, which limits the spread of this species and other species with similar distribution patterns. Protecting

patches and linear elements, both containing high-quality habitat, in human-dominated landscapes, therefore seems crucial for successful conservation of these species. With these rules of thumb for management of the two butterfly species, this paper illustrates that spatial constraints can limit newly reintroduced species and details how these constraints can be removed to promote successful population growth and spread after reintroduction.

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